BEHAVIOURAL RESPONSES OF NOCTURNALLY STRANDED SEABIRDS

TOWARD ARTIFICIAL LIGHT, AND IMPLICATIONS FOR RESCUE PROGRAMS

A Thesis Submitted to the Committee on Graduate Studies

in Partial Fulfilment of the Requirements for the Degree of

Doctor of Philosophy

in the Faculty of Arts and Science

TRENT UNIVERSITY

Peterborough, Ontario, Canada

Environmental and Life Sciences Ph.D. Graduate Program

September 2025

ABSTRACT

Behavioural Responses of Nocturnally Stranded Seabirds Toward Artificial Light, and
Implications for Rescue Programs

Taylor M. Brown

Globally, fledglings of more than 50 seabird species are vulnerable to stranding in human
settlements near their colonies as they leave their nests for the first time. This
phenomenon has been attributed to attraction toward and disorientation by artificial light
at night (ALAN). Grassroots rescue programs find more birds in illuminated locations
than in dark ones, but it is unclear to what extent this pattern is driven by seabird versus
rescuer behaviour. I studied behavioural responses to ALAN in stranding-prone Atlantic
puffin (*Fratercula arctica*) and Leach's storm-petrel (*Hydrobates leucorhous*) fledglings
and investigated detection probabilities of 3D-printed puffin fledgling decoys by rescuers.
I hypothesized that seabird strandings are due to attraction toward ALAN; that post-
stranding behaviour varies with taxon and lighting conditions; and that post-stranding
behaviour (e.g., concealment) and lighting conditions drive variance in detection
probability of stranded seabirds by rescuers. To address my first hypothesis, I alternately
illuminated two beaches near a Newfoundland puffin colony and found significantly
more puffin fledglings stranded when the beaches were illuminated than when they were
dark, supporting the light attraction hypothesis. Stranded puffins similarly moved toward
light over darkness in a Y-maze choice experiment and were less active under LED light

than in darkness or under high-pressure sodium light, demonstrating a preference toward certain light conditions post-stranding. In contrast, storm-petrels predominantly avoided lit conditions in a Y-maze and were less active in darkness than under light. Further, when provided with a place to hide, more than half of storm-petrels concealed themselves when in light conditions versus none in darkness. To test my third hypothesis, I deployed puffin decoys and found that rescuers detected them more easily in higher light levels, in less concealed locations, and with increased search effort. My results support historical deductions that seabird fledgling strandings are caused by attraction toward artificial light but demonstrate that post-stranding behavioural responses to ALAN depend on species and light type, which may in turn affect detection probability by rescuers.

KEYWORDS

ALAN, light attraction, procellariiform, charadriiform, detection probability, leach's storm-petrel, Atlantic puffin, phototaxis

PREFACE

This thesis is presented in manuscript format. Chapter 1 (the general introduction), as well as two of the three data chapters in this thesis, have been published, with me as the first author. The general introduction was published in *Conservation Science and Practice* (volume 5); Chapter 2 was published in *Animal Behaviour* (volume 218); and Chapter 3 was published in *Ornithological Applications* (duaf018). Chapter 4 will be submitted for publication upon program completion. The pronoun "we" is used throughout these chapters because authorship of the published papers included multiple people, without whom the work would have been impossible. These co-authors and their contributions are detailed in the preface of each chapter. Copyright permissions for use of the published papers in this thesis are included in the General Appendix. I am the sole author of Chapter 5 (General Discussion), and the pronoun "I" is thus used therein.

ACKNOWLEDGEMENTS

Firstly, I am grateful to Gary Burness and Gaby Mastromonaco for their multifaceted support, unending patience, and ability to intellectually challenge me far beyond my comfort zone without ever making me feel stupid. Thank you, Gary, for the genuine interest and enthusiasm you always showed for my project and for bringing out the best scientist in me. Our various lab get-togethers at your place, Ashburnham Alehouse, Publican House, and trivia night will be cherished among my favourite memories from graduate school, as will be our numerous quirky jokes and "aha!" moments. To Gaby – I am also extremely indebted to you. Regardless of the technical "role" you played in the supervision of my research at any point in time, I knew that I could reach out to you for guidance on any given issue I encountered and that you would offer the exact clear and concise answers I needed, along with a confidence boost that I often sorely needed. You are a role model for me as a powerful woman in STEM, far beyond what you realize.

I hope I made you both proud in some way.

Speaking of powerful female role models in STEM: I'm looking at you, Sabina Wilhelm, Christina Davy, Suzanne Dooley, Erica Nol, and Sarah Jamieson. Sabina, you never cease to inspire me with your intellect, creativity, and enthusiasm. I remember when I finally met you in-person in 2021, after all the COVID zoom meetings, I was surprised you weren't six feet tall because you have such a presence and authority about you (in the best of ways). Yet, you are not too proud to show your absolute love for the birds you work with, your care for colleagues and mentees, and excitement for awesome findings and sightings (like that storm-petrel flying over our boat in broad daylight!

v

Something I will never forget). I am so grateful to now call you a friend. Christina, you are a fantastic mentor, and I admire your combined superpowers of intelligence and empathy, which helped get me through many a committee meeting. Thank you for being a member of my supervisory committee and for always bringing to the table a plethora of simultaneously sensible and exciting ideas. Suzanne – thank you for your endless support of my research and for providing essential material, logistical, gastronomical, and emotional support to me when I needed them most during fieldwork and throughout my PhD journey. Thanks for introducing me to toutons and bay ball, for late-night girl talk in the trailer, annual invitations to your and Colton's birthday party, and of course the endless laughs. You really are the best. Erica, I know you never played a formal role in my supervisory committee or even my project at large but every encounter I had with you throughout my PhD left me feeling positive, energized, and intellectually stimulated. Sarah, you were always a pleasure to work with and talk to, and I admire your focus on students and building them (/us) up with each interaction, which is something I will try to emulate whenever I am in a mentorship role. All five of you have significantly shaped, and will continue to shape, my self-image and goals as a woman in science.

Members of my supervisory and examining committees (most of them detailed above), as well as those people who peer-reviewed chapters one through three prior to publication, contributed essential feedback, without which this thesis would be of significantly poorer quality. Special thanks go to Mark Mallory for his close reading of this thesis, his thoughtful comments for the sake of its improvement, and for his role in making my defense both challenging and enjoyable.

There were many other folks who either helped with fieldwork, provided a comfortable and welcoming place to stay with great food and conversation, or gave freely of their time and knowledge to help me make my experiments come to life. I owe all of you my gratitude: the Sutton family, Sherry Green and Philip Walsh, Sofia Karabatsos, Jenny Herbig, Galina Sherren, Dustin Porta, Jasmin Dawson, Brayden Johnson, Laura Taylor, Steven Duffy, Brendan Kelly, Bobby Blackmore, Noah O'Brien, Mohammad Fahmy, Tori Burt, Dave Fifield, Dr. Hugo Lehmann and his lab at Trent, Dr. Wesley Burr, Hannah Moon, Francesco Bonadonna, and Lincoln Savi (of SaviMade), among still others. My thanks are also toward the countless people who interned and volunteered with the Puffin Patrol (especially those who participated in my experiment[s]), as well as Ani at the "Grocery Deli and More" and those who worked at the Quinlan Brothers seafood processing plant in Bay de Verde and at the BGI crab plant in Witless Bay, for their good nature at me being in their way all the time.

I had the privilege to do my research alongside many talented and inspirational academic "siblings" and "cousins", including but not limited to Joshua Tabh, Simon Tapper, Chantelle Penney, Kayla Martin, Michael Campbell, Megan Heft, Sandra Klemet-N'Guessan, and a number of folks from other labs. Thank you all for the laughs, lightbulb moments, pep talks, birding walks, and for getting me out to fun events in Peterborough.

My last expression of gratitude goes toward those nearest and dearest to me. I will be forever grateful for the encouragement I received from my parents from an early age: to Mum, for loving and supporting me equally through all my successes and failures; to Dad, for fostering in me an interest in all things biological from a very early age; and to

Gord, for emphasizing the importance of hard work, dedication, and education, and always reminding me that I can do whatever I put my mind to. To my brothers Shawn and Steven – one of you I've been fortunate to grow up with and be tormented by my whole life, and the other of you I was fortunate enough to reconnect with during my PhD and find out I'm a sister-in-law and an aunt to four wonderful kids. I am so lucky to have both of you in my life. To all of my extremely supportive aunts, uncles, cousins, and extended family: I am grateful to be so close with all of you, and to have had you following along with my academic journey and continuing to keep in touch after all these years. I know that I can always turn to any of you at any time for hugs, advice, and cups of hot tea. And lastly, to Michael: you came into my life fairly late in my PhD journey, but I am so grateful that in such a twist of fate, the PhD journey itself is what led me to you. Finding you, and finishing this thesis, are my two greatest achievements in life! Not to mention, the last stages of writing a thesis are the most difficult, and you have been the most wonderful and supportive partner that I could ever ask for. Thank you for being by my side and helping me make this a reality.

DEDICATION

I dedicate this dissertation to my beloved grandparents. The losses of my Papa (John Saxton), Nana (Marie Saxton), and Grandma (Ruth Steele) in three consecutive years during my PhD wrought in me a heartache that I was not sure I could bear; for the love I have for all four of my grandparents – including of course my ever-steady Grandpa (Eric Steele) – is beyond measure. To all of you: you helped raise me from the moment I was born, and you will continue to guide me until I myself leave this earth. Each of you infused in me a unique lesson that was distilled from your lifetimes of experience and wisdom, for which I will be forever grateful: Papa, to listen well, chuckle often, and not take life too seriously; Nana, to be tough and not let people take advantage, while still giving as much as possible; Grandma, to love with all one's heart and never give up the silliness of youth; and Grandpa, to keep one's mind sharp and always maintain integrity.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

General Introduction

Preface

A version of this chapter has been published in Conservation Science and Practice.

Brown, T.M., Wilhelm, S.I., Mastromonaco, G.F., and Burness, G. (2023). A path forward in the investigation of seabird strandings attributed to light attraction. *Conservation Science and Practice*, *5*(1), e12852. https://doi.org/10.1111/csp2.12852

Author contributions

T.M.B., G.B. and G.F.M. conceived the idea for the manuscript; T.M.B. wrote the first draft. S.I.W., G.F.M., and G.B provided subsequent input and revisions.

Effects of artificial light at night

Artificial light at night (ALAN) is associated with disruptions to the physiology and behaviour of, as well as ecological interactions among, numerous species (Rich and Longcore 2006; Gaston et al. 2021; Jägerbrand and Spoelstra 2023). Furthermore, effects of ALAN on wildlife are expected to worsen due to both its increasing global emittance (Sánchez de Miguel et al. 2021) and increases in the use of light-emitting diodes (LED) specifically, which emit higher proportions of particularly disruptive blue light than most traditional (i.e., incandescent) lightbulb types (Pawson and Bader 2014; Longcore et al. 2018). Artificial light can cause disorientation, object collisions, and grounding of flighted nocturnal animals, oftentimes leading to predation (Rich and Longcore 2006; Rodríguez et al. 2017a; Marangoni et al. 2022; Fabian et al. 2024).

Among seabirds, fledglings of at least 56 of 140 procellariiform species (40%) and one charadriiform species (Atlantic puffin *Fratercula arctica*) are affected by mass nocturnal strandings in coastal human settlements during their inaugural flights from the nest (Rodríguez et al. 2017a; Wilhelm et al. 2021). The phenomenon has been termed "fallout", and it is thought to be caused by attraction to and disorientation by artificial lights (hereafter the "light attraction hypothesis"; reviewed in Rodríguez et al. 2017a). Over the course of a fledging season, fallout may affect anywhere from a handful to a couple of thousand individuals (reviewed in Rodríguez et al. 2017a; Wilhelm et al. 2021; Chevillon et al. 2022; Urmston et al. 2022; Burt et al. 2023; Borsa et al. 2024). These mass strandings of mostly fledglings (but sometimes high proportions of adults; see Borsa et al. 2024; Raine et al. 2024) are usually reported in coastal communities near breeding colonies (but see Friswold et al. 2023) on nights throughout each species' local

fledging season. Strandings are thus relatively predictable and even anticipated at the same time each year in the communities where they occur (Rodríguez et al. 2017a). This phenomenon contrasts with the more widely known and widespread but less predictable passerine light attraction and strandings, which occur throughout both vernal and autumnal migration in locations not necessarily near the affected species' place of breeding, and involve adults as well as fledglings (Evans Ogden 1996; Gauthreaux and Belser 2006; Gjerdrum et al. 2021).

Seabird fledgling fallout can occur under several different scenarios. For example, individuals may fly from inland, sometimes mountainous, breeding colonies to strand in coastal communities (e.g., Day et al. 2003; Rodríguez et al. 2012a). Some fly from island breeding colonies over water to adjacent coastal communities (Wilhelm et al. 2021) or other islands (Friswold et al. 2023). Fledglings may fly from coastal breeding colonies to communities immediately beside them (i.e., flying short distances over land; e.g., Rodríguez et al. 2017b) or, rarely, from high elevation breeding colonies to adjacent high elevation communities (Le Corre et al. 2002). Seabird strandings have also been reported on ocean-going vessels (Dick and Donaldson 1978; Black 2005; Merkel and Johansen 2011) and oil platforms (Ronconi et al. 2015; Gjerdrum et al. 2021), although not all of these instances are seasonally predictable or involve predominantly fledglings. The estimated proportion of fledglings produced by a population that become stranded varies widely from <1% to ~34% (with higher proportions of affected fledglings usually occurring in small populations; Rodríguez et al. 2017a and tables therein). Although procellariiforms are long-lived, and populations thus tend to be more resilient to juvenile mortality than shorter-lived taxa, fallout has been identified as having a significant

negative effect on population growth in at least three species (Simons 1984; Ainley et al. 2001; Fontaine et al. 2011; Griesemer and Holmes 2011). Such population-level effects could be even greater for species with higher proportions of adults affected (e.g., Rodríguez and Rodríguez 2009; Borsa et al. 2024; Raine et al. 2024). Data collected over multiple years by some volunteer-driven rescue programs reveal increases in raw stranding numbers concurrent with increases in human populations and light pollution indices (Le Corre et al. 2002; Rodríguez et al. 2012a), although part of this trend can likely be attributed to increased search effort over time (Rodríguez et al. 2017a). Decreases or plateaus in stranding numbers across multiple years are less common and have been interpreted as indicators of overall seabird population decline or stability, respectively (e.g., Rodríguez et al. 2012a).

Current evidence in support of the light attraction hypothesis

The vast majority of seabird fallout research has focused on procellariiforms, but mass strandings of all species of nocturnal seabird fledglings, and even of adults, have largely been attributed to light attraction (Rodríguez et al. 2017a). This hypothesis originated from observations of fledgling shearwaters, petrels, and puffins wandering lighted areas or flying into buildings in coastal towns and cities after leaving their colonies for the first time (Hadley 1961, as cited in Reed et al. 1985; Swales 1965; Sincock and Swedberg 1969; Imber 1975; Harris 1982). Individuals have also been observed circling artificial lights (Montevecchi 2006), and Global Positioning System (GPS) tracks of Cory's shearwater (*Calonectris diomedea*) fledglings have shown them flying to areas of increased light emittance instead of out to sea (Rodríguez et al. 2015;

Rodríguez et al. 2022). Modeling has also suggested that patterns of fallout are related to regional patterns in artificial light (Troy et al. 2013; Borsa et al. 2024). There may indeed be an adaptive benefit of positive phototaxis, e.g., in nocturnal navigation or seeking bioluminescent prey (Imber 1975; Montevecchi 2006; Rodríguez et al. 2017a; Wilhelm et al. 2021). It has also been suggested that inherent inexperience and latent visual system development of young birds (Nevitt 2008; Mitkus et al. 2018) may lead to misinterpretation of visual stimuli (Atchoi et al. 2020).

Imber (1975) has often been cited as the formulator of the light attraction hypothesis, although there had been previous reports implicating light attraction in procellariiform strandings (e.g., Hadley 1961; Swales 1965; Sincock and Swedberg 1969). Rather than developing the light attraction hypothesis or showing experimental evidence to support it, Imber (1975) was the first to propose an explanation for it (that is, an innate preference for bioluminescent prey), while simply making the unspoken assumption that light attraction was what caused strandings. Other proposed mechanisms for assumed light attraction include fledglings associating the light of their burrow entrances with food provided by their parents, or mistakenly using artificial lights as navigational cues in place of the moon and stars, causing phototactic behaviour (Reed et al. 1985; Rodríguez et al. 2017a). Alternatively, practitioners are now recognizing that what was historically perceived as pure phototaxis – that is, seabirds flying around lights and landing in illuminated areas – may have been evidence of disorientation (Atchoi et al. 2024), although the two are not mutually exclusive in their potential to cause fallout.

The light attraction hypothesis is nonetheless still widely accepted to explain seabird strandings, regardless of the mechanism. A small but growing number of studies

have tested this assumed causal relationship by manipulating the quality or quantity of artificial lights present in communities and observing subsequent effects on seabird stranding numbers (Reed et al. 1985; Reed 1987; Miles et al. 2010; Rodríguez et al. 2014; Rodríguez et al. 2017b; Burt et al. 2024). In support of the light attraction hypothesis, experiments with Newell's shearwaters (*Puffinus newelli*) on Kauai found that some of the largest decreases in stranding rates occurred when upward radiation was shielded (Reed et al. 1985). Fewer short-tailed shearwaters (*Ardenna tenuirostris*) were stranded in a grassy lot on Phillip Island, Australia, under sodium vapour bulbs compared with light-emitting diode and metal halide lights (but without a "dark" control; Rodríguez et al. 2017b), and on a bridge when lights were turned off (Rodríguez et al. 2014). Similarly, Miles et al. (2010) turned off lights in Village Bay, Hirta, St. Kilda, and noted a decrease in the number of stranded Leach's storm-petrels (*Hydrobates leucorhous*) but not Manx shearwaters (*Puffinus puffinus*). Light reductions also resulted in decreased numbers of stranded Leach's storm-petrels at a seafood processing plant near their largest breeding colony in Newfoundland and Labrador, Canada (Burt et al. 2024). Barau's petrels (*Pterodroma baraui*) on Réunion Island were less attracted to yellow and red light treatments than white, green, or blue (Salamolard et al. 2001, as cited in Minatchy 2004), but it is not clear how this was tested or quantified since the Salamolard et al. study is not peer-reviewed nor publicly available. The light attraction hypothesis is further bolstered by studies on passerines that have found effects of different light types and colours on attraction behaviour (Jones and Francis 2003; Evans et al. 2007; Poot et al. 2008; Rebke et al. 2019).

Young wedge-tailed shearwaters (*Ardenna pacifica*) are susceptible to stranding (e.g., Friswold et al. 2020; Urmston et al. 2022) and are one of the only procellariiform species to have had its photoreceptors fully characterized to date. They have four cone-based visual pigments that are most sensitive to light wavelengths of 406, 450, 503, and 566 nm (Hart 2004), approximately corresponding to violet, blue-violet, green, and yellow-green light, respectively. They possess violet-sensitive cones in roughly twice the proportion of most terrestrial birds, which is thought to confer advantages in their ability to forage at and just below the ocean's surface (Hart 2004). A heightened sensitivity to wavelengths of <400 to 500 nm (Hart 2004) may explain observations of "increased attraction" to blue and "cool" colour temperature light by fledglings (Salamolard et al. 2001, as cited in Minatchy 2004; Rodríguez et al. 2017b). Electroretinography has indeed revealed that blue light elicits stronger retinal responses in Newell's shearwater fledglings compared to wedge-tailed shearwater fledglings, which has been taken as a reflection of the differences in foraging ecology between the two species (although sample sizes in this study were low; Moon 2024). However, procellariiform visual systems and physiological responses to light remain understudied, and it is unknown to what degree those physiological responses correspond to phototactic behaviour.

Behavioural responses of adult procellariiforms to experimental and incidental ALAN may not be directly applicable to the study of fledgling fallout (or especially to that of fledgling charadriiforms, which are much less studied). However, studies thereof point to additional nuance in phototactic behaviour even among adults, both within and among species. Breeding adults of various species are known to reduce colony attendance, abandon sub-colonies, and shift preferences to nest in darker areas in

response to nearby artificial night lighting (Oro et al. 2005; Bourgeois et al. 2008; Sultana et al. 2011, as cited in Austad et al. 2023). Experimentally shining amber or white light above a fairy prion (*Pachyptila turtur*) colony at night resulted in an increase in the number of adult birds in flight over the colony and elicited increased attraction and disorientation behaviours relative to darkness (control treatment), while red light caused no change in behaviour (Middlemiss et al. 2025). Meanwhile, experimentally shining white, green, or blue lights above a Manx shearwater colony significantly reduced the number of adult birds in flight relative to darkness (control treatment), indicating negative phototaxis (Syposz et al. 2021a). Again, red light elicited no behavioural differences compared to darkness. Despite this evidence for light avoidance in Manx shearwaters, collisions of adult birds with the walls of a research station on a foggy night were drastically increased when interior lights (which emanated through windows) were turned on versus off in an alternating design (Guilford et al. 2018). It is not clear what drives these seemingly contradictory results between adults of the same, and different, species of procellariiform.

Limitations of rescue programs to inform our understanding of strandings

Most data on seabird strandings have been collected through rescue, rehabilitation, and release programs that are intended to reduce mortality of stranded seabirds. Such programs have been successfully implemented in places such as Tenerife, Canary Islands (Rodríguez and Rodríguez 2009); Kauai, Hawaii (Telfer et al. 1987; Ainley et al. 2001); Réunion Island (Le Corre et al. 2002); the Azores Archipelago (Fontaine et al. 2011; Rodrigues et al. 2012); Phillip Island, Australia (Rodríguez et

al. 2014); Grande Terre, New Caledonia (Borsa et al. 2024); New Zealand (Deppe et al. 2017); and Newfoundland, Canada (Wilhelm et al. 2021). These programs rely on dedicated volunteer searchers and/or members of the public (who are not engaged in search efforts) to capture or report stranded seabirds (or both) to local authorities and conservation organizations so that they can be assessed, banded, and released (with as yet unknown survival rates of released individuals). With limited human resources at their disposal, organizers of seabird rescue patrols must delegate volunteers and time to a limited number of search locations at the expense of a balanced search effort across an entire potential fallout zone (e.g., Rodríguez et al. 2014, 2017a; Wilhelm et al. 2021), resulting in spatial coverage bias. This potential bias would be particularly pronounced in programs that rely almost entirely on opportunistic finding and capture by community members who are not strictly engaged in formal seabird search efforts (e.g., Le Corre et al. 2002; Salamolard et al. 2007; Rodrigues et al. 2012; Rodríguez and Rodríguez 2009; Rodríguez et al. 2012a, 2012b; Deppe et al. 2017; Borsa et al. 2024). The same problem exists at many industrial sites, including offshore oil infrastructure, where searching for and reporting of stranded seabirds tends to be opportunistic (Fraser and Carter 2018; Gjerdrum et al. 2021). At night, detection probability of stranded seabirds by the public is presumably increased in areas of higher human activity and lighting levels, e.g., roads, parking lots, public buildings, private dwellings, etc., thereby inadvertently resulting in a bias toward searching in well-lit areas. Hence, data collected under these initiatives should be used with caution to inform our understanding of the causes of seabird strandings, specifically acknowledging the limitation of spatially biased data in their ability to support the light attraction hypothesis.

Natural factors influencing seabird strandings

Data from seabird rescue and release programs suggest that lunar illumination has a strong negative influence on numbers of birds found stranded, regardless of species, location, and artificial lighting conditions. When the moon is full, fewer birds than expected are found stranded, even when it coincides with the estimated timing of peak strandings based on multi-year averages (Telfer et al. 1987; Rodríguez and Rodríguez 2009; Rodríguez et al. 2014; Deppe et al. 2017; Syposz et al. 2018; Gjerdrum et al. 2021; Wilhelm et al. 2021; Rodríguez et al. 2023; Burt et al. 2024; Raine et al. 2024; and figures therein). Decreased numbers of stranded individuals on moonlit nights appear to be due to higher proportions of fledglings safely reaching the sea (Rodríguez et al. 2023), since lunar phase does not appear to influence the number of fledglings departing the colony (Byrd et al. 1984; Collins et al. 2023; Raine et al. 2023; Rodríguez et al. 2023). Furthermore, GPS tracks of Cory's shearwater fledglings revealed their first flights were more tortuous in areas of higher light pollution, but less so with greater moon luminance; in turn, the probability of grounding was positively associated with flight tortuosity (Rodríguez et al. 2022). It is unclear exactly by which mechanism increased natural light at night reduces the disorienting effect of its artificial counterpart on fledging seabirds. Higher ambient light may cause some visual effect whereby point sources of artificial light are rendered less disorienting (Reed et al. 1985; Montevecchi 2006; Rodríguez et al. 2017a) or landforms and obstructions are rendered more visible (Telfer et al. 1987) to the underdeveloped eyes of fledgling procellariiforms (Mitkus et al. 2018; Atchoi et al. 2020). Alternatively, but not mutually exclusively, fledglings may use the moon and other bright stellar objects for orientation (Reed et

al. 1985; Telfer et al. 1987). In the absence of the moon, then, it may seem reasonable that distant point sources of artificial light may very closely resemble stars. Clearly, further research is needed to explore the mechanisms by which moonlight may ameliorate the disorienting effects of ALAN.

Nightly variation in stranding numbers can also be influenced by weather conditions. Wind direction and speed appear to be important predictors of stranding for some species and, where they have not yet been explored as potential influencing factors, they deserve further attention. For example, more Leach's storm-petrels were found stranded on the Avalon Peninsula of Newfoundland on nights when winds had a northerly (onshore) component, suggesting also that stranded birds originated from the large colony on Baccalieu Island, which sits at the northern tip of the Peninsula (Wilhelm et al. 2021; Burt et al. 2024). Similarly, a multi-year study found that onshore winds contributed significantly (third in importance only to year and moon phase) to strandings of Manx shearwaters in a coastal community in Scotland (Syposz et al. 2018). Wind direction was also potentially important in predicting numbers of short-tailed shearwaters that became stranded in communities to the northeast of breeding colonies on Phillip Island, Australia: strong prevailing southerly and southwesterly winds likely helped to push fledging birds into well-lit areas (Rodríguez et al. 2014). Adverse weather conditions such as cloud, precipitation, and fog have been anecdotally noted as being associated with higher stranding numbers (e.g., Harris 1982; Telfer et al. 1987; Black 2005; Ronconi et al. 2015; Guilford et al. 2018), but these effects remain largely unexamined from a statistical standpoint. Effects of adverse weather on stranding numbers could occur by one or more of several modes: reduced visibility for navigation,

increased light reflection off wet surfaces causing increased attraction (Telfer et al. 1987), or refraction of light which either increases the area of illumination in which attraction can occur (Wiese et al. 2001; Syposz et al. 2018) or disrupts dark-adaptation and/or light-dependent magnetoreception (Guilford et al. 2018). However, an analysis of Atlantic puffin strandings showed no difference in stranding numbers between foggy and clear nights (Wilhelm et al. 2013), and neither fog nor cloud cover had significant effects on Leach's storm-petrel stranding numbers (Burt et al. 2024). Visibility similarly contributed little to the modeling of Manx shearwater stranding predictors (Syposz et al. 2018). Adding to the mystery, strandings observed during the latter study were associated with extremes (both high and low) in visibility (Syposz et al. 2018).

The number of fledglings that become stranded is undoubtedly related, at least in part, to the number of fledglings produced at the colony where those stranded individuals originate; however, the paucity of data on this topic means that it remains ripe for study. For example, interannual variation in stranding numbers at a given location has yet to be directly linked to interannual variation in fledging success at the nearest colony. However, some anecdotal evidence suggests a link may exist: when cold, wet weather reduced the fledging success at a colony of Atlantic puffins, stranding numbers were also drastically reduced, but this was only in comparison to one subsequent year (Wilhelm et al. 2013). Mass chick starvation at the same colony in 2023 similarly coincided with an extreme drop in stranding numbers compared to prior years (S.I.W. and T.M.B., pers. obs.). On the other hand, the coincidence of a full moon with peak fledging timing is suggested to have a positive effect on the number of fledglings successfully reaching the ocean, thereby reducing overall stranding numbers in a given season compared to one in

which a new moon coincides with the fledging peak, resulting in higher stranding

numbers overall (Rodríguez et al. 2023).

Among colonies, one that numbers in the millions of breeding adults will likely

result in more fledglings produced, and therefore, stranded (by raw numbers alone), than

one much smaller, all else being equal. That said, the estimated proportions of fledglings

stranded divided by fledglings produced can vary widely by species and location

(Rodríguez et al. 2017a). It is unknown what drives this variation in the proportion of

fledglings stranded. Some potential factors that deserve further inquiry include proximity

of the colony to the stranding location(s); natural history and biological characteristics of

each species such as the presence of bioluminescent prey in the diet or the ability to

maneuver in high winds; local topography; and interspecific variation in sensitivity to

artificial light and other anthropogenic stimuli (discussed below).

Alternative factors potentially influencing seabird strandings

There remain a null hypothesis and several alternative hypotheses to light

attraction that should be explored. Any further research on the cause(s) of strandings

needs to carefully consider and provide refuting evidence for the null hypothesis that

fledgling strandings are due to random dispersal, or long-range attraction to stimuli

besides light but which may be confounded with it.

The number of fledglings found stranded annually as a function of the total

fledgling cohort can vary widely (discussed previously; Rodríguez and Rodríguez 2009;

Rodríguez et al. 2017a). In many cases, however, and especially in larger populations

(e.g., thousands or hundreds of thousands of breeding pairs), the estimated proportion of

fledglings affected by fallout is relatively low, and in the range of 0-5% (Deppe et

al. 2017; Rodríguez et al. 2017a; Wilhelm et al. 2021). Such a small proportion becoming

stranded, rather than attraction to light, might suggest random dispersal from the colony

with individuals becoming stranded due to navigational inexperience. In other words, if

light (or any other stimulus on land) truly had an "attractive" effect, one would

presumably expect the proportion of fledglings stranded to be much higher. It could be

argued that strandings on offshore ships and well-lit oil and gas platforms are evidence

for attraction toward point-source stimuli (Ronconi et al. 2015; Gjerdrum et al. 2021)

since they are often quite distant from the fledglings' colony of origin. Both in the case of

strandings on land and offshore, the number of stranded fledglings expected to be due to

random dispersal could be modelled and compared against models that include

components of attraction. On the spectrum between fully random dispersal and

"attraction", however, lies an alternative possibility that would still be in keeping with the

stranding rates observed: that of disorientation. Fledglings may be dispersing in

ecologically appropriate directions and only become stranded after close-range exposure

to and disorientation by (rather than attraction toward) ALAN (Rodríguez et al. 2022;

Atchoi et al. 2024).

Additionally, nocturnal, burrow-nesting members of the Procellariiformes are

receptive to sound: many members of this taxon are vocal at colonies and mates can

recognize each other's acoustic call signatures (Bretagnolle 1996; Curé et al. 2016).

Further, recordings of conspecific vocalizations have been used to lure burrow-nesting

procellariiforms into establishing new breeding colonies (Podolsky and Kress 1989;

Miskelly and Taylor 2004). Attraction to noise (e.g., produced by generators) may play a

role in seabird strandings (Harris 1982; Harris et al. 1998; Miles et al. 2010; Wilhelm et al. 2013), although some types of anthropogenic noise may actually suppress activity (e.g., disco music; Cianchetti-Benedetti et al. 2018). Miles et al. (2010) suggested that perhaps the continued stranding of Manx shearwaters during experimentally reduced lighting conditions was in fact due to noise attraction; this was bolstered by the finding of stranded individuals near extractors and generators. Calls produced by procellariiforms range in frequency from 0-10 kHz, with many species producing the highest amplitudes in the 0-1 kHz range (James 1984; Curé et al. 2012; Totterman 2014; Curé et al. 2016). Similarly, Atlantic puffin hearing is most sensitive to frequencies of 0.75-3 kHz (Mooney et al. 2020). The majority of noise from internal combustion (e.g., gasoline) generators is 0-1 kHz in frequency (Cuesta and Cobo 2000), putting it well within hearing range for these taxa. Anthropogenic lights may mask the potential attractive effect of anthropogenic noise in locations where the stimuli co-occur. For example, cars and boats produce light as well as sound; their engines emit sound profiles similar in minimum, maximum, and peak-amplitude frequencies to generators (e.g., Versfeld and Vos 1997; Tripovich et al. 2012); and they can be heard at great distances over water, especially in calm and foggy conditions (Wilhelm et al. 2013). To our knowledge, there are no studies exploring anthropogenic noise attraction in any stranding-prone seabird.

Anthropogenic olfactory stimuli can also be confounded with artificial light and may contribute to strandings. Volatile compounds emanating from fish or paper processing plants; sewage and sewage treatment plants; car, truck, boat, or generator exhaust; or other smells associated with coastal industry or settlement may act as potential attractants to seabirds, and they occur in anthropogenically lighted places. In

burrow-nesting procellariiforms, the olfactory bulbs are among the first brain structures to develop and are highly functional upon fledging, conferring an excellent sense of smell (Nevitt 2008; Mitkus et al. 2018). In contrast, the visual system and optic bulbs are relatively poorly developed at fledging age (Nevitt 2008; Mitkus et al. 2018). To illustrate the potential implications of these coincident factors, blue petrel (*Halobaena caerulea*) chicks are negatively phototactic but orient to vapourized dimethyl sulfide at ages as young as 15 days (Bonadonna et al. 2006).

Olfaction is one of the primary senses used by adult procellariiforms in navigation (Nevitt 2008; Gagliardo et al. 2013), with special importance at night (Dell'Ariccia and Bonadonna 2013). Of the few volatile compounds tested experimentally, dimethyl sulfide appears to be a major attractant to those procellariiforms that use it to find patchily distributed prey in the open ocean (Nevitt et al. 1995). Other compounds such as 3-methyl pyrazine are also attractive to several species (Nevitt et al. 2004). Dimethyl sulfide and other volatile sulfur compounds that are potentially attractive to seabirds (Nevitt 2008) are also produced by pulp and paper mills (both aerosolized and in wastewater effluent; Lichutina et al. 2012; Giri et al. 2014), sewage and sewage treatment plants (Glindemann et al. 2006; Giri et al. 2014), biomass burning (Meinardi et al. 2003), marine microplastics (Savoca et al. 2016), and other sources (Guo et al. 2010). Many procellariiforms are also unsurprisingly highly attracted to fish offal and oils (e.g., Hutchison and Wenzel 1980; Nevitt et al. 1995; Nevitt et al. 2004), which can be suspended and discharged in wastewater of fish processing plants if it is not adequately treated (Islam et al. 2004; Chowdhury et al. 2010; de Melo Ribeiro and Naval 2019). Indeed, some of the biggest "hotspots" for Leach's storm-petrel and Atlantic puffin

strandings in Newfoundland are the fish processing plants in Bay de Verde (it is also noteworthy that plant workers say birds appear to approach the plant primarily from downwind) and Witless Bay, respectively (Wilhelm et al. 2021). Fish offal and oils are also sometimes discharged from fishing vessels at sea or in harbor, making them notoriously attractive to seabirds (e.g., Pierre et al. 2010), as are cage fish farms (Aguado-Giménez et al. 2016). The possibility should also be considered that prey species (e.g., plankton, fish) may be attracted by any of these anthropogenic discharges, which in turn may emit olfactory cues that attract seabirds. For these reasons, olfactory attraction should be experimentally tested as a potential cause of or contributor toward seabird strandings. In fact, since the publication of this chapter (Brown et al. 2023), experiments have been underway to evaluate effects of both light and scent as potentially interacting factors causing fallout, but it appears that, at least at a colony of breeding adult Leach's storm-petrels and in fledgling Atlantic puffins subjected to a cue preference test, there is no effect of scent on attraction behaviour (T.M.B., unpubl. data; T. Burt, unpubl. data).

Barring attraction toward any kind of stimulus, disorientation caused by interference of anthropogenic or natural phenomena with magnetoreception could cause strandings. Magnetoreception is the ability of birds and some other animals to detect the direction and intensity of Earth's magnetic field, and use it to navigate (Wiltschko and Wiltschko 2005; Wiltschko and Wiltschko 2019). It can be especially important to those organisms that migrate at night (e.g., Engels et al. 2012). The disruption of this ability may be a plausible mechanism for strandings of animals with magnetoreception, but this area of research remains largely unexplored. There is evidence that cetaceans use Earth's

magnetic field to navigate (Kirschvink et al. 1986; Walker et al. 1992), and strandings of some whale species increase significantly when ambient radio-frequency noise is high during solar storms, possibly indicating magnetoreception interference (Granger et al. 2020). Similarly, higher proportions of homing pigeons become lost on days with more sunspots, which are indicators of higher solar activity and can result in geomagnetic disturbance (Schreiber and Rossi 1976). A broad spectrum of relatively low-level anthropogenic electromagnetic noise can disrupt songbird magnetoreception, causing birds to orient in ecologically inappropriate directions (Engels et al. 2014). The frequencies shown to be effective at causing disorientation (2 kHz to 5 MHz) correspond to a range from very low to high frequency radio waves and are produced by AM radio transmissions, or during the operation of electronic appliances common to businesses and households (Engels et al. 2014).

Although its mechanisms may differ from those in other taxa, there is some evidence for the existence of magnetoreception in procellariiforms. Shearwaters fledging from a colony on the north side of Japan crossed its treacherous mountainous interior on a direct southward route toward their wintering grounds instead of circumnavigating the island in either direction, as experienced adults did (Yoda et al. 2017), indicating an innate compass sense (and one that adults can override with experience). Some fledgling procellariiforms also appear to imprint to the geomagnetic field, influencing their eventual nesting locations (Putman 2020; Wynn et al. 2020). It stands to reason, then, that radio-frequency anthropogenic noise could cause disorientation in this taxon if it disrupts their sense of magnetoreception in similar ways to other taxa. However, evidence for magnetoreception in procellariiforms remains equivocal (Gagliardo et al. 2013;

Pollonara et al. 2015; Syposz et al. 2021b) and, to the best of my knowledge, has not even been considered in Atlantic puffins.

It has been suggested that object collisions by adult seabirds may be due to close-range light-induced disruption of magnetoreception and flight maneuvering (Guilford et al. 2018). It is worth noting that object collisions are also often associated with "light attracted" fledglings (Rodríguez et al. 2017a). The limited evidence obtained so far points to blue, green, and other "cool" colour temperature light being more disruptive to fledgling (and adult) seabirds than "warm", yellow, or red lights (Salamolard et al. 2001, as cited in Minatchy 2004; Rodríguez et al. 2017b; Syposz et al. 2021a; Atchoi et al. 2024; but for contrasting results see Atchoi et al. 2023). It is possible that the differential effects observed of various light types on procellariiform stranding numbers may result from differential disruption of magnetoreception by certain wavelengths of light. The presence and potential disruption of magnetoreception in seabirds (by visible light or low-frequency electromagnetic noise) clearly warrants more attention in its potential to cause strandings.

Determining causal factors through experimental approaches

Despite the historically prevalent acceptance of the light attraction hypothesis to explain mass seabird fledgling strandings, there remain biases in the existing data and gaps in our current understanding of the phenomenon (as discussed; and as also suggested by Rodríguez et al. 2017a). At the same time, there are viable alternative hypotheses that remain to be explored (detailed above). Over the last few years alone (approximately 2021 to present), our understanding of seabird behavioural responses to ALAN has grown

19

significantly and has led to a small but tangible shift in expert opinion on the proximate

cause of stranding, from an attraction-based hypothesis to one disorientation-based.

Considered together, it can be concluded that there is yet a need for more behavioural and

natural history observations, and more rigorous experimental testing of all hypothesized

causes of seabird strandings.

Currently, the behaviour of nocturnally fledging seabirds as they depart their

colonies is relatively unknown and understudied, although it is likely affected by

topography, weather conditions, taxon-specific natural history traits, and possibly other

factors. Likewise, the behaviour of those fledglings as they approach developed areas and

become stranded has scarcely been studied (although there are plenty of anecdotal

observations of birds after they reach land). Basic information on the behaviour of

nocturnally fledging burrow-nesting seabirds can inform our understanding of stranding

mechanisms and potential avenues toward mitigation. For example, in which direction(s)

do procellariiform fledglings orient during their initial flights from the burrow and does

this orientation change throughout their flight? What factors influence changes in

direction? How do fledging behaviour and stranding behaviour differ between species

that nest inland versus coastally? Some researchers have begun addressing these

questions using GPS tracking technology (Rodríguez et al. 2015; Rodríguez et al. 2022),

manual observation augmented by visible markers (Syposz et al. 2021b), and thermal

imagery (but so far only in adults; Syposz et al. 2021a). We suggest more widespread

uptake of these methods as well as radar and night vision technology to study fledging

and stranding behaviour of nocturnally fledging seabirds. A basic understanding of the

natural histories and fledging behaviours of the affected species needs to come first and

foremost, because it is essential in informing the execution of future stranding and attraction experiments.

Studies involving stimulus (e.g., light) alterations in settings where strandings occur may be compromised due to externally imposed constraints borne out of working in public and private spaces beyond the experimenters' control (e.g., Miles et al. 2010; Burt et al. 2024). Such studies need to occur over several fledging seasons and at multiple locations to ensure sufficient replication (e.g., Rodríguez et al. 2017b), or otherwise should be conducted in locations where there are no environmental sources of the stimulus in the immediate area. In addition, one of the greatest challenges in designing tests of attraction is identifying and implementing an appropriate control treatment (i.e., randomized absence of the stimulus of interest). For example, in experiments testing light attraction in passerines, various coloured light periods were alternated with dark periods to observe the resulting number and behaviours of birds nearby (e.g., Evans et al. 2007; Poot et al. 2008; Rebke et al. 2019). Without dark control treatments, it would have been more difficult to attribute changes in passerine abundance and behaviour to the light. Similar issues may arise in field studies of seabird light attraction.

In addition to field experiments, a lab-like experimental approach where environmental factors can be controlled, and which includes proper control treatments, is also helpful to test causal relationships. This approach can help inform effective mitigative measures in a shorter period (e.g., one fledging season). For example, preferences for various visual, auditory, or olfactory stimuli associated with stranding locations can be investigated using cue preference tests (using e.g., Y-maze and T-maze apparatuses; Brooke 1989; Nevitt and Bonadonna 2005; Bonadonna et al. 2006;

Jouventin et al. 2007; Atchoi et al. 2024) and other behaviour-based stimulus response experiments (e.g., Porter et al. 1999). Orientation and disorientation behaviour in response to various stimuli could be investigated with modified orientation experiments (e.g., Engels et al. 2014). Importantly, we also need a better understanding of the sensory capabilities of the affected species. This could be achieved in part by continuing to examine and characterize the various (not only visual) sensory organs of the species affected by stranding (e.g., Hart 2004; Mitkus et al. 2016; Mitkus et al. 2018; Atchoi et al. 2020) and experimentally measure their physiological and neurological responses to stimuli of interest (e.g., Nevitt and Bonadonna 2005; Baden and Osorio 2019; Mooney et al. 2020).

Additional research is needed to confirm the effects of weather variables (such as wind and visibility) and fledging numbers on stranding numbers. Firstly, we suggest further studying the effects of wind speed and direction on stranding numbers: fledglings could simply be getting blown ashore during certain wind conditions, or they could be preferentially fledging during certain wind conditions (e.g., stronger winds provide greater lift, which would be advantageous for inexperienced flyers), or both. Fledglings might also preferentially fledge in conditions of lower visibility to hide themselves from potential predators, leading to observations of increased strandings. The disentangling of weather and other emergent environmental variables to determine their effects on fledging and stranding numbers could be accomplished by quantifying the relative number of fledglings departing each night from a colony throughout the fledging period (as in Collins et al. 2023), simultaneously to quantifying fallout. For species where only fledglings are active at night (e.g., Atlantic puffin), radar could potentially be used (as

suggested by Wilhelm et al. 2021). Across all species, one could monitor a subset of burrows observationally or using Passive Integrated Transponder tags throughout the fledging season and document fledging timing (while controlling for other variables, such as age) to determine if wind conditions and potentially other environmental factors affect departure timing (such as was recently done by Collins et al. [2023] in relation to moon phase and incident illumination).

Conducting (ideally nightly) systematic searches in a defined area is critical to establish baseline stranding rates as it allows for quantification of search effort and comparisons across years (Fraser and Carter 2018; Friswold et al. 2020; Gjerdrum et al. 2021). This in turn allows the investigation of possible factors influencing strandings, and just as importantly, what factors are present and absent when birds are not found stranded, resulting in higher-resolution data for targeted mitigation efforts. Nightly systematic searches for stranded birds are also effective at reducing mortality by increasing the likelihood of finding live birds (Rodríguez et al. 2014), conferring a conservation benefit. Search areas should include areas with and without factors of interest, such as artificial light, across a gradient of proximity to the nearest colony or colonies, to eliminate or reduce the search bias that is inherent to non-systematic (i.e., community- and volunteer-based) search efforts. Indeed, over eight years Friswold et al. (2020) systematically searched for downed wedge-tailed shearwater fledglings along a 25.7-km transect that varied in proximity to the largest colonies in southeast Oʻahu (Hawaiʻi) and which included sections of varying streetlight density. The authors found more than one-quarter of the 376 downed fledglings next to only two light poles located in an area of relatively low streetlight density within 5 km from the nearest

colonies; fallout was negligible beyond 5 km from the colony even in the areas of highest

streetlight density (Friswold et al. 2020). Targeted mitigation measures at those two light

poles associated with the most strandings would therefore likely be more effective in

reducing overall fallout than if mitigation measures simply targeted areas of highest

streetlight density.

It is also important to estimate as accurately as possible the proportion of stranded

birds that remain undetected by rescuers. The search for stranded fledglings during rescue

programs is largely opportunistic, meaning that numbers reported in any study using this

approach must be viewed as minimums. Once stranded, birds may blend into the

landscape and hide in unsearched areas. Smaller species such as the Leach's storm-petrel

are particularly vulnerable to predation (e.g., gulls, foxes, owls, domestic cats) and can

quickly disappear from the searched area without a trace. Implementing detection

probability and carcass persistence studies (e.g., van Pelt and Piatt 1995; Wiese and

Robertson 2004) to estimate the number of stranded birds that disappear between

searches, coupled with comprehensive systematic searches (discussed above), would

provide a more accurate assessment of the total numbers of fledglings that become

stranded. This, in turn, would further inform our understanding of the true effects of

strandings on a given population.

There is a need for more intra- and inter-species comparative studies to evaluate

the reasons why some birds may become stranded while others do not, despite most

things seeming to be equal. For example, strandings in most cases are largely dominated

by fledglings, with only few adults becoming stranded (Rodríguez et al. 2017a; but see

Borsa et al. 2024; Raine et al. 2024). However, it is insufficient to only focus on the

causes of fledgling strandings; it is also necessary and complementary to investigate why

adults do not strand (or importantly, in rare cases, why they do strand). That is to say, the

various alternative hypotheses presented previously (light attraction, sound attraction,

olfactory attraction, random dispersal, magnetoreception, etc.) should be rigorously tested

in not only the demographics that are most affected by strandings but also in those that

are least affected (e.g., Syposz et al. 2021a; Middlemiss et al. 2025). There are scenarios

in which cross-species comparisons would also provide insight. For example, Leach's

storm-petrels and Atlantic puffins are both susceptible to stranding (Wilhelm et al. 2021).

However, where both of these species breed in great numbers near Witless Bay,

Newfoundland, only puffins become stranded while Leach's storm-petrels appear to be

minimally affected (despite stranding elsewhere in Newfoundland after departing from a

different colony; Wilhelm et al. 2021; pers. obs.). Clearly, more in-depth investigation of

the factors that differentially affect fallout probability amongst demographics and species

would be useful.

In contrast to the current working hypothesis of light attraction, which suggests

that seabirds are drawn to artificial lights over distances of up to several kilometers

(Troy et al. 2013; Rodríguez et al. 2015), we suggest for consideration an alternative,

short-range light attraction hypothesis. It is possible that individuals become disoriented

and subsequently stranded only once they approach lighted areas, e.g., via random

dispersal, rather than being drawn there. To our knowledge, there currently exists no

evidence that would exclusively support the long-range attraction hypothesis (e.g., GPS

tracks or radar imagery of fledglings exhibiting directed long-distance movement toward

lighted areas in an otherwise ecologically inappropriate direction). In contrast, results of

Guilford et al. (2018) suggest only a short-range effect of light on numbers of adult Manx shearwaters that collided with a lighted structure. Radar can help test the short-range light attraction hypothesis, thanks to its ability to resolve and make measurable the movement speed and direction of hundreds of birds over distances of one to several kilometers as they depart their colonies in darkness (Day and Cooper 1995; Hamer et al. 1995; Bertram et al. 1999; Day et al. 2015; reviewed in Hüppop et al. 2019). There are numerous types of radar technology that can be used for this purpose, many of them capable of resolving individual birds (reviewed in Hüppop et al. 2019). Multiple radar units can also be used to expand the area of detection. The management and policy implications of the short-range light attraction hypothesis may go so far as to suggest that artificial lighting schemes in settlements affected by seabird strandings remain unchanged, so as to funnel and concentrate birds that would become stranded regardless, into places where they are more easily found and captured. Taking this concept one step further, these areas could in turn be managed so that they are safe for birds to become stranded (i.e., lowered risk of injuries or death related to collisions and predation) and combined with a release program.

Summary

In this review, we have described the literature surrounding the effects of artificial light at night (ALAN) on stranding behaviour in a variety of seabird species. We have also highlighted areas in which future research efforts can be made, including the direct testing of the light attraction hypothesis using dark control treatments and standardized search effort; the investigation of null (i.e., random fledging dispersal) and alternative

hypotheses of stranding; the use of diverse methods to evaluate effects of natural and anthropogenic factors on both stranding and post-stranding behaviour in both fledglings and adults of affected species; and an estimation of the number of stranded individuals that remain undetected by rescuers. In my thesis, I address several of the aforementioned areas of research that are ripe for study. Additionally, most research on ALAN-induced seabird fallout to date has focused on procellariiforms. However, Atlantic puffins are numerically (i.e., in terms of number of individuals stranded per year) more highly affected (Rodríguez et al. 2017a) and are affected in more locations in the world than most procellariiforms, and are also declining across parts of their range, which begs the question of why they have been relatively neglected in the seabird stranding literature to date. I have thus attempted to remedy this shortfall by focusing much of my research on this species in the following chapters.

Thesis structure and objectives

In this thesis, I examine the effects of artificial light at night on seabird behaviour and detection probability. Specifically, I study behavioural responses toward light of seabird fledglings prone to becoming stranded in coastal settlements during their maiden flights from the nest, using Atlantic puffins and Leach's storm-petrels as model species. I also explore the effects of search effort, illumination and concealment levels on detection probability of puffin fledglings by rescue volunteers. Until recently, the hypothesis that light attraction was the cause of seabird strandings throughout the world was largely anecdotal in nature, with plenty of observations of stranded birds in illuminated areas but little experimental evidence to demonstrate that this was the sole result of seabird

phototactic behaviour and not partially an artefact of detectability bias. An important step in the effort to understand, quantify, and mitigate seabird strandings is to disentangle these various factors.

In the following chapters, I investigate phototactic responses and activity levels of Atlantic puffin and Leach's storm-petrel fledglings in a series of experiments on two different scales and across a variety of light types. In Chapter 2, I hypothesized that puffin fledglings become stranded due to attraction toward artificial lights, and that attraction responses differ based on preferences for certain light types over others. I also hypothesized that different spectra of artificial light elicit different activity levels in puffin fledglings. Phototactic behaviour was tested through a coarse-scale beach illumination experiment near the breeding colony and with a fine-scale Y-maze choice experiment to test for preferences among various combinations of darkness and several light types, while activity levels were quantified using an open field test. In Chapter 3, I replicated the Y-maze choice experiment and open field test with Leach's storm-petrel fledglings to test my hypotheses that juveniles of this species are also attracted to light and that activity levels also vary under different light types after grounding. Furthermore, I leveraged the results from these experiments to design an additional open field test experiment in which a hide box was provided, to test my hypothesis that Leach's storm-petrel fledglings would conceal themselves in the box at different rates under light versus dark conditions.

When predicting the impact of strandings at the population level, one of the major difficulties is in identifying how many individuals may be missed by rescue programs and under what conditions individuals are most likely to be found. Thus, in Chapter 4 I

investigated detection probability of realistic puffin fledgling decoys by rescue program volunteers. Specifically, I hypothesized that detection probability varies with varying levels of illumination, concealment, and search effort. Finally, in Chapter 5 I summarize my main findings related to the effects of artificial light at night on seabird behavioural responses and detection probability. I complete Chapter 5 by synthesizing my results to infer potential conservation and mitigation measures aimed at reducing the impact of night lighting on seabird populations globally. Considering the imperiled nature of many stranding-affected seabird species and the myriad other threats they face, it is critical that we rapidly increase our understanding, quantification, and mitigation of seabird mortality induced by artificial night lighting.

Chapter 2

Effects of artificial light on the behaviour of Atlantic puffin fledglings

This chapter has been published in Animal Behaviour:

Author Contributions

T.M.B.: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing – Original draft preparation. S.I.W.: Conceptualization, Supervision, Methodology, Resources, Writing – review and editing. A.D.S.: Resources, Methodology, Writing – review and editing. K.B.: Methodology, Investigation. G.F.M.: Supervision, Methodology, Funding acquisition, Writing – review and editing. G.B.: Conceptualization, Supervision, Methodology, Resources, Funding acquisition, Writing – review and editing.

Abstract

Every year in Newfoundland, young Atlantic puffins, *Fratercula arctica*, departing their nests at night for the first time become stranded in towns near their breeding colonies, a phenomenon thought to be caused by attraction towards artificial light. To test this hypothesis, we conducted three behavioural experiments. First, we illuminated beaches near a breeding colony to determine whether more fledglings would become stranded in illuminated versus dark conditions. Next, we conducted a Y-maze experiment to test stranded fledglings for phototactic behaviour in general and for preferences among high-pressure sodium (HPS), warm white light-emitting diode (LED), cool white LED, blue LED and orange LED light. Lastly, we quantified activity levels of stranded fledglings in an open field test during exposure to several different light types. We found significantly more fledglings stranded when beaches were illuminated, and fledglings significantly preferred light over darkness in the Y-maze, supporting our hypothesis that Atlantic puffin fledglings become stranded due to light attraction. Fledglings displayed no preferences for certain light types over others in the Y-maze, potentially suggesting that strandings in this species may not be mitigable by changing the streetlight type in stranding-prone towns. Interestingly, fledglings exhibited higher activity levels in darkness and HPS light than in LED light, potentially holding implications for rescue, rehabilitation and husbandry programmes. Overall, our findings demonstrate that the only evidence-based strategy for the reduction of Atlantic puffin strandings is the reduction of coastal artificial lighting; however, further research is needed to determine whether aspects of artificial light besides bulb type may be altered to effectively reduce light attraction in this species.

Introduction

As global human development continues to increase, artificial light at night (ALAN) is of growing concern as a pollutant of dark nightscapes (Jägerbrand and Spoelstra 2023). In addition, the widespread conversion to energy-efficient light-emitting diode (LED) lighting is expected to worsen the ecological impacts of ALAN through a variety of mechanisms (Pawson and Bader 2014; Davies and Smyth 2018). These mechanisms are both physiological (e.g., many organisms are more sensitive to short-wavelength light, which is prevalent in LED outputs, than to the long-wavelength light that dominates light types used previously, such as sodium vapour) and logistical (e.g., greater energy-efficiency allows for increased light production at the same or lower energy cost as other lighting technologies; Pawson and Bader 2014; Davies and Smyth 2018) in nature. Across taxa, disruption of natural diel light cycles by the presence of ALAN can dysregulate circadian rhythms and lead to endocrinological dysfunction, behavioural changes, and decreased fitness, among other effects (Sanders et al. 2021; Yang et al. 2024). One way in which ALAN can alter behaviour, especially that of nocturnal animals, is by acting as a supernormal visual stimulus that induces phototactic behaviour (either positive or negative; Rich and Longcore 2006). Positive phototaxis (or photopositivity), which is often ascribed to light attraction, has been documented in various animal taxa including insects, amphibians, fish, sea turtles, migratory songbirds, and seabirds, among others (Rich and Longcore 2006; Rodríguez et al. 2017a; Jägerbrand and Spoelstra 2023; Fabian et al. 2024). Positive phototaxis toward sources of ALAN can result in mortality due to collisions with glass windows, lighted structures, and vehicles; stranding and dehydration or desiccation in unfamiliar locations; and predation of

32

stranded individuals following disorientation and/or collision (Witherington 1997; Rich

and Longcore 2006; Rodríguez et al. 2017a; Van Doren et al. 2021).

Seabirds of the orders Procellariiformes and Charadriiformes (family Alcidae) are

prone to becoming stranded in human settlements following phototaxis toward and

disorientation by ALAN (Rodríguez et al. 2017a; but there are other non-mutually

exclusive hypotheses for stranding such as simple navigation error during natural

dispersal; Brown et al. 2023, Chapter 1). Fledglings of burrow-nesting and night-fledging

seabird species appear to be the most susceptible to light-induced stranding, although

adults of some species are also affected (Rodríguez et al. 2017a; Burt et al. 2024). There

is mounting evidence that suppression of ALAN near colonies of burrow-nesting,

night-fledging procellariiform seabirds can reduce the number of stranded fledglings

(Reed et al. 1985; Miles et al. 2010; Rodríguez et al. 2014; Burt et al. 2024). However, it

is not always possible to eliminate or suppress the use of ALAN, especially at industrial

and commercial sites where lighting is necessary for regular operation and human safety.

There is thus a growing interest from industry, non-governmental conservation

organizations, and various levels of government in investigating and implementing

alternate "less attractive" light types where suppression or elimination of ALAN is not

possible (e.g., Mercer 2018). Limited evidence suggests that lights with high correlated

colour temperature (CCT; a relatively crude but simple and widely-used metric of the

perceived colour of a nominal white light source; Durmus 2022) and predominantly

blue-violet wavelengths (such as metal halide types) may be more attractive to fledgling

procellariiforms and other wildlife than those with low CCT and red-orange dominant

spectra (such as sodium vapour types; Salamolard et al. 2001, as cited in Minatchy 2004;

Rodríguez et al. 2017b; Longcore et al. 2018), but other findings suggest the opposite

(Atchoi et al. 2024) and some indicate no difference (Urmston et al. 2022). An increased

attraction toward blue-violet wavelengths may be explained by an increased sensitivity to

these wavelengths by the visual systems of the affected taxa (Reed 1986; Bowmaker et

al. 1997; Hart 2004; Pawson and Bader 2014; Davies and Smyth 2018).

While research interest in procellariiform light attraction has increased in recent

years, comparatively little attention has been given to other seabirds that are similarly

affected by ALAN. Most notably, the Atlantic puffin (*Fratercula arctica*) represents the

only non-procellariiform seabird species that gets stranded routinely in coastal

communities, with insular Newfoundland (Newfoundland and Labrador, Canada) and

Iceland being the best-known affected locations (Rodríguez et al. 2017a; Wilhelm et

al. 2021; Katz 2023). Adults are diurnal, but fledglings leave their burrows on maiden

flights to the sea at night, unattended by parents, leaving them susceptible to the influence

of ALAN. Although populations in the western Atlantic remain robust and are even

increasing (Wilhelm et al. 2015), those in the eastern Atlantic are declining, likely due to

low recruitment (Miles et al. 2015; Fayet et al. 2021). Thus, with increasing coastal

development, understanding the extent and spectral attributes through which ALAN

impacts post-fledging behaviour in this species is urgently needed.

In Newfoundland, certain well-lit commercial and industrial locations near

Atlantic puffin breeding colonies are known to consistently yield stranded puffin

fledglings (hereafter, "pufflings") and have thus been deemed stranding "hotspots"

(Canadian Parks and Wilderness Society, Newfoundland and Labrador Chapter,

unpublished data). The existence of such "hotspots" has been taken as anecdotal evidence

in support of the light attraction hypothesis of stranding in puffins, although it is unclear to what degree this pattern may be driven by a spatial bias in non-systematic search effort (e.g., toward well-lit areas, where people are also presumably more comfortable searching at night). Furthermore, while hundreds of puffins are stranded annually, this represents only a very small proportion of the total number of individuals fledging from the colonies (Wilhelm et al. 2021), providing support to the natural random dispersal hypothesis which suggests that young birds become stranded because of their inexperience in navigating a new environment (Brown et al. 2023, Chapter 1). To date, no experimental study has been conducted to directly test the light attraction hypothesis and confirm the role of ALAN in causing Atlantic puffin strandings. To do so would require a coarse-scale experimental approach wherein, at a minimum, light levels (including specifically a "dark" condition), geographic location, and search effort are all tightly controlled (Brown et al. 2023, Chapter 1).

At small geographic scales, the behaviour of pufflings and other stranding-prone seabird fledglings exposed to ALAN remains largely unknown but can be studied ex- or in-situ (e.g., in a Y- or T-maze choice experiment). In the only alcid whose fine-scale phototactic behaviour has been studied to date, ancient murrelet (*Synthliboramphus antiquus*) chicks oriented more often toward a reflected light source than toward darkness (Gaston et al. 1988). Stranded Cory's shearwater (*Calonectris borealis*) fledglings, however, consistently chose darkness over light in a similar experiment (Atchoi et al. 2024). In addition to testing for the presence of photopositivity in general (i.e., comparing taxic responses to light versus dark), it is also of interest whether stranding-prone seabird fledglings exhibit fine-scale preferential phototactic responses or

differential activity levels in response to certain spectra of artificial light over others. For example, Atchoi et al. (2024) found that both fledgling and adult Cory's shearwaters significantly preferred red over blue light when both were provided as options simultaneously. Such fine-scale experiments may not perfectly mimic what occurs in nature, but they nonetheless inform our understanding of behavioural responses to light, especially in ground-based contexts. This information holds implications for rescue efforts in predicting where stranded seabirds are likely to go and how they will behave following stranding, which should allow for higher rescue success.

In this study, we tested the effect of ALAN on puffin behaviour at both a coarse and fine scale. At a coarse scale, we experimentally tested the light attraction hypothesis of stranding in the field by directing a 30,000 lumen LED light toward the Gull Island (Witless Bay) Atlantic puffin breeding colony, on alternate nights from two different dark beaches during the fledging season. Given the hypothesis that pufflings become stranded by light attraction, we expected that more pufflings would be observed at the beaches when they were illuminated than when the beaches were dark. To test for effects of ALAN on a fine scale, we used a Y-maze to evaluate the propensity of already-stranded pufflings to exhibit phototactic behaviour and preferences for various artificial light spectra. We expected that fledglings would exhibit positive phototaxis in the Y-maze by preferentially choosing light over darkness when both were provided as options. We further expected that when pufflings were exposed to two different artificial light types, they would preferentially choose those with "cooler" hues (e.g., cool white LED; blue LED) over those with "warmer" hues (e.g., high-pressure sodium (HPS); warm white LED; orange LED). This reasoning is based on the peak optical sensitivity of

closely-related auks to 406 nm violet light and that of stranding-prone procellariiforms to 402-405 nm violet light (Ödeen and Håstad 2003). To determine if different spectra of artificial light induce different activity levels in pufflings, we conducted an open field test. Although we expected to observe differences in activity levels among the light treatments, particularly when compared with darkness, we could not predict directionality a priori.

Methods

Ethical Note

All procedures involving the use of animals for research were performed in accordance with Trent University's Animal Care Protocol guidelines under the Canadian Council on Animal Care (CCAC), protocols #26223 and #28033, and Canadian Wildlife Service guidelines under scientific permit # SC4051. All experiments were compliant with current Canadian law. Birds were captured using handheld mesh nets, were not manipulated beyond simple handling, and were held in captivity for as short a time as possible. We further attempted to reduce the stress experienced by birds by housing them individually in quiet and dimly lit conditions for the duration of captivity.

Study Sites and Species

In Newfoundland, most stranded pufflings are found along a ~15 km section of coastline between the communities of Bay Bulls and Bauline East (Figure 2.1). This section forms the focal search area for the Canadian Parks and Wilderness Society – Newfoundland and Labrador Chapter's (CPAWS-NL) "Puffin Patrol", a volunteer-based

puffling rescue program that operates each year during the fledging (and stranding) season (Wilhelm et al. 2013, 2021). The Witless Bay Ecological Reserve, which borders this coastline, hosts close to 400,000 breeding pairs of Atlantic puffins, forming the largest concentration in North America (Lowther et al. 2020; S.I.W., unpubl. data). Stranded pufflings are thought to largely originate from the two largest breeding colonies on Gull Island (47.262297°N, 52.773389°W, estimated at 168,000 pairs; S.I.W., unpubl. data) and Great Island (47.187182°N, 52.813495°W, estimated at 205,000 pairs; S.I.W., unpubl. data), both part of the reserve and located less than 3 km from shore at their closest points (Figure 2.1).

To study the behavioural response of pufflings to light at coarse spatial scales, we performed an "illuminated beach experiment" (hereafter, beach experiment) in August 2022 at two sites near Witless Bay, Newfoundland: Lower Pond Beach (47.281464°N, 52.810982°W) and Ragged Beach (47.262068°N, 52.811644°W; Figure 2.1). Both of these beaches face Gull Island: Lower Pond Beach at a distance of approximately 3.1 km, and Ragged Beach at a distance of approximately 2.5 km.

To study the fine-scale spatial behavioural response of pufflings to lights of differing spectra, we performed both a Y-maze "choice experiment" and an open field test in August 2021 in Bay Bulls, Newfoundland and Labrador, Canada (47.315178°N, 52.813887°W; Figure 2.1). In 2021, we conducted the fine-scale experiments in one of two identical "field labs" (storage trailers, 2.4 × 1.4 × 2.1 m) located adjacent to the headquarters for CPAWS-NL's annual Puffin Patrol rescue program (and the designated drop-off location for all rescued pufflings). One "lab" was used for the choice experiment, while the other was for the open field test. In August 2022, we tested one

additional choice experiment combination in a building in Saint Michaels (47.187247°N, 52.843990°W; Figure 2.1).

Response of Pufflings to Light at a Coarse Spatial Scale

Materials

We illuminated one of two beaches (Lower Pond beach or Ragged Beach; Figure 2.1) over 11 nights during the fledging season between 15-27 August 2022, coinciding with a transition from 85% to 0% lunar illumination (moongiant.com). Experiments were not conducted on 17-18 August due to inclement weather. At both beaches, a 30,000 lumen, 6390 K LED light apparatus (Willpower 52-inch, 675-Watt LED light bar: Xalapa, Veracruz, Mexico; spectrum displayed in Appendix Figure A2.1) was mounted to a 1.5-metre wooden fence board and placed on two overturned plastic buckets at the highest point of the beach (approximately 2 m above sea level) such that the light sat horizontal and parallel to the beach, facing Gull Island. On each night during the experimental period, we illuminated one beach while the other remained dark. At the light beach, the light apparatus was connected to a Discover 12V 35AH/20HR rechargeable deep cycle marine battery (Richmond, B.C., Canada) via a wiring harness with an in-line fuse and toggle power switch; at the dark beach the battery and the light apparatus with attached wiring harness were set up but not connected.

Experimental procedure

A coin was flipped to determine which of the two beaches was illuminated on the first night of the experiment; thereafter, the light treatment was alternated between

beaches. Because there was one illuminated beach and one unilluminated beach every night, we have $N = 11$ "light" and $N = 11$ "dark" experimental trials. Regardless of treatment (light or dark), there was a team of usually two to three (one instance of four, and one instance of five) biologists and trained volunteers stationed at each beach to operate the light apparatus and to observe and capture pufflings for the duration of the experiment. Trials ran for exactly two hours, sometime between 2130 and 0030 hours (to coincide with the peak stranding period; CPAWS-NL, unpubl. data), depending on the night. On two nights there was an equipment malfunction in the middle of the trial, but by extending the light treatment trial we ensured the total duration of two hours of light exposure remained the same.

Approximately 10 minutes before the experiment start time, 1-2 team members at each beach conducted a brief survey to a minimum of 25 m on either side of the light apparatus and scanned the water with the unaided eye and night vision binoculars (Bestguarder NV900 4.5-22.5 × 40 HD; Shenzhen, China) as thoroughly as allowable by the weather conditions, to ensure no pufflings were already present in the vicinity prior to the start of the experiment. We then placed two reflective safety vests 25 m on either side of the light apparatus and two vests closer to the water's edge at the same distance (total four vests on each beach) to delineate the focal observation area (50 m long and varying from 15-20 m wide = ~750-1000 m^2). This distance was chosen based on preliminary tests of the resolution and range of the night vision binoculars and the width of the light beam. There was no way to consistently delineate the focal observation area over water, but the best effort was made to estimate the relative distances of pufflings observed.

During the two-hour experiment period on the light and dark beaches, observations principally consisted of one team member at each beach visually scanning the focal beach observation area with night vision binoculars; however, it should be noted that on most nights, even the unaided eye could resolve details of the beach topography (and therefore also presumably resolve the stark white chests of any pufflings present) with ambient light alone. Observers took turns (of no set duration) using the night vision binoculars to avoid fatigue. The remaining team members scanned the beach, water, and airspace with the unaided eye and recorded each puffling observation, including notes on whether a puffling was suspected or known to be the same individual as one observed earlier. Team members stood next to one another and visually tracked each individual puffling as long as it was within view, continuously communicating about positions and movements of birds to keep track of unique individuals. Whenever visual contact with a puffling was lost, subsequent visual contact with a puffling in the same general location was judged in its likelihood of being the same individual based on the amount of time that had elapsed since previous visual contact. If less than ~10 seconds elapsed between initial and subsequent visual contact, the second observation was considered to be the same bird; otherwise, it was recorded as a "potential duplicate".

Any pufflings that became stranded were captured by hand as they were observed and placed individually into a vented plastic holding container (40 cm long × 30 cm wide × 25 cm tall) in a quiet, dark and sheltered location. We took care to limit our time on the beach during capture to a minimum (less than 5 minutes) and only executed a capture attempt when no other birds were seen nearby (either in the water or on land), so as not to influence their behaviour. During a capture attempt, the remaining observer(s) divided

their attention amongst scanning the beach, water, and airspace with both night vision

binoculars and the unaided eye to ensure all new puffling observations were documented.

At the end of the evening (maximum time in captivity, three hours), pufflings were

measured and banded by Environment and Climate Change Canada personnel and

released at the water's edge of the same site where they became stranded (always in dark

conditions).

Data extraction

From the recorded observational data, we extracted minimum, maximum, and

best-estimate counts of unique individual pufflings observed each night at each beach.

Minimum counts for each beach, on each night were calculated by summing the number

of observations known to be of unique individuals, omitting all observations that were

potentially duplicates; this was our most conservative count. Maximum counts were

calculated by summing the number of observations known to be of unique individuals

plus all those that were potentially duplicates. Best-estimate counts were calculated by

summing the number of observations known to be of unique individuals plus only the

potential duplicates that were (according to qualitative field notes) likely to be unique

individuals; this count is likely the most accurate. On six of eleven nights, the number of

pufflings present at the illuminated beach at any one time was low enough to facilitate

continuous visual tracking of all or nearly all individuals, resulting in few (if any)

potential duplicates and minimum, maximum, and best-estimate counts that vary little

from one another. On the other five nights, numbers were high enough that continuous

visual tracking of all individuals was not possible despite our best efforts; this is when the

number of potential duplicates was highest, and the greater difference between minimum and maximum counts on these nights reflects this difficulty. We also tabulated on a per-treatment basis the number of pufflings observed in the water, in the air, and on the beach; however, it is important to note that because of the difficulty in tracking unique individuals (see above), these are counts of observations rather than estimated counts of unique individuals.

Response of Pufflings to Light at Fine Spatial Scales

Animal collection, housing, and release

To measure phototactic behaviour and activity levels we mainly used stranded pufflings provided by the Puffin Patrol between 8-24 August 2021. Although it is possible that stranded pufflings do not represent a truly random sample of the entire fledgling population, it is this population in which we are most interested since it appears to be most affected by ALAN and also the population from which we would expect the greatest response to our experimental light stimuli. Puffin Patrol volunteers captured pufflings by hand using long-handled butterfly nets, placed them individually into vented plastic holding containers (described above) and then transported them to Puffin Patrol headquarters by vehicle within 2 hours of capture, but usually sooner. CPAWS-NL staff recorded the location and time of capture (if the information was not already submitted electronically by the volunteer(s)) and placed the crated pufflings in a quiet, dark and sheltered location.

Each night between ~2000 and 2100 hours, we brought the first rescued pufflings in their crates to a grassy area next to our "field labs," approximately 25 m away.

Pufflings rested in their crates for a minimum of 10 minutes before being brought into the lab and participating in the choice experiment described below. Pufflings were then returned to their crates and allowed to rest outside at ambient temperature for a minimum of 10 minutes before beginning the open field test in the second field lab. Once the open field test was completed, pufflings were returned to the Puffin Patrol's designated holding area. All pufflings were then measured, banded, and released the following morning by Environment and Climate Change Canada personnel.

In 2022, we performed one additional choice experiment combination (we did not do an open field test in 2022). We captured stranded pufflings between 10-14 August 2022 in the same focal search area as that of the Puffin Patrol, placed individuals in crates, and brought them to Saint Michaels by vehicle (20 minutes travel). Pufflings rested in their crates in a small, dark, quiet room (~20°C) for a minimum of 10 minutes before we placed them in the choice experiment. After the experiment, we returned pufflings to their crates and released them the following morning from a nearby beach.

Materials for choice experiment to measure phototactic behaviour

We used a Y-maze to measure phototactic behaviour and assess pufflings' preferences for various light spectra (Figure 2; Appendix Figure A2.2). The metal "acclimation box" (height: 15 cm) opened into the "main box" (height: 22 cm), a large, opaque, blue Rubbermaid container, via a vertically sliding door. Attached to the main box were two adjacent and parallel "choice arms" constructed of 15 cm-diameter thick-walled expandable blue dryer vent hose, each of which led to a small, opaque, blue Rubbermaid container ("choice box"; height: 18 cm). In the middle of the terminal end of

each choice box we cut a round hole, approximately 3 cm in diameter and with its centre approximately 8 cm above the ground, which allowed light from the light source to enter the Y-maze. Except for this hole, we covered the exterior light-facing side of each choice box with aluminum foil to prevent light from passing through the wall of the choice box and thereby affecting the spectrum of light visible inside the Y-maze. Further, we placed a 100 × 50 cm Masonite sheet between the two choice arms and choice boxes to eliminate crossover of the different light types (except in the bright HPS vs. dim HPS group, where the incident light crossing over from the bright HPS choice box was used for the dim HPS choice box). Another small hole (1 cm in diameter) was cut into the outer-most sides of both choice boxes to allow an infrared baby monitor camera (VTech, VM5262-2; British Columbia, Canada) to view the doorway between each choice arm and its corresponding choice box, allowing us to detect when an individual had made a choice (Figure 2.2).

Three different types of lights were used in combination with various filters to produce six spectral choice combinations (spectra displayed in Appendix Figure A2.2): HPS with a correlated colour temperature (CCT) of 2100 K (Light EnerG, 400 Watt; manufacturer location unknown); warm white LED with a CCT of 2700 K (Philips, 5W / 40W-equivalent Soft White LED); and cool white LED with a CCT of 5000 K (Philips, 5W / 40W-equivalent Daylight LED). In total, there were six choice combinations, with number of trials for each bracketed: 1) bright HPS vs darkness ($N = 15$); 2) bright HPS vs dim HPS ($N = 22$); 3) bright HPS vs warm white LED ($N = 23$); 4) warm white LED vs cool white LED ($N = 21$); 5) dim blue LED vs orange LED ($N = 25$); 6) bright blue LED vs orange LED ($N = 25$, in 2022 only).

When used, LED lights were fixed to a retort stand and positioned approximately 5 cm from the choice box's distal hole. The HPS light fixture had an attached rectangular metal reflector on one side, which was bent around the lightbulb to create a cylindrical shape to focus the light out of the distal end of the cylinder. When HPS light was used, the end of the light reflector was placed approximately 15 cm away from the hole. These distances were calibrated with the use of variable neutral density filters (crossed sheets of polyvinyl alcohol-iodine polarizer films; Alight Polarizers, PF006 linear polarizer; Texas, USA) and diffusers (parchment paper) to ensure that the amount of light entering the Y-maze at the peak wavelength of each light type's respective spectrum was approximately equal across light types, as measured by a calibrated spectrometer (see Appendix Figure A2.2). The two blue LED light options and the orange LED light option were created by pairing the cool white and warm white LED lightbulbs, respectively, with neutral density filters and diffusers as well as coloured acrylic (ePlastics; California, USA) and glass filters (see Appendix Table A2.3). We tested pufflings in blue and orange LED light in an attempt to distinguish effects of "warm"- and "cool"-coloured light on phototaxis, following distinctions reported in the literature for other seabird species (Salamolard et al. 2001, as cited in Minatchy 2004; Rodríguez et al. 2017b).

Procedure of choice experiment to measure phototactic behaviour

In 2021, 106 pufflings were randomly chosen from those that were stranded and rescued by the Puffin Patrol and divided among five choice combinations. We tested only one combination each night via selection out of a hat (i.e., it took five consecutive nights

to conduct trials in all five combinations, after which they were drawn nightly again in random order), except in the last few days of the field season when we selected the choice combination each night to correct for sample-size deficiencies (all choice combinations tested over a minimum of two non-sequential nights). In 2022, 25 pufflings were tested in bright blue LED vs orange LED, resulting in a total choice experiment sample size of $N = 131$.

Before each trial, the light stimuli were put in their positions and turned on. Each puffling was brought into the field lab, removed from its holding container, and placed in the acclimation box of the Y-maze. After precisely 2 minutes the inner sliding door was removed and the puffling was allowed 13 minutes to make a "response". If the puffling did not voluntarily exit the acclimation box by 5 minutes after removal of the inner door, it was gently prodded with the experimenter's hand reaching through the outer sliding door until the puffling entered the main box. In total, 21% (27 of 131) of pufflings needed prodding. A response was considered to have been made when a bird reached the end of a choice arm and any part of the body was visible on the monitor (even if it did not fully enter the choice box). The bird was removed from the apparatus after making a choice or after 15 minutes had elapsed (deemed "No Response"), whichever came first, and returned to its holding container in preparation for the open field test. Between each individual's trial, the entirety of the Y-maze was cleaned with 70% isopropyl alcohol and a disposable cloth to eliminate possible olfactory cues, and the two lights were alternated between the two choice boxes to account for any potential side bias on part of the birds.

Materials to measure activity levels under various light spectra

The cube-shaped open field test arena was constructed from 6 semi-opaque white twin wall polycarbonate panels (1 m × 1 m), held together by acrylonitrile butadiene styrene (ABS) strips. The floor was left unattached for easy removal and cleaning between trials. A 20 cm × 20 cm grid composed of 25 squares (i.e., 5 squares × 5 squares) was created on the floor using black electrical tape. A flap door (approximately 20 cm wide × 15 cm tall) was cut into the bottom edge of one side of the arena to allow pufflings to be placed into and removed from the apparatus. To eliminate any ambient light, an opaque blackout curtain was placed over the roof and sides of the arena. Two holes were cut in the center of the roof and overlaying curtain: one hole, approximately 3 cm in diameter, accommodated the lens of a miniature action camera (Activeon, CCA10W, Activeon Inc.; San Diego, CA, USA) with a wide-angle lens to allow for full view of the floor of the arena. The other hole, approximately the same size and 5 cm away, allowed for a controlled amount of light to enter the arena from an overhanging light source. When in use, LED lights rested directly on the hole, while the HPS light was suspended approximately 20 cm above the hole. This was done to decrease the amount of heat applied to the arena roof (since the HPS light was warmer than the LED lights), and because the HPS light was brighter than the LED lights (this distance resulted in a relatively equal amount of light entering the arena). Median illuminance was similar across the three light treatments when measured at 25 different locations at floor level (Kruskal-Wallis test: $H_2 = 1.3696$, $P = 0.5$) using a spectrometer (SRI-2000 Spectral Light Meter; Allied Scientific Pro; Gatineau, Quebec, Canada). The median illuminance from HPS was 26.35 lux (IQR 21.08 – 33.18), while that from warm white LED was

24.34 lux (IQR 20.30 – 27.80), and that from cool white LED was 23.88 lux (IQR

19.46 – 28.62). These median illuminance values are comparable to that of a similar

behavioural study, wherein illuminance was approximately 30 lux (Atchoi et al. 2023).

Experimental procedure to measure activity levels under various light spectra

To determine whether puffling activity level was affected by light type, we

performed an open field test. In 2021, 96 of the 106 Atlantic puffin fledglings used in the

choice experiment were used in the open field test, whereby we exposed them to either

darkness or one of three light spectra. Five individuals were removed from the final

dataset due to camera malfunction, resulting in a final sample size of $N = 91$. Treatments

were: 1) darkness ($N = 23$); 2) HPS ($N = 19$); 3) warm white (2700 K) LED ($N = 24$); and

4) cool white (5000 K) LED ($N = 25$). We did not measure activity in response to blue or

orange light to focus our testing on spectra from light sources currently used in human

settlements (i.e., HPS and LED). Each night, we used only two light treatments in the

open field test, and they were never the same as the two light types used in the Y-maze on

the same night. The initial treatment each night was chosen randomly, and treatments

were alternated for the rest of the night.

Prior to each open field trial, the appropriate light was set up and turned on

(except in the dark treatment), and a video recording (with audio) was started. The

puffling was placed just inside the flap door of the arena, and an electronic timer started.

After 10 minutes, the video and audio recording were stopped. The puffling was removed

from the arena, replaced in its holding container, and returned to Puffin Patrol

headquarters. The floor of the arena was not cleaned between trials unless a puffling

defecated during its trial, in which case the affected area was cleaned with 70% isopropyl alcohol and allowed to dry before the next trial. As many trials as possible were completed each night (median 10 trials; range 3-13 trials per night).

Activity level data extraction

Prior to reviewing any open field test videos, we determined the order in which to watch each video using the random number "sequence generator" on random.org (Randomness and Integrity Services Ltd., Dublin, Ireland). We used behavioural scoring software JWatcher (Version 1.0, Macquarie University and University of California, Los Angeles) to score two levels of behaviour for 10 minutes: "mobile" behaviour included walking, running, or flying; otherwise, birds were considered "immobile". The software automatically calculated the total amount of time spent mobile and immobile by each puffling in milliseconds, based on the timing of our key presses, and we subsequently converted each score of time spent mobile into seconds.

In the case of "dark" treatment videos, only the audio was discernible. Puffins have large, webbed feet and claws, which allowed us to hear them as they walked over the polycarbonate floor of the arena. Instead of viewing the file, we listened to its audio and recorded instances when we heard the bird moving (mobile) or halting (immobile). Billing (tapping or scraping the arena walls with the bill) and scratching (clawing at the arena floor with the feet) could also be heard but were not scored as "mobile" behaviour on their own. Each time a key code was pressed, the previous behaviour was automatically assumed to have ceased. We decided to score only "dark" videos audially (rather than scoring all videos audially) because: 1) we reasoned that visual scoring is

both more accurate (i.e., truer to the correct value) and more precise (i.e., repeatable) than audial scoring, and is therefore preferable when three of our four treatments can be scored visually; 2) the noise associated with the HPS light's ballast fan would have made audial scoring of those videos difficult and therefore introduce a new source of scoring bias; and 3) extra care was taken during the dark treatment specifically to ensure that noises similar in quality to those of puffling footsteps were reduced to an absolute minimum so as to increase the accuracy of those audial scores, whereas only reasonable care was taken to reduce similar noises in the lighted treatments.

To determine whether the time spent mobile and immobile in the dark treatment could be accurately scored by listening to the audio alone, we selected a subset of 25 videos from the three lighted conditions (HPS, warm white LED, cool white LED) that had already been scored. We listened to all 25 videos in random order with headphones and scored them audially as normal. A single observer did all visual and audial scoring.

Statistical Analysis

All analysis was performed in program R (ver. 4.3.0; R Core Team, 2023). We report results to a significance level of $\alpha = 0.05$.

Response of pufflings to light at a coarse spatial scale

We tabulated the minimum, maximum, and best-estimate counts of pufflings seen during the "light" and "dark" treatments each night, as well as counts of observations of pufflings in the water, in the air, and on the beach. To control for search effort, we calculated "estimated observation rate" (reported as birds per observer) by dividing the best-estimate counts of pufflings during a given treatment on a given night (over the

51

two-hour experimental period) by the number of observers present. We report medians and interquartile ranges. For a more conservative approach we also compared median estimated observation rates on the beach only (estimated count on the beach divided by number of observers), between light and dark. This was because the night vision binoculars worked best while looking at a solid backdrop (i.e., the beach itself) and because our land-based search area at both beaches was standardized. The results of this experiment were definitive in demonstrating higher numbers of pufflings at the beaches during the "light" treatment regardless of the metric used, obviating the need for formal statistical analysis.

Response of pufflings to light at fine spatial scales

Phototactic behaviour

In the choice experiment we tested a final sample size of $N = 131$ pufflings. To test whether pufflings displayed evidence for positive phototaxis or preferences for certain light spectra over others we excluded individuals who exhibited No Response ($N = 23$) since this behavioural outcome indicates no preference. For the remaining individuals, we performed a binomial test (package "stats", v. 4.3.0) of the light stimuli chosen in each of the six choice combinations to determine if choices significantly differed from hypothesized proportions of 0.5, and we report 95% confidence intervals of the estimated true proportions. We then conducted a Fisher exact test (package "stats", v. 4.3.0) on the number of pufflings from each combination that were "prodded" to determine if the proportion of prodded individuals differed among combinations.

<u>Activity levels</u>

To determine if scoring videos audially may have artificially biased our estimates of time spent mobile in the "dark" treatment group (in comparison to scoring the light videos, which was done visually), we conducted a simple linear regression of time spent mobile scored visually as a function of time spent mobile scored audially of the 25 selected lighted videos that were scored both visually and audially. The regression equation was statistically significant ($r^2 = 0.985$, $F_{1,23} = 1478$, $P < 0.001$); audial scores slightly overestimated but nonetheless strongly predicted visual scores of time spent mobile ($\beta = 0.9228$, $P < 0.001$, Appendix Figure A2.3). We converted the "dark" data using the regression equation and used these "converted" values in statistical comparisons with the unmodified visual scores from the other treatment groups (see Appendix 2). Note that the average difference between raw and converted scores of time spent mobile in the "dark" group was a decrease of only eight seconds (maximum difference, -21 seconds).

We identified one outlier in the entire dataset: an individual exposed to warm white LED light that spent 353 seconds mobile (a deviation from that treatment group's 75% quartile by approximately +2.3 times the interquartile range). Because it is unclear what caused this individual to behave so differently from the rest of the individuals exposed to warm white LED light, we removed it from all analyses (both choice experiment and open field test). Retention of this outlier causes a loss of statistical significance in one out of three comparisons, but the general trends remain unchanged (to see results with the outlier included, see Appendix 2). Because activity level data did not meet assumptions of normality or homogeneity of variance, we used non-parametric statistics. To test whether individuals differed in the time spent mobile across treatment

groups, we performed a Kruskal-Wallis H test (package "stats", v. 4.3.0) and a post hoc Dunn test (package "FSA", v. 0.9.4; Ogle et al. 2023) for multiple comparisons.

Results

Response of Pufflings to Light at a Coarse Spatial Scale

We calculated a best-estimate total of 136 pufflings that arrived at the beaches (observed in the water, on the beach, and in the air combined) during the light treatment, and only 2 pufflings during the dark treatment, over the 11 nights of the experiment. Similar patterns emerged between the light and dark treatments when we expressed best-estimate count data on a nightly basis (Figure 2.3A): during the light treatment the median best-estimate count was 7.0 (IQR 4.5 – 14.5) individuals per night compared to 0.0 (IQR 0.0 – 0.0) in the dark. When numbers are compared within the same experimental night, minimum, best estimate, and maximum counts of pufflings observed, as well as observation rates that control for search effort, all tell a similar story: the frequency of pufflings was consistently higher during light treatments than during dark treatments (Appendix Tables A2.1, A2.2). When we controlled for search effort, median estimated observation rate was 2.0 (IQR 1.2 – 6.0) birds per observer in the light and 0.0 (IQR 0.0 – 0.0) birds per observer in the dark (Figure 2.3B). Focusing only on the standardized 50-metre-long beach search areas for which we have greatest confidence, pufflings were observed 54 times during the light treatment, which greatly outnumbered the dark treatment's single observation. Controlling for search effort, a median of 0.7 birds per observer (IQR 0.4 – 2.3) was seen on the beach in the light treatment, compared to 0.0 birds per observer (IQR 0.0 – 0.0) in the dark. Behavioural observations

indicated that pufflings in flight generally flew at altitudes of 15 m or less, in straight lines either along the shoreline (in both directions) or overhead going inland, and pufflings in the water and on the beach approached the light to varying distances (approximately 15-40 m) and then either stopped moving (to preen, rest, etc.) or proceeded back to the water and swam away (if not captured first).

Assessment of Phototactic Behaviour and Light Preferences

Significantly more individuals responded to bright HPS light than dark ($P = 0.002$; 95% CI of estimated true proportion of bright HPS: 0.69-1.00; Table 2.1) in the choice experiment. Although not statistically significant, more individuals responded to bright HPS over dim HPS ($P = 0.1$; 95% CI of estimated true proportion of bright HPS: 0.46-0.88). There was no significant preference of any light type in any other remaining choice combination (Table 2.1). There was no statistical evidence for side bias, as pufflings chose Choice Box 1 ($N = 57$) relatively equally to Choice Box 2 ($N = 52$; binomial test: $P = 0.7$; 95% CI of estimated true proportion of Choice Box 1: 0.43-0.62). There was no difference among choice combinations in the number of pufflings prodded out of the acclimation box after 5 minutes (Fisher Exact Test: $P = 0.6$).

Assessment of Activity Levels in Different Light Types

In our open field test, there was a significant effect of light type on time spent mobile by pufflings (Kruskal-Wallis test: $H_3 = 18.396$, $P = 0.0004$). Pufflings spent more time mobile in darkness (median time spent mobile = 120 seconds) and in HPS light (median 111 seconds) than in cool white LED light (median 32 seconds; Dunn test:

P = 0.003 and *P* = 0.004, respectively; Figure 2.4). Pufflings also spent more time mobile in darkness than in warm white LED light (median 54 seconds; Dunn test: *P* = 0.045). Pufflings spent more time mobile, but only marginally, in HPS light compared to warm white LED light (Dunn test: *P* = 0.050; Figure 2.4). If the statistical outlier is included (see Methods), the difference between warm white LED and darkness is no longer significant, although the trend remains the same (*P* = 0.09; see Appendix 2).

Discussion

Our results provide strong experimental evidence that light attraction behaviour is a causal mechanism behind the stranding of Atlantic puffin fledglings (pufflings) in coastal areas during their initial fledging flights. This evidence emerges at both coarse and fine spatial scales. Even after controlling for search effort and size of the search area, in our coarse-scale beach illumination experiment we found significantly more pufflings stranded during the light treatment than during the dark treatment. Further, consistent with a light attraction hypothesis of stranding, in our Y-maze experiments pufflings significantly preferred light over darkness and somewhat preferred bright HPS light over dim HPS light (although the latter was not statistically significant). Contrary to our expectation that pufflings would prefer "cool" light spectra over "warm" light spectra (based on results of Salamolard et al. 2001, as cited in Minatchy 2004; Rodríguez et al. 2017b), we found no preferences when pufflings were simultaneously presented with two different light spectra. Our open field test experiment, in which we exposed pufflings to either darkness or one of three light types, revealed that pufflings were more active in darkness than in any LED light, and more active in HPS light than under cool white LED

light. Pufflings also tended to be more active in HPS light than in warm white LED light, but this difference only bordered on statistical significance.

We are first to demonstrate a reduction in stranding numbers of an alcid through the experimental reduction of ALAN. Our finding that more pufflings became stranded at our two beach sites during the light treatment compared to the dark treatment is consistent with similar studies on procellariiforms (Reed et al. 1985; Miles et al. 2010; Rodríguez et al. 2014; Burt et al. 2024). Our results therefore provide further support for recommendations to reduce or eliminate sources of ALAN near breeding colonies of seabirds affected by stranding, especially where populations are already in decline (e.g., Rodríguez et al. 2017a). However, it should be noted that the number of pufflings stranded during our experiment, and indeed during the entire Puffin Patrol rescue program, is small relative to the estimated total fledging cohort (e.g., in 2019 an estimated $246,069 \pm 25,988$ juveniles successfully fledged from the Witless Bay Ecological Reserve and 326 were found stranded; Wilhelm et al. 2021). It is possible, then, that navigational errors during natural dispersal movements inevitably bring a small proportion of fledglings close to land, where they become attracted to and stranded by nearby artificial lights (Brown et al. 2023, Chapter 1).

Previously, we expressed concern that human visual perception is more acute, and therefore the detection of stranded birds is likely more efficient in light conditions compared to darkness, potentially leading to a bias in detection probability (Brown et al. 2023, Chapter 1). As such, in our coarse-scale light attraction experiment we attempted to reduce the bias between our two treatments by: 1) using identical night vision binoculars at each of our sites on each night of the experiment; 2) clearly

delineating a search area of the same size (area of approximately 50 m × 15-20 m) on

both beaches that took into account the maximum visual range of the binoculars; and

3) controlling for the number of observers present at each site in our data analysis. Even

if our light treatment was still subject to bias toward elevated detection probability, it is

highly unlikely that the large difference in number of pufflings found within the beach

search areas ($N = 54$ in Light vs $N = 1$ in Dark) is attributable to missing a significant

number of pufflings in the dark treatment. In fact, the single puffling we detected within

the search area during the dark treatment was on a night with very low lunar illumination

(13.3%), after the moon had already set, and during overcast and rainy conditions. That

pufflings were visible to observers even in the worst of visibility conditions suggests that

if more individuals were indeed present in the dark treatment, they would have been

detected. Additionally, by alternating each night which site received the light treatment,

we simultaneously controlled for the potential effects of date, moon phase (see

Wilhelm et al. 2021) and site on the numbers of pufflings we observed.

In addition to the stark difference in number of pufflings observed within the

delineated beach search areas in the light versus dark treatment, more individuals were

also observed swimming and flying in the light treatment ($N = 77$ and $N = 78$,

respectively) than in the dark treatment ($N = 1$ and $N = 1$, respectively).

Support for the light attraction hypothesis of stranding in pufflings is bolstered by

the positive phototactic behaviour pufflings displayed in our choice experiment. Pufflings

chose bright HPS light significantly more often than darkness and chose bright HPS light

slightly (but insignificantly) more often than dim HPS. These results agree with those of a

similar study in which ancient murrelet chicks chose light significantly more often than

darkness in a T-maze just after leaving their nests (Gaston et al. 1988), but interestingly are contrary to results of a Y-maze experiment in which Cory's shearwater fledglings chose darkness over light (Atchoi et al. 2024). Ancient murrelet chicks leave the nest at night under parental care on average only two days after hatching (Gaston and Shoji 2020), long before they are capable of flight. It is this lack of flight ability, combined with breeding in mostly remote areas away from human settlement, that presumably precludes them from stranding in areas with ALAN. That our Atlantic puffin Y-maze results are consistent with those of ancient murrelets but not Cory's shearwaters possibly suggests a taxonomic difference in fine-scale behavioural responses to ALAN between the two main seabird groups affected by light-induced stranding (i.e., alcids and procellariiforms); however, more research is necessary to confirm this trend.

Contrary to our expectations, pufflings did not display any preferences for certain light spectra over others when presented with a choice. We based our expectations on two premises: first, previous studies have found that attraction behaviour and stranding numbers of fledgling procellariiforms increase under exposure to short wavelength-dominant (i.e., high CCT) light types like metal halide (~4500 K CCT) compared to long wavelength-dominant (low CCT) light types like high-pressure sodium (~2000 K CCT; Salamolard et al. 2001, as cited in Minatchy 2004; Rodríguez et al. 2017b), although this is not always the case (e.g., shielding of long wavelength light from radiating upward may negate the effect; Urmston et al. 2022; Atchoi et al. 2024) and evidence is limited. Second, the procellariiform eye is quite sensitive to short wavelengths (Reed 1986; Bowmaker et al. 1997; Hart 2004), implying a potential link between the wavelengths of highest spectral sensitivity and those that induce the

strongest phototactic responses. Atlantic puffins likely have similar spectral sensitivities given the similarities in photoreceptor profiles between auks and procellariiforms (Ödeen and Håstad 2003), which is why we expected they would choose blue light over orange and cool white over warm white LED light in our Y-maze. It is therefore unclear why these choice combinations did not elicit differences in phototactic behaviour. Most of our light stimuli were calibrated such that the amount of light irradiated at the peak wavelength of each spectrum was relatively equal; we did this because the calibration of spectra based on perceived "brightness", although valuable, is difficult without a complete understanding of spectral sensitivities in the species of interest. To a puffling's eyes our provided light options were therefore not necessarily perceived as all being of the same "brightness", and there may thus have been unquantified effects of perceived brightness on the choice behaviour they exhibited in some of our choice combinations. Another possible explanation is that the locomotory context of the birds (i.e., standing and walking) and/or the spatial scale of the experimental apparatus are so contextually different from flying in a three-dimensional airspace that they elicit a completely different mode of behaviour as it relates to lighting conditions. A coarse-scale beach illumination experiment that compares phototactic responses and stranding numbers across several different light spectra (ideally calibrated according to perceived brightness) may provide insight in a more realistic context (as per Rodríguez et al. 2017b).

When we measured the activity levels of pufflings exposed to darkness and various spectra of artificial light in our open field test, they spent significantly more time active in darkness than in cool or warm white LED light (despite the effect of "converting" the dark treatment scores to reduce the significance of these differences),

and significantly more time active in HPS light than in cool white LED light. It is unclear what factors drove our results, especially in darkness. It is possible that in the HPS light treatment the low-level noise of the associated ballast fan (unlike the LED lights which have no ballast fan) elicited an attractive response, which has been anecdotally observed in stranded pufflings (Harris 1982; Harris et al. 1998; reviewed in Wilhelm et al. 2013). Conversely, it is possible that the greater proportion of cool-hued light in LED spectra compared to HPS has a calming effect on pufflings that results in reduced activity, as blue light does in domestic ducks (Sultana et al. 2013) and in black-headed buntings (*Emberiza melanocephala*) experiencing periods of migratory restlessness (but with this pattern reversed outside these periods; Yadav et al. 2015). A fear-based freezing response toward some aspect of LED light could also drive the reduced activity levels we observed in that light type, similar to that observed in some poultry lines when placed in an open field arena (Forkman et al. 2007; Campbell et al. 2019), although our anecdotal observations of pufflings preening themselves in the arena during bouts of immobility would appear to contradict this hypothesis. Ultimately, the true cause of the reduced activity levels that we observed in pufflings exposed to LED light, especially in cool white LED light, remains a matter of conjecture. Regardless of the reason, these differences in activity patterns may hold implications for detection probability following stranding; for example, pufflings may be easier to find in darkness and under HPS light if they are more mobile there, whereas comparatively less active birds under LED light may be less noticeable, all else being equal.

Conservation Implications

Globally, there is a concerted effort to reduce the impact of ALAN on wildlife, which includes efforts to mitigate and prevent the stranding of various seabird species. To date, most research has focused on procellariiforms, with comparatively little attention paid to the Atlantic puffin. We have demonstrated experimentally that the addition of sources of ALAN near Atlantic puffin breeding colonies has the potential to drastically increase the number of fledglings that become stranded, which in turn would almost certainly contribute to decreased juvenile survival. However, perhaps counter-intuitively, we suggest that light could also be used to lure wayward puffins away from areas of high mortality risk (i.e., towns and roads) to those of low risk (e.g., supervised remote sites) as part of a dynamic rescue effort, and this potential application of ALAN in a conservation context deserves further research. From fine-scale behavioural experiments, we demonstrated that Atlantic puffin fledglings display positive phototactic behaviour in response to all tested bulb colours, without a preference for either blue- or red-dominant spectra. Although there may also be compounding effects of perceived brightness, this implies that changes to street lighting from historically prevalent HPS lamps to more energy-efficient LED, or (if specifically attempting to reduce attraction) from cool-hued to warm-hued lamps, may not be effective in reducing strandings in Atlantic puffins and that the reduction and shielding of ALAN sources remain the best recommendations. Our open field test results imply that post-stranding LED light exposure may have either a calming or startling effect on stranded pufflings, with potential implications for rescue, rehabilitation, and even husbandry of puffins and other auks.

Tables

Table 2.1. Quantity of pufflings that chose each of the two light options in each choice combination.

Choice combination				95% CI	*P*	No response
Light type 1	Quantity	Light type 2	Quantity			
Bright HPS	10	Dark	0	0.69–1.00	0.002	5
Bright HPS	14	Dim HPS	6	0.46–0.88	0.1	2
Bright HPS	10	Warm LED	11	0.26–0.70	1.0	2
Warm LED	10	Cool LED	10	0.27–0.73	1.0	2
Dim blue LED	13	Orange LED	9	0.36–0.79	0.5	2
Bright blue LED	9	Orange	6	0.32–0.84	0.6	10

Note: Individual binomial tests assessed evidence for a preference for one light type over the other in each choice combination (excluding "no response" individuals), using 0.5 as the theoretical (null) proportion for each of the two options. We report the 95% confidence intervals of the true proportion of "Light type 1" as a reference. We also present the number of individuals that displayed "no response" in each combination.

Figures
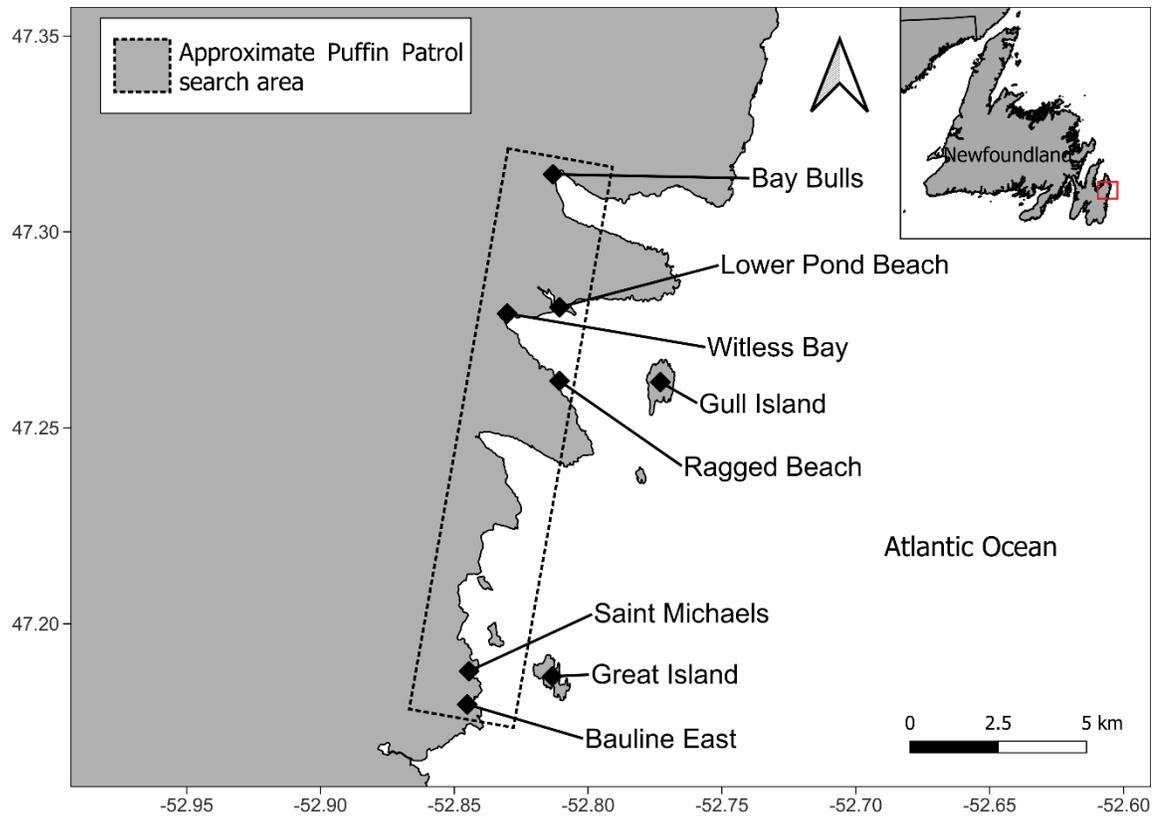
Figure 2.1. Map of Puffin Patrol search area in Newfoundland, Canada, including all relevant locations of research activities (Bay Bulls, Lower Pond Beach, Ragged Beach, Saint Michaels) and the two largest Atlantic puffin breeding colonies (Gull Island, Great Island).
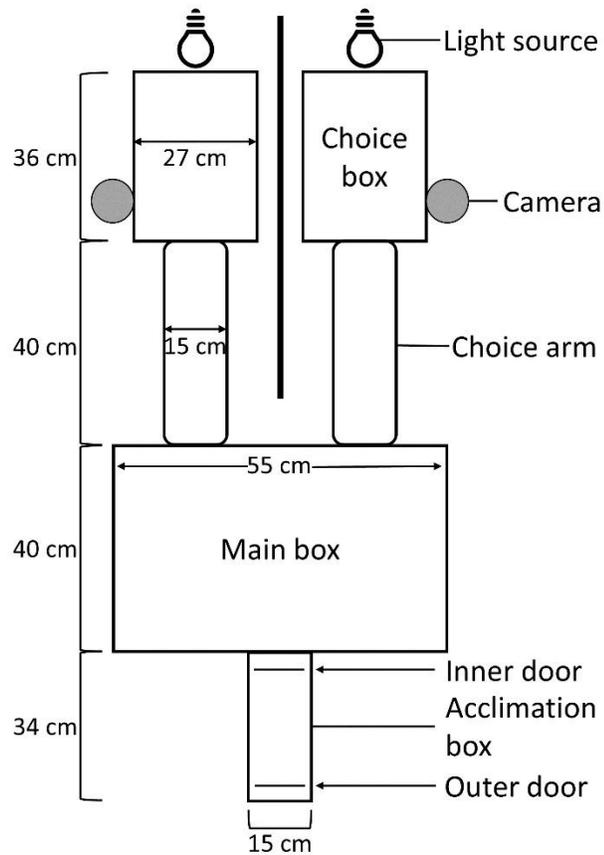
Figure 2.2. View from above the Y-maze apparatus used for our choice experiment. We placed an individual puffling inside the acclimation box prior to the start of a behavioural trial. The inner door was then opened, and the bird was allowed to enter and explore the main box, choice arms, and choice boxes. An infrared camera detected when an individual became visible at the doorway of a choice box. Note that the diagram is not to scale.

Figure 2.3. Number of fledgling puffins observed per night at artificially lit and dark beaches. A) Best-estimate total counts of pufflings (in the water, on the beach, and in the air combined) seen each night during the dark (black circle) and light (yellow circle) treatments, 15-27 August 2022. Note that points overlap on August 26 due to zero birds being observed during either treatment. B) Observation rates (same best-estimate counts of pufflings observed, divided by the number of observers present) at the two beach sites during dark and light treatments. Each data point represents the observation rate on one experimental night at each site and points have been offset from one another to improve readability.

Figure 2.4. Time spent mobile by fledgling puffins when exposed to each of four light treatment groups. Figure combines a violin plot and boxplot with overlaid individual data points. Sample sizes: warm white LED light ($N = 24$), cool white LED light ($N = 25$), darkness ("converted" data; $N = 23$, see text), and high-pressure sodium (HPS) light ($N = 19$). The single data point >300 seconds in the warm LED treatment (outlined in red) was considered a statistical outlier and was not included in analysis. Individuals were significantly less mobile when exposed to warm white LED and cool white LED than when exposed to darkness, and significantly less mobile under cool white LED than under HPS.

Chapter 3

Effects of artificial light on the behaviour of Leach's storm-petrel fledglings

Author contributions

T.M.B. conceived the ideas and formulated hypotheses, designed the field protocols and methods, collected and analyzed data, and co-wrote the first version of the manuscript. K.B. helped design methods and analyze data and co-wrote the first version of the manuscript. S.I.W. helped supervise the research, design field protocols and edited the manuscript. G.B. supervised the research, helped design field protocols and methods, and substantially edited the manuscript.

Abstract

Artificial light at night is an anthropogenic pollutant that has wide-ranging effects on wildlife. Fledgling seabirds of order Procellariiformes exhibit phototaxis toward artificial lights on their first flights from the nest, causing them to become grounded in human settlements, where they are subject to increased predation risk. Limited evidence suggests certain light types may be less attractive than others, yet there is also evidence for an aversion to light under certain circumstances. We investigated differences in phototactic behaviour, activity level, and shelter-seeking behaviour of grounded Leach's storm-petrel *Hydrobates leucorhous* fledglings exposed to artificial light in three experiments: a Y-maze choice experiment, an open field test, and a modified open field test with a hide box provided ("Safe Haven test"). When provided with combinations of different light types in the Y-maze, storm-petrels typically remained stationary in the darkest parts of the apparatus (farthest from light stimuli) and exhibited no preferred response toward one light type over another. This was consistent with results from the open field test: individuals were less active in darkness than when exposed to two of three light conditions (warm white light-emitting diode and high-pressure sodium). More than half of individuals entered the hide box in light conditions, compared to none in darkness. Considered together, our results indicate that most (but not all) Leach's storm-petrel fledglings exhibit photophobic behaviour after stranding, which may be part of a behavioural strategy to avoid predation. Further, we demonstrate the utility of providing hide boxes to protect stranded seabird fledglings in locations where lighting cannot be eliminated or where rescue efforts are limited in spatial or temporal coverage. However, hide boxes would have limited utility in dark locations. Hide boxes constitute a novel

mitigation measure that merits future testing for its ability to reduce stranding-induced

mortality, especially in imperiled procellariiform species.

Introduction

Nightscapes across our planet are increasingly subject to light pollution from anthropogenic sources. Further, the widespread conversion to energy-efficient light-emitting diode (LED) lighting is expected to worsen ecological impacts through a variety of mechanisms, including an increase in the usage of short light wavelengths that are especially disruptive to wildlife (Pawson and Bader 2014; Davies and Smyth 2018; Jägerbrand and Spoelstra 2023). The presence of artificial light at night (ALAN) can alter the physiology and behaviour of a growing list of animals (Sanders et al. 2021; Yang et al. 2024). Especially in nocturnal animals, artificial light can act as a supranormal visual stimulus that induces phototactic behaviour (movement either toward or away from light; Rich and Longcore 2006). Positive phototaxis has been observed in many animal groups including insects, amphibians, fish, sea turtles, migratory songbirds, and seabirds, among others (Rich and Longcore 2006; Rodríguez et al. 2017a; Jägerbrand and Spoelstra 2023). Phototaxis toward ALAN sources can result in mortality through a variety of mechanisms including trauma from collision with buildings, vehicles, and other structures; dehydration or desiccation after stranding in unfamiliar locations; and predation or poaching of disoriented individuals (Witherington 1997; Rich and Longcore 2006; Rodríguez et al. 2017a; Van Doren et al. 2021).

Seabirds of the order Procellariiformes are one of the most imperiled groups of birds, with anthropogenic threats including fisheries bycatch, plastic ingestion, climate change, and predation by introduced predators (Dias et al. 2019). In addition, fledglings of burrow-nesting and largely nocturnal procellariiform species, such as storm-petrels and shearwaters, are susceptible to stranding in developed coastal areas and at offshore

71

industrial sites after disorientation by, and sometimes collision with, lighted structures during their first flights from the nest (sometimes termed "fallout"; Montevecchi 2006; Burke et al. 2012; Rodríguez et al. 2017a; Gjerdrum et al. 2021). Fledgling mortality following stranding can be high without rescue intervention (Rodríguez et al. 2017a; Burt et al. 2024). Even where rescue programs are implemented, many stranded fledglings are not found as they tend to hide in concealed locations (Reed et al. 1985; Rodríguez et al. 2017a). Although procellariiforms are generally K-selected and their populations are therefore relatively robust against juvenile mortality, light-induced fallout has had a significant negative effect on population growth in several species (Ainley et al. 2001; Fontaine et al. 2011; Griesemer and Holmes 2011; Simons 1984) and adults can also be affected (Rodríguez et al. 2017a; Burt et al. 2024).

Increasing experimental evidence suggests that reductions in ALAN near colonies of burrow-nesting, night-fledging seabirds can decrease stranding numbers (Reed et al. 1985; Miles et al. 2010; Rodríguez et al. 2014; Brown et al. 2024, Chapter 2; Burt et al. 2024). At finer scales and in ground-based contexts, however, behavioural patterns are more equivocal and vary among species. For example, in the charadriiform ancient murrelet (*Synthliboramphus antiquus*), chicks orient more often toward reflected light sources than toward darkness, yet because they nest in remote areas and go to sea before they can fly are not prone to fallout (Gaston et al. 1988). Stranding-prone Atlantic puffin (Order Charadriiformes) fledglings similarly orient toward light over darkness in a Y-maze (Brown et al. 2024, Chapter 2), but stranded Cory's shearwater (*Calonectris diomedea*; Order Procellariiformes) fledglings consistently move toward darkness in a similar experiment (Atchoi et al. 2024). The latter result may indicate a

72

context-dependent phototactic response in which behaviour toward ALAN on a broad scale (especially in flight) differs from fine-scale responses (especially on the ground, post-stranding). Combined with observational and tracking data of fledgling seabirds as they encounter ALAN (e.g., Rodríguez et al. 2022), it has been suggested that procellariiform fledglings may be attracted to artificial lights from a distance but disoriented by them at close range (Atchoi et al. 2024).

In instances where total or near-total suppression of ALAN is not possible (e.g., industrial sites with nocturnal operations), other mitigation measures are needed to reduce fallout. The shielding of light from radiating upward toward birds flying overhead has demonstrated effectiveness (Reed et al. 1985; Urmston et al. 2022). Implementation of potentially "less attractive" light types also has potential. Limited evidence suggests that long wavelength-dominant (i.e., "redder") lights (such as sodium vapour types) with low correlated colour temperature (CCT; a relatively crude but simple and widely-used metric of the perceived colour of a nominal white light source; Durmus 2022) may be less attractive to fledgling procellariiforms and other wildlife than those with high-CCT, short wavelength-dominant (i.e., "bluer") spectra (such as many LEDs; Rodríguez et al. 2017b; Longcore et al. 2018). Increased attraction toward blue-violet wavelengths may be explained by an increased sensitivity to these wavelengths by the optical systems of the affected taxa (Reed 1986; Bowmaker et al. 1997; Hart 2004; Pawson and Bader 2014; Davies and Smyth 2018).

Contrary results, however, have been found in Y-maze experiments with Cory's shearwaters, which preferentially oriented toward red over blue light (Atchoi et al. 2024); and with Atlantic puffins, which showed no differences in response between blue and

73

orange light or between low- and high-CCT LED light (Brown et al. 2024, Chapter 2). Interestingly, however, activity levels of puffin fledglings did appear to vary by light type: birds were more active when exposed to high-pressure sodium (HPS) light compared to LED light (Brown et al. 2024, Chapter 2). These results imply effects of light type on behaviour beyond simple phototaxis: for example, varying activity levels following stranding under different light types could have implications for detection probability of individuals by rescue programs. To date, no similar research has been conducted on activity levels under various light types of any procellariiform, despite this group's overwhelming representation in the list of light-affected seabirds.

Leach's storm-petrels (*Hydrobates leucorhous*; Order Procellariiformes, Family Hydrobatidae) are one of many seabird species affected by stranding. They are a small (approximately 60 grams at fledging), long-lived (20-30+ years), colonial, burrow-nesting species that breeds on islands in the North Atlantic and North Pacific oceans (Pollet et al. 2021). The largest colony of this species is on Baccalieu Island in Newfoundland and Labrador, Canada, with an estimated breeding population of 1.95 million pairs (down from an estimated 3.4-5.1 million pairs in 1984; Wilhelm et al. 2020). Juveniles fledge on average two hours after sunset in September through November (Collins et al. 2023), going directly to the open ocean without parental guidance (Pollet et al. 2021). At this time, some fledglings become stranded both inland and at offshore oil production and other industrial facilities (Miles et al. 2010; Gjerdrum et al. 2021; Wilhelm et al. 2021; Burt et al. 2023, 2024). Leach's storm-petrels fledge throughout the lunar cycle but stranding increases when moon illumination is low (Miles et al. 2010; Collins et al. 2023; Burt et al. 2024), potentially implying that

artificial light has a greater attractive or disorienting effect on birds during nights with lower natural light levels (Rodríguez et al. 2023).

On the Avalon Peninsula of Newfoundland and Labrador, hundreds to thousands of Leach's storm-petrels are found stranded each year and many likely remain unfound, especially given the large geographic area over which strandings occur (Gjerdrum et al. 2021; Wilhelm et al. 2021; Burt et al. 2023). High predation on grounded individuals by herring gulls (*Larus argentatus*), foxes (*Vulpes* spp.), feral cats (*Felis catus*), and other predators at "hotspot" stranding sites (Burt et al. 2024), as well as high mortality of stranded procellariiforms from other causes even with the use of rescue programs (Rodríguez et al. 2017a) imply the need for additional mitigation measures where lights cannot be extinguished and where rescuers cannot be constantly present. For example, the targeted placement and monitoring of protective hiding places at stranding "hotspots" may be beneficial to reduce predation (Burt et al. 2024), as procellariiforms often seek shelter in concealed locations after grounding (Reed et al. 1985; Rodríguez et al. 2017a).

In this study, we assessed post-grounding behavioural responses toward artificial light by Leach's storm-petrel fledglings. Our three initial objectives were to: 1) measure phototactic behavioural responses of grounded Leach's storm-petrel fledglings (hereafter "storm-petrels") to artificial lights; 2) test their preferences among various artificial light spectra; and 3) measure their activity under various lighting conditions. Last, based on anecdotal observations of grounded storm-petrels seeking shelter in rodent bait stations (Burt et al. 2024), we leveraged the results from objectives 1-3 to test a fourth objective: whether different lighting conditions would influence an individual's propensity to seek shelter in a hide box (termed a "Safe Haven" box). To address our first objective of

measuring phototactic behaviour, we used a Y-maze and hypothesized that fledglings would exhibit differential responses toward light versus dark portions of the apparatus; specifically, we predicted that fledglings would preferentially respond to (i.e., move toward) light stimuli and avoid or move away from dark portions of the apparatus. We used the same Y-maze apparatus to address our second objective of testing for light preferences, whereby we hypothesized that phototactic responses toward artificial light would depend on the spectra used. We predicted that when storm-petrels were exposed to two different artificial light types, they would respond more often to those with "cooler" hues (e.g., cool white LED; blue LED) than to those with "warmer" hues (e.g., high-pressure sodium; warm white LED; orange LED). We addressed objective 3 using an open field test to measure activity levels and hypothesized that storm-petrels would exhibit differences in activity levels among different light types, particularly when compared with darkness. However, we could not predict directionality a priori. We used the same open field test with an added hide box to address objective 4. Based on the unexpected results we obtained in the above experiments, we hypothesized that storm-petrels would interact differently with the hide box under light versus dark conditions, with the prediction that they would seek shelter when the open field was illuminated and not seek shelter in darkness. Objective 4 has the potential to inform local-scale rescue efforts and conservation measures.

Methods

Study Site and Species

Experiments were conducted with stranded storm-petrels in October 2021 and 2023 at the Quinlan Brothers seafood processing plant in Bay de Verde (48.085°N, 52.895°W), Newfoundland and Labrador, Canada. Hundreds of storm-petrels strand at the seafood processing plant on an annual basis (Wilhelm et al. 2021; Burt et al. 2023, 2024), most of which likely originate from Baccalieu Island, approximately 7 km to the northeast (Figure 3.1). We conducted experiments in two sheds, and housed birds in a third shed, on the wharf between 2100 and 0430 hours on 2-11 October 2021 and 3-8 October 2023.

Animal Collection, Housing, and Release

We collected stranded storm-petrels during opportunistic walking surveys (single "laps") around the processing plant from approximately 2000 to 2400 hours. We conducted experiments throughout the night between or at the same time as walking surveys, depending on the number of field personnel available (range: 1-5). Although it is possible that stranded storm-petrel fledglings do not represent a truly random sample of the entire population, it is this population whose responses to artificial light were of greatest interest to us, since we were specifically assessing post-stranding behaviour. When individuals were found, we placed them in cardboard pet carriers, approximately 47 cm long × 25 cm wide × 30 cm tall and lined with disposable absorbent multipurpose pads (up to 25 individuals per carrier). We kept the carriers containing rescued birds in

darkness in the third shed (dedicated to housing birds) until experimentation and/or release.

Prior to experimentation (described below), we removed each storm-petrel from the group housing and placed it individually in a cardboard box (30 cm × 20 cm × 25 cm) outdoors in a sheltered location for a minimum 10-minute rest period. Following the phototactic behaviour experiment, we returned the bird to its cardboard box and allowed it to rest for at least 10 minutes before proceeding with the activity level experiment. In 2023, we focused solely on objective 4, the Safe Haven test, which involved two trials conducted in quick succession. Storm-petrels used in this experiment rested for at least 10 minutes before the first trial, but only about 5 minutes between the first and second trials. In both years, individuals that had completed the experimental trials were placed together in a cardboard pet carrier until release.

Choice Experiment to Measure Phototactic Behaviour

To measure phototactic responses of storm-petrels to various light spectra we used a Y-maze, following Brown et al. (2024; Figure 2.2). Briefly, the apparatus consisted of a dark, metal "acclimation box" (34 cm × 15 cm × 15 cm) which opened into a plastic "main box" (40 cm × 55 cm × 22 cm) via a vertical sliding door. Two corrugated plastic pipes (i.e., choice arms) connected the main box to two plastic choice boxes (36 cm × 27 cm × 18 cm), each with a 3 cm-diameter hole through which each experimental light shone into each choice arm. We anecdotally judged relative movement and position of the bird within the apparatus by the sound of its footsteps (or lack thereof) and determined responses to light stimuli by placing infrared baby monitor cameras (VTech, VM5262-2;

British Columbia, Canada) at small holes in the walls of the choice boxes. We considered the storm-petrel to have made a response when it reached the end of a choice arm, and any part of the body was visible on the baby monitor screen (even if it did not fully enter a choice box); otherwise, the trial outcome was deemed "No Response".

We used three different types of lights (high-pressure sodium [HPS] with a CCT of 2100 K; warm white LED with a CCT of 2700 K; and cool white LED with a CCT of 5000 K) in combination with various filters to produce four stimulus combinations (for materials and spectra of all light-filter combinations see Appendix Table A3.1 and Figure A3.1). We randomly selected 76 stranded storm-petrel fledglings and divided them amongst four light stimulus combinations. The combinations (with number of trials each, in brackets) were: HPS vs darkness ($N = 19$); HPS vs warm white LED ($N = 19$); warm white LED vs cool white LED ($N = 17$); and blue LED vs orange LED ($N = 21$). The blue and orange LED light options were created by adding to the cool and warm white LED options filters made of coloured acrylic and glass (Appendix Table A3.1). We tested only one combination each night, selected randomly without replacement until all four had been tested over the course of four nights; they were then selected again in random order (all light combinations tested over two non-sequential nights).

We brought the storm-petrel into the choice experiment shed and placed it in the acclimation box of the Y-maze. After two minutes, we removed the inner sliding door to allow the bird to make a "response". If the bird did not exit the acclimation box within 5 minutes (as discerned by a lack of audible footsteps), the experimenter gently prodded it by hand until it entered the main box ($N = 53$ out of 76 storm-petrels, or 70%, were prodded). Note that prodding was used in an attempt to elicit a response, but not all

prodded birds responded. We removed the bird from the apparatus when it made a

response or 13 minutes after removal of the inner door, whichever came first, and

returned it to its cardboard box. The experiment was thus a maximum of 15 minutes in

duration. In most cases of "No Response," storm-petrels sat still in the apparatus, but "No

Response" also included the few individuals that audibly wandered around inside the

apparatus without ever becoming visible on the monitor screen. Between trials, we

cleaned the entire Y-maze with 70% isopropyl alcohol and a disposable cloth and allowed

it to dry completely. We then swapped the two lights between the two choice boxes to

account for any potential side bias on part of the birds.

Measuring Activity Levels under Various Light Spectra

To address objective 3, we used an open field test to measure differences in

activity level of fledgling storm-petrels under various artificial light spectra, as described

in Brown et al. (2024, Chapter 2) (for apparatus description, see Appendix 3).

The same 76 storm-petrel fledglings used in the Y-maze were divided into four

treatment groups for trials in the open field test, where each individual was exposed to

darkness or one of three light spectra. Two individuals were removed from the final

dataset due to camera malfunction, resulting in a final sample size of $N = 74$. Treatments

were: darkness ($N = 21$); HPS ($N = 18$); warm white (2700K) LED ($N = 16$); and cool

white (5000K) LED ($N = 19$). We did not measure activity in response to blue or orange

light to ensure adequate sample sizes in the light treatments that most closely resemble

actual light spectra used in human settlements and at industrial sites. Median illuminance

at floor level in the arena was 23 – 26 lux and did not differ significantly across the three

light treatments (Brown et al. 2024, Chapter 2). Each night, we tested two light types in the open field test (chosen randomly), and they were never the same as the two light types used in the Y-maze on the same night. From the remaining light options, the initial treatment each night was chosen randomly, followed by the second treatment, and these were alternated for the rest of the night.

Prior to each open field trial, we started a video recording (with audio) and placed the storm-petrel just inside the access door of the arena. Unfortunately, a thermal imaging camera was not available for this experiment. After 10 minutes, we stopped recording, removed the storm-petrel from the arena, and replaced it in its cardboard holding box. We did not clean the floor of the arena between trials unless a storm-petrel defecated during trial, in which case the affected area was cleaned with 70% isopropyl alcohol and allowed to dry before the next trial. We completed as many trials as possible each night (median: 11 trials; range: 3-13 trials per night).

We scored open field test videos in a random order. We used the behavioural scoring software JWatcher (Version 1.0, Macquarie University and University of California, Los Angeles) to code two levels of behaviour for each 10-minute trial: "mobile", which included walking, running, or flying, and "immobile" whenever birds were stationary. The software automatically calculated the total amount of time each storm-petrel spent mobile and immobile.

For storm-petrels in the "dark" treatment group, only audio data were discernible. Storm-petrels were audible when they walked on the polycarbonate floor of the arena, which allowed us to hear and score their movement. As such, rather than viewing the file, we instead listened to the audio file and coded "mobile" behaviours when we heard the

bird walking or flying, and "immobile" when we heard the bird stop moving. Scratching (clawing at the arena floor with the feet) could also occasionally be heard but was not scored as "mobile" behaviour on its own. To determine whether the time spent mobile in the dark treatment could be accurately scored by listening to the audio alone, we selected a random subset of 10 videos from the three lighted conditions (HPS, warm white LED, cool white LED) that had already been scored visually. We listened to all 10 of these videos in random order and scored them audially in the same way that we scored the dark videos. A single observer (K.B.) did all visual and audial scoring. We then performed a linear regression and used the resulting equation ($y = 0.7x + 56$) to convert the Dark treatment data for use in later analyses (see Appendix 3).

Safe Haven Test

We used the same polycarbonate arena for the Safe Haven test as the open field test; however, we removed the roof and overlaying blackout curtain. To address objective 4, we placed an empty black plastic rodent bait station (approximately 29 cm × 25 cm × 15 cm; Bell Laboratories Protecta Evo Express; Wisconsin, USA) inside the arena (see Appendix Figure A3.2). We hereafter refer to this bait station as the "Safe Haven box" (for further description, see Appendix 3).

This experiment consisted of two treatments: light and dark. The light treatment used a cool white 5000 K LED bulb as in the previous experiments, hung approximately 160 cm above the centre of the arena floor. In the dark treatment, all light sources in the experiment arena were extinguished and windows in the shed were covered. To record the behaviour of individuals in the arena, we used a thermal imaging camera (Teledyne FLIR

C5; Oregon, USA) affixed to a tripod and positioned such that it could record the entire arena floor.

Between 3-8 October 2023, we tested 14 storm-petrels in a paired design, such that each individual experienced one light trial and one dark trial (light trials, $N = 14$; dark trials, $N = 14$). We chose randomly whether the first bird experienced light or dark first and alternated the first treatment experienced by each bird thereafter, to obtain a roughly equal number of individuals that experienced light first ($N = 6$) versus dark first ($N = 8$). After each 10-minute trial, we removed the storm-petrel from the arena (or from the Safe Haven box, when applicable), placed it back into the cardboard holding box, and allowed it to rest for 5 minutes until the arena was ready for the second trial (for details, see Appendix 3).

Statistical Analyses

All analyses were performed in R (ver. 4.3.0; R Core Team 2023) and we report results to the nearest significance level.

To test whether storm-petrels displayed phototactic responses toward light (objective 1), we conducted an exact two-tailed binomial test through the basic stats R package (v. 4.3.0; R Core Team 2023) on the combined number of storm-petrels that exhibited "No Response" compared to the combined number of storm-petrels that responded to one of the light options, in three stimulus combinations: HPS vs warm white LED, warm white LED vs cool white LED, and blue LED vs orange LED. To test for preferential phototactic responses toward certain light spectra over others (objective 2), we conducted exact two-tailed binomial tests on the numbers of storm-petrels in each

stimulus combination that responded to each of the two provided light options. We tested against a hypothesized proportion of 0.5 and report 95% confidence intervals of the estimated true proportions.

To quantify differences in activity level under exposure to the four light treatments (objective 3), we first converted the "dark" data according to a regression equation of the relationship between auditory versus visual-based scoring and used these "converted" values in comparisons with the unmodified visual scores from the other treatment groups (see Appendix 3; Appendix Figure A3.3). We then tested for homogeneity of variance in time spent mobile across treatments using a Levene Test with car package v. 3.1-2 (Fox and Weisberg 2019). We also tested for normality by conducting a Shapiro-Wilk test on the residuals of a standard ANOVA of time spent mobile across treatments, from the stats package v. 4.3.0 (R Core Team 2023). Variance differed significantly across treatments ($F = 7.5594$; df = 3 and 70; $P < 0.001$), but there was no evidence for deviation from normality (W = 0.984, $P = 0.5$). We therefore used a Welch's one-way ANOVA to determine if the time spent mobile differed significantly among treatment groups, followed by a pairwise post-hoc Games-Howell test since it does not assume homogeneity of variance or equal sample sizes, using rstatix package v. 0.7.2 (Kassambara 2023).

Lastly, we tested whether individual storm-petrel fledglings differed in their probability to enter the Safe Haven box depending on the light treatment used (light or dark; objective 4) by conducting a classical version of McNemar's chi-squared test for paired data (Pembury Smith and Ruxton 2020).

84

Results

Choice Experiment to Measure Phototactic Behaviour

Sixty-three percent, i.e. 48 of the 76 storm-petrels in all stimulus combinations combined displayed "No Response" (Appendix Table A3.2). Considering only the three combinations in which there were two light options provided (i.e., excluding HPS vs dark), 38 individuals exhibited "No Response" while 19 responded to one of the light options (total $N = 57$ individuals). There was a significant preference by storm-petrels to exhibit "No Response" rather than choosing one of the provided light options (binomial test $P < 0.05$; 95% CI of estimated true proportion of "No Response": 0.53, 0.79).

The following results include all four stimulus combinations but exclude from further consideration the 48 individuals that made "No Response". Of the remaining 28 individuals that responded to one of the two provided options, 43% ($N = 12$ individuals) were prodded out of the acclimation box into the main box after 5 minutes of inactivity, while 57% ($N = 16$ individuals) voluntarily left the acclimation box before making their response (Appendix Table A3.2). We found no significant response toward any one light type in our stimulus combinations (Table 3.1). There was also no statistical evidence for side bias, as 15 storm-petrels chose Box 1 and 13 storm-petrels chose Box 2 (binomial test $P = 0.9$; 95% CI of estimated true proportion of Box 1: 0.34, 0.72).

Measuring Activity Levels under Various Light Spectra

The time that storm-petrels spent mobile differed significantly among light treatments (Welch's one-way ANOVA $F_{3,30.28} = 9.306$, $P < 0.001$). Specifically, we found that on average, individuals spent significantly less time mobile in Darkness ($t_{mobile} = 84$

sec) than in warm white LED light (t_{mobile} = 210 sec) and in HPS light (t_{mobile} = 172 sec; P < 0.01 and P < 0.05, respectively; Figure 3.2). None of the other light treatments differed significantly from each other in time spent mobile. No individuals spent less than 56 seconds mobile in the dark group, as the conversion we applied to t_{mobile} in that group used a linear equation with intercept y = 56 (see Appendix Figure A3.3).

Safe Haven Test

Storm-petrels were significantly more likely to enter the Safe Haven box in light conditions than in the dark (classical McNemar's test $\chi^2(1)$ = 6.125, P < 0.05). In the dark, none of the 14 individuals entered the Safe Haven box. In contrast, when exposed to the Light treatment, eight of the same 14 storm-petrels entered the Safe Haven box while six did not enter.

Discussion

We expected that storm-petrels, which are prone to light-induced grounding, would display evidence of positive phototaxis when tested in a laboratory setting after becoming grounded. In contrast, most fledglings either displayed no response to light stimuli or displayed evidence of negative phototaxis. Across our three experiments, birds tended to remain stationary in darkness, while in light conditions they exhibited increased movement. In the Y-maze, storm-petrels exhibited little response to the light options provided and most remained relatively immobile in both the dark acclimation box and, after being prodded out of the acclimation box, in the (also relatively dark) main box of the apparatus. Further, although there were no significant responses displayed in any

stimulus combination, numerically more birds moved toward darkness in the only combination that had it as an option (HPS vs darkness; chosen by three and six storm-petrels, respectively). The apparent photophobic behaviour of the majority of storm-petrels in the Y-maze choice experiment was consistent with the lower activity levels they exhibited in darkness in our open field test, and with their increased probability to enter hide boxes in light compared to dark conditions. Specifically, our Safe Haven Test results provide evidence that the purpose of increased activity levels in light conditions was to seek out a dark place to hide. However, that 29% (22 of 76) of grounded storm-petrels chose a light option in the Y-maze and that 43% (6 of 14) chose to remain unhidden in light conditions of the Safe Haven test together indicate substantial variation in post-stranding phototactic behaviour that merits further attention.

Our findings are consistent with those of Atchoi et al. (2023, 2024), who found evidence for photophobic behaviour in fallout-susceptible Cory's shearwater chicks and fledglings (but not adults), when they were exposed to light in controlled experimental apparatuses. Anecdotally, seabird fledglings are sometimes found in dark and concealed locations after grounding, implying negative phototaxis (Reed et al. 1985; Rodrigues et al. 2012; Burt et al. 2024). Our results also concur with the photophobia exhibited by adult burrow-nesting procellariiforms (including Leach's storm-petrels) in the form of reduced attendance levels at their breeding colonies and arrival from foraging trips later at night, when light is at naturally high levels (Watanuki 1986; Riou and Hamer 2008; Silva et al. 2011) or artificially introduced (Syposz et al. 2021a; Austad et al. 2023). In these cases, photophobia may be part of a behavioural strategy to reduce predation risk, although there are invariably at least small numbers of individuals that are active even

under higher illumination levels (Watanuki 1986; Riou and Hamer 2008; Silva et al. 2011; Syposz et al. 2021a; Austad et al. 2023; Middlemiss et al. 2025).

Instead of attraction toward ALAN being the sole mechanism driving procellariiform strandings, lights may attract birds from a distance and then cause disorientation at close range, as evidenced in part by the highly tortuous flights of fledglings as they navigate over brightly illuminated areas in comparison with dark areas (Rodríguez et al. 2022). Negative phototaxis by fledgling procellariiforms in Y-maze apparatus (where light stimuli are presented at very close range) has been interpreted as birds attempting to avoid the disorientating stimulus (Atchoi et al. 2024). Alternatively, but not mutually exclusively, once birds are grounded and more vulnerable to predation, they may become negatively phototactic and seek the safety of darkness. Our experiment cannot distinguish these competing hypotheses; future studies might seek to test them by introducing artificial visual, auditory, or even olfactory predator cues into an open field or Y-maze experiment to determine if photophobic behaviour is increased in the presence of a perceived predator.

Our prediction that storm-petrel fledglings would be positively phototactic in our Y-maze choice experiment (hypothesis 1) was based on the observations that fledglings of this and other burrow-nesting seabird species are found grounded each year in anthropogenically developed areas, presumably due to light attraction (Rodríguez et al. 2017a; Wilhelm et al. 2021; Burt et al. 2023), and that fallout increases with increased ALAN (e.g., Miles et al. 2010; Brown et al. 2024, Chapter 2; Burt et al. 2024). Instead, we found no evidence for positive phototaxis, as the majority of storm-petrels chose not to respond to the provided light stimuli. In contrast to fledgling procellariiforms,

88

fledglings of burrow-nesting charadriiforms display positive phototaxis on the ground (specifically those in the family Alcidae; Gaston et al. 1988; Brown et al. 2024, Chapter 2). It is unclear why the two groups differ despite their shared tendencies to develop in burrows, fledge nocturnally and become grounded by ALAN. It has been suggested that in burrow-nesting procellariiforms the visual system is not fully developed at the time of fledging (itself due to a lack of light exposure in the burrow throughout development; Mitkus et al. 2018), which may contribute to the disorientation they experience in response to ALAN encountered on their first flights from the nest (Atchoi et al. 2020); presumably, the same would be true of burrow-nesting charadriiforms. In general, burrow-nesting charadriiforms also share with procellariiforms the same rod and cone photoreceptors and their associated spectral sensitivities (Reed 1986; Ebrey and Koutalos 2001; Ödeen and Håstad 2003). However, still little is known about variation in ocular anatomy, physiology, and development across stranding-prone seabird species and how they may contribute to observed differences in phototactic behaviour.

When provided with different light spectra in a Y-maze, we expected storm-petrels to preferentially respond to short wavelength-dominant spectra (e.g., cool white LED and blue LED) over those that are long wavelength-dominant (e.g., warm white LED and orange LED), based on increased numbers of stranded individuals in the presence of short wavelength-dominant light (hypothesis 2) (Salamolard et al. 2001, as cited in Minatchy 2004; Rodríguez et al. 2017b). Our current results demonstrating no differences in response by storm-petrels to different light types agree with those of our previous Y-maze experiment with Atlantic puffin fledglings (Brown et al. 2024, Chapter 2), but

differ from those of Cory's shearwaters, in which both fledglings and adults oriented more toward red than blue light (Atchoi et al. 2024). This behaviour was speculated to be an adaptation for Cory's shearwaters to avoid disorientation (Atchoi et al. 2024), since procellariiforms may be especially sensitive to and disoriented by blue-rich light (Hart 2004; Rodríguez et al. 2017b; Syposz et al. 2021a). In comparison, few storm-petrel fledglings responded to either blue or orange light in our Y-maze, with 86% (18 out of 21) exhibiting "No Response" in that combination. This suggests either a tendency to remain in the dark, or an aversion to both types of spectra in storm-petrels. Alternatively, storm-petrels may have perceived differences in brightness among our provided light options, which led to unquantified effects on the behavioural responses (or lack thereof) they exhibited in our experiments. We calibrated most of our light stimuli such that the amount of light irradiated at the peak wavelength of each spectrum was relatively equal (Appendix Figure A3.1), but this does not mean that all spectra were perceived as equally bright. Nevertheless, we did this because the calibration of spectra based on perceived "brightness" is difficult without a complete understanding of the spectral sensitivities and ocular physiology in the species of interest.

In our open field test, storm-petrels spent significantly less time mobile in darkness than when exposed to either warm white LED or HPS light, supporting our third hypothesis that activity levels would differ across light treatments. This was true in spite of the conversion applied to scores from the dark group, which inflated them such that comparisons with other groups were even more conservative (see Appendix 3). This suggests that storm-petrels are particularly stimulated by spectra rich in long-wavelength (i.e., "reddish"), but not short wavelength (i.e., "bluish"), light. We did not find any

differences in activity levels among the three light treatments (HPS, warm white LED, or cool white LED). These results are in direct contrast with those of Atlantic puffin fledglings, which are highly active in darkness, as well as HPS light and less active in both warm and cool white LED light (Brown et al. 2024, Chapter 2). To our knowledge, activity levels in response to artificial light have not been quantified in any other seabird species. Low activity levels of storm-petrels in darkness could imply either a calming or startling effect from the lack of light; the mechanism underlying this behavioural pattern remains unexplained. Nonetheless, these results hold implications for detection probability of stranded birds by rescuers whereby mobile individuals are presumably more conspicuous than stationary ones, all else being equal.

As grounded fledglings are vulnerable to increased predation risk (Rodríguez et al. 2017a; Burt et al. 2024), we tested the propensity of storm-petrel fledglings to enter a provided dark hiding place under light versus darkness (hypothesis 4). We found that more than half of individuals entered in light conditions, compared to none in the dark. This clearly demonstrates the value of placing Safe Haven boxes (in this case empty rodent bait stations) in lit areas to provide stranded storm-petrels with protection until rescue, as had previously been suggested by Burt et al. (2024). Additionally, anecdotal preliminary trials revealed that birds never entered the Safe Haven box when its doors were oriented away from the wall of the open field apparatus, so this needs to be considered when deploying them. Storm-petrels also do not appear to leave Safe Haven boxes on their own and thus still require rescue intervention in the hours following grounding. During initial deployments of Safe Haven boxes at our study site (beginning April 2021; Burt et al. 2024), we noted up to 11 individuals sheltering inside a single box

after a single night (T.M.B. and S.I.W., pers. obs.), demonstrating their effectiveness in a field setting. Safe Haven boxes therefore provide an effective and inexpensive means to protect at least a portion of grounded seabirds and potentially further reduce stranding-related mortality in stranding "hotspots", a tactic especially helpful in trying to further conserve already declining and threatened populations affected by ALAN.

Conclusion

We found evidence for photophobic behaviour in fledgling storm-petrels that have been grounded in areas illuminated by ALAN, despite substantial variation overall in their behavioural responses to light. Importantly, we have also demonstrated that negative phototaxis tends to be exhibited regardless of the spectrum of light to which birds are exposed. Our study focused on small-scale behavioural responses to light in a ground-based context and it does not predict phototactic behaviour of birds in flight or how it may relate to stranding. Furthermore, the storm-petrels used in our experiments were already grounded and may have encountered any number of stressors prior to capture that could have influenced their behaviour. In fact, seabird umwelt remains largely a mystery and behavioural responses in artificial versus natural settings will inevitably differ to some degree. Our findings nonetheless have implications for seabird rescue programs: procellariiforms that become grounded in dark areas will likely remain there, as evidenced by their low activity levels and lack of hiding response (i.e., remaining exposed in the open field) in experimentally dark conditions. This contrasts with procellariiform fledglings grounded in light areas, which likely exhibit high activity levels and seek out dark hiding places (as also observed anecdotally in

previous studies). Given that individuals become stranded in large numbers in lighted areas and rescue efforts are typically focused there, our results emphasize the need to also search more concealed dark locations where stranded birds may remain hidden for hours or days following stranding. Our results also confirm the utility of an additional mitigation measure not previously tested in the global effort to reduce mortality of seabirds grounded by artificial light at night. As it is not always possible to extinguish ALAN, especially in industrial settings where human safety during nocturnal operations is a priority, deploying Safe Haven boxes in illuminated stranding "hotspots" takes advantage of the negatively phototactic behaviour displayed by stranded fledglings. This will assist in the safe rescue of fledglings and provide an additional measure to help conserve seabird populations affected by ALAN.

Tables

Table 3.1. Number of storm-petrels that responded to each of the two light options in each stimulus combination (in parentheses, column 1) or exhibited no response for one light type over the other ("No Response"). Total responses to both light options combined is provided. We also report the 95% confidence intervals of the true proportion of individuals that chose the first light type named in the combination, and the p-value of the exact two-tailed binomial test on the quantities that responded to each light option.

Stimulus Combination	95% CI	P-value	Total Responses	No Response
HPS (3) vs dark (6)	0.07, 0.70	0.5	9	10
HPS (5) vs warm white (3)	0.24, 0.91	0.7	8	11
Warm white (4) vs cool white (4)	0.16, 0.84	1.0	8	9
Blue (2) vs orange (1)	0.09, 0.99	1.0	3	18

Figures
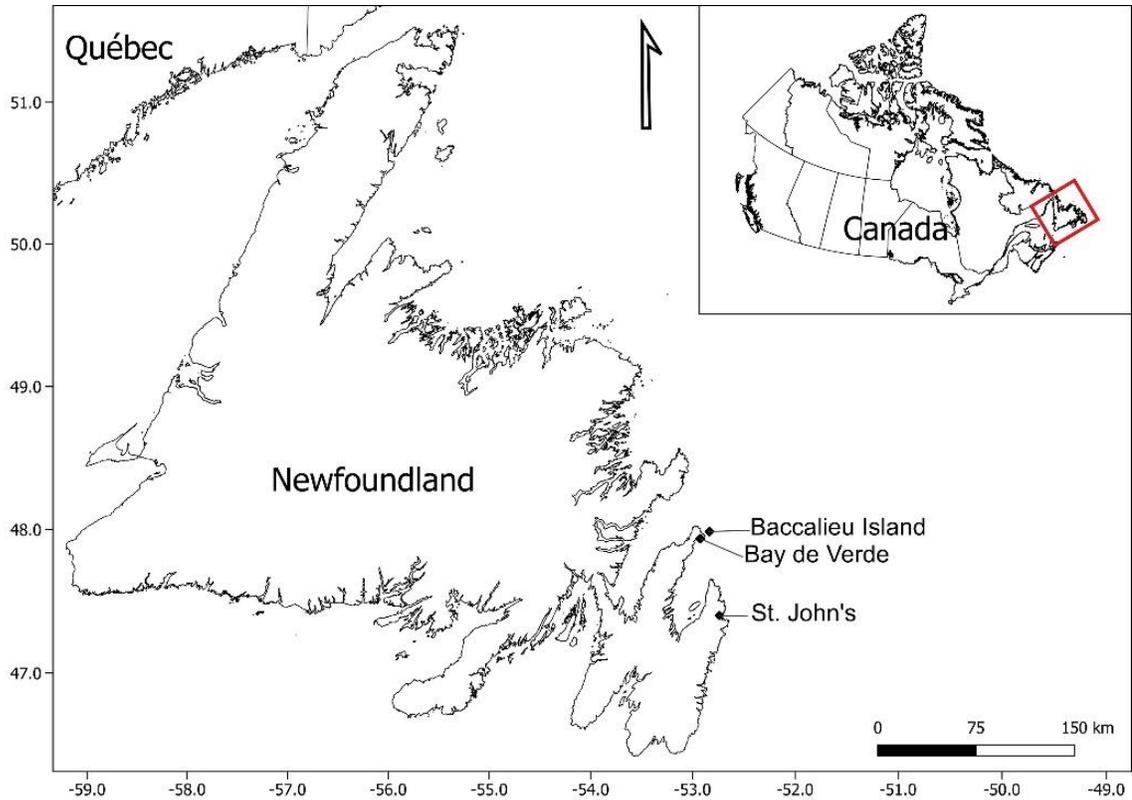
Figure 3.1. Leach's storm-petrel colony location (Baccalieu Island) and study location (Bay de Verde) with reference to the capital city (St. John's) of the province of Newfoundland and Labrador, Canada.
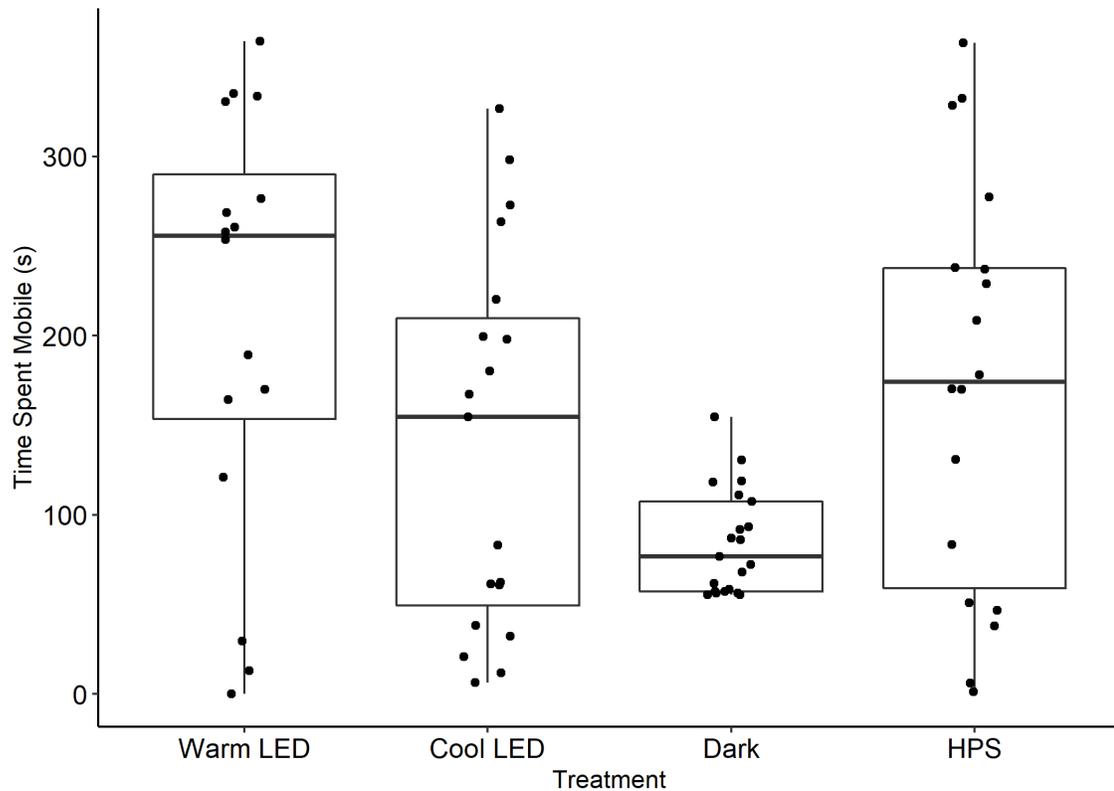
Figure 3.2. Fledgling storm-petrels were significantly less mobile in the Dark than when exposed to warm white LED or high-pressure sodium (HPS). There were no other significant differences. Figure shows a boxplot of time spent mobile (in seconds) by individuals exposed to one of four light treatment groups. Note that, because of the conversion applied to dark data (see text), data points of birds that truly spent zero or near-zero time mobile have been artificially inflated and statistical comparisons are therefore more conservative.

Chapter 4

Concealment and light levels affect detection probability of stranded seabirds: a study with 3D puffin decoys

This chapter has not yet been submitted for publication but is written in manuscript format.

Authors: Brown, T.M., L. Van Haaften, S.I. Wilhelm, and G. Burness.

Author Contributions

T.M.B.: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing – Original draft preparation. L.V.: Methodology, Investigation. S.I.W.: Supervision, Methodology, Resources, Writing – review and editing. G.B.: Conceptualization, Supervision, Methodology, Resources, Funding acquisition, Writing – review and editing.

Abstract

Fledglings of burrow-nesting seabirds are vulnerable to disorientation by artificial light at night (ALAN) and grounding in coastal human settlements, where most individuals presumably perish if not rescued. Many affected species are already threatened, such that ALAN-induced grounding represents an additional risk to population persistence. Opportunistic rescue programs have collected extensive data instrumental to studying the phenomenon, yet accurate estimates of the effects of stranding on seabird populations remain elusive due to several levels of uncertainty, such as the number of stranded seabirds estimated to remain undiscovered by rescuers. One species subjected to stranding is the Atlantic puffin (*Fratercula arctica*). We hypothesized that the detection probability of puffin fledglings by the Puffin Patrol rescue program, operating in Newfoundland, Canada, is affected by search effort, light level, and concealment level. We deployed realistic puffin decoys in locations of varying light and concealment levels throughout two sites that are searched nightly by rescuers and measured the amount of time and search effort required until each decoy was found. We also measured the total search effort to which each site was subjected on each night and found that each additional minute of search effort increased detection rate by 0.6%. Up to 100% more search effort was required to find a decoy placed in concealed conditions (35.5 min) than one in the open (17.5 min), and 78% more search effort was required to find a decoy in darkness (32.0 min) compared to illuminated conditions (18.0 min). In combination with recent advances in our knowledge of seabird post-stranding behaviour, these insights may be used to train rescuers in more effective search techniques and to

estimate correction factors to account for the number of stranded seabirds overlooked by

rescue programs. Application of such correction factors will hopefully result in better

estimation of mortality rates and their resultant effects on populations.

Introduction

The presence of artificial light at night (ALAN) has been linked to the dysregulation of biological systems in myriad species (Rich and Longcore 2006; Gaston et al. 2021; Jägerbrand and Spoelstra 2023), and between 1992 and 2017 (the most recent timespan over which it was estimated) its emittance increased by at least 49% globally (Sánchez de Miguel et al. 2021). Furthermore, the increasing adoption of energy-efficient light-emitting diode (LED) lights, which emit a relatively higher proportion of blue light compared to historically prevalent incandescent light types, is poised to worsen the effects of ALAN on wildlife due to a greater sensitivity in many animal taxa to that part of the visible spectrum (Pawson and Bader 2014; Longcore et al. 2018). One way in which ALAN affects animal behaviour specifically is by causing disorientation and disruption of natural movement patterns, leading to exhaustion, collision with anthropogenic structures, stranding, and/or predation (Rich and Longcore 2006; Rodríguez et al. 2017a; Marangoni et al. 2022; Fabian et al. 2024).

More than 50 seabird species worldwide are affected by nocturnal stranding (or "grounding") in artificially-illuminated spaces. Most of them are burrow-nesting seabirds of order Procellariiformes, but Atlantic puffins of order Charadriiformes are also impacted (Rodríguez et al. 2017a; Wilhelm et al. 2021; Brown et al. 2024, Chapter 2). Puffins strand in human settlements near their colonies in Scotland (island of Hirta; Harris 1982), Iceland (island of Heimaey; E. Hansen, pers. comm., South Iceland Nature Research Centre, 31 August 2024), Denmark (various of the Faroe islands; S. Hammer, pers. comm., Faroese Environment Agency, 28 August 2024; B. Porter, pers. comm., Cardiff University, 9 September 2024), and Canada (island of Newfoundland; Wilhelm et

al. 2013), with ALAN identified as the likely causal factor (Rodríguez et al. 2017a; Brown et al. 2024, Chapter 2). Across species, fledglings on maiden voyages from their nests appear to be most susceptible to becoming stranded, likely due to their inexperience in flight and navigation as well as an underdeveloped visual system (Rodríguez et al. 2017a; Mitkus et al. 2018; Atchoi et al. 2020; Atchoi et al. 2023). Grounded fledglings are rarely able to regain flight in anthropogenic landscapes (where they are thought to most often become stranded) and are therefore highly susceptible to mortality by predation, vehicle collisions, and dehydration despite generally high initial survival rates (Telfer et al. 1987; Ainley et al. 2001; Le Corre et al. 2002; Rodríguez and Rodríguez 2009; Miles et al. 2010; Fontaine et al. 2011). Many affected seabird species are globally imperiled and already face a number of compounding threats (Croxall et al. 2012; IUCN 2024), but additional mortality due to ALAN-induced grounding has been identified as having further negative effects on population growth in at least three species (Simons 1984; Ainley et al. 2001; Fontaine et al. 2011; Griesemer and Holmes 2011).

It is essential to basic seabird population monitoring and conservation efforts that mortality rates of ALAN-affected fledglings (and adults) are estimated accurately. In most locales affected by seabird strandings, there are no standardized survey programs in place to estimate the number of birds grounded by ALAN. Instead, non-standardized nocturnal rescue programs that rely on public participation allow for at least a crude approximation of the magnitude of stranding-related mortality, but accurate estimation is hindered by various levels of uncertainty, including the total number of fledglings produced by a population, the number of fledglings that become grounded by lights, and the number of stranded fledglings that go undiscovered or unreported (Rodríguez et al. 2017a). Rescue

programs universally find more birds in illuminated compared to dark areas (Rodríguez et al. 2017a), but it is unclear to what extent this pattern is driven by seabird versus rescuer behaviour. For example, procellariiform fledglings are known to seek shelter and prefer dark spaces following stranding (Reed et al. 1985; Rodríguez et al. 2017a; Brown et al. 2025, Chapter 3). If rescuers are biased toward searching or more efficient at finding birds in illuminated areas, or both (Brown et al. 2023, Chapter 1), then a considerable proportion of stranded individuals may remain undiscovered. In comparison, stranded fledglings that continue to move toward light after stranding, such as puffins (Brown et al. 2024, Chapter 2), are probably less subject to potential light level-related biases in rescuer search efficiency. In either case, however, an estimation of seabird detection probability across light as well as concealment levels would be useful in the global effort to accurately quantify ALAN-related seabird stranding and mortality rates.

In the province of Newfoundland and Labrador, Canada, the Witless Bay Ecological Reserve protects a group of islands hosting close to 400,000 breeding pairs of Atlantic Puffins, the largest breeding concentration of the species in North America (Lowther et al. 2020; Iles et al. 2025). In August of each year, fledgling puffins (hereafter "pufflings") leave their nests for the first time and several hundred are found stranded along an approximate 15-km section of coastline near the reserve annually (Wilhelm et al. 2013, 2021). In comparing population estimates and observed reproductive success to the numbers of stranded pufflings, and in a band-recapture study, it has been estimated that a minimum of 0.2% of puffin fledglings are affected by stranding (Wilhelm et al. 2021).

Since 2004, the volunteer-based "Puffin Patrol" rescue program has conducted nightly searches for stranded pufflings along the affected section of coastline and has identified several distinct "hotspots" where stranded pufflings are reliably found. These hotspots are generally well-illuminated areas of human infrastructure along the coastline, within approximately 3 km of the main puffin colonies in the reserve (Wilhelm et al. 2021; Brown et al. 2024, Chapter 2). Volunteers (especially those with children) eager to find a puffling are often informed by organizers of the reliability of these hotspots; also, volunteers who have found pufflings at these hotspots previously are presumably more likely to search there; both of these circumstances may thus drive a bias toward increased search effort and increased numbers of pufflings found in those areas (T.M.B., pers. obs.; Brown et al. 2023, Chapter 1).

To our knowledge, no study to date has attempted to estimate the effects of either intrinsic or extrinsic factors on variation in seabird detection probability. We hypothesized that three extrinsic factors affect detection probability of stranded pufflings by the Puffin Patrol: illumination level, concealment level, and search effort. To eliminate potential biases in detection probability caused by mobility, behaviour, and variation in body size of live birds, and to control for the possible effects of predation and number of puffins available to be found, we used realistically-sized and -coloured 3D-printed puffling decoys for this experiment. We placed decoys in dark, dimly illuminated, and brightly illuminated locations which also varied in level of concealment, throughout two hotspots visited regularly by rescue volunteers. By monitoring the sites in real time, every evening for 12 nights, we were able to measure search effort as well as the time to detection of each decoy at each site with relatively high precision. We predicted that

detection would increase with illumination level, decrease with concealment level, and increase with search effort; and that more search effort would be required to find decoys in low illumination or high concealment. We used three different analyses to assess the effects of our three chosen covariates: first, we compared proportions of decoys found across illumination and concealment levels; next, we assessed the effects of illumination, concealment, and search effort on detection rate (the likelihood of a detection event at a particular point in time); and lastly, we compared the amount of search effort required to find decoys in each level of illumination and concealment. To visualize the point of diminishing returns on search effort, we also modeled the relationship between search effort expended and proportion of decoys found.

Methods

Ethical Note

All procedures were performed in accordance with Trent University's Research Ethics Board guidelines under protocol #28055. We created an informed consent agreement which was approved by the Trent University Research Ethics Board before the experiment (see Appendix 4). As part of the stipulations of the protocol, we as Experimenters were not in contact with study participants during the signup process and we were not privy to their identities or information. When volunteers arrived at the Puffin Patrol headquarters in Bay Bulls (47.315178°N, 52.813887°W) at the beginning of their search shift at 22:00 on the nights of this experiment, program organizers read to them a short script requesting their participation in this experiment and administered a consent agreement to those who consented to participate (Appendix 4). A total of $N = 55$

agreements were signed by Puffin Patrol volunteers who chose to participate in the study

(i.e., to collect decoys) and who are hereafter referred to as anonymous "Participants" in

those contexts pertaining to decoy detection specifically. Otherwise, we refer to

volunteers more generally because in the field it was not always possible to guess, and we

as the Experimenters were not permitted to ask, a volunteer's participatory status in this

experiment. Puffin Patrol organizers showed volunteers a sample decoy to familiarize

them with its appearance, and specifically asked volunteers who decided not to

participate to leave decoys in place whenever they encountered them. Participants were

not told how many decoys would be deployed, so as not to influence their search effort.

Participants who participated on two or more nights of the experiment were not required

to sign new consent agreements. As such, any repeat Participants are not necessarily

accounted for in the $N = 55$ consent agreements collected and it is therefore unknown

exactly how many Participants were involved in this experiment. All volunteers

(Participants and non-Participants alike) searched for real puffins and were counted

toward metrics of search effort in this experiment, but only Participants were responsible

for collecting decoys. Personal information of Participants was kept separate from any

experimental data to maintain anonymity.

Materials

We printed 60 life-size, three-dimensional (3D) puffin fledgling decoys following

an initial 3D file design (by SaviMade; savimade.ca) created using photographs and

measurements of live Atlantic Puffin fledglings (see Appendix 4). Each decoy was 18 cm

tall × 10.5 cm wide × 23 cm from beak tip to tail tip and was painted to mimic real

pufflings (Figure 4.1). Although we only needed 20 decoys for our experiment, we created 60 decoys in total to account for potential loss, damage, and theft.

Study Sites

We conducted our experiment on 12 nights between 6-27 August 2023, at two sites in Witless Bay, Newfoundland and Labrador, Canada: a small commercial building that included a convenience store (hereafter "convenience store"; 47.279272°N, 52.831533°W) and the BGI crab plant (hereafter "crab plant"; 47.279404°N, 52.823854°W; Figure 4.2; Table 4.1). We chose these sites as they are considered to be stranding "hotspots" where rescue volunteers can reliably find stranded pufflings, and as such they are two of the most heavily searched areas. We conducted the experiment on the properties surrounding each of the two buildings and delineated the boundaries of the total area to ensure that the area searched for the experiment at each site was approximately equal (approximately 5330 m^2; Figure 4.2): the search area of the convenience store site was 5265 m^2 (total area = 5709 m^2 minus the area occupied by the building on site; the search area at the crab plant was only accessible on two sides of the building and was estimated at 5396 m^2 (Figure 4.2).

Location Selection

We subjectively selected 15 illuminated locations (including both dimly and brightly illuminated locations) and 15 dark locations at each of the two sites for the placement of puffling decoys (60 locations total) and marked their coordinates with a GPS unit (Garmin GPSMAP 64s or 64sx; Olathe, KS, USA; Table A4.1). After the

experiment was complete (on 28 August 2023; a relatively clear night with the moon 91% illuminated; moongiant.com) we measured light levels at all 60 locations with a spectrometer (SRI-2000 Spectral Light Meter; Allied Scientific Pro; Gatineau, Quebec, Canada) and with an app ("Lux"; Doggo Apps) on a cell phone (Samsung Galaxy S22; Samsung Electronics Co., Ltd.; Suwon-si, South Korea). The spectrometer could not detect illuminance readings below 10 lux (e.g., approximately the illuminance perceived by the human eye during civil twilight; AMS 2025) and therefore was not precise enough to quantify real differences between dark and dimly illuminated locations; nor would it have been sensitive enough to detect differences in illuminance between nights of high and low ambient (i.e., lunar) light. As such, we opted to use qualitative categories of light level in statistical analysis and include spectrometer and cell phone app readings of illuminance in Table A4.1 for information purposes only. Although we acknowledge that the use of spectrometer-quantified differences in illuminance among the three light levels in our analysis would be ideal, the inclusion of these measurements would not change the results, which are nonetheless based on subjective human perception of light level (as are units of lux). It was not possible to equalize the number of "dim" and "bright" illuminated locations between the two sites due to differences in site lighting and layouts, but we accounted for this by stratifying by site in our analysis (see *Statistical Analysis*, below).

To mimic true stranding behaviour of live pufflings, at least in terms of where they are found by rescuers, we only selected locations on the ground (i.e., never on top of objects) and selected locations that varied in levels of illumination and concealment which reflected the variation observed across real stranding locations (Table A4.1).

Across locations we varied the level of concealment on a scale based on an imaginary cube of 1 m³ surrounding the decoy's precise location, not including the ground: e.g., if the decoy was concealed by a wall or other object to within 1 m on only one side, the decoy received a concealment score of 1 (Figure 4.3). We chose locations that typically ranged from 0-3 (median 1, $N = 60$), with a singular location (and four deployments thereof) of concealment score 4 which we omitted from final analysis (Table 4.1; Table A4.1). Due to the heterogeneity of the two sites in terms of topography, obstacles, and business activities it was not possible to perfectly equalize the number of locations with each level of concealment between the two sites, although the best effort was made to do so.

Experimental Procedure

Each night, we (the two "Experimenters": T.M.B. and L.V.H.) deployed 20 decoys, 10 at each site. Of the ten decoys at each site, five were placed in dark locations and five in illuminated locations (dim and bright combined; separated during analysis). Because there were 30 possible locations at each site, we randomly determined which ten locations we would use at each site on each night of the experiment, sampling without replacement over three-day intervals. That is, all locations at each site were used over a three-day period before randomly re-sampling. Because the experiment spanned 12 nights and we deployed 20 decoys per night, we used each location four times (total of 240 deployments). Despite using each individual decoy location four times throughout the experiment, we treated each deployment as an independent sub-sample for two primary reasons. First, precision of deployment location varied by up to several metres due to

imperfect GPS locational accuracy and intra- and inter-Experimenter variability in decoy

placement (when this variation resulted in a decoy receiving a different category of light

or concealment level than intended, we omitted this particular deployment from

subsequent analysis; see *Statistical Analysis*, below, and Table 4.1). Second, the use of

each deployment location was randomized over three-day intervals without replacement.

This was important because most Participants were tourists/visitors who would have

searched for decoys on a single night only or, if on more than one night, would have

searched on consecutive nights. As a result, most Participants would have encountered a

decoy at a specific deployment location only once.

Between 2130-2200 hours on each night of the experiment, the two Experimenters

(one stationed at each of the two sites) deployed the 10 decoys allocated to that site in

time for the experiment to begin at approximately 2200 hours (range in start time

2143-2159 hours). The experiment began whenever the last decoy was deployed at each

site; as such, the start time was allowed to vary slightly between sites (median variation

in start time between the two sites on the same night was 6 minutes; maximum 12

minutes). The start time of 2200 hours was chosen to coincide both with complete

darkness (sunset time varied from 2027 to 1951 hours in the experimental period) and

with the beginning of the second "shift" of Puffin Patrol volunteers (2200-2400 hours).

To reduce any potential bias in the direction of decoy placement and resulting differences

in visibility, we randomly assigned to each decoy on each night one of the four main

cardinal directions (north, east, south, and west), toward which it would be faced. During

deployment, Experimenters used GPS units both to locate the designated locations where

decoys were to be placed and to ensure the decoys faced their assigned cardinal

directions. Following decoy deployment, Experimenters stationed themselves at a designated location in each site that was chosen to maximize the visibility of site entrances/exits and minimize potential effects on decoy detection by Participants.

As an index of search effort for each site on each night, Experimenters recorded when and how many volunteers arrived and departed from each site. Volunteers were only considered to be present at the site if they were seen wearing reflective vests (issued by the Puffin Patrol) and searching on foot within the site boundary; people in cars within the site boundary were not counted and those not wearing reflective vests were not counted. Arrival time of volunteers was recorded as the time at which they were first seen on foot within the site boundary. Because all volunteers were included in estimates of search effort, this metric is thus inflated as compared with the search effort of Participants alone, but in a way that is consistent across both sites and across all illumination and concealment levels. We assumed that search effort of Participants alone (which was unquantified in this study) and search effort by volunteers in general (which is reported in this study) were highly correlated. Note also that we were not concerned about equivalency in search effort among different group sizes; we assumed that, e.g., two volunteers searching for 10 minutes was equivalent to 10 volunteers searching for two minutes (i.e., both equal 20 search-minutes).

If volunteers arrived or were already present at the site during decoy deployment, they were excluded from search effort metrics for that particular site and were asked by the deploying Experimenter to refrain from collecting decoys at that site. However, these volunteers were allowed to collect decoys at the other site and were counted toward search effort at the other site. We quantified search effort for each site on each

experimental night in units of "search-minutes" (i.e., one search-minute is equivalent to one volunteer searching for one minute). For example, if there were no volunteers present for 80 minutes of the experiment ($0 \times 80 = 0$), then five volunteers were present for 10 minutes ($5 \times 10 = 50$), and then two volunteers were present for 30 minutes ($2 \times 30 = 60$), the search effort calculated for that site on that night would be $0 + 50 + 60 = 110$ search-minutes.

Experimenters recorded the time at which each decoy was found. Experimenters had planned to also record the time and number of real pufflings found by volunteers, so that this potential source of distraction from search effort expended on decoy detection could be accounted for in analysis, but because of mass chick mortality at the colony in 2023 there were few pufflings grounded overall and zero pufflings found grounded at either of the two experiment sites on our experimental nights. Occasionally, Participants collected multiple decoys while out of view of the Experimenter, and it was only possible to assign a single "time found" to all these decoys, which was the time that they were given to the Experimenter. In the one instance when a decoy was collected from one site and brought to the Experimenter at the other site, the assigned "time found" was the time that the Participants departed the original site; although not perfect, this decoy's "time found" would presumably not be much less accurate than that of a decoy given to the Experimenter after Participants found it while out of view (see above). The experiment ended at a given site when all decoys at that site were found, or when all volunteers had returned to Puffin Patrol headquarters to sign out, or at 2400 hours, whichever occurred first (median experiment duration, 117.5 minutes; range 22-132 minutes). Experimenters collected any undetected decoys at the end of each night.

Statistical Analysis

Due to external circumstances beyond our control (i.e., lighting changes at the businesses we used as our study sites) and miscommunication among Experimenters, there were ten deployments in which light levels at deployed decoys differed from their original allocations, four deployments (all at the same location) with concealment score of four, and two deployments wherein decoys were accidentally placed on top of objects, all of which were omitted from final analysis (Table 4.1). We also removed from analysis two deployments in which the decoy was stolen and one deployment in which the decoy location was accidentally revealed to volunteers by the Experimenter. In total there were thus 19 deployments, distributed across all 12 nights of experiments, which hereafter have been excluded from analysis (Table 4.1), leaving a final sample size of $N = 221$ deployments. Of these, 110 were in darkness and 111 were in light (38 in dim light; 73 in bright light); in terms of concealment level, 80 deployments were in concealment $= 0$, 76 deployments in concealment $= 1$, 36 deployments in concealment $= 2$, and 29 deployments in concealment $= 3$. All statistical analyses were conducted in program R (ver. 4.3.0; R Core Team 2023), and we report results with exact *P*-values ($\alpha = 0.05$ was used to denote statistical significance).

Proportions of decoys found in each level of illumination and concealment

First, we calculated the percentages of decoys found in each of the three light levels (dark, dim, and bright) and separately in each of the four concealment levels (0, 1, 2, 3). We then conducted Chi-square tests for homogeneity to determine if the

proportions of detected versus undetected decoys differed among levels of each of these

two variables (without controlling for or holding constant any other factors).

Decoy detection rate relative to levels of illumination, concealment, and search effort

For the purpose of this analysis, detection rate was calculated relative to regular

elapsed time, which included time spans in which there were no volunteers present. We

conducted this analysis to understand, on an average night when the Puffin Patrol is

operational, how our variables of interest affect the detection rate of decoys. This allowed

us to estimate how long (in elapsed time) real pufflings may await rescue (visualized as

persistence probability over time) across different levels of illumination, concealment,

and search effort, with the effect of each covariate assessed while adjusting for those of

the others. We first determined the "fate" of each deployed decoy as either detected ("1")

or undetected ("0"). We then calculated the "fate time" of each decoy as the number of

minutes that elapsed until it was found, using the time at which all decoys had been

deployed at a given site as the reference start time. If the decoy remained undetected until

the end of the experiment, its "fate time" was the duration of the experiment (in minutes).

Any decoys that remained undetected at the end of an experiment with a duration <120

minutes (no less than 116 minutes) were "censored"; our analysis contained 22 such

censored observations. Censored individuals were dropped from the model as having

persisted at the time that they became censored, and thus did not affect estimates of

persistence probability or detection rate beyond that time.

We tested for effects of light level (ordinal: dark [0], dim [1], or bright [2]; at the

level of the individual decoy location), concealment level (ordinal: 0, 1, 2, or 3; at the

level of the individual decoy location), and search effort (continuous, numeric: in search-minutes; at the level of each site on each night) on "detection rate" using Cox proportional hazards (CPH) models (Cox 1972) with the *survival* (v. 3.6-4; Therneau 2024) and *survminer* (v. 0.4.9; Kassambara et al. 2021) packages. "Detection rate" was defined as the likelihood of a detection event occurring at a particular point in time and was encoded by the CPH model incorporating both the "fates" and "fate times" of decoys. We calculated the magnitude of difference in detection rate between individual levels of a variable using the hazard ratio ("HR") provided in the CPH model output. An HR >1 indicated that the variable level in question increased detection rate from the reference level by a factor of the HR minus one. An HR <1, meanwhile, indicated that the variable level in question decreased detection rate from the reference level by a factor of one minus the HR. For example, an HR of 1.45 for variable level 1 would indicate that detection rate was increased by (1.45 - 1 = 0.45) 45% for that variable level relative to the reference level (e.g., 0), and an HR of 0.45 for variable level 1 would indicate that detection rate was decreased by (1 - 0.45 = 0.55) 55% for that variable level relative to the reference level (e.g., 0).

We tested for differences in search effort between the two sites using a Wilcoxon rank-sum test (package *stats*, v. 4.3.0; R Core Team 2023) since variances were not homogeneous. Search effort differed significantly between sites ($W = 31.5$, $P = 0.02$) and was approximately twice as high at the crab plant (median 99 search-minutes per night; total 1277 search-minutes across all 12 nights) than at the convenience store (median 44.5 search-minutes per night; total 676 search-minutes across all 12 nights; Table 4.1). We accounted for these differences between the two sites in our CPH model both by testing

for the effect of search effort directly, as a covariate, and by stratifying the data according to site (convenience store and crab plant) using the *strata()* function. Stratification allowed the baseline hazard functions to differ between sites while still assuming a common effect of the chosen covariates.

We tested the proportional hazards assumption using the *cox.zph()* function (package *survival*, v. 3.6-4) and found no violations (light level $\chi^2_2 = 0.14$, $P = 0.93$; concealment $\chi^2_3 = 2.06$, $P = 0.56$; search effort $\chi^2_1 = 0.05$, $P = 0.83$; global $\chi^2_6 = 2.27$, $P = 0.89$). We additionally checked for multicollinearity by calculating variance inflation factors using the *vif()* function in package *car* (v. 3.1-2; Fox and Weisberg 2019) and detected no collinearity among our three covariates (light level, concealment, and search effort), as their $\text{GVIF}^{(1\div(2\times df))}$ values were all between 1.00-1.02, where $\text{GVIF}^{(1\div(2\times df))} = 1$ signifies zero collinearity and $\text{GVIF}^{(1\div(2\times df))} > 2.24$ indicates potentially problematic multicollinearity.

For visualization and description purposes only, we modeled persistence probability of decoys relative to each level of our three covariates of interest (light level, concealment level, and search effort). Persistence probability is the probability of decoys remaining undiscovered over time, whereby a high persistence probability generally indicates a low detection rate (i.e., it took longer for Participants to find the decoys) and vice versa. Because search effort was a continuous variable measured in search-minutes, we created three arbitrary bins (i.e., categories) for better visualization. These bins of search effort were "low" (≤ 60 search-minutes), "medium" (61-120 search-minutes), and "high" (≥ 121 search-minutes). Across persistence probability models for all three covariates of interest, we modeled only the main effect, with no random effects, stratified

variables, or determinants of significance, again because these models were created for visualization purposes of the main effects only. It is important to note that the main way in which modeled persistence probabilities visually reflect significant differences in detection rate is in the absence of model intersections and overlaps; lack of differences in detection rate are visualized as intersecting and overlapping persistence probability models throughout the duration of the experiment. Confidence intervals should therefore be interpreted with caution.

Differences in search effort required to find decoys across illumination and concealment levels

We assessed whether the amount of search effort required to find an individual decoy (y) differed among our three light levels (x) or, separately, among our four concealment levels (x). Because search effort data were severely non-normal, we compared medians using non-parametric statistics. Specifically, we performed two separate Kruskal-Wallis H tests (package "*stats*", v. 4.3.0) and subsequent post hoc Dunn tests (package "*FSA*", v. 0.9.4; Ogle et al. 2023) for multiple comparisons. Note that concealment level was not controlled for or held constant in the comparisons among light levels, or vice versa.

Relationship between search effort and proportion of decoys found each night

In our final analysis, we wanted to explore the shape of the relationship between search effort and proportion of decoys found, so that we could estimate the point of diminishing returns. First, we omitted all undetected decoys ($N = 58$), leaving a sample

size of $N = 163$ found decoys for further analysis. We then calculated for each decoy: (1) the search effort (in search-minutes) expended to find it; and (2) the cumulative proportion of decoys found that it represented on a per-site, per-night basis. We modeled the relationship between search effort and proportion of decoys found using a quasibinomial generalized additive mixed model (GAMM) with logit link function, coding "site" as a random effect, using the *gamm* function in package *mgcv* (v. 1.9-1; Wood 2023). The model was then visualized using the functions *gratia* (v. 0.10.0; Simpson 2024) and *ggplot2* (v. 3.5.1; Wickham 2016).

Results

Note that there were zero real pufflings found at either of the two experimental sites on any of the experimental nights.

Proportions of Decoys Found in Each Level of Illumination and Concealment

Of 221 deployed decoys, 163 (74%) were found by Participants. Seventy-three decoys were found at the convenience store out of 110 deployed (66% detected), versus 90 found out of 111 deployed at the crab plant (81% detected). Separated according to light level, Participants found 66% ($N = 73$ of 110) of decoys deployed in "dark" locations, 76% ($N = 29$ of 38) of decoys in "dim" locations, and 84% ($N = 61$ of 73) of decoys in "bright" locations (Table 4.2); these differences were statistically significant ($\chi^2_{2, 221} = 6.86$, $P = 0.03$). When "dim" and "bright" deployments were considered together as simply "illuminated" locations, 81% of decoys were found ($N = 90$ of 111;

Table 4.2), suggesting that even when there is some light, close to 20% of decoys still remain undetected after two hours.

Separated according to concealment level, Participants found 80% (N = 64 of 80) of decoys placed in the open (concealment score = 0), and this did not differ from when decoys were concealed on one, two, or three sides ($\chi^2_{3, 221}$ = 5.33, P = 0.15; Table 4.3). When deployments with concealment scores of 1-3 are considered together as simply "concealed" locations, 70% of decoys were found (N = 99 of 141; Table 4.3).

Decoy Detection Rate Relative to Levels of Illumination, Concealment, and Search Effort

According to our Cox proportional hazards model, search effort and concealment level each had significant effects on detection rate (the likelihood of a detection event occurring at a particular point in time) while adjusting for the effects of the other covariates. For each additional minute spent searching by one person (i.e., one "search-minute") at a given site on a given night, detection rate increased by 0.6% (coefficient = 0.006; SE = 0.002; P < 0.001; hazard ratio = 1.006; 95% CI = 1.003, 1.009; Table 4.4). Note that for the concealment and illumination level covariates, the CPH model only provides comparisons for each level compared to the reference level (i.e., reference levels are concealment = 0 and light level = dark, respectively), and therefore does not compute pairwise comparisons among all levels (Table 4.4). Concealment played a significant role in predicting detection rate, but only up to a concealment score of two. Decoys concealed on one side (concealment score = 1) had a detection rate 40% lower than those placed in the open (concealment score = 0) (coefficient = -0.506; SE = 0.201; P = 0.012; hazard ratio = 0.603; 95% CI = 0.406,

0.894; Table 4.4) and the detection rate of decoys concealed on two sides (concealment score = 2) was 57% lower than those placed in the open (coefficient = -0.852; SE = 0.268; P = 0.001; hazard ratio = 0.427; 95% CI = 0.253, 0.721; Table 4.4). Interestingly, concealment on three sides (concealment score = 3) did not result in any significant reduction in detection rate compared to decoys placed in the open (P = 0.134; Table 4.4). Detection rate was higher, but not statistically significant, in brightly illuminated conditions compared to darkness (coefficient = 0.321; SE = 0.188; P = 0.087; hazard ratio = 1.378; 95% CI = 0.954, 1.991; Table 4.4) and detection rate did not differ between darkness and dimly illuminated locations (P = 0.167; Table 4.4).

To visualize differences in detection rate among levels of each parameter, we modeled persistence probability. As was the case in our formal detection rate analysis (i.e., Cox proportional hazards model, above), decoys deployed in bright light trended toward having a lower probability of persistence (i.e., were more easily found) over the course of the experiment than those in the dark, but models intersected several times during the first half of the experiment (Figure 4.4). Meanwhile, puffling decoys in dim light had intermediate persistence probability. Our models demonstrated that if a decoy had not been found within approximately 90 minutes from the beginning of the experiment, it was unlikely to be found, irrespective of lighting conditions (Figure 4.4).

Persistence probability decreased steadily but irregularly across the four concealment levels, with several equivalence points (i.e., model crossovers) in the first 40 minutes of the experiment (Figure 4.5). After 90 minutes, few of the remaining decoys were found and persistence probability leveled off at approximately 0.2 for decoys in the

open and those concealed on three sides, approximately 0.3 for decoys concealed on one side, and approximately 0.4 for decoys concealed on two sides.

Persistence probabilities decreased over time but did not vary among decoys subjected to different levels of search effort (Figure 4.6). Although detection rate increased by 0.6% per minute of expended search effort, the only visible trend in the plotted persistence probabilities was that persistence was higher when a site was subjected to low search effort, compared to medium or high (Figure 4.6).

Differences in Search Effort Required to Find Decoys across Illumination and Concealment Levels

There was a significant effect of light level on the amount of search effort required to find each individual decoy (Kruskal-Wallis test: $H_2 = 12.621$, $P = 0.002$, Figure 4.7). Seventy-eight percent more search effort was required to find a decoy placed in darkness (median search effort = 32 search-minutes) than in dim illumination (median 18 search-minutes) or bright illumination (median 18 search-minutes; Dunn test: $P = 0.010$ and $P = 0.007$, respectively; Figure 4.7). There was no difference in search effort required to find a decoy between dim and bright illumination ($P = 0.541$).

There was also a significant effect of concealment level on the amount of search effort required to find decoys (Kruskal-Wallis test: $H_3 = 20.702$, $P = 0.001$; Figure 4.8). More search effort was required when decoys were concealed on one side (median search effort = 32.5 search-minutes), two sides (median 35.5 search-minutes), and three sides (median 26 search-minutes) than when they were placed in the open (median 17.5 search-minutes; Dunn test: $P = 0.001$, 0.003, and 0.030, respectively; Figure 4.8). There

were no significant differences in the amount of search effort required to find decoys among concealment levels 1, 2, or 3. It should be noted that in these comparisons we did not control for or hold constant light level.

Relationship Between Search Effort and Proportion of Decoys Found each Night

The goal of visualizing the relationship between search effort and the proportion of decoys found each night was to identify the threshold at which approximately 90% of decoys were detected. The following results were obtained after omitting all undetected decoys and pooling the results of the proportions of decoys found at each site, irrespective of illumination and concealment levels. Our quasibinomial GAMM was significant in predicting the highly non-linear positive relationship between search effort and proportion of decoys found (effective degrees of freedom = 3.431, $F = 56.350$, $P < 0.001$, adjusted $R^2 = 0.601$; Figure 4.9). Proportions of decoys found increased steeply until approximately $x = 75$ search-minutes, at which point the slope levels off just above $y = 0.9$ proportion found (Figure 4.9). That is, after an expenditure of approximately 75 search-minutes of search effort, it is estimated that Participants would have found approximately 90% of the decoys (assuming a denominator of approximately 10 decoys available to be found at each site, as in our experiment). The intercept of the relationship did not significantly differ from zero (estimate = 0.245, SE = 0.165, $T = 1.484$, $P = 0.140$).

Discussion

Our study, as far as we know, is the first to estimate variation in detection probability of stranded seabirds by rescue program volunteers. By placing 3D-printed decoys throughout two puffin stranding "hotspots" over 12 nights and measuring search effort and detection times, we found support for our hypothesis that detection probability of stranded pufflings by the Puffin Patrol is affected by all three factors studied: namely, light level, concealment level, and search effort. Most of the decoys deployed at a given site on a given night were detected with the expenditure of at least 75 search-minutes of search effort, regardless of light and concealment levels. In the conditions that we expected the highest detection probability of puffin decoys (i.e., in open areas and under bright illumination), approximately 10-15% of decoys still remained undetected by Participants.

Our Cox proportional hazards regression of detection rate offered insights into how light level, concealment level, and search effort affect detection rate and resulting persistence probability across an average late shift of the Puffin Patrol, with all its natural gaps in search effort. It gave us a first glimpse at how long a real puffling may actually wait to be rescued in real life, an insight we could not have gleaned by quantifying search effort alone. The results of our various analyses combined provide intriguing and nuanced insights regarding Puffin Patrol volunteers' search patterns across the various levels of illumination and concealment.

Effects of Illumination Level on Decoy Detection Probability

Increased light levels resulted in higher proportions of decoys detected (Table 4.2). However, the *rate* at which decoys were detected (i.e., the likelihood of a detection event occurring at a particular point in time) did not vary significantly with illumination level (Table 4.4, although the difference between darkness and bright light approached significance, $P = 0.087$). This lack of difference in detection rate among illumination levels was surprising given that an individual needed to expend almost twice as much search effort to find a decoy in darkness (median 32 search-minutes) than in either of the two illuminated conditions (median 18 search-minutes) (Figure 4.7). Our calculated detection rates and the resulting inverse persistence probabilities of decoys placed in the three different light levels point to a lack of effect of illumination on puffling detection over the duration of an average late shift (2200-2400 hours) of the Puffin Patrol. The lack of difference in detection rate among decoys in different levels of illumination can be visualized as overlapping lines in modeled persistence probability over the duration of the experiment (Figure 4.4). Trends were similar across all three light levels in the first 20 minutes of the experiment, after which time decoys in bright locations had lower persistence probability (i.e., higher detection rates); this was reflected in the trend toward significance in detection rate differences between decoys in darkness versus bright illumination (Table 4.4). Trends in modeled persistence probability continued to be similar between darkness and dim illumination until approximately 60 minutes of the experiment had elapsed, reflecting the lack of difference in detection rate between the two groups (Figure 4.4).

Effects of Concealment Level on Decoy Detection Probability

The relationship between concealment level and detection probability was more complex, but in general concealment on any number of sides decreased detection probability compared to placing decoys in the open (Table 4.3). Significantly more search effort was required to find decoys concealed on at least one side compared to unconcealed ones (Figure 4.8). Yet, surprisingly, decoys concealed on three sides were detected in a similar proportion (Table 4.3) and rate (Table 4.4) to those placed in the open, and slightly (not significantly) less search effort was required to find decoys concealed on three sides than those concealed on one or two sides (Figure 4.8). These results suggest that volunteers were preferentially or perhaps initially searching locations that were open and those of high concealment before searching locations with low and intermediate concealment. It may also be that decoys in the open were found first only by virtue of their conspicuousness, and then volunteers quickly began searching highly concealed locations, perhaps under the impression that puffins hide after grounding. Modeled persistence probabilities of decoys in each concealment level also reflect this: for approximately the first 30 minutes of the experiment (and also approximately the last 75 minutes), persistence of decoys concealed on three sides closely mirrored that of decoys placed in the open (Figure 4.5). However, to truly quantify search effort across the various light and concealment levels, a systematic tracking study of rescuer search effort would be required.

Implications for Live Birds and Rescue Programs

Using actual volunteers from the Puffin Patrol rescue program, our results demonstrate that rescuers show differences in detecting stranded seabirds across illumination and concealment levels. This finding of differential detection probability is important in the effort to increase the effectiveness of rescue programs, particularly in the context of post-stranding behaviour in response to light, which can vary widely across affected taxa. For example, fledgling puffins (Charadriiformes) ground at higher rates in light areas than dark ones and preferentially move toward light even after becoming stranded (Brown et al. 2024, Chapter 2). In contrast, Procellariiforms also become stranded at higher rates when illumination is higher (Rodríguez et al. 2014; Burt et al. 2024) but, once grounded, individuals remain within or move toward dark areas and even preferentially hide in concealed locations when given the opportunity (Reed et al. 1985; Rodríguez et al. 2017a; Atchoi et al. 2024; Burt et al. 2024; Brown et al. 2025, Chapter 3). Therefore, seabird rescue efforts should employ different strategies for maximizing detection rate between e.g. charadriiforms and the much more widely-affected procellariiforms, with greater focus in the latter case on searching dark and concealed locations. From our results, it would appear that Puffin Patrol rescuers employ relatively effective strategies for finding decoys in illuminated and open conditions, which is where we would expect most stranded puffins to be (Brown et al. 2024, Chapter 2). Puffin Patrol rescuers are also relatively effective at searching highly concealed, but not intermediately concealed or dark locations. This implies that they might not be quite as effective in finding stranded procellariiforms as they were at finding pufflings. That said, volunteers (many of whom have never rescued seabirds

before) may unknowingly be using a relatively effective intermediate search strategy that balances search effort across illumination and concealment levels: after all, our model demonstrated they were able to find approximately 90% of decoys scattered over approximately a half hectare (1.3 acres) area within a 75 minute total search-effort interval (Figure 4.9). It is also important to note that this measure of search effort is actually inflated by the inclusion of non-Participant search effort; the amount of Participant-only search effort required to find 90% of decoys would be less than 75 search-minutes.

When considering living birds, the time until detection is arguably just as important as the proportion of individuals found, considering time is likely the main difference between a seabird found alive and one found deceased (e.g., Rodríguez et al. 2014) or not found at all (e.g., Podolsky et al. 1998). Despite the fact that our decoys were detected in statistically similar proportions across concealment levels (Table 4.3), when decoys were placed in locations of intermediate concealment (i.e., concealment level 2), the rate at which they were detected was approximately half that of those placed in the open (Table 4.4: hazard ratio = 0.427). Further, the search effort required to find decoys of intermediate concealment (median = 35.5 search-minutes) was up to double that of those placed in the open (median = 17.5 search-minutes; Figure 4.8). This means that stranded birds that have managed to only partially conceal themselves may face greater predation risk than those in more fully concealed locations not only because they are more exposed, but also because volunteers are less efficient at finding them (Table 4.4; Figure 4.8). Rapid response times are important in ensuring high survival rates: significantly more stranded seabirds are found during nocturnal surveys (Rodríguez et al. 2014; Burt et

al. 2024), and a higher proportion of them are found alive (Rodríguez et al. 2014), compared to when surveys are conducted the next morning. Podolsky et al. (1998) calculated that rapid removal of seabirds (in this case carcasses thereof) by scavengers could cause daily surveys to underestimate counts of stranded individuals by at least 17%. Similarly, over a one-month period during peak fledging of Leach's storm-petrels, Burt et al. (2024) estimated that a minimum of 300 individuals perished due to predation at one stranding "hotspot" in Newfoundland based on counts of the body parts left behind, with an unknown number of individuals completely removed from the site, despite a routine of almost daily morning surveys. Clearly, high detection rates are essential in maximizing the survival of stranded seabirds, and our study offers insights on where efficiency may be lacking.

Across species and rescue programs, the proportion of stranded seabirds found dead or dying ranges from 3-43% (Rodríguez et al. 2017a; Wilhelm et al. 2021). These values may mistakenly be taken at face value as the true range in mortality rates of stranded seabirds, yet they do not include the individuals that remain undetected, which probably suffer mortality rates approaching 100% given their extreme difficulty in regaining flight and reorienting themselves back to the ocean (Rodríguez et al. 2017a). Our data suggest that despite their best efforts, volunteers will overlook >30% of stranded individuals in dark and intermediately-concealed locations and >10% of stranded individuals even in bright and open locations (Tables 4.2 and 4.3). These estimates are based on relatively small sites that were searched relatively intensely every single night and using decoys representing a relatively large body size (Atlantic puffin fledglings on average weigh approximately 250 g; Wilhelm et al. 2021). We expect the proportion of undetected

individuals to only increase in cases where the area to be searched is larger or has less search coverage, or when the target species is smaller, such as in the ~50 gram Leach's storm-petrel (Wilhelm et al. 2021). In fact, smaller body sizes are linked to lower detection probability in carcass detection studies (Barrientos et al. 2018). Potentially making detection even more difficult, Leach's storm-petrels, and possibly other procellariiform seabirds, tend to move very little in darkness after becoming stranded (Brown et al. 2025, Chapter 3), as opposed to puffins which are highly active in the absence of light (Brown et al. 2024, Chapter 2). Further study of detection probabilities of ideally live stranded seabirds that includes interactive effects of body size, activity level, light level, and concealment level will be helpful in the development of accurate stranding data correction factors.

Study Limitations and Future Directions

Our study has several limitations in its estimation of detection probability of stranded pufflings (and of seabirds more generally). Our primary sources of error included a lack of experimental control over the study sites (including the number and timing of volunteers entering and exiting the sites) and the inability of Experimenters to know which or exactly how many volunteers were participating in the experiment. These sources of error have several implications. Firstly, we could not determine whether the number of Participants nor their expended search effort was correlated with those of volunteers in general. We assumed that the two were highly correlated. However, if this assumption proved to be false, our conclusions regarding the effects of search effort on seabird detection probability would be weakened. At best, we could conclude that even

128

with noise introduced into the data we found trends toward increased detection probability with increased search effort. Regardless, we expect that our metrics of search effort were inflated to some unknown degree because they included efforts of volunteers not responsible for detecting decoys. In future, it would be ideal to quantify the exact numbers of volunteers and Participants each night, and calculate their degree of correlation. Even better, a more tightly controlled experiment would include only Participants searching the experimental sites, rather than having to assume or calculate the proportionality of search effort between experiment Participants and volunteers in general.

We were also limited in our ability to draw specific and precise conclusions regarding the effects of illumination level on decoy detection probability. Due to a lack of precision in the instruments we used to measure illuminance at the level of each decoy, we could not with confidence use our quantified values of illumination level (in lux) in our analysis but instead relied upon qualitative categories. Nonetheless, we expect that because the unit of "lux" (which characterizes illuminance) is based upon the perception of brightness by the human eye, we expect that quantified measures of illuminance would only provide higher resolution confirmation of the trends we observed.

Our study used stationary plastic decoys to represent living birds. As such, our experiment did not take account of the many additional parameters that may affect detection of living birds, the majority of which survive stranding (Rodríguez et al. 2017a) and likely move away from their original stranding locations (Telfer et al. 1987; Rodríguez et al. 2017a; S.I.W. and T.M.B., pers. obs.). These parameters should thus be estimated and incorporated into seabird stranding data correction factors: namely, spatial

fallout patterns, post-stranding movement patterns, and predation rates of live stranded

seabirds; persistence and reporting rates of carcasses; and rescuer search patterns. For

example, spatial fallout patterns could be better discerned by radio- or GPS-tagging

fledglings before they depart the colony and tracking their movements (e.g., Rodríguez et

al. 2022), or by conducting standardized searches across all light and dark areas in the

potential fallout zone (as suggested in Brown et al. 2023, Chapter 1). The fates of

individuals that remain undetected by rescuers are also largely unknown but could be

studied by tracking movements and predation of stranded seabirds using cameras

mounted at stranding hotspots, thermal imaging drones, or radio-frequency tags and

handheld receivers. Carcass persistence and reporting rates could be quantified by

deploying already-deceased puffin fledglings (or individuals of other species, in areas

where they are affected) across the stranding-affected area(s) during the stranding period,

and their persistence in the environment and reporting rate by rescuers quantified over

time (Podolsky et al. 1998; Barrientos et al. 2018). Alternatively, carcass persistence and

reporting rates could be quantified by leaving in place and monitoring individuals found

deceased in the course of regular stranding rescue or survey operations (as by Santos et

al. 2016). Lastly, rescuer search patterns, which may be biased toward illuminated areas

(Brown et al. 2023, Chapter 1; this study), could be tracked across the entire search area

using individual GPS units and subsequent characterization of the light levels and

calculation of proportions of time spent searching in each sector of the search area. A

useful additional factor to explore in such a study would be the actual level of

equivalence between, for example, a group of two volunteers searching for 10 minutes

and a group of 10 volunteers searching for two minutes. In our experiment we treated all

search-minutes as equal, but in reality, a large number of volunteers (assuming they enter a site at the same time and location) can only cover so much search area in a short time, compared with the area that may be covered by fewer people over a longer time. An evaluation of the differences in effectiveness across different group sizes and search times in seabird detection probability would be valuable to rescue programs in their efforts to improve rescue efficiency.

Conclusion

Using our approximations of detection probability calculated using randomly-placed, stationary, plastic decoys, we estimate that at least 10% of stranded pufflings go undetected by Puffin Patrol rescuers at hotspot stranding sites. While it has not been estimated how many pufflings become stranded at these hotspots specifically, in total across the entire Puffin Patrol search area volunteers recover an average of 359 living pufflings per year (range 13-759; Wilhelm et al. 2021). As such, at a conservative 10% miss rate, we would expect approximately 36 pufflings (range 1-76) to remain undetected each year. In areas of fallout zones that receive lower search effort, in locations that are dark and intermediately concealed, and in smaller-bodied seabirds, the proportion of undetected individuals may actually be much higher. Our study offers a first step in the development of correction factors for rescue program stranding data to estimate the numbers of birds that remain undetected. This will allow for more accurate estimations of mortality rates of stranded seabirds and for understanding the broader effects of ALAN-induced fallout on populations. Without accurate estimates of the proportion of seabirds that remain undetected following grounding, mortality may be

severely underestimated (Rodríguez et al. 2017a), with potentially grave consequences especially for those seabird populations already in decline.

Tables

Table 4.1. Characteristics of each of the two sites where puffling decoys were deployed.

Characteristic	Convenience Store	Crab plant
Area (m^2)	5265	5396
Illumination Levels	(*N* locations)	(*N* locations)
Dark	15	15
Dim	9	1
Bright	6	14
Concealment Levels		
0	17	6
1	7	12
2	4	6
3	3	5
4[a]	0	1
Search effort	(search-min)	(search-min)
Median, nightly	44.5	99
Range, nightly	5, 115	42, 240
Total	676	1277
Omitted deployments[b]	10	9
Deployments used in analysis	110	111

[a]We omitted the location with concealment score of 4 from further analysis (see also [b], below)
[b]For descriptions of omitted deployments, see *Statistical Analysis*.

Table 4.2. Number of decoys deployed and found in each light level, along with calculated percentage of decoys found.

|	Dark	Dim	Bright	Total
Deployed	110	38	73	**221**
Found	73 (66%)	29 (76%)	61 (84%)	**163 (74%)**

Table 4.3. Total numbers of decoys deployed and found, along with calculated percentage of decoys found, according to each concealment level.

|	Concealment Level				Total
	0	**1**	**2**	**3**	
Deployed	80	76	36	29	**221**
Found	64 (80%)	54 (71%)	22 (61%)	23 (79%)	**163 (74%)**

Table 4.4. Results of a Cox proportional hazards model of decoy persistence based on light level, concealment level, and search effort as fixed effects, with data stratified by site. The hazard ratio ("HR") refers to the magnitude of change in detection rate from the reference level of each parameter (light level = dark; concealment = 0) to the parameter level indicated in column 1, whereby a hazard ratio >1 indicates an increase in detection rate from the reference value by a factor of HR-1 and a hazard ratio <1 indicates a decrease in detection rate from the reference value by a factor of 1-HR. HR = 1 or 95% confidence intervals overlapping with 1.00 would indicate no difference in detection rate.

Parameter (level)	Coefficient	Hazard Ratio (Exponentiated Coefficient)	Standard Error of Coefficient	*P*-value	95% Confidence Interval
Light Level (Dim)	0.326	1.386	0.236	0.167	0.873, 2.201
Light Level (Bright)	0.321	1.378	0.188	0.087	0.954, 1.991
Concealment (1)	-0.506	0.603	0.201	**0.012**	**0.406, 0.894**
Concealment (2)	-0.852	0.427	0.268	**0.001**	**0.253, 0.721**
Concealment (3)	-0.376	0.686	0.251	0.134	0.420, 1.122
Search Effort	0.006	1.006	0.002	**<0.001**	**1.003, 1.009**

Figures
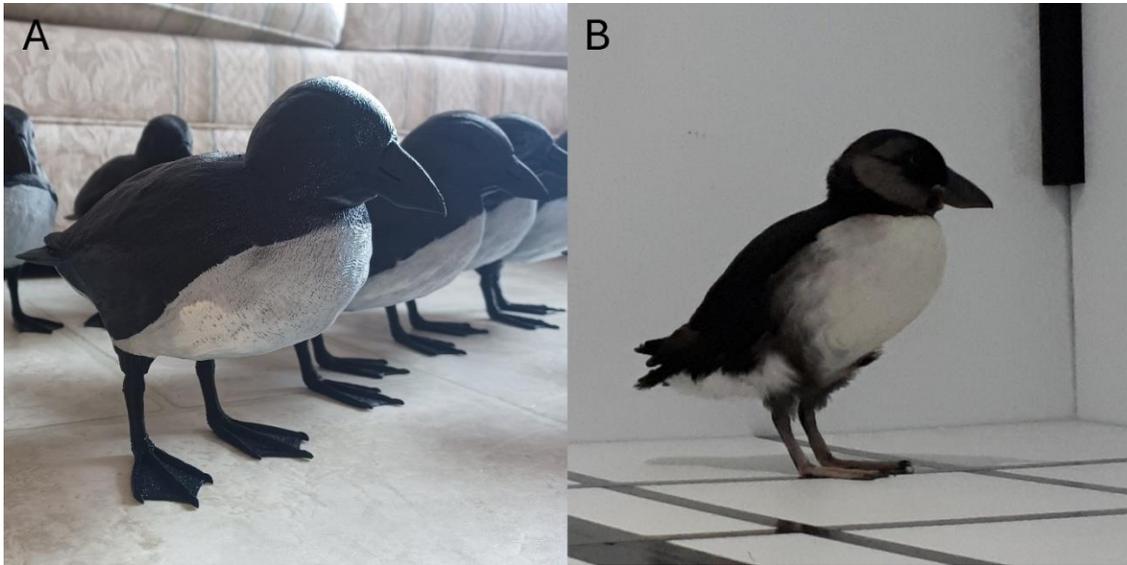
Figure 4.1. A) Several puffling decoys all assembled, painted, and ready to be deployed. B) A living puffling, used as a visual reference for the creation of puffling decoys.
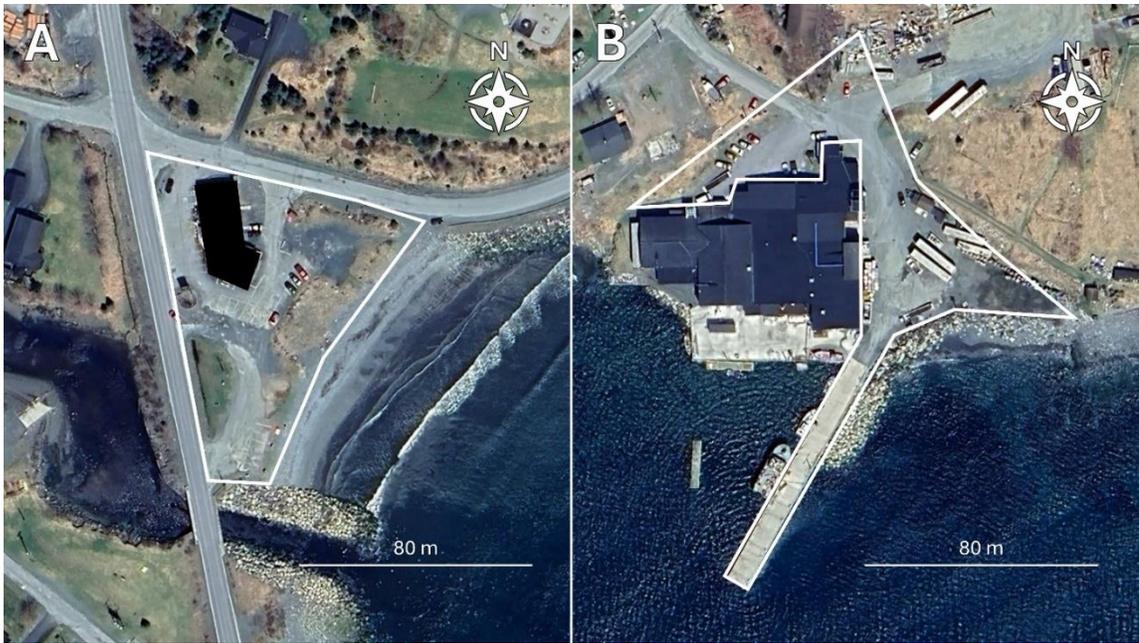
Figure 4.2. Satellite imagery (courtesy of Google Earth) of the two sites used in this experiment, with associated white perimeters demarcating the boundaries used for decoy deployment. A) Convenience store (note the black box, denoting the area of the building which was excluded from area calculations). B) Crab plant.

Figure 4.3. A) Example of a "dim" illuminated location with concealment score of 0 at the convenience store site. A puffling decoy is indicated by white arrow. B) Example of a "bright" location with concealment score of 1 (indicated by black arrow) at the crab plant site (note that a decoy is not present in picture).
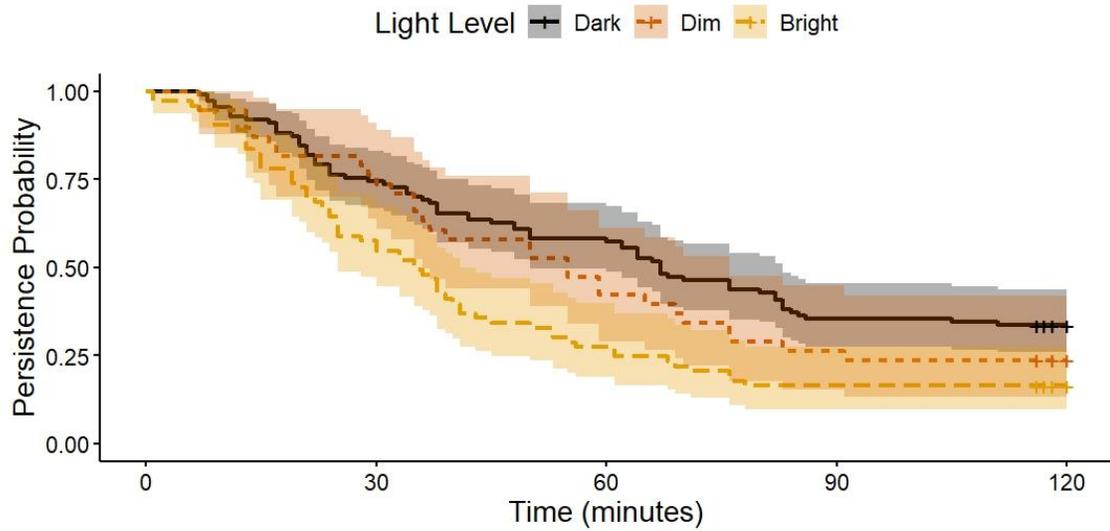
Figure 4.4. Light level persistence curves, depicting main effects for visualization purposes only. Persistence probability of decoys (as a proportion of 1.00) over the duration of the experiment (in minutes) deployed in three different light level conditions: darkness, dim illumination, and bright illumination. Persistence probability is the probability of decoys remaining undiscovered over time, whereby a high persistence probability indicates a low detection rate over time. Censored individuals are indicated on the figure by "+", which in these cases were deployed decoys that persisted the entire experiment, but the experiment duration was slightly less than 120 minutes ($N = 22$ occasions). Shaded areas represent 95% confidence intervals.
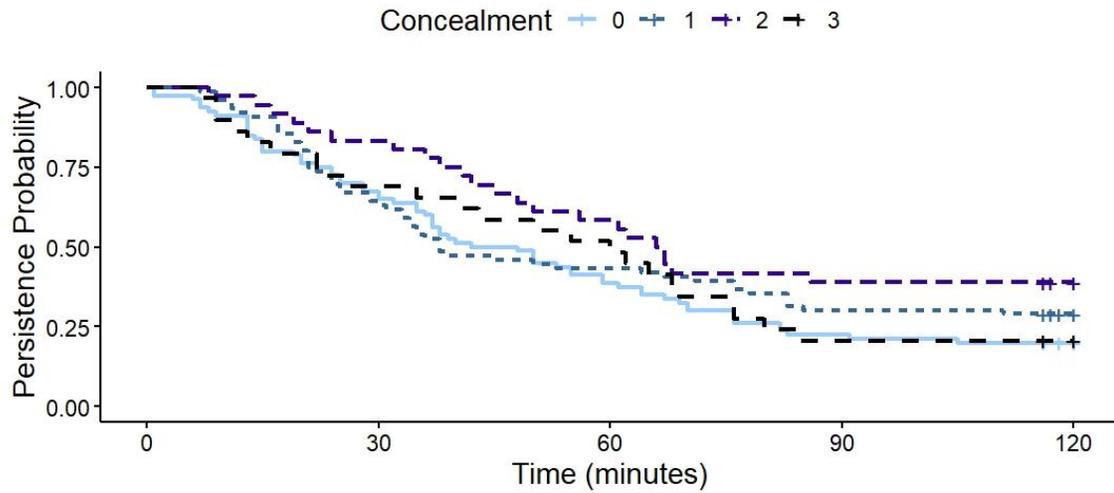
Figure 4.5. Concealment level persistence curves, depicting main effects for visualization purposes only. Persistence probability of decoys (as a proportion of 1.00) over the duration of the experiment (in minutes) deployed in four different concealment levels: completely unconcealed (score of 0), and concealed on one, two, and three sides. See Figure 4.4 for an explanation of persistence probability and details of censored individuals. Confidence intervals overlapped across concealment levels and were removed for readability.
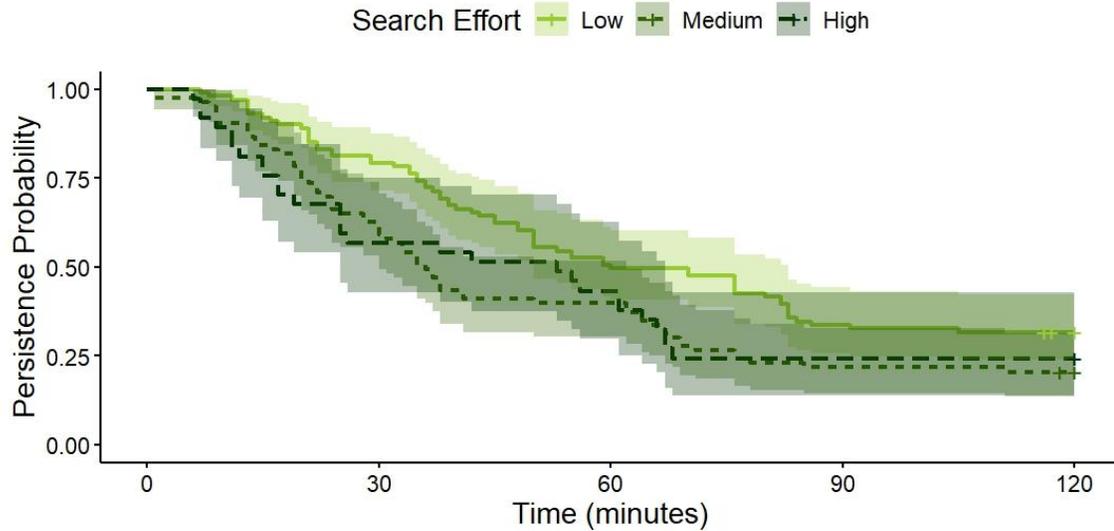
Figure 4.6. Search effort persistence curves, depicting main effects for visualization purposes only. Persistence probability of decoys (as a proportion of 1.00) over the duration of the experiment (in minutes) when exposed to different levels of search effort. Search effort was statistically analyzed as a continuous variable, but for visualization purposes we created three bins: low (≤60 search-minutes; $N = 101$), medium (61-120 search-minutes; $N = 83$), and high (≥121 minutes; $N = 37$) search effort. See Figure 4.4 for an explanation of persistence probability and details of censored individuals. Shaded areas represent 95% confidence intervals.
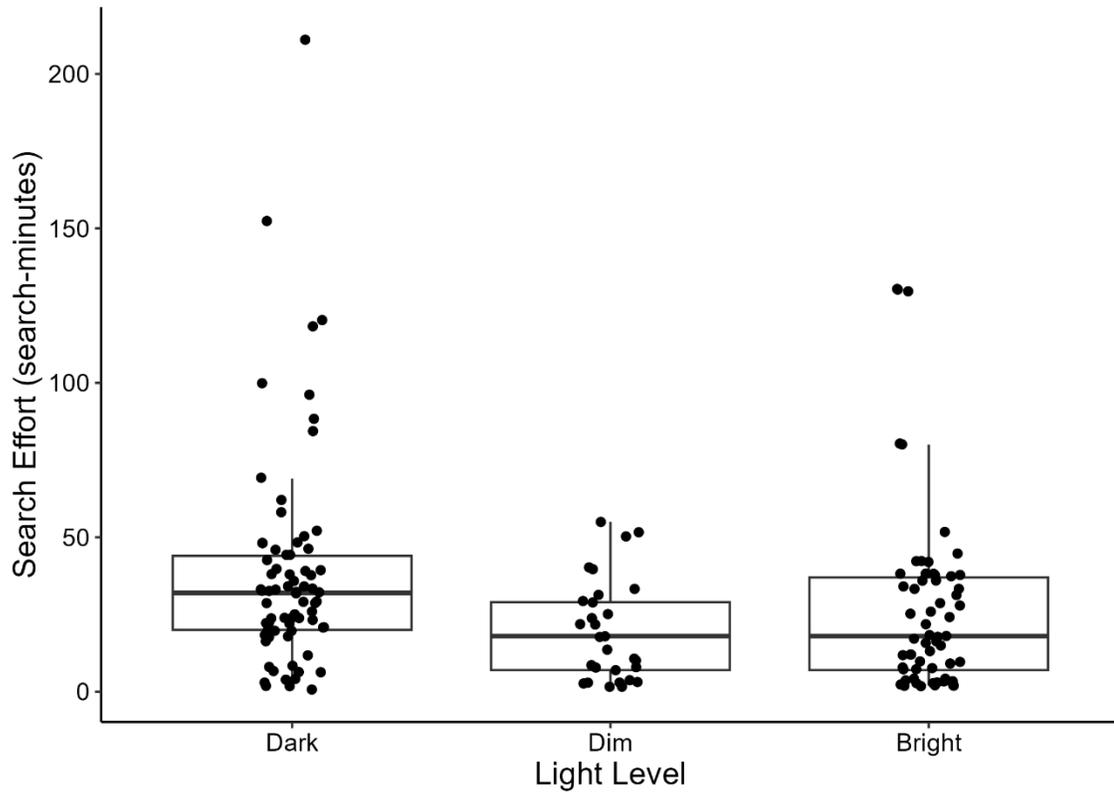
Figure 4.7. Amounts of search effort (in search-minutes) required to find each decoy (represented by individual data points) under each of three light levels (represented by one of three boxplots): dark (median = 32 search-minutes; $N = 73$), dim (median = 18 search-minutes; $N = 29$), and bright (median = 18 search-minutes; $N = 61$). Search effort required to find decoys in darkness was significantly higher than under dim or bright illumination; there was no difference between dim and bright.
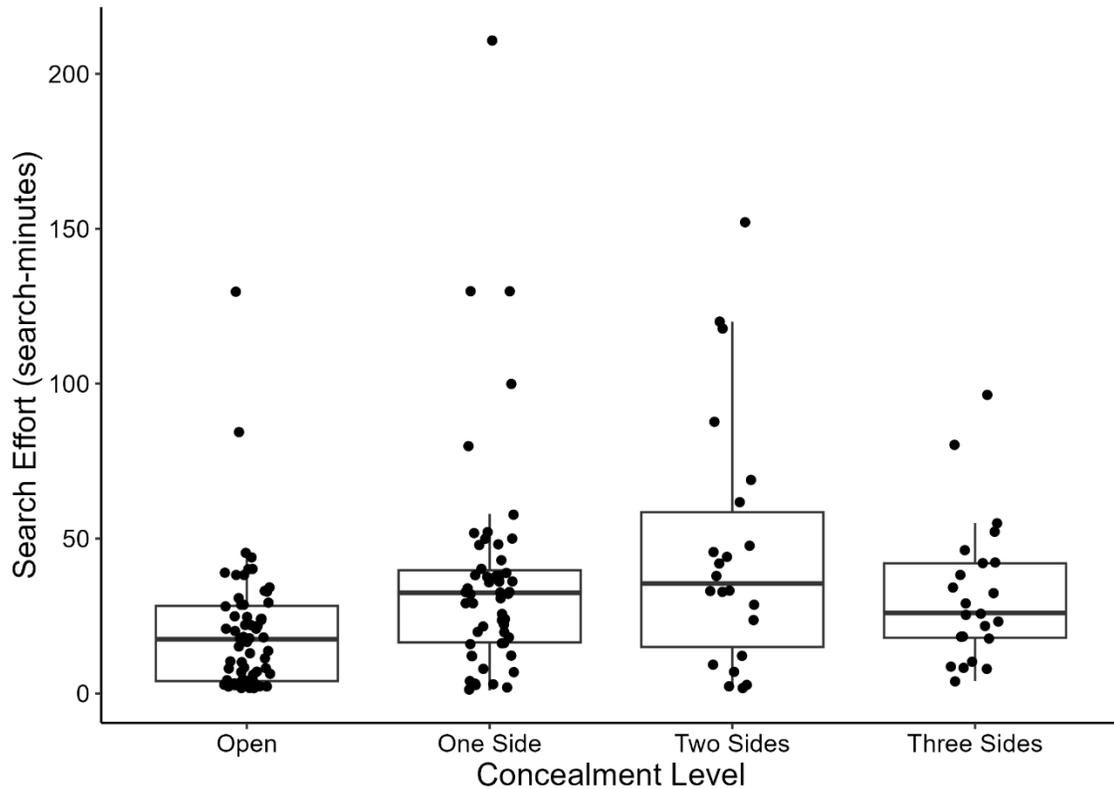
Figure 4.8. Amounts of search effort (in search-minutes) required to find each decoy (represented by individual data points) under each of four concealment levels (represented by one of four boxplots): those unconcealed in the open (median = 17.5 search-minutes; $N = 64$), concealed on one side (median = 32.5 search-minutes; $N = 54$), concealed on two sides (median = 35.5 search-minutes; $N = 22$), and concealed on three sides (median = 26 search-minutes; $N = 23$). Search effort required to find decoys was significantly less when decoys were placed in the open than when they were concealed on one, two, and three sides.
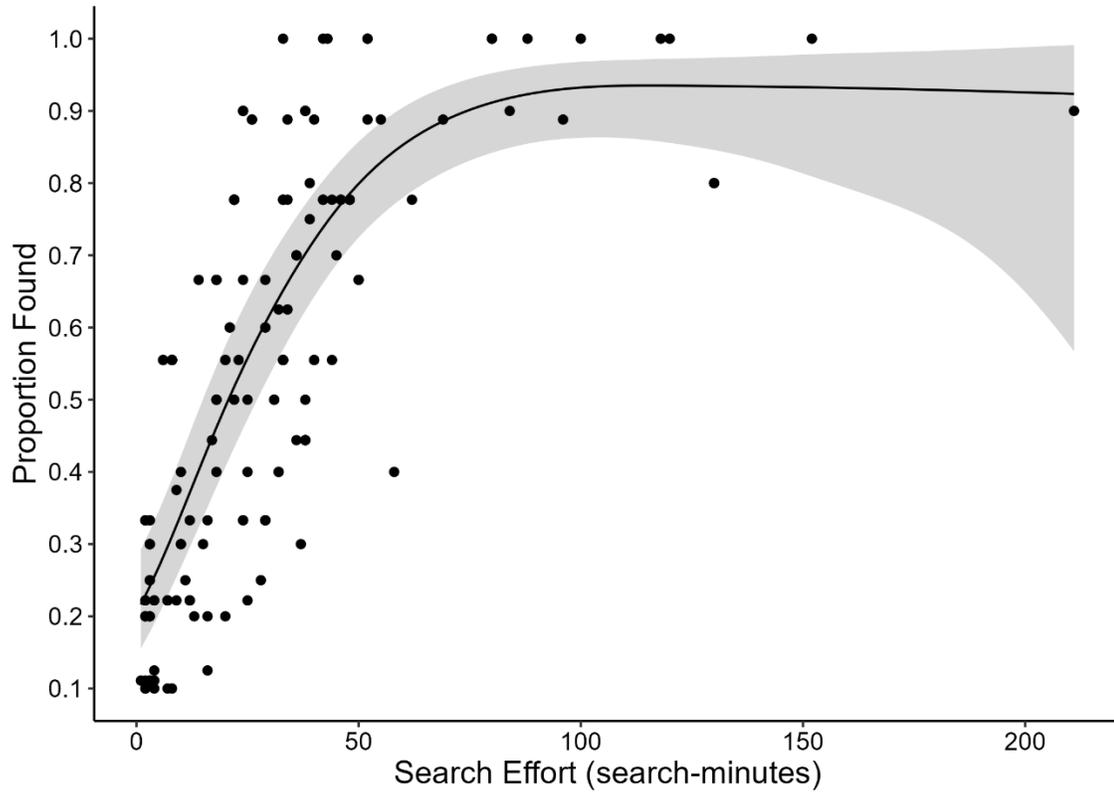
Figure 4.9. Increased search effort resulted in higher proportions of decoys found until approximately 75 minutes of search effort had been expended, at which point the slope levels off just above $y = 0.9$. Individual data points represent the cumulative proportion of decoys found (y) at a given site on a given night, with the expenditure of x search-minutes of search effort. Trendline depicts generalized additive mixed model of the relationship, with associated 95% confidence intervals (shaded areas).

Chapter 5

General Discussion

My research examined aspects of seabird and rescuer behaviour that contribute to patterns of fallout observed by rescue programs: namely, that more stranded seabird fledglings are found in illuminated compared to dark areas. Specifically, I investigated behavioural responses to artificial light by fledglings of two stranding-prone seabird species, Atlantic puffin and Leach's storm-petrel, with particular focus on quantifying phototactic behaviour both during (in puffins only) and after stranding (both species). I observed differences between the two species mainly in that puffin fledglings are largely photopositive, while storm-petrel fledglings appear to be mainly photonegative. Both species exhibited differences in activity levels among light types, but in nearly inverse patterns from each other, with implications for detectability by rescuers across varying artificial lightscapes. Lastly, I investigated factors that contribute to variation in detection probability of stranded puffins by rescuers using 3D-printed puffin decoys and found nuanced effects of illumination level, concealment level, and search effort. Collectively, these three studies highlight the various contributions of both seabird and rescuer behaviour to the patterns of fallout historically observed by rescue programs and offer avenues for further investigation and mitigation of ALAN-related strandings.

Chapter summaries

In Chapter 2, I examined effects of artificial light on Atlantic puffin fledgling behaviour by: 1) alternately illuminating two beaches near a breeding colony and quantifying the corresponding differences in fledgling stranding numbers between light

146

and dark treatments; 2) offering various two-choice combinations of different light types and darkness to stranded fledglings in a Y-maze and measuring phototactic behaviour; and 3) measuring activity levels of stranded fledglings in an open field test, when individuals were exposed to various types of artificial light. I found significantly more pufflings stranded on beaches when I experimentally illuminated them, compared to when they were dark, which supports the light attraction hypothesis to explain annual fledgling strandings. Further, pufflings were positively phototactic in the Y-maze choice experiment but displayed no significant preferences for any one light type over any other. In the open field test, individuals were highly active under high-pressure sodium light and in darkness, and less active under the two tested hues of LED light. Positive phototaxis exhibited by pufflings in the Y-maze is similar to that of other charadriiform chicks (Gaston et al. 1988), but opposite to the negative phototaxis of procellariiform fledglings (Atchoi et al. 2024; Brown et al. 2025, Chapter 3), in similar Y-maze cue preference experiments. Pufflings also appear to differ from procellariiforms in that the latter have demonstrated some level of preference for cool-hued over warm-hued light (Salamolard et al. 2001, as cited in Minatchy 2004; Rodríguez et al. 2017b; but contrary to Brown et al. 2025, Chapter 3) whereas we found no preferences among light spectra in puffins. Taken together, my results suggest that pufflings become stranded due to light attraction, and that after stranding they continue to exhibit positive phototaxis. Differences I observed in activity levels under different light types may hold implications for detection probability by rescuers, whereby more mobile pufflings (e.g., under high-pressure sodium streetlights) might be detected more easily than less mobile ones (e.g., under LED streetlights), all else being equal.

In Chapter 3, I examined effects of artificial light on the behaviour of a procellariiform seabird impacted by ALAN-induced grounding: the Leach's storm-petrel. I began by replicating my Y-maze choice experiment and open field test using stranded fledglings of this species to measure their phototactic behaviour and activity levels in response to several different artificial light spectra. I also placed storm-petrel fledglings in a modified version of the open field test with a Safe Haven hide box provided, to quantify differences in their propensity to conceal themselves in light versus dark conditions.

In the Y-maze, most storm-petrel fledglings remained in the darker portions of the apparatus where they were initially placed, rather than move toward any of the provided light types or even toward darkness; there were thus no significant preferences among the light spectra tested. Fledglings were significantly more active when exposed to warm white LED light and high-pressure sodium light than when exposed to darkness, which we hypothesized was the result of negative phototaxis and possibly an instinct to escape the illuminated area, especially in response to warm-hued light. This hypothesis was supported when we found that more than half of tested individuals concealed themselves in the provided Safe Haven box under LED light, but none of the same birds did so in darkness. The predominant behaviour of Leach's storm-petrel fledglings to remain in the darker portions of the Y-maze, combined with low activity in dark conditions and a propensity to conceal themselves rather than remain in the open field under light conditions, all point to an aversion to artificial light in this species after becoming stranded. Up to now, negative phototaxis has been anecdotally reported in grounded Leach's storm-petrels and other procellariiforms (Reed et al. 1985; Rodríguez et

al. 2017a; Atchoi et al. 2024; Burt et al. 2024), but my results provide the first experimental confirmation of the behaviour under tightly controlled conditions. Previous work has demonstrated that more procellariiform fledglings become stranded when artificial illumination is more intense (Rodríguez et al. 2014; Burt et al. 2024); my findings further suggest that procellariiform rescuers should ensure that dark and concealed locations within illuminated stranding hotspots are adequately searched, in order to maximize recoveries.

In Chapter 4, I explored various factors that may influence the detection probability of Atlantic puffin fledglings by Puffin Patrol rescuers. I did so by deploying 3D-printed puffin decoys in locations of varying concealment and light levels throughout two "hotspot" stranding locations that were searched nightly, and by quantifying both the amount of time that elapsed and the amount of search effort that was expended until each decoy was found.

Greater search effort resulted in higher decoy detection rates, and approximately 75 minutes of collective search effort was needed to detect approximately 90% of the deployed decoys. Significantly more decoys were detected in illuminated conditions compared to darkness, and median search effort required to find a decoy in darkness was almost double that required to find a decoy in either dim or bright light. However, detection rate of decoys over time did not differ among the three light levels, likely because they were detected at similar rates at the beginning of the experiment (perhaps as all the decoys placed in the open – both light and dark – were found first; see below). There were no significant differences among concealment levels in the proportion of decoys found. However, detection rate over time differed between decoys placed in the

149

open and those concealed on one or two sides (but not 3 sides, Table 4.4), and median

search effort to find a decoy concealed on any number of sides (1-3) was significantly

higher than to find one placed in the open (Figure 4.8). Together, these results suggest

that Participants may have searched in open and highly concealed (concealment

level = 3) areas before searching in areas of low and intermediate concealment

(concealment level = 1 and 2, respectively), but more research that includes

spatiotemporal tracking of search effort would be needed to confirm this.

Overall, my results indicate that Puffin Patrol rescuers, who are mostly naïve to

the practice of nocturnal seabird detection and rescue, are relatively effective in the

detection of stranded puffin fledglings, which are expected to stay in or move toward

illuminated locations after stranding (Brown et al. 2024, Chapter 2). However, rescuers

may be slightly less effective in finding stranded seabirds that preferentially stay in or

move toward dark and/or intermediately concealed locations after stranding, as many

procellariiform fledglings do (Reed et al. 1985; Rodríguez et al. 2017a; Atchoi et

al. 2024; Burt et al. 2024; Brown et al. 2025, Chapter 3). Based on my results, I suggest

at least 10% of puffin fledglings remain undetected by Puffin Patrol rescuers at hotspot

stranding locations, with probably a higher proportion that remain undetected outside of

hotspots, which are searched less intensely. Additional study of post-stranding behaviour,

rescuer search patterns, carcass detection probability, and carcass removal rates (as in

e.g., Podolsky et al. 1998; Santos et al. 2016; Barrientos et al. 2018) will be essential to

develop a more accurate estimate of the number of undetected fledglings, which may then

be used to estimate population-level impacts of ALAN-induced seabird fallout.

Synthesis

Prior to my research, relatively little was known about post-stranding seabird behaviour and its implications for rescue programs. There was also much that remained unknown regarding the exact environmental and anthropogenic predictors of ALAN-induced seabird fallout and why, for example, stranding appears to be most prevalent in fledglings specifically of burrow-nesting procellariiforms and charadriiforms. Concurrent with my research (beginning in 2019) and the publication of three chapters of this thesis (Chapter 1 published in 2023, Chapter 2 in 2024, and Chapter 3 in 2025), research on seabird fallout accelerated and diversified rapidly and continues to do so. As such, to better contextualize the contributions of my thesis and its overall place in the literature, the following synthesis is presented approximately chronologically.

As far back as the first anecdotal literature report of a procellariiform becoming grounded on a ship (Ridgway 1885), and even decades later with the first reports of large numbers of individuals becoming grounded in artificially illuminated areas on land (Hadley 1961, as cited in Reed et al. 1985; Swales 1965; Sincock and Swedberg 1969; Imber 1975 and citations therein), procellariiform strandings were assumed to be caused by artificial light via a mechanism of attraction. This assumption existed despite a complete absence at the time of experimental tests of the light attraction hypothesis. In the 1980s, the effect of the illuminated moon to decrease fallout numbers was confirmed, as was the effectiveness of shielding lights, lending evidence to the light attraction hypothesis (Reed et al. 1985; Telfer et al. 1987). However, it was unclear whether the lunar effect observed was primarily to suppress fledging itself or to suppress attraction

toward artificial light after fledging (Reed et al. 1985). Further, Reed et al. (1985) made the surprising observation that stranded fledglings seek out dark hiding places after stranding in an apparent behavioural switch from light attraction. Around the same time that these effects of variation in moonlight and artificial light shielding were quantified in procellariiform fallout on Hawai'i (Reed et al. 1985; Telfer et al. 1987), the first report of charadriiform (Atlantic puffin) strandings was published from Europe, again with light attraction as the presumed cause (Harris 1982). A potential role of noise attraction was also suggested in this instance but was never investigated. The first-ever cue preference test that evaluated behavioural responses to artificial light in a seabird was also conducted in the 1980s and found that ancient murrelet chicks preferentially oriented to light over darkness (Gaston et al. 1988). This study was prescient as it suggested that juveniles of at least one alcid species display positive phototaxis during "fledging" (the chicks of this species go to sea at night only a couple days after hatching).

The first of many volunteer-based seabird rescue programs was implemented in 1978 for downed Newell's shearwater fledglings in Hawai'i (Telfer et al. 1987), and models later showed that without such rescue interventions, mortality from ALAN-induced grounding likely would have contributed to significant declines in this population (Ainley et al. 2001). Salamolard et al. (2001, as cited in Minatchy 2004) claimed in a non-publicly available report that experiments with Barau's petrels revealed a greater attraction toward blue-rich compared to yellow- or red-rich light, while Hart's (2004) characterization of ocular spectral sensitivities in another species of stranding-prone procellariiform (the wedge-tailed shearwater) revealed a potential mechanism for this in the form of increased sensitivity to short, blue-violet wavelengths.

152

In the 2010s, the global negative ecological effects of ALAN on ecosystems were becoming more widely recognized and research efforts on the subject were increasing (Gaston et al. 2012; Gaston et al. 2013; Pawson and Bader 2014; Davies and Smyth 2018). Experimental studies during this decade demonstrated that fallout numbers of some seabird species could be reduced by large-scale reductions to light emissions (despite constraints on experimental design; Miles et al. 2010) or by changing the type of light used, with the greatest reductions seemingly obtained by changing from blue-rich (e.g., metal halide) to orange-rich (e.g., high-pressure sodium) lights (although this study did not employ a "dark" control; Rodríguez et al. 2017b). At this time, practitioners also tracked fledglings' first flights from the nest with GPS data-loggers and mapped their fallout locations relative to artificial light emittance (Rodríguez et al. 2015). Others focused on quantifying the effects of factors besides light on stranding numbers and found clear effects of wind and varying effects of fog (Wilhelm et al. 2013; Syposz et al. 2018). Still others investigated ocular development in fledglings of one affected procellariiform and found that it was not nearly so advanced upon fledging as the olfactory system (Mitkus et al. 2018). Indeed, olfaction was found to be a key component of navigation and foraging in many procellariiforms (Nevitt 2008; Dell'Ariccia and Bonadonna 2013; Gagliardo et al. 2013). In 2017, Rodríguez et al.(a) published a review on ALAN-induced seabird fallout in which they summarized the species affected, the locations at which strandings occur, the estimated proportions of fledgling cohorts affected and mortality rates of stranded birds. Further, the authors summarized evidence for ALAN-induced attraction and disorientation (both were discussed as co-occurring to cause fallout) and proposed future directions of research including better quantification of

the number of stranded fledglings that remain undiscovered by rescuers. This is approximately where the literature stood when I began my PhD in 2019.

It is important to note that the above discussion is not meant to be an exhaustive account of all the developments in seabird stranding research; numerous researchers not mentioned also contributed in various ways to the immense growth in our collective understanding of seabird strandings over the last several decades. However, in general, I have described the main sequence of findings that led to the early conceptualization of my dissertation. Initially, I sought to conduct a meta-analysis of the importance of factors in addition to ALAN that may contribute to seabird strandings. However, I soon discovered there were relatively few empirical, experimental, systematically-collected data to work with. For example, most locational fallout data had been collected opportunistically by volunteers; there had as yet been no fully controlled experimental tests of the light attraction hypothesis itself; other potential hypotheses for stranding were as yet untested; stranding-prone charadriiforms (namely Atlantic puffins) were little studied in their behavioural responses to artificial light; adults of the various affected species were understudied in the reason(s) why they generally become stranded in smaller numbers than fledglings (Rodríguez et al. 2017a; but see Rodríguez and Rodríguez 2009); evidence for a difference in the attractive potential of different light types remained equivocal; and environmental effects on stranding rates had only been studied in few cases (excepting moon phase/illumination), with mixed results (Wilhelm et al. 2013; Rodríguez et al. 2014; Syposz et al. 2018).

I therefore sought to build upon the work of Rodríguez et al. (2017a) and to encourage a diversification of research efforts within the field to directly address some of

the above issues by publishing Chapter 1 as a review paper in 2023. Therein, I proposed

direct experimental tests of the light attraction hypothesis through the controlled (and

ideally randomized) use of light and dark treatments and measurement of resulting fallout

(proposed in Brown et al. 2023, Chapter 1; addressed in Brown et al. 2024, Chapter 2). I

also suggested that, given the generally small proportions of the fledgling cohort that

appear to be affected by fallout in most species (Rodríguez et al. 2017a), individual

fledglings may be randomly dispersing from their colonies and only become attracted or

disoriented by ALAN at close range (proposed in Brown et al. 2023, Chapter 1). And

lastly, I proposed some ways in which the research could go forward: for example, by

conducting systematic searches for stranded birds with substantially reduced spatial and

temporal biases in search effort; by testing alternative hypotheses for stranding

(e.g., olfactory attraction, noise attraction, magnetoreceptive disruption); by further

studying the species and demographics (e.g., adults) that are not as susceptible to fallout;

by confirming the effects (and ideally also the mechanisms of the effects) of

environmental factors on stranding, including whether moon phase influences stranding

rates by way of influencing fledging rates; and by testing behavioural responses to

artificial light in stranding-prone species *ex situ*, for example in cue preference tests or

other closed experimental apparatuses (proposed in Brown et al. 2023, Chapter 1;

addressed in Brown et al. 2024, 2025, Chapters 2 and 3).

Directly in response to my published review (Brown et al. 2023, Chapter 1), in

which I suggested that greater lunar illumination may reduce stranding numbers by

suppressing fledging, Rodríguez et al. (2023) demonstrated using a long-term dataset that

the effect of increased moonlight on fallout rates actually appears to be in reducing the

attractive or disorienting effect of ALAN on fledgling seabirds. Further confirmation of this effect was found and published by Collins et al. (2023), who tracked fledging dates of stranding-prone Leach's storm-petrels using radio frequency identification (RFID) and found that they fledged throughout the lunar cycle. My review (Brown et al. 2023, Chapter 1) has also been cited by several other works, including those which measured the effect on the behaviour of procellariiform chicks of repeated exposure to artificial light (Atchoi et al. 2023), and preferential phototaxis toward different light colours by both fledgling and adult procellariiforms of the same species (Atchoi et al. 2024), in closed experimental apparatuses. Directly in line with my review's recommendation to further study adult procellariiform behaviour toward artificial light (Brown et al. 2023, Chapter 1), Middlemiss et al. (2025) shone various intensities and colours of lights in a fairy prion colony during the breeding season and offered confirmation on previous reports of differences in behavioural responses toward different light types (Salamolard et al. 2001, as cited in Minatchy 2004; Rodríguez et al. 2017b).

My experiments on the behavioural responses of Atlantic puffin fledglings to artificial light at two different spatial scales (Brown et al. 2024, Chapter 2) included one of the first and few direct *in situ* tests of the light attraction hypothesis (i.e., by systematically testing for effects of light versus darkness on fallout numbers) in any stranding-prone seabird (after Burt et al. 2024; and after the more logistically-constrained experiment by Miles et al. 2010). My *ex situ* cue preference test using a Y-maze was the second to be conducted in a charadriiform (after Gaston et al. 1988) and the second conducted in any stranding-prone species (after Atchoi et al. 2024). Lastly, my open field test, which quantified activity levels of stranded puffin fledglings across light spectra and

darkness, was the first of its kind to be conducted with any seabird species. My results (Brown et al. 2024, Chapter 2) have the potential to affect coastal development policy in any region affected by puffin strandings. Simply, I demonstrated that eliminating or reducing ALAN wherever possible remains the only evidence-based strategy to reduce strandings. These results may also be used by puffin rescue programs to improve the efficiency of their search strategies.

Results from my experiments on stranded Leach's storm-petrel fledglings also have the potential to influence future research and policy in locations where this and other procellariiforms become grounded. In agreement with observations of Reed et al. (1985) and experimental results of Atchoi et al. (2023, 2024), I found evidence for photophobia in grounded procellariiform fledglings (Brown et al. 2025, Chapter 3). Evidence for photophobia allowed me to test and confirm the utility of a novel mitigation measure against stranding-induced mortality: that of hide boxes (repurposed rodent bait stations; Brown et al. 2025, Chapter 3), which storm-petrels were already anecdotally observed to use as shelters at hotspot stranding sites (Burt et al. 2024). If hide boxes were to be employed at all the major procellariiform stranding hotspots around the world, especially where endangered and declining species are affected, there is potential to dramatically increase survival after stranding by reducing predation rates of grounded birds.

Rodríguez et al. (2017a) called for better estimates of the number of stranded seabirds that remain undiscovered by rescue groups, which would then help inform estimates of total stranding-related mortality and its overall effect on populations. In my review (Brown et al. 2023, Chapter 1) I further suggested that the probability of rescuers

detecting stranded seabirds is likely higher in illuminated compared to dark locations. In Chapter 4, I used 3D-printed decoys to quantify relative variation in detection probability of Atlantic puffin fledglings by rescuers across light and concealment levels at two puffin stranding hotspots. Although this chapter has not yet been published, to my knowledge it was the first-ever study to measure detection probability of any bird species using decoys. My results demonstrate that there are indeed negative impacts on detection probability of lower light levels and intermediate concealment levels (Chapter 4). My results also allow conservation practitioners to estimate a crude rate of at minimum 10% of individuals that remain undiscovered by seabird rescue programs that operate in similar contexts (Chapter 4).

Research on seabird fallout continues to develop at a rapid pace and to diversify into topics highlighted in my review, which was exactly the goal of its publication (Brown et al. 2023, Chapter 1). Many research projects aimed at disentangling and quantifying various environmental and anthropogenic effects on fallout rates, as well as studies that further investigate behavioural responses to light and other stimuli across species and demographics, are currently in progress. For example, I suggested olfactory attraction should be considered a valid and testable alternative hypothesis to light attraction in causing strandings (Brown et al. 2023, Chapter 1). Results of a recent, as yet unpublished experiment by Burt et al. suggest avoidance of light and ambivalence toward scent (i.e., no evidence of olfactory attraction) in adult Leach's storm-petrels at their colony on Gull Island, Newfoundland (T. Burt, unpubl. data). At a separate colony (Outer Island, Nova Scotia), experimental evidence suggests that adults and possibly juveniles of this species are susceptible to collisions with illuminated vertical surfaces, and that white

vertical surfaces induce higher collision rates than black ones (Rutherford 2025). In my

review I also called for additional experimentation testing for light attraction behaviour

which employs (fully) dark controls (Brown et al. 2023, Chapter 1), which were absent

from previous studies (Reed et al. 1985; Miles et al. 2010; Rodríguez et al. 2017b). A

study currently in progress, which directly tests the light attraction hypothesis with proper

dark controls, has found higher collision rates of adult and fledgling Leach's storm-

petrels with a boat as it passed by Baccalieu Island with its lights on, compared to when

they were off (P. Doiron, unpubl. data; Elliot 2025). Evidently, in the few years since I

began my PhD, our collective knowledge base of seabird behavioural responses to light

has grown substantially, and research efforts continue to home in on understanding those

more nuanced aspects of fallout that will hopefully allow for targeted mitigation efforts in

the near future.

Future directions

In spite of all the aforementioned recent developments in research on seabird

fallout, there remain several areas that deserve further attention, many of them

highlighted already by Rodríguez et al. (2017a), Rodríguez et al. (2019), Brown et

al. (2023, Chapter 1), and throughout Chapters 2-4. Firstly, there have been few attempts

to either quantify or reduce bias in search effort of opportunistic seabird rescue programs.

Friswold et al. (2020) conducted surveys along a defined transect that varied in streetlight

density using standardized methodology to quantify spatial patterns in procellariiform

fallout across several years. The authors found the highest number of stranded individuals

in an area that was only of intermediate streetlight density, but which was relatively close

to the largest local colony. Such efforts are much more valuable to understanding actual seabird fallout patterns than opportunistic rescue data. Predation and carcass persistence rates of stranded seabirds are also largely unknown but, in combination, further quantifications thereof would represent significant progress in attempts to quantify the number of seabirds that remain undetected by rescuers. The estimated numbers of seabirds that remain undetected by rescuers may then be used to develop correction factors applied to opportunistically-collected rescue data to more accurately estimate total fallout. Detection probability likely varies significantly among species (e.g., dependent on body size, colouration, behaviour) and locations (e.g., dependent on the geographic extent of fallout, presence of obstructions to search efforts), and none of this variation has yet been quantified for any stranding-prone species.

In situ experiments testing the light attraction hypothesis using controlled light and dark treatments and standardized search effort in a defined area (as in my illuminated beach experiment; Chapter 2) are imperative in confirming the effect of light on seabird stranding behaviour. However, a logical next extension of this line of investigation would be to continue measuring fallout *in situ* in response to different light types and hues, as did Rodríguez et al. (2017b) with short-tailed shearwaters. Theirs has been the only *in situ* experimental test of the effect of light type on fallout but because their tested lights varied in emittance, this should be controlled for in future experiments. Such experiments should target species representative of the various taxonomic families affected by stranding (e.g., shearwaters and petrels *Procellariidae*, northern storm-petrels *Hydrobatidae*, and puffins *Alcidae*), since perception and interpretation of light likely differ across taxa to some extent.

Lastly, it is obvious that artificial light at night is here to stay and will only continue to increase in emittance, necessitating creative solutions to mitigate seabird fallout and its resultant mortality whenever or wherever ALAN cannot be fully eliminated. In Chapter 2, I suggested that designated safe (i.e., predator-free) illuminated areas with dedicated rescuers be employed near towns affected by puffin strandings and tested in their capacity to lure wayward puffins away from the more dangerous potential stranding locations (e.g., roads, parking lots, yards, industrial sites). This strategy is not likely to work for procellariiforms, however, due to their propensity to become stranded in locations sometimes quite distant from their natal colonies. For this reason, in Chapter 3, I proposed the more widespread development and testing of hide boxes in their capacity to effectively reduce predation rates of downed procellariiforms at stranding hotspots. Given the positive phototaxis displayed by Atlantic puffins after stranding (Chapter 2), these hide boxes could also potentially be adapted for use by this species with the installation of internal lighting that lures individuals inside and thereby increases usage rates. Going forward in this ever-brightening world, practitioners intimately familiar with the ecological, anthropogenic, and biological/behavioural contexts in which strandings of other seabird species occur will need to continue to think creatively about how fallout can be mitigated or mortality reduced, potentially by harnessing what we already know about the affected species' responses to various stimuli including light, noise, and intraspecific social cues.

Conclusion

There were several key findings of my PhD research that advance our understanding of seabird behavioural responses to light and the resulting implications for rescue programs. First, I experimentally confirmed that Atlantic puffin fledglings come to land in much larger numbers in response to light versus dark conditions, supporting the light attraction hypothesis for stranding in this species. Second, I found interspecific differences in post-stranding behaviour between Atlantic puffin and Leach's storm-petrel fledglings that have implications for where they would be expected to go and how they would be expected to behave following stranding *in situ*. For example, I expect puffin fledglings would remain in or move toward illuminated areas and would be more active (and therefore possibly easier to detect) under high-pressure sodium compared to light-emitting diode streetlights, in comparison to Leach's storm-petrel fledglings which I expect would stay in or move toward dark and concealed areas. Lastly, I discovered that volunteer seabird rescuers were more skilled at finding puffin decoys in illuminated and open locations, as well as in highly concealed locations, compared to dark or intermediately concealed locations. When these findings are considered in the context of real puffin fledglings' post-stranding behaviour, I expect that rescuers are reasonably efficient at finding living puffins, but detection probabilities of living stranded birds have yet to be quantified in any species. In contrast, considering storm-petrels' small size and propensity to stay in or move toward dark and concealed locations after stranding, my detection probability experiment suggests that rescuers would be somewhat less skilled in finding living storm-petrels; again, this needs to be confirmed experimentally. Considered together, my results provide considerable insight into behavioural responses

162

toward artificial light of seabirds both during and after stranding, as well as implications thereof for rescue programs.

References

Aguado-Giménez, F., Sallent-Sánchez, A., Eguía-Martínez, S., Martínez-Ródenas, J., Hernández-Llorente, M. D., Palanca-Maresca, C., Molina-Pardo, J. L., López-Pastor, B., García-Castellanos, F. A., Ballester-Moltó, M., Ballesteros-Pelegrín, G., García-García, B., and Barberá, G. G. (2016). Aggregation of European storm-petrel (*Hydrobates pelagicus ssp. melitensis*) around cage fish farms. Do they benefit from the farms' resources? *Marine Environmental Research* **122**, 46-58.

Ainley, D. G., Podolsky, R., Deforest, L., Spencer, G., and Nur, N. (2001). The status and population trends of the Newell's shearwater on Kaua'i: insights from modeling. *Studies in Avian Biology* **22**, 108-123.

American Meteorological Society (AMS). (2025). Glossary of Meteorology: "civil twilight". Available from https://glossary.ametsoc.org/wiki/Civil_twilight

Atchoi, E., Mitkus, M., and Rodríguez, A. (2020). Is seabird light-induced mortality explained by the visual system development? *Conservation Science and Practice* **2**, e195. https://doi.org/10.1111/csp2.195

Atchoi, E., Mitkus, M., Vitta, P., Machado, B., Rocha, M., Juliano, M., Bried, J., and Rodríguez, A. (2023). Ontogenetic exposure to light influences seabird vulnerability to light pollution. *Journal of Experimental Biology* **226**, jeb245126. https://doi.org/10.1242/jeb.245126

Atchoi, E., Mitkus, M., Machado, B., Medeiros, V., Garcia, S., Juliano, M., Bried, J., and Rodríguez, A. (2024). Do seabirds dream of artificial lights? Understanding light preferences of Procellariiformes. *Journal of Experimental Biology* **227**, jeb247665. https://doi.org/10.1242/jeb.247665

Austad, M., Oppel, S., Crymble, J., Greetham, H. R., Sahin, D., Lago, P., Metzger, B. J., and Quillfeldt, P. (2023). The effects of temporally distinct light pollution from ships on nocturnal colony attendance in a threatened seabird. *Journal of Ornithology* **164**, 527-536. https://doi.org/10.1007/s10336-023-02045-z

Baden, T., and Osorio, D. (2019). The retinal basis of vertebrate color vision. *Annual Review of Vision Science* **5**, 177-200. https://doi.org/10.1146/annurev-vision-091718-014926

Barrientos, R., Martins, R. C., Ascensão, F., D'Amico, M., Moreira, F., and Borda-de-Água, L. (2018). A review of searcher efficiency and carcass persistence in infrastructure-driven mortality assessment studies. *Biological Conservation* **222**, 146-153. https://doi.org/10.1016/j.biocon.2018.04.014

Bertram, D. F., Cowen, L., and Burger, A. E. (1999). Use of radar for monitoring colonial burrow-nesting seabirds. *Journal of Field Ornithology* **70**, 145-157.

Black, A. (2005). Light induced seabird mortality on vessels operating in the Southern Ocean: incidents and mitigation measures. *Antarctic Science* **17**, 67-68. https://doi.org/10.1017/S0954102005002439

Bonadonna, F., Caro, S., Jouventin, P., and Nevitt, G. A. (2006). Evidence that blue petrel, *Halobaena caerulea*, fledglings can detect and orient to dimethyl sulfide. *Journal of Experimental Biology* **209**, 2165-2169.

Borsa, P., Mareschal, J., and Chartendrault, V. (2024). Light-induced petrel groundings in New Caledonia. *Zoological Studies* **63**, 59.

Bourgeois, K., Vidai, E., Comor, V., Legrand, J., and Dromzee, S. (2008). Colony-site selection drives management priorities for Yelkouan shearwater populations. *Journal of Wildlife Management* **72**, 1188-1193.

Bowmaker, J. K., Heath, L. A., Wilkie, S. A., and Hunt, D. M. (1997). Visual pigments and oil droplets from six classes of photoreceptor in the retinas of birds. *Vision Research* **37**, 2183-2194. https://doi.org/10.1016/S0042-6989(97)00026-6

Bretagnolle, V. (1996). Acoustic communication in a group of nonpasserine birds, the petrels. In: Ecology and evolution of acoustic communication in birds. Cornell University Press, Ithaca, New York, pp 160-178.

Brooke, M. de L. (1989). Determination of the absolute visual threshold of a nocturnal seabird, the Common Diving Petrel *Pelecanoides urinatrix*. *Ibis* **131**, 290-300.

Brown, T. M., Wilhelm, S. I., Mastromonaco, G. F., and Burness, G. (2023). A path forward in the investigation of seabird strandings attributed to light attraction. *Conservation Science and Practice* **5**, e12852. https://doi.org/10.1111/csp2.12852

Brown, T. M., Wilhelm, S. I., Slepkov, A. D., Baker, K., Mastromonaco, G. F., and Burness, G. (2024). Navigating the night: effects of artificial light on the behaviour of Atlantic Puffin fledglings. *Animal Behaviour* **218**, 135-148. https://doi.org/10.1016/j.anbehav.2024.09.008

Brown, T. M., Baker, K., Wilhelm, S. I., and Burness, G. (2025). Under cover of darkness: refuge from artificial light at night may mitigate risks to stranded seabirds. *Ornithological Applications* **duaf018**. https://doi.org/10.1093/ornithapp/duaf018

Burke, C. M., Montevecchi, W. A., and Wiese, F. K. (2012). Inadequate environmental monitoring around offshore oil and gas platforms on the Grand Bank of Eastern Canada: are risks to marine birds known? *Journal of Environmental Management* **104**, 121-126. https://doi.org/10.1016/j.jenvman.2012.02.012

Burt, T. V., Collins, S. M., and Montevecchi, W. A. (2023). Social media reports inform the spatio-temporal distribution of Leach's storm-petrel strandings across the island of Newfoundland. *Northeastern Naturalist* **30**, 151-160. https://doi.org/10.1656/045.030.0204

Burt, T. V., Collins, S. M., Green, S., Doiron, P. B., Wilhelm, S. I., and Montevecchi, W. A. (2024). Reduction of coastal lighting decreases seabird strandings. *PLoS ONE* **19**, e0295098. https://doi.org/10.1371/journal.pone.0295098

Byrd, G. V., Sincock, J. L., Telfer, T. C., Moriarty, D. I., and Brady, B. G. (1984). A cross-fostering experiment with Newell's race of Manx shearwater. *Journal of Wildlife Management* **48**,163-168.

Campbell, D. L. M., Dickson, E. J., and Lee, C. (2019). Application of open field, tonic immobility, and attention bias tests to hens with different ranging patterns. *PeerJ* **7**, e8122. http://doi.org/10.7717/peerj.8122

Chevillon, L., Tourmetz, J., Dubos, J., Soulaimana-Mattoir, Y., Hollinger, C., Pinet, P., Couzi, F.-X., Riethmuller, M., and Le Corre, M. (2022). 25 years of light-induced petrel groundings in Reunion Island: retrospective analysis and predicted trends. *Global Ecology and Conservation* **38**, e02232. https://doi.org/10.1016/j.gecco.2022.e02232

Chowdhury, P., Viraraghavan, T., and Srinivasan, A. (2010). Biological treatment processes for fish processing wastewater – a review. *Bioresource Technology* **101**, 439-449.

Cianchetti-Benedetti, M., Becciu, P., Massa, B., and Dell'Omo, G. 2018. Conflicts between touristic recreational activities and breeding shearwaters: short-term effect of artificial light and sound on chick weight. *European Journal of Wildlife Research* **64**, 19. https://doi.org/10.1007/s10344-018-1178-x

Collins, S. M., Hedd, A., Montevecchi, W. A., Burt, T. V., Wilson, D. R., and Fifield, D. A. (2023). Small tube-nosed seabirds fledge on the full moon and throughout the lunar cycle. *Biology Letters* **19**, 20230290. http://doi.org/10.1098/rsbl.2023.0290

Cox, D. R. (1972). Regression models and life-tables. *Journal of the Royal Statistical Society: Series B* **34**, 187-202. https://doi.org/10.1111/j.2517-6161.1972.tb00899.x

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., and Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International* **22**, 1-34.

Cuesta, M., and Cobo, P. (2000). Active control of the exhaust noise radiated by an enclosed generator. *Applied Acoustics* **61**, 83-94.

Curé, C., Mathevon, N., Mundry, R., and Aubin, T. (2012). Acoustic cues used for species recognition can differ between sexes and sibling species: evidence in shearwaters. *Animal Behaviour* **84**, 239-250.

Curé, C., Mathevon, N., and Aubin, T. (2016). Mate vocal recognition in Scopoli's shearwater *Calonectris diomedea*: do females and males share the same acoustic code? *Behavioural Processes* **128**, 96-102.

Davies, T. W., and Smyth, T. (2018). Why artificial light at night should be a focus for global change research in the 21st century. *Global Change Biology* **24**, 872-882. https://doi.org/10.1111/gcb.13927

Day, R. H., and Cooper, B. A. (1995). Patterns of movement of dark-rumped petrels and Newell's shearwaters on Kauai. *Condor* **97**, 1011-1027.

Day, R. H., Cooper, B. A., and Telfer, T. C. (2003). Decline of Townsend's (Newell's) shearwaters (*Puffinus auricularis newelli*) on Kauai, Hawaii. *Auk* **120**, 669-679.

Day, R. H., Rose, J. R., Prichard, A. K., and Streever, B. (2015). Effects of gas flaring on the behavior of night-migrating birds at an artificial oil-production island, Arctic Alaska. *Arctic* **68**, 367-379.

de Melo Ribeiro, F. H., and Naval, L. P. (2019). Reuse alternatives for effluents from the fish processing industry through multi-criteria analysis. *Journal of Cleaner Production* **227**, 336-345.

Dell'Ariccia, G., and Bonadonna, F. (2013). Back home at night or out until morning? Nycthemeral variations in homing of anosmic Cory's shearwaters in a diurnal colony. *Journal of Experimental Biology* **216**, 1430-1433. https://doi.org/10.1242/jeb.082826

Deppe, L., Rowley, O., Rowe, L. K., Shi, N., McArthur, N., Gooday, O., and Goldstien, S. J. (2017). Investigation of fallout events in Hutton's shearwaters (*Puffinus huttoni*), associated with artificial lighting. *Notornis* **64**, 181-191.

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., and Croxall, J. P. (2019). Threats to seabirds: a global assessment. *Biological Conservation* **237**, 525-537.

Dick, M. H., and Donaldson, W. (1978). Fishing vessel endangered by crested auklet landings. *Condor* **80**, 235-236.

Durmus, D. (2022). Correlated color temperature: use and limitations. *Lighting Research & Technology* **54**, 363-375. https://doi.org/10.1177/14771535211034330

Ebrey, T., and Koutalos, Y. (2001). Vertebrate photoreceptors. *Progress in Retinal and Eye Research* **20**, 49-94. https://doi.org/10.1016/S1350-9462(00)00014-8

Elliot, J. (2025). Using nocturnal at-sea bird density to conceptualize buffer zones for vessels around seabird colonies. Hons. Thesis. Memorial University of Newfoundland, St. John's, NL.

Engels, S., Hein, C. M., Lefeldt, N., Prior, H., and Mouritsen, H. (2012). Night-migratory songbirds possess a magnetic compass in both eyes. *PLoS ONE* **7**, e43271. https://doi.org/10.1371/journal.pone.0043271

Engels, S., Schneider, N.-L., Lefeldt, N., Hein, C. M., Zapka, M., Michalik, A., Elbers, D., Kittel, A., Hore, P. J., and Mouritsen, H. (2014). Anthropogenic electromagnetic noise disrupts magnetic compass orientation in a migratory bird. *Nature* **509**, 353-356.

Evans, W. R., Akashi, Y., Altman, N. S., and Manville, A. M. II (2007). Response of night-migrating songbirds in cloud to colored and flashing light. *North American Birds* **60**, 476-488.

Evans Ogden, L. J. (1996). Collision course: the hazards of lighted structures and windows to migrating birds. World Wildlife Fund Canada and Fatal Light Awareness Program (FLAP), **3**.

Fabian, S. T., Sondhi, Y., Allen, P. E., Theobald, J. C., and Lin, H.-T. (2024). Why flying insects gather at artificial light. *Nature Communications* **15**, 689. https://doi.org/10.1038/s41467-024-44785-3

Fayet, A. L., Clucas, G. V., Anker-Nillsen, T., Syposz, M., and Hansen, E. S. (2021). Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic puffin. *Journal of Animal Ecology* **90**, 1152-1164. http://doi.org/10.1111/1365-2656.13442

Fontaine, R., Gimenez, O., and Bried, J. (2011). The impact of introduced predators, light-induced mortality of fledglings and poaching on the dynamics of the Cory's shearwater (*Calonectris diomedea*) population from the Azores, northeastern subtropical Atlantic. *Biological Conservation* **144**, 1998-2011.

Forkman, B., Boissy, A., Meunier-Salaün, M.-C., Canali, E., and Jones, R. B. (2007). A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiology & Behavior* **92**, 340-374. https://doi.org/10.1016/j.physbeh.2007.03.016

Fox, J., and Weisberg, S. (2019). An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA. Available from https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Fraser, G. S., and Carter, A. V. (2018). Seabird attraction to artificial light in Newfoundland and Labrador's offshore oil fields: documenting failed regulatory governance. *Ocean Yearbook* **32**, 265-282. https://doi.org/10.1163/22116001-03201011.

Friswold, B., Swindle, K., Hyrenbach, D., and Price, M. R. (2020). Wedge-tailed shearwater *Ardenna pacifica* fallout patterns inform targeted management. *Marine Ornithology* **48**, 245-254.

Friswold, B., Idle, J. L., Learned, J., Penniman, J., Bolosan, T., Cotin, J., Young, L., and Price, M. R. (2023). From colony to fallout: artificial lights pose risk to seabird fledglings far from their natal colonies. *Conservation Science and Practice* **5**, e13000.

Gagliardo, A., Bried, J., Lambardi, P., Luschi, P., Wikelski, M., and Bonadonna, F. (2013). Oceanic navigation in Cory's shearwaters: evidence for a crucial role of olfactory cues for homing after displacement. *Journal of Experimental Biology* **216**, 2798-2805. doi:10.1242/jeb.085738

Gaston, A. J., and Shoji, A. (2020). Ancient Murrelet (*Synthliboramphus antiquus*), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.

Gaston, A. J., Jones, I. L., Noble, D. G., and Smith, S. A. (1988). Orientation of ancient murrelet, *Synthliboramphus antiquus*, chicks during their passage from the burrow to the sea. *Animal Behaviour* **36**, 300-303. https://doi.org/10.1016/S0003-3472(88)80277-X

Gaston, K. J., Davies, T. W., Bennie, J., and Hopkins, J. (2012). Reducing the ecological consequences of night-time light pollution: options and developments. *Journal of Applied Ecology* **49**, 1256-1266.

Gaston, K. J., Bennie, J., Davies, T. W., and Hopkins, J. (2013). The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biological Reviews* 88, 912-927.

Gaston, K. J., Ackermann, S., Bennie, J., Cox, D. T. C., Phillips, B. B., Sánchez de Miguel, A., and Sanders, D. (2021). Pervasiveness of biological impacts of artificial light at night. *Integrative and Comparative Biology* **61**, 1098-1110.

Gauthreaux, S. A. Jr., and Belser, C. G. (2006). Effects of artificial night lighting on migrating birds. In *Ecological Consequences of Artificial Night Lighting*. Rich, C., and Longcore, T., editors. Island Press, Washington, D.C., USA.

Giri, B. S., Kim, K. H., Pandey, R. A., Cho, J., Song, H., and Kim, Y. S. (2014). Review of biotreatment techniques for volatile sulfur compounds with an emphasis on dimethyl sulfide. *Process Biochemistry* **49**, 1543-1554. http://dx.doi.org/10.1016/j.procbio.2014.05.024

Gjerdrum, C., Ronconi, R. A., Turner, K. L., and Hamer, T. E. (2021). Bird strandings and bright lights at coastal and offshore industrial sites in Atlantic Canada. *Avian Conservation and Ecology* **16**, 22. https://doi.org/10.5751/ACE-01860-160122

Glindemann, D., Novak, J., and Witherspoon, J. (2006). Dimethyl sulfoxide (DMSO) waste residues and municipal waste water odor by dimethyl sulfide (DMS): the north-east WPCP plant of Philadelphia. *Environmental Science and Technology* **40**, 202-207.

Granger, J., Walkowicz, L., Fitak, R., and Johnsen, S. (2020). Gray whales strand more often on days with increased levels of atmospheric radio-frequency noise. *Current Biology* **30**, R135-R158.

Griesemer, A. M., and Holmes, N. D. (2011). Newell's shearwater population modeling for Habitat Conservation Plan and Recovery Planning. Technical Report No. 176. The Hawai`i-Pacific Islands Cooperative Ecosystem Studies Unit & Pacific Cooperative Studies Unit, University of Hawai`i, Honolulu, Hawai`i. 68 pp.

Guilford, T., Padget, O., Bond, S., and Syposz, M. M. (2018). Light pollution causes object collisions during local nocturnal manoeuvring flight by adult Manx Shearwaters *Puffinus puffinus*. *Seabird* **31**, 48-55.

Guo, H., Simpson, I. J., Ding, A. J., Wang, T., Saunders, S. M., Wang, T. J., Cheng, H. R., Barletta, B., Meinardi, S., Blake, D. R., and Rowland, F. S. (2010). Carobnyl sulfide, dimethyl sulfide and carbon disulfide in the Pearl River Delta of southern China: impact of anthropogenic and biogenic sources. *Atmospheric Environment* **44**, 3805-3813.

Hadley, T. H. (1961). Shearwater calamity on Kauai. *'Elepaio* **21**, 60.

Hamer, T. E., Cooper, B. A., and Ralph, C. J. (1995). Use of radar to study the movements of marbled murrelets at inland sites. *Northwestern Naturalist* **76**, 73-78.

Harris, M. P. (1982). Seasonal variation in fledging weight of the puffin *Fratercula arctica*. *Ibis* 124, 100-103.

Harris, M. P., Murray, S., and Wanless, S. (1998). Long-term changes in breeding performance of puffins *Fratercula arctica* on St Kilda. *Bird Study* **45**, 371-374. https://doi.org/10.1080/00063659809461109

Hart, N. S. (2004). Microspectrophotometry of visual pigments and oil droplets in a marine bird, the wedge-tailed shearwater *Puffinus pacificus*: topographic variations in photoreceptor spectral characteristics. *Journal of Experimental Biology* **207**, 1229-1240. http://doi.org/10.1242/jeb.00857

Hüppop, O., Ciach, M., Diehl, R., Reynolds, D. R., Stepanian, P. M., and Menz, M. H. M. (2019). Perspectives and challenges for the use of radar in biological conservation. *Ecography* **42**, 912-930. https://doi.org/10.1111/ecog.04063

Hutchison, L. V., and Wenzel, B. M. (1980). Olfactory guidance in foraging by procellariiforms. *Condor* **82**, 314-319.

Iles, D., Gutowsky, S., Wilhelm, S. I., Rail, J. F., Hedd, A., Calvert, A., Robertson, G., and Major, H. (2025). Estimating regional trajectories and trends of seabirds from sparse and inconsistent colony counts: Case studies from eastern Canada with Leach's storm-petrel and Atlantic puffin. Manuscript submitted.

Imber, M. J. (1975). Behaviour of petrels in relation to the moon and artificial lights. *Notornis* **22**, 302-306.

Islam, M. S., Khan, S., and Tanaka, M. (2004). Waste loading in shrimp and fish processing effluents: potential source of hazards to the coastal and nearshore environments. *Marine Pollution Bulletin* **49**, 103-110.

IUCN (2024). The IUCN Red List of Threatened Species. Version 2024-1. Available from https://www.iucnredlist.org

Jägerbrand, A. K., and Spoelstra, K. (2023). Effects of anthropogenic light on species and ecosystems. *Science* **380**, 1125-1130. https://doi.org/10.1126/science.adg3173

James, P. C. (1984). The vocal and homing behaviour of the Manx Shearwater *Puffinus puffinus* with additional studies on other Procellariiformes. PhD thesis, Oxford University, Oxford, UK.

Jones, J., and Francis, C. M. (2003). The effects of light characteristics on avian mortality at lighthouses. *Journal of Avian Biology* **34**, 328-333.

Jouventin, P., Mouret, V., and Bonadonna, F. (2007). Wilson's storm petrels *Oceanites oceanicus* recognise the olfactory signature of their mate. *Ethology* **113**, 1228-1232.

Kassambara, A. ((2023). rstatix: Pipe-Friendly Framework for Basic Statistical Tests. R package version 0.7.2. Available from https://CRAN.R-project.org/package=rstatix

Kassambara, A., Kosinski, M., and Biecek, P. (2021). survminer: drawing survival curves using 'ggplot2'. R package version 0.4.9. Available from https://CRAN.R-project.org/package=survminer

Katz, C. (2023). An Icelandic town goes all out to save baby puffins. Smithsonian Magazine online. Available from https://www.smithsonianmag.com/science-nature/icelandic-town-goes-all-out-save-baby-puffins-180981518/

Kirschvink, J. L., Dizon, A. E., and Westphal, J. A. (1986). Evidence from strandings for geomagnetic sensitivity in cetaceans. *Journal of Experimental Biology* **120**, 1-24. https://doi.org/10.1242/jeb.120.1.1

Le Corre, M., Ollivier, A., Ribes, S., and Jouventin, P. (2002). Light-induced mortality of petrels: a 4-year study from Réunion Island (Indian Ocean). *Biological Conservation* **105**, 93-102.

Lichutina, T. F., Bogolitsyn, K. G., and Gusakova, M. A. (2012). Environmental performance assessment for pulp and paper enterprises: promising waste utilization options. *Russian Journal of General Chemistry* **82**, 1040-1047.

Longcore, T., Rodríguez, A., Witherington, B., Penniman, J. F., Herf, L., and Herf, M. (2018). Rapid assessment of lamp spectrum to quantify ecological effects of light at night. *Journal of Experimental Zoology Part A* **329**, 511-521. https://doi.org/10.1002/jez.2184

Lowther, P. E., Diamond, A. W., Kress, S. W., Robertson, G. J., Russell, K., Nettleship, D. N., Kirwan, G. M., Christie, D. A., Sharpe, C. J., Garcia, E. F. J., and Boesman, P. F. D. (2020). Atlantic Puffin (*Fratercula arctica*), version 1.0. In Birds of the World (Billerman, S. M., editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.atlpuf.01

Marangoni, L. F. B., Davies, T., Smyth, T., Rodríguez, A., Hamann, M., Duarte, C., Pendoley, K., Berge, J., Maggi, E., and Levy, O. (2022). Impacts of artificial light at night in marine ecosystems – a review. *Global Change Biology* **28**, 5346-5367.

Meinardi, S., Simpson, I. J., Blake, N. J., Blake, D. R., and Rowland, F. S. (2003). Dimethyl disulfide (DMDS) and dimethyl sulfide (DMS) emissions from biomass burning in Australia. *Geophysical Research Letters* **30**, 1454. DOI:10.1029/2003GL016967

Mercer, J. (2018). N.L. biologist worries offshore lights stranding seabirds. Saltwire. Available from https://www.saltwire.com/newfoundland-labrador/news/nl-biologist-worries-offshore-lights-stranding-seabirds-236694/

Merkel, F. R., and Johansen, K. L. (2011). Light-induced bird strikes on vessels in southwest Greenland. *Marine Pollution Bulletin* **62**, 2330-2336.

Middlemiss, K. L., Cieraad, E., Mander, S., Fischer, J. H., and Goad, D. (2025). Understanding the impacts of LED light pollution in marine ecosystems: phototaxis response in fairy prion. *Journal of Ornithology*. https://doi.org/10.1007/s10336-024-02245-1

Miles, W., Money, S., Luxmoore, R., and Furness, R. W. (2010). Effects of artificial lights and moonlight on petrels at St Kilda. *Bird Study* **57**, 244-251. https://doi.org/10.1080/00063651003605064

Miles, W. T. S., Mavor, R., Riddiford, N. J., Harvey, P. V., Riddington, R., Shaw, D. N., Parnaby, D., and Reid, J. M. (2015). Decline in an Atlantic Puffin population: evaluation of magnitude and mechanisms. *PLoS ONE* **10**, e0131527. http://doi.org/10.1371/journal.pone.0131527

Minatchy, N. (2004). Stratégie de réduction de la mortalité des pétrels induite par les éclairages publics. Internal report, Laboratoire d'ECOlogie MARine (ECOMAR) de l'université de La Réunion. 129 pp.

Miskelly, C. M., and Taylor, G. A. (2004). Establishment of a colony of common diving petrels (*Pelecanoides urinatrix*) by chick transfers and acoustic attraction. *Emu* **104**, 205-211. https://doi.org/10.1071/MU03062

Mitkus, M., Nevitt, G. A., Danielsen, J., and Kelber, A. (2016). Vision on the high seas: spatial resolution and optical sensitivity in two procellariiform seabirds with different foraging strategies. *Journal of Experimental Biology* **219**, 3329-3338. https://doi.org/10.1242/jeb.140905

Mitkus, M., Nevitt, G. A., and Kelber, A. (2018). Development of the visual system in a burrow-nesting seabird: Leach's storm petrel. *Brain Behavior and Evolution* **91**, 4-16. https://doi.org/10.1159/000484080

Montevecchi, W. A. (2006). Influences of artificial light on marine birds. In *Ecological Consequences of Artificial Night Lighting*. Rich, C., and Longcore, T., editors. Island Press, Washington, D.C., USA.

Moon, H. E. (2024). The physiology and molecular ecology of vision in Hawaiian seabirds. PhD thesis, University of Hawai'i at Mānoa – Honolulu, Hawai'i, USA.

Mooney, T. A., Smith, A., Larsen, O. N., Hansen, K. A., and Rasmussen, M. (2020). A field study of auditory sensitivity of the Atlantic puffin, *Fratercula arctica*. *Journal of Experimental Biology* **223**, jeb228270. https://doi.org/10.1242/jeb.228270

Nevitt, G. A. (2008). Sensory ecology on the high seas: the odor world of the procellariiform seabirds. *Journal of Experimental Biology* **211**, 1706-1713.

Nevitt, G. A., and Bonadonna, F. (2005). Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Biology Letters* **1**, 303-305.

Nevitt, G. A., Veit, R. R., and Kareiva, P. (1995). Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. *Nature* **376**, 680-682.

Nevitt, G., Reid, K., and Trathan, P. (2004). Testing olfactory foraging strategies in an Antarctic seabird assemblage. *Journal of Experimental Biology* **207**, 3537-3544.

Ödeen, A., and Håstad, O. (2003). Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Molecular Biology and Evolution* **20**, 855-861. https://doi.org/10.1093/molbev/msg108

Ogle, D. H., Doll, J. C., Wheeler, A. P., and Dinno, A. (2023). FSA: Simple Fisheries Stock Assessment Methods. R package version 0.9.4. Available from https://CRAN.R-project.org/package=FSA

Oro, D., de Léon, A., Minguez, E., and Furness, R. W. (2005). Estimating predation on breeding European storm-petrels (*Hydrobates pelagicus*) by yellow-legged gulls (*Larus michahellis*). *Journal of Zoology* **265**, 421-429.

Pawson, S. M., and Bader, M.K.-F. (2014). LED lighting increases the ecological impact of light pollution irrespective of temperature. *Ecological Applications* **24**, 1561-1568. https://doi.org/10.1890/14-0468.1

Pembury Smith, M. Q. R., and Ruxton, G. D. (2020). Effective use of the McNemar test. *Behavioral Ecology and Sociobiology* **74**, 133. https://doi.org/10.1007/s00265-020-02916-y

Pierre, J. P., Abraham, E. R., Middleton, D. A. J., Cleal, J., Bird, R., Walker, N. A., and Waugh, S. M. (2010). Reducing interactions between seabirds and trawl fisheries: responses to foraging patches provided by fish waste batches. *Biological Conservation* **143**, 2779-2788.

Podolsky, R. H., and Kress, S. W. (1989). Factors affecting colony formation in Leach's storm-petrel. *Auk* **106**, 332-336.

Podolsky, R., Ainley, D. G., Spencer, G., Deforest, L., and Nur, N. (1998). Mortality of Newell's shearwaters caused by collisions with urban structures on Kauai. *Colonial Waterbirds* **21**, 20-34.

Pollet, I. L., Bond, A. L., Hedd, A., Huntington, C. E., Butler, R. G., and Mauck, R. (2021). Leach's Storm-Petrel (*Hydrobates leucorhous*), version 1.1. In Birds of the World (editor not available). Cornell Lab of Ornithology, Ithaca, NY, USA.

Pollonara, E., Luschi, P., Guilford, T., Wikelski, M., Bonadonna, F., and Gagliardo, A. (2015). Olfaction and topography, but not magnetic cues, control navigation in a pelagic seabird: displacements with shearwaters in the Mediterranean Sea. *Scientific Reports* **5**, 16486.

Poot, H., Ens, B. J., de Vries, H., Donners, M. A. H., Wernand, M. R., and Marquenie, J. M. (2008). Green light for nocturnally migrating birds. *Ecology and Society* **13**, 47.

Porter, R. H., Hepper, P. G., Bouchot, C., and Picard, M. (1999). A simple method for testing odor detection and discrimination in chicks. *Physiology & Behavior* **67**, 459-462.

Putman, N. F. (2020). Animal navigation: seabirds home to a moving magnetic target. *Current Biology* 30, R802–R830. https://doi.org/10.1016/j.cub.2020.05.061

Raine, A. F., Driskill, S., Rothe, J., and Travers, M. S. (2023). Evaluating the breeding phenology of the endangered ʻaʻo (Newell's Shearwater *Puffinus newelli*) on Kauaʻi to better focus conservation actions and management decisions. *Bird Conservation International* **33**, e35, 1–11. https://doi.org/10.1017/S0959270922000387

Raine, A. F., Driskill, S., Rothe, J., Rossiter, S., Gregg, J., Anderson, T., and Travers, M. S. (2024). The impact of light attraction on adult seabirds and the effectiveness of minimization actions. *Pacific Science* **78**, 85-102.

R Core Team (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/

Rebke, M., Dierschke, V., Weiner, C. N., Aumüller, R., Hill, K., and Hill, R. (2019). Attraction of nocturnally migrating birds to artificial light: the influence of colour, intensity and blinking mode under different cloud cover conditions. *Biological Conservation* **233**, 220-227.

Reed, J. R. (1986). Seabird vision: spectral sensitivity and light-attraction behavior. PhD thesis, University of Wisconsin – Madison, Wisconsin, USA.

Reed, J. R. (1987). Polarizing filters fail to reduce light attraction in Newell's shearwaters. *Wildlife Society Bulletin* **15**, 596-598.

Reed, J. R., Sincock, J. L., and Hailman, J. P. (1985). Light attraction in endangered procellariiform birds: reduction by shielding upward radiation. *Auk* **102**, 377-383.

Rich, C., and Longcore, T. (editors) (2006). Ecological consequences of artificial night lighting. Island Press. Washington, D.C., USA.

Ridgway, R. (1885). A new petrel for North America. *Auk* **2**, 386-387.

Riou, S., and Hamer, K. C. (2008). Predation risk and reproductive effort: impacts of moonlight on food provisioning and chick growth in Manx shearwaters. *Animal Behaviour* **76**, 1743-1748.

Rodrigues, P., Aubrecht, C., Gil, A., Longcore, T., and Elvidge, C. (2012). Remote sensing to map influence of light pollution on Cory's shearwater in São Miguel Island, Azores Archipelago. *European Journal of Wildlife Research* **58**, 147-155. DOI 10.1007/s10344-011-0555-5

Rodríguez, A., and Rodríguez, B. (2009). Attraction of petrels to artificial lights in the Canary Islands: effects of the moon phase and age class. *Ibis* **151**, 299-310.

Rodríguez, A., Rodríguez, B., and Lucas, M. P. (2012a). Trends in numbers of petrels attracted to artificial lights suggest population declines in Tenerife, Canary Islands. *Ibis* **154**, 167-172.

Rodríguez, A., Rodríguez, B., Curbelo, Á. J., Pérez, A., Marrero, S., and Negro, J. J. (2012b). Factors affecting mortality of shearwaters stranded by light pollution. *Animal Conservation* **15**, 519-526.

Rodríguez, A., Burgan, G., Dann, P., Jessop, R., Negro, J. J., and Chiaradia, A. (2014). Fatal attraction of short-tailed shearwaters to artificial lights. *PLos ONE* **9**, e110114. doi:10.1371/journal.pone.0110114

Rodríguez, A., Rodríguez, B., and Negro, J. J. (2015). GPS tracking for mapping seabird mortality induced by light pollution. *Scientific Reports* **5**, 10670. https://doi.org/10.1038/srep10670

Rodríguez, A., Holmes, N. D., Ryan, P. G., Wilson, K.-J., Faulquier, L., Murillo, Y., Raine, A. F., Penniman, J. F., Neves, V., Rodríguez, B., Negro, J. J., Chiaradia, A., Dann, P., Anderson, T., Metzger, B., Shirai, M., Deppe, L., Wheeler, J., Hodum, P., Gouveia, C., Carmo, V., Carreira, G. P., Delgado-Alburqueque, L., Guerra-Correa, C., Couzi, F.-X., Travers, M., and Le Corre, M. (2017a). Seabird mortality induced by land-based artificial lights. *Conservation Biology* **31**, 986-1001.

Rodríguez, A., Dann, P., and Chiaradia, A. (2017b). Reducing light-induced mortality of seabirds: high pressure sodium lights decrease the fatal attraction of shearwaters. *Journal for Nature Conservation* **39**, 68-72.

Rodríguez, A., Arcos, J. M., Bretagnolle, V., Dias, M. P., Holmes, N. D., Louzao, M., Provencher, J., Raine, A. F., Ramírez, F., Rodríguez, B., Ronconi, R. A., Taylor, R. S., Bonnaud, E., Borrelle, S. B., Cortés, V., Descamps, S., Friesen, V. L., Genovart, M., Hedd, A., Hodum, P., Humphries, G. R. W., Le Corre, M., Lebarbenchon, C., Martin, R., Melvin, E. F., Montevecchi, W. A., Pinet, P., Pollet, I. L., Ramos, R., Russell, J. C., Ryan, P. G., Sanz-Aguilar, A., Spatz, D. R., Travers, M., Votier, S. C., Wanless, R. M., Woehler, E., and Chiaradia, A. (2019). Future directions in conservation research on petrels and shearwaters. *Frontiers in Marine Science* **6**, 1-27. https://doi.org/10.3389/fmars.2019.00094

Rodríguez, A., Rodríguez, B., Acosta, Y., and Negro, J. J. (2022). Tracking flights to investigate seabird mortality induced by artificial lights. *Frontiers in Ecology and Evolution* **9**, 786557. https://doi.org/10.3389/fevo.2021.786557

Rodríguez, A., Atchoi, E., Rodríguez, B., Pipa, T., Le Corre, M., and Ainley, D. G. (2023). Moonlight diminishes seabird attraction to artificial light. *Conservation Science and Practice* **5**, e13014. https://doi.org/10.1111/csp2.13014

Ronconi, R. A., Allard, K. A., and Taylor, P. D. (2015). Bird interactions with offshore oil and gas platforms: review of impacts and monitoring techniques. *Journal of Environmental Management* **147**, 34-45.

Rutherford, A. (2025). Changing vertical substrate color to reduce seabird collisions associated with artificial light. Hons. Thesis, Acadia University, Wolfville, Nova Scotia, Canada.

Salamolard, M., Couzi, F.-X., Pellerin, M., and Ghestemme, T. (2001). Etude complémentaire concernant la protection du Puffin de Baillon dans le cadre de la Route des Tamarins. Rapp. SEOR/DDE-Réunion. 30 pp. + Annexes 4 pp.

Salamolard, M., Ghestemme, T., Couzi, F.-X., Minatchy, N., and Le Corre, M. (2007). Impacts des éclairages urbains sur les pétrels de Barau, *Pterodroma baraui* sur l'Ile de la Réunion et mesures pour réduire ces impacts. *Ostrich* **78**, 449-452. http://doi.org/10.2989/OSTRICH.2007.78.2.52.132

Sánchez de Miguel, A., Bennie, J., Rosenfeld, E., Dzurjak, S., and Gaston, K. J. (2021). First estimation of global trends in nocturnal power emissions reveals acceleration of light pollution. *Remote Sensing* **13**, 3311.

Sanders, D., Frago, E., Kehoe, R., Patterson, C., and Gaston, K. J. (2021). A meta-analysis of biological impacts of artificial light at night. *Nature Ecology & Evolution* 5, 74-81. https://doi.org/10.1038/s41559-020-01322-x

Santos, R. A. L., Santos, S. M., Santos-Reis, M., Picanço de Figueiredo, A., Bager, A., Aguiar, L. M. S., and Ascensão, F. (2016). Carcass persistence and detectability: Reducing the uncertainty surrounding wildife-vehicle collision surveys. *PLoS ONE* 11, e0165608. https://doi.org/10.1371/journal.pone.0165608

Savoca, M. S., Wohlfeil, M. E., Ebeler, S. E., and Nevitt, G. A. (2016). Marine plastic debris emits a keystone infochemical for olfactory foraging seabirds. *Science Advances* 2, e1600395.

Schreiber, B., and Rossi, O. (1976). Correlation between race arrivals of homing pigeons and solar activity. *Italian Journal of Zoology* 43, 317-320. https://doi.org/10.1080/11250007609430148

Silva, M. C., Granadeiro, J. P., Boersma, P. D., and Strange, I. (2011). Effects of predation risk on the nocturnal activity budgets of thin-billed prions *Pachyptila belcheri* on New Island, Falkland Islands. *Polar Biology* 34, 421-429.

Simons, T. R. (1984). A population model of the endangered Hawaiian Dark-rumped Petrel. *Journal of Wildlife Management* 48, 1065-1076.

Simpson, G. (2024). gratia: An R package for exploring generalized additive models. *Journal of Open Source Software* 9, 6962. https://doi.org/10.48550/arXiv.2406.19082

Sincock, J. L., and Swedberg, G. E. (1969). Rediscovery of the nesting grounds of Newell's Manx shearwater (*Puffinus puffinus newelli*), with initial observations. *Condor* 71, 69-71.

Sultana, S., Hassan, M. R., Choe, H. S., and Ryu, K. S. (2013). Impact of different monochromatic LED light colours and bird age on the behavioural output and fear response in ducks. *Italian Journal of Animal Science* 12, e94. https://doi.org/10.4081/ijas.2013.e94

Swales, M. K. (1965). The sea-birds of Gough Island. *Ibis* 107, 215-229.

Syposz, M., Gonçalves, F., Carty, M., Hoppitt, W., and Manco, F. (2018). Factors influencing Manx shearwater grounding on the west coast of Scotland. *Ibis* 160, 846-854.

Syposz, M., Padget, O., Willis, J., Van Doren, B. M., Gillies, N., Fayet, A. L., Wood, M. J., Alejo, A., and Guilford, T. (2021a). Avoidance of different durations, colours and intensities of artificial light by adult seabirds. *Scientific Reports* **11**, 18941.

Syposz, M., Padget, O., Wynn, J., Gillies, N., Fayet, A. L., and Guilford, T. (2021b). An assay to investigate factors influencing initial orientation in nocturnally fledging seabirds. *Journal of Avian Biology* e02613.

Telfer, T. C., Sincock, J. L., Byrd, G. V., and Reed, J. R. (1987). Attraction of Hawaiian seabirds to lights: conservation efforts and effects of moon phase. *Wildlife Society Bulletin* **15**, 406-413.

Therneau, T. (2024). A package for survival analysis in R. R package version 3.7-0. Available from https://CRAN.R-project.org/package=survival.

Totterman, S. L. (2014). Sexual and individual differences in wedge-tailed shearwater (*Puffinus pacificus*) burrow calls and vocal recognition. *Notornis* **61**, 121-130.

Tripovich, J. S., Hall-Aspland, S., Charrier, I., and Arnould, J. P. Y. (2012). The behavioural response of Australian fur seals to motor boat noise. *PLoS ONE* **7**, e37228. http://doi.org/10.1371/journal.pone.0037228

Troy, J. R., Holmes, N. D., Veech, J. A., and Green, M. C. (2013). Using observed seabird fallout records to infer patterns of attraction to artificial light. *Endangered Species Research* **22**, 225-234.

Urmston, J., Hyrenbach, K. D., and Swindle, K. (2022). Quantifying wedge-tailed shearwater (*Ardenna pacifica*) fallout after changes in highway lighting on Southeast Oʻahu, Hawaiʻi. *PLoS ONE* **17**, e0265832. https://doi.org/10.1371/journal.pone.0265832

Van Doren, B. M., Willard, D. E., Hennen, M., Horton, K. G., Stuber, E. F., Sheldon, D., Sivakumar, A. H., Wang, J., Farnsworth, A., and Winger, B. M. (2021). Drivers of fatal bird collisions in an urban center. *PNAS* **118**, e2101666118. https://doi.org/10.1073/pnas.2101666118

van Pelt, T. I., and Piatt, J. F. (1995). Deposition and persistence of beachcast seabird carcasses. *Marine Pollution Bulletin* **30**, 794-802.

Versfeld, N. J., and Vos, J. (1997). Annoyance caused by sounds of wheeled and tracked vehicles. *Journal of the Acoustical Society of America* **101**, 2677. https://doi.org/10.1121/1.418556

Walker, M. M., Kirschvink, J. L., Ahmed, G., and Dizon, A. E. (1992). Evidence that fin whales respond to the geomagnetic field during migration. *Journal of Experimental Biology* **171**, 67-78.

Watanuki, Y. (1986). Moonlight avoidance behavior in Leach's storm-petrels as a defense against Slaty-backed gulls. *Auk* **103**, 14-22.

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, USA.

Wiese, F. K., and Robertson, G. J. (2004). Assessing seabird mortality from chronic oil discharges at sea. *Journal of Wildlife Management* **68**, 627-638.

Wiese, F. K., Montevecchi, W. A., Davoren, G. K., Huettmann, F., Diamond, A. W., and Linke, J. (2001). Seabirds at risk around offshore oil platforms in the north-west Atlantic. *Marine Pollution Bulletin* **42**, 1285-1290.

Wilhelm, S. I., Schau, J. J., Schau, E., Dooley, S. M., Wiseman, D. L., and Hogan, H. A. (2013). Atlantic Puffins are attracted to coastal communities in eastern Newfoundland. *Northeastern Naturalist* **20**, 624-630.

Wilhelm, S. I., Mailhiot, J., Arany, J., Chardine, J. W., Robertson, G. J., and Ryan, P. C. (2015). Update and trends of three important seabird populations in the western North Atlantic using a geographic information system approach. *Marine Ornithology* **43**, 211-222.

Wilhelm, S. I., Hedd, A., Robertson, G. J., Mailhiot, J., Regular, P. M., Ryan, P. C., and Elliot, R. D. (2020). The world's largest breeding colony of Leach's Storm-petrel *Hydrobates leucorhous* has declined. *Bird Conservation International* **30**, 40-57.

Wilhelm, S. I., Dooley, S. M., Corbett, E. P., Fitzsimmons, M. G., Ryan, P. C., and Robertson, G. J. (2021). Effects of land-based light pollution on two species of burrow-nesting seabirds in Newfoundland and Labrador, Canada. *Avian Conservation and Ecology* **16**, 12. https://doi.org/10.5751/ACE-01809-160112

Wiltschko, W., and Wiltschko, R. (2005). Magnetic orientation and magnetoreception in birds and other animals. *Journal of Comparative Physiology A* **191**, 675-693.

Wiltschko, R., and Wiltschko, W. (2019). Magnetoreception in birds. *Journal of the Royal Society Interface* **16**, 20190295. http://dx.doi.org/10.1098/rsif.2019.0295

Witherington, B. E. (1997). The problem of photopollution for sea turtles and other nocturnal animals. In *Behavioral approaches to conservation in the wild* (Clemmons, J. R., and Buchholz, R. (editors)). pp. 303-328. Cambridge University Press.

Wood, S. (2023). mgcv: Mixed GAM computation vehicle with automatic smoothness estimation. R package version 1.9-1. http://doi.org/10.32614/CRAN.package.mgcv

Wynn, J., Padget, O., Mouritsen, H., Perrins, C., and Guilford, T. (2020). Natal imprinting to the Earth's magnetic field in a pelagic seabird. *Current Biology* **30**, 2869-2873. https://doi.org/10.1016/j.cub.2020.05.039

Yadav, G., Malik, S., Rani, S., and Kumar, V. (2015). Role of light wavelengths in synchronization of circadian physiology in songbirds. *Physiology & Behavior* **140**, 164-171. http://dx.doi.org/10.1016/j.physbeh.2014.12.032

Yang, Y., Liu, Q., Pan, C., Chen, J., Xu, B., Liu, K., Pan, J., Lagisz, M., and Nakagawa, S. (2024). Species sensitivities to artificial light at night: a phylogenetically controlled multilevel meta-analysis on melatonin suppression. *Ecology Letters* **27**, e14387. https://doi.org/10.1111/ele.14387

Yoda, K., Yamamoto, T., Suzuki, H., Matsumoto, S., Müller, M., and Yamamoto, M. (2017). Compass orientation drives naïve pelagic seabirds to cross mountain ranges. *Current Biology* **27**, R1141-R1155.

Appendices

Appendix – Chapter 2

Methods

Conversion of "dark" treatment activity levels

To determine if we should "convert" the audial scores of time spent mobile by pufflings in the "dark" treatment (x) to estimated scores of time spent mobile had been scored visually (y), we calculated 95% confidence intervals of the slope and intercept estimates (that is, 0.92 and 2.30, respectively). We decided a priori that if either the slope estimate's 95% confidence intervals did not contain 1.00 or if the intercept estimate's 95% confidence intervals did not contain 0.00, we would convert the "dark" data using y = 2.3 + 0.92x; otherwise, we would use the raw "dark" data for analysis. The 95% confidence interval of the slope was [0.87, 0.97] and that of the intercept was [-5.29, 9.95]. The slope estimate's 95% confidence intervals therefore did not contain 1.00, so we converted the "dark" data for analysis.

Results

Assessment of activity levels in different light types when outlier is included

The following results were obtained when the individual identified as an outlier (in the warm white LED light treatment of the open field test; spent 353 seconds mobile) was retained in our analysis. There was a significant effect of light type on time spent mobile by pufflings (Kruskal-Wallis test: H_3 = 17.184, P < 0.001); post-hoc testing revealed that pufflings spent more time mobile in darkness (median time spent mobile = 120 seconds) and in HPS light (median 111 seconds) than in cool white LED

light (median 32 seconds; $P = 0.004$ for both comparisons). Pufflings also tended to spend more time mobile in darkness and in HPS light than in warm white LED light (median 56 seconds; $P = 0.09$ and $P = 0.10$, respectively), but these differences failed to reach significance.

Tables

Table A2.1. Minimum ("Min"), best-estimate ("Est"), and maximum ("Max") counts of pufflings observed at the two beaches during Dark and Light treatments over the course of 11 experimental nights, accompanied by percent moon illumination on each night ("% Moon") and qualitative observations of weather conditions at the sites.

Night	% Moon	Weather	Dark			Light		
			Min	Est	Max	Min	Est	Max
1	85	Clear	0	0	0	10	14	23
2	76	Cloud & fog	0	0	0	34	44	52
3	47	Cloud & rain	1	1	1	11	12	17
4	38	Drizzle[1]	0	0	0	27	28	30
5	29	Clear	0	0	0	14	15	19
6	20	Clear	0	0	0	6	6	6
7	13	Cloud & rain	1	1	2	5	5	5
8	8	Cloud & wind	0	0	0	4	4	4
9	3	Cloud	0	0	0	6	7	8
10	1	Cloud & wind	0	0	0	0	0	0
11	0	Clear	0	0	0	1	1	1

Note: All counts for both treatments were conducted over the same experimental duration each night (two hours). Percent moon illumination data were collected from moongiant.com. Weather conditions were not recorded at the sites on night 4; conditions on this night were obtained from Environment and Climate Change Canada (climate.weather.gc.ca).

[1]Weather data obtained from Environment and Climate Change Canada for St. John's International Airport (47.618611°N, 52.752500°W), located 38-40 km from the two beach sites used in this experiment.

Table A2.2. Minimum ("Min"), best-estimate ("Est"), and maximum ("Max") "observation rates" (pufflings seen, divided by number of observers) at the beaches during Dark and Light treatments over the course of 11 experimental nights. All observation rates for both treatments apply to a two-hour experimental duration.

Night	Dark			Light		
	Min	Est	Max	Min	Est	Max
1	0	0	0	5	7	11.5
2	0	0	0	11.3	14.7	17.3
3	0.5	0.5	0.5	3.7	4	5.7
4	0	0	0	9	9.3	10
5	0	0	0	4.7	5	6.3
6	0	0	0	2	2	2
7	0.5	0.5	1	1.7	1.7	1.7
8	0	0	0	0.8	0.8	0.8
9	0	0	0	1.5	1.75	2
10	0	0	0	0	0	0
11	0	0	0	0.5	0.5	0.5

Table A2.3. Materials used to create each of the eight light options used in the choice experiment, including the specific lightbulbs used, whether a neutral-density filter or diffuser were used, and any other materials used.

Light option	Lightbulb	NDF[a]	Diffuser[b]	Other
Dim HPS	2100 K HPS[c,d]	none	yes	none
Bright HPS	2100 K HPS[d]	yes	yes	none
Cool white LED	5000 K LED[e]	yes	yes	none
Warm white LED	2700 K LED[f]	yes	yes	none
Bright blue LED	5000 K LED[e]	none	none	ePlastics #2424 dark blue acrylic; cobalt glass
Dim blue LED	5000 K LED[e]	yes	yes	ePlastics #2424 dark blue acrylic; cobalt glass
Orange LED	2700 K LED[f]	yes	yes	ePlastics #2422 amber orange acrylic
Darkness	none	none	none	light hole covered

[a]A variable neutral density filter (NDF) consisted of two pieces of polyvinyl alcohol-iodine polarizing film, overlapping at varying degrees of polarization depending on the light option.

[b]Diffuser consisted of one piece of parchment paper.

[c]Incident light only (i.e., crossover light from Bright HPS on other choice box).

[d]High pressure sodium; Light EnerG, 400 Watt

[e]Light-emitting diode; Philips, 5W / 40W-equivalent Daylight LED

[f]Light-emitting diode; Philips, 5W / 40W-equivalent Soft White LED
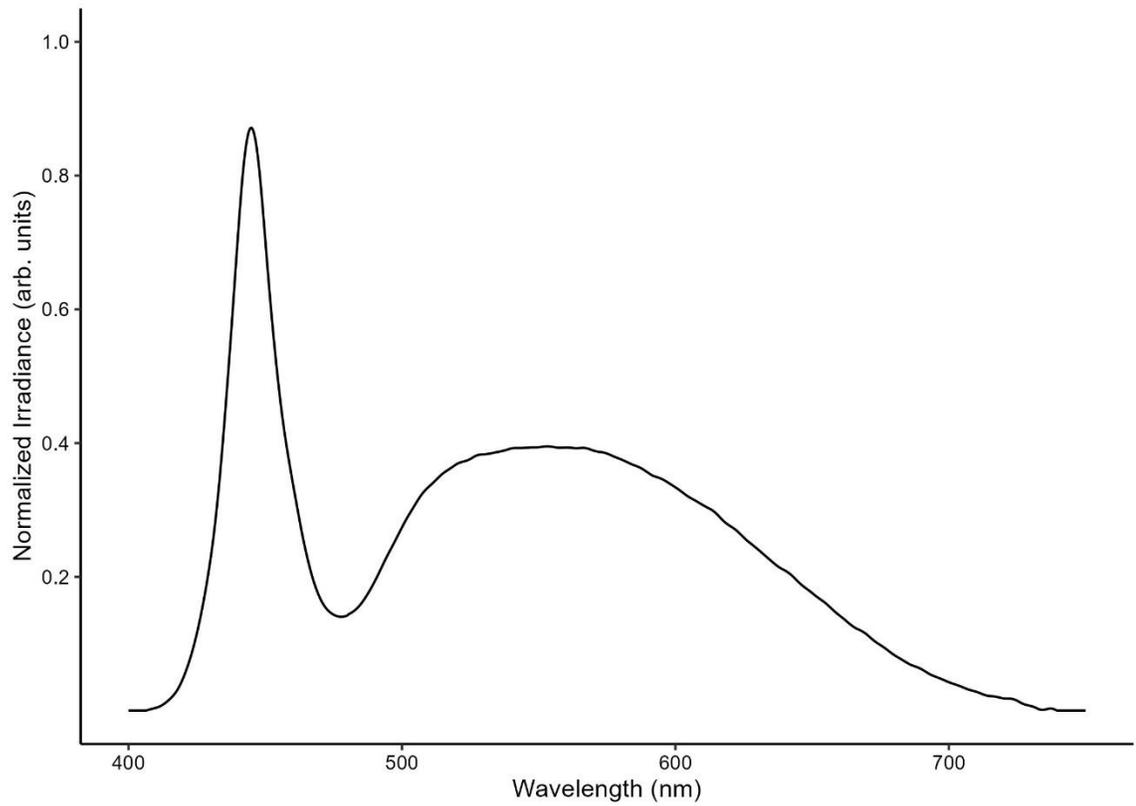
Figure A2.1. Spectrum of the 6390 K, 30,000 lumen LED light apparatus used on two beach sites to test the responses of pufflings to light at a coarse spatial scale. Note that the y-axis has been normalized to arbitrary units with a maximum of 1.0.
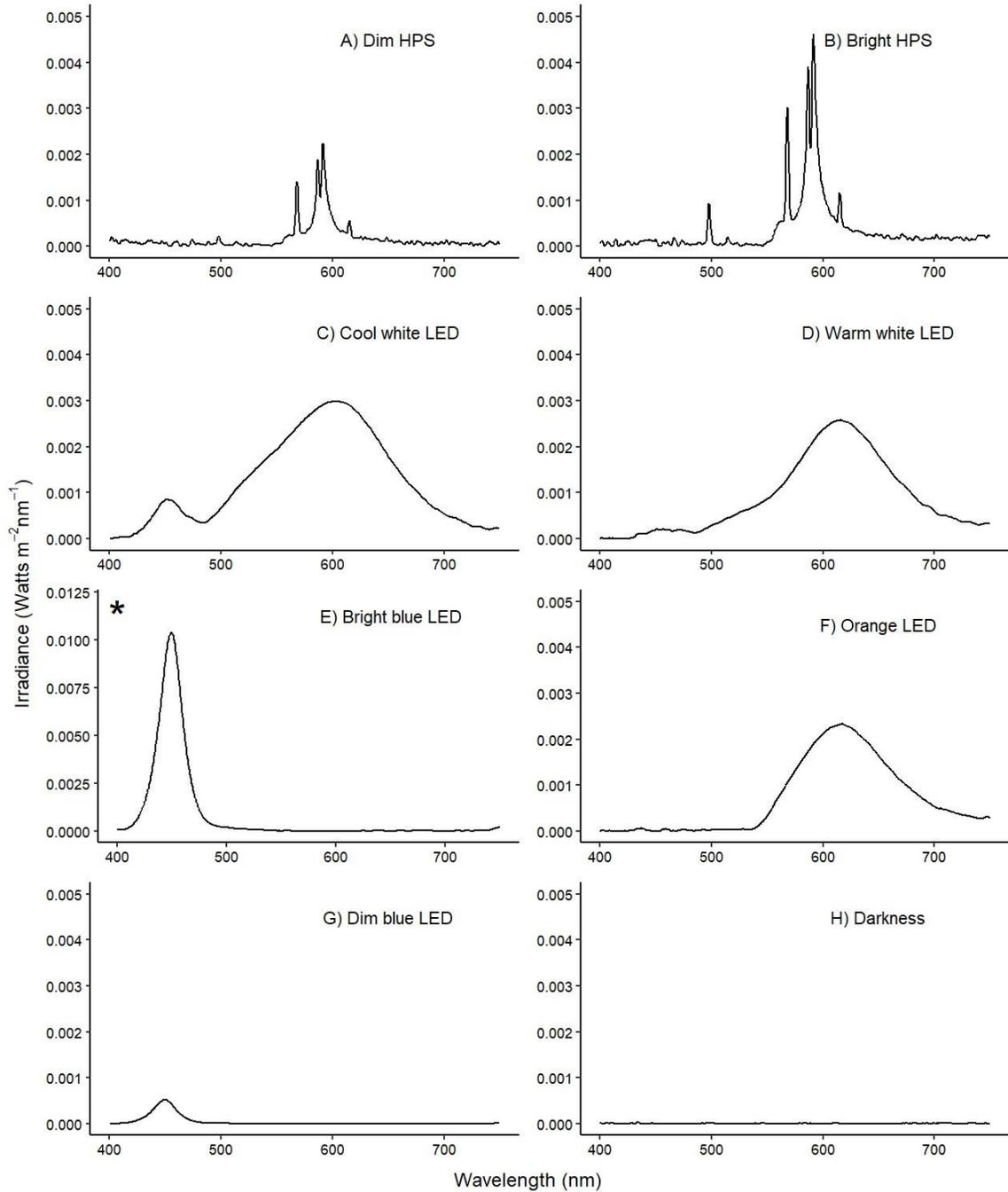
Figure A2.2. Spectra of all light options used in the choice experiment: A) Dim HPS; B) Bright HPS; C) Cool white (5000 K) LED light; D) Warm white (2700 K) LED light; E) Bright blue LED light; F) Orange LED light; G) Dim blue LED light; and H) Darkness. Irradiance is as measured by a spectrometer with its sensor placed at the entrance of the "choice arm", inside the "main box" of the Y-maze. * = note the change in y-axis scale.
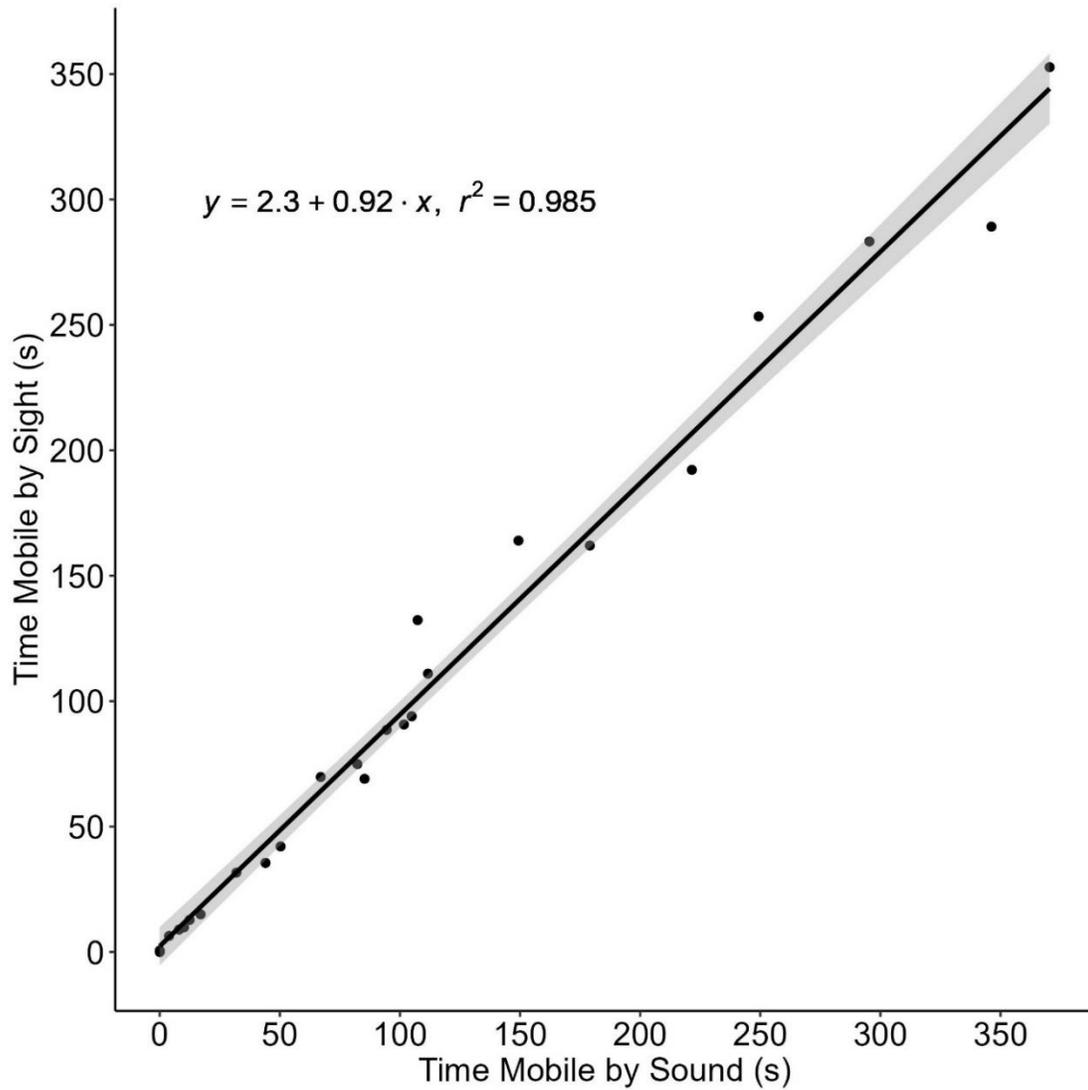
Figure A2.3. Comparison of time spent mobile by 25 pufflings in a 600 second trial in 25 lighted videos (including HPS, warm white LED, and cool white LED), as scored by watching the video (*y*-axis) versus listening to the video (*x*-axis). Note that there are two overlapping points around (0, 0).

Appendix – Chapter 3

Methods

Measuring activity levels under various light spectra

The 1-m³ cube-shaped open field test arena was constructed from polycarbonate panels, with the floor left unattached for easy removal. We created a 20 cm × 20 cm grid composed of 25 squares (in a 5 × 5 squares arrangement) on the floor, cut an access door into the lower part of one wall of the arena for easy insertion and removal of storm-petrels from the apparatus, and cut two small holes in the ceiling: one for the light source and one for the camera (Activeon, CCA10W, Activeon Inc.; San Diego, CA, USA). We placed an opaque blackout curtain over the whole arena to prevent any ambient light from entering.

Safe haven test

The Safe Haven box has two small openings (approximately 6 cm in diameter) through which storm-petrels can enter; one on each of the two short sides. We placed the Safe Haven box against the middle of the wall opposite the arena's access door, with its two openings oriented along the wall. Inside the Safe Haven box, a ramp angles upward from each opening until dropping off to the interior floor of the box, such that after an individual goes over the ramp, it has difficulty escaping the box.

In each trial, we started the video camera, placed each storm-petrel just inside the access door of the arena, and started a timer. At the end of each 10-minute trial, we noted whether the storm-petrel was inside the Safe Haven box and, if it was not, we later used the thermal imaging video footage to verify that the bird had not entered the Safe Haven box during the experiment (note that there were zero occurrences of this). The floor of the

arena was not cleaned between trials unless a storm-petrel defecated during its trial. If a

storm-petrel entered the Safe Haven box, we cleaned the entire Safe Haven box with 70%

isopropyl alcohol and allowed it to dry before the next trial.

Statistical Analysis

<u>Measuring activity levels under various light spectra</u>

  To determine if scoring videos using auditory information may have artificially

increased or decreased our estimates of time spent mobile in darkness (in comparison to

scoring the light videos, which was done visually), we conducted a simple linear

regression of time spent mobile scored visually (y) as a function of time spent mobile

scored audially (x) of the 10 selected lighted videos that were scored both visually and

using auditory information (package "stats", v. 4.3.0; R Core Team 2023). The regression

equation was statistically significant ($r^2 = 0.823$; $F_{(1, 8)} = 37.12$; $P < 0.001$), and auditory

scores predicted visual scores ($\beta = 0.6980$; $P < 0.001$; Appendix Figure A3.3). We

converted the "dark" data using the regression equation and used these "converted"

values in subsequent statistical comparisons with the unmodified visual scores from the

other treatment groups. We decided to score only "dark" videos using auditory

information (rather than scoring all videos this way) because: 1) we reasoned that visual

scoring is both more accurate (i.e., truer to the correct value) and more precise

(i.e., repeatable) than auditory scoring, and is therefore preferable when three of our four

treatments can be scored visually; 2) the noise associated with the high-pressure sodium

light's ballast fan would have made auditory scoring of those videos difficult and

therefore introduce another source of scoring bias; and 3) extra care was taken during the

dark treatment specifically to ensure that noises similar in quality to those of storm-petrel

footsteps were reduced to an absolute minimum to increase the accuracy of those auditory

scores.

Table A3.1. Materials used to create each of the six light options used in the choice experiment, including the specific lightbulbs used, whether a neutral-density filter or diffuser were used, and any other materials used.

Light option	Lightbulb	NDF[a]	Diffuser[b]	Other
HPS	2100 K HPS[c]	yes	yes	none
Warm white LED	2700 K LED[d]	yes	yes	none
Cool white LED	5000 K LED[e]	yes	yes	none
Blue LED	5000 K LED[e]	none	none	ePlastics #2424 dark blue acrylic; cobalt glass
Orange LED	2700 K LED[d]	yes	yes	ePlastics #2422 amber orange acrylic
Darkness	none	none	none	light hole covered

[a]A variable neutral density filter (NDF) consisted of two pieces of polyvinyl alcohol-iodine polarizing film, overlapping at varying degrees of polarization depending on the light option.

[b]Diffuser consisted of one piece of parchment paper.

[c]High-pressure sodium; Light EnerG, 400 Watt

[d]Light-emitting diode; Philips, 5W / 40W-equivalent Soft White LED

[e]Light-emitting diode; Philips, 5W / 40W-equivalent Daylight LED

Table A3.2. Contingency table comparing the number of storm-petrels that required prodding out of the acclimation box after 5 minutes of inactivity with the number of individuals that eventually made a response, or not, in the Y-maze choice experiment. The total experimental sample size was $N = 76$

		Prodded		
		Yes	**No**	**Total**
Responded	Yes	12	16	28
	No	41	7	48
	Total	53	23	**76**
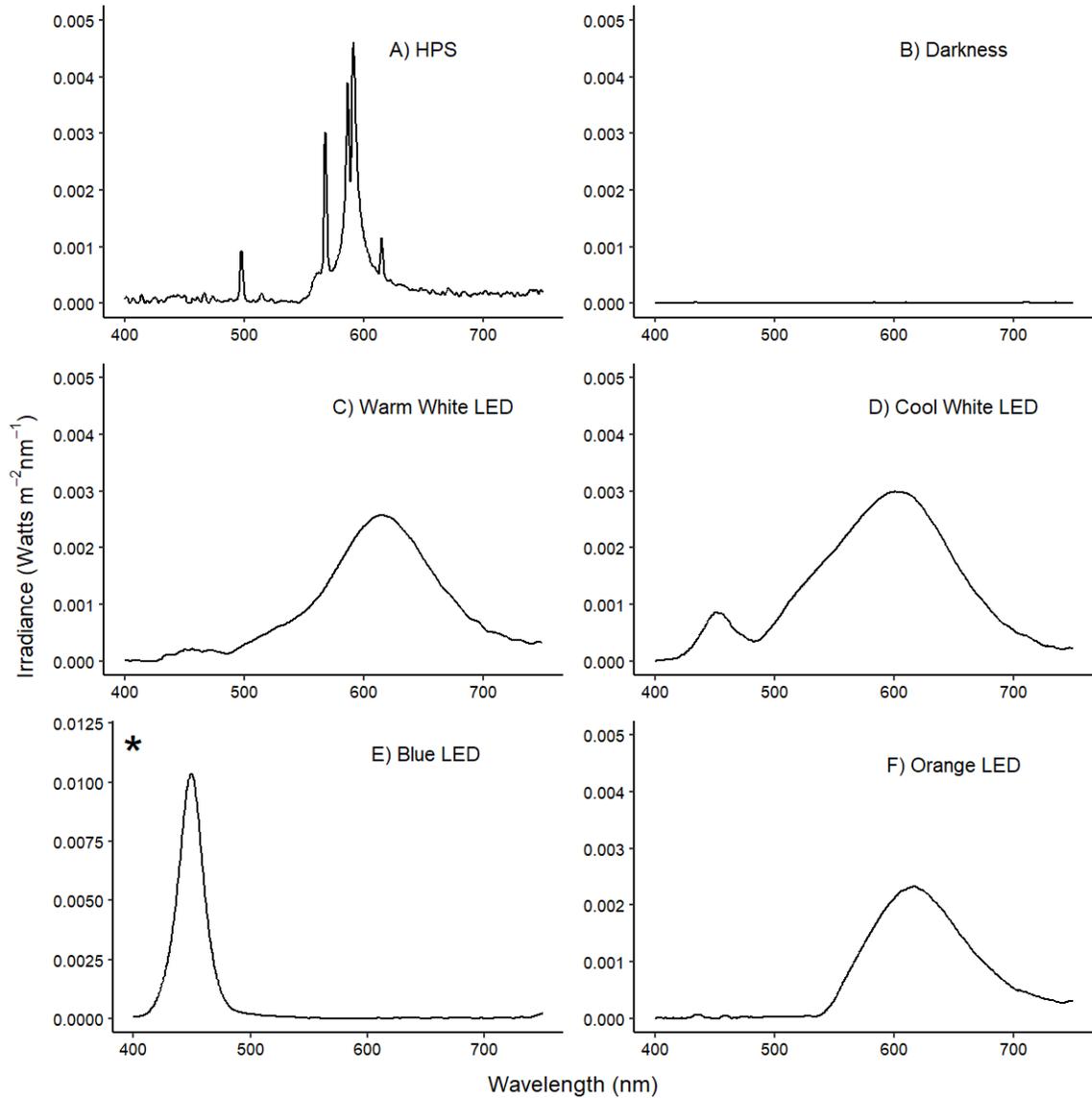
Figure A3.1. Spectra of all light options used in the choice experiment: A) High-pressure sodium; B) Darkness; C) Warm white (2700 K) LED light; D) Cool white (5000 K) LED light; E) Blue LED light; and F) Orange LED light. Irradiance is as measured by a spectrometer with its sensor placed at the entrance of the "choice arm", inside the "main box" of the Y-maze. * = note the difference in y-axis scale compared to the other spectra.
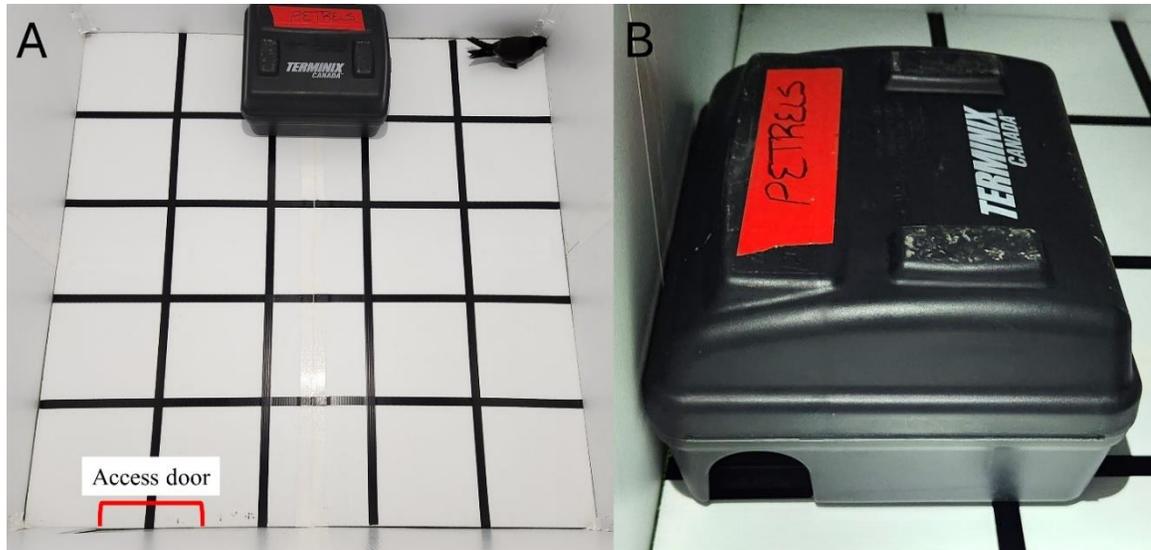
Figure A3.2. A) Floor layout of the Safe Haven test arena, including Safe Haven box and storm-petrel. Note the access door at the bottom of the picture, through which storm-petrels were placed inside the arena. Each floor grid square is 20 cm × 20 cm. B) Orientation of the Safe Haven box such that the openings were both along the wall of the arena.

$$y = 56 + 0.7 \cdot x, \quad r^2 = 0.823$$
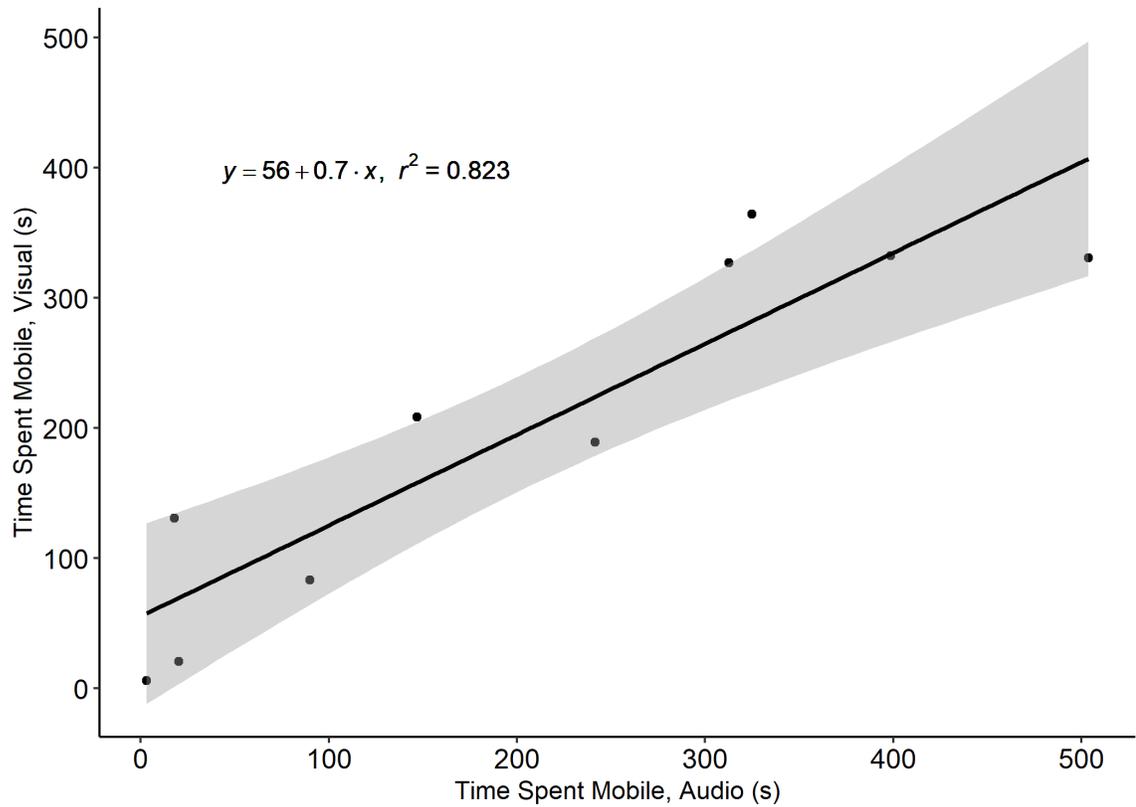
Figure A3.3. Comparison of time spent mobile by 10 randomly selected Leach's storm-petrels, each tested in a 600-second trial under either high-pressure sodium, warm white LED, or cool white LED light, as scored by watching the video (*y*-axis) versus listening to the audio (*x*-axis). Gray area represents 95% confidence limits.

Appendix – Chapter 4

Methods

Ethical Note

<u>Pre-experiment script to be read to volunteers</u>

"This year, the Puffin Patrol is working with a PhD student at Trent University named Taylor Brown. Taylor is studying puffins and why they get stranded here in coastal Newfoundland. She is running an experiment with our help, and we are wondering if you would like to participate in it. It is completely optional. Taylor has put some fake, plastic puffins like this [show them the puffin model] in random places where you will be searching for real puffins. If you want to participate in this experiment, all you have to do is sign this consent form and bring back to us any plastic puffins that you find while you are out looking for real ones. Alternatively, you can give the plastic puffins to Taylor or her assistant Lucy, who will be present in the area with vests on that say their names. Your name and signature on the form will be kept separate from any data you help collect, so you will stay totally anonymous. If you sign the consent form but change your mind about participating, just let us know by the end of the night."

<u>Consent Agreement</u>

The formal consent agreement for this study is on file with Trent University's Research Ethics Board under protocol #28055.

Materials

Decoys were constructed of black polylactic acid plastic using a filament-based 3D printer (Creality CR10S; Shenzhen, China). Right and left legs were designed and printed separately, then inserted and glued into sockets in the main body of the decoy. We spray-painted decoy undersides white in a pattern similar to that of real pufflings (Krylon Fusion All-In-One Paint and Primer in Gloss Dover White; Sherwin-Williams; Cleveland, OH, USA) and used black permanent marker to write a unique identifying number (1-60) on the underside of the tail.

Tables

Table A4.1. All decoy locations at both of the experimental sites, including their coordinates (easting and northing), illuminance (lux), qualitative light level, and concealment level. Note that the spectrometer used to measure illuminance was not capable of detecting <10 lux, so both "dim" and "dark" locations register as 0 lux (except location B06, the only "dim" location for which we received a spectrometer reading). "Spec" refers to the spectrometer measurement and "App" refers to that of the phone app ("Lux").

Site	Location	Easting	Northing	Illuminance (lux)		Light Level	Concealment Level
				Spec	**App**		
Store	B01	361486	5237789	0	2	Dim	0
Store	B02	361477	5237808	30	19	Bright	2
Store	B03	361513	5237828	0	3	Dim	3
Store	B04	361493	5237810	0	4	Dim	0
Store	B05	361514	5237838	14	8	Bright	0
Store	B06	361510	5237822	9	5	Dim	0
Store	B07	361501	5237834	0	3	Dim	0
Store	B08	361496	5237826	29	20	Bright	1
Store	B09	361487	5237814	0	1	Dim	0
Store	B10	361476	5237831	19	12	Bright	0
Store	B11	361477	5237816	13	8	Bright	0
Store	B12	361509	5237832	14	8	Bright	1
Store	B13	361507	5237823	0	4	Dim	0
Store	B14	361477	5237798	0	1	Dim	0
Store	B15	361480	5237824	0	3	Dim	2
Store	B16	361483	5237818	0	1	Dark	2
Store	B17	361508	5237769	0	0	Dark	0
Store	B18	361500	5237765	0	1	Dark	0
Store	B19	361483	5237767	0	0	Dark	1
Store	B20	361494	5237748	0	0	Dark	0
Store	B21	361494	5237745	0	0	Dark	2
Store	B22	361525	5237811	0	0	Dark	0
Store	B23	361502	5237755	0	0	Dark	0
Store	B24	361504	5237781	0	3	Dark	0
Store	B25	361513	5237810	0	0	Dark	1
Store	B26	361479	5237784	0	0	Dark	1
Store	B27	361530	5237826	0	0	Dark	1
Store	B28	361492	5237834	0	0	Dark	1
Store	B29	361499	5237814	0	1	Dark	3
Store	B30	361480	5237842	0	0	Dark	3
Plant	C01	362100	5237785	10	6	Bright	1
Plant	C02	362111	5237797	13	6	Bright	2
Plant	C03	362099	5237802	66	43	Bright	0

Plant	C04	362112	5237803	16	10	Bright	0
Plant	C05	362118	5237800	0	1	Dim	1
Plant	C06	362120	5237832	32	19	Bright	0
Plant	C07	362116	5237838	46	35	Bright	1
Plant	C08	362095	5237839	24	13	Bright	0
Plant	C09	362112	5237845	35	21	Bright	3
Plant	C10	362110	5237852	21	12	Bright	0
Plant	C11	362096	5237856	21	9	Bright	1
Plant	C12	362066	5237866	10	6	Bright	1
Plant	C13	362063	5237850	38	22	Bright	3
Plant	C14	362042	5237845	42	34	Bright	1
Plant	C15	362079	5237764	10	5	Bright	3
Plant	C16	362069	5237736	0	0	Dark	1
Plant	C17	362131	5237804	0	0	Dark	1
Plant	C18	362136	5237819	0	0	Dark	0
Plant	C19	362131	5237831	0	0	Dark	3
Plant	C20	362122	5237862	0	1	Dark	1
Plant	C21	362090	5237861	0	3	Dark	1
Plant	C22	362089	5237878	0	1	Dark	2
Plant	C23	362082	5237862	0	0	Dark	3
Plant	C24	362084	5237855	0	1	Dark	1
Plant	C25	362047	5237845	0	0	Dark	2
Plant	C26	362035	5237841	0	0	Dark	1
Plant	C27	362040	5237842	0	0	Dark	2
Plant	C28	362109	5237869	0	0	Dark	2
Plant	C29	362093	5237825	0	0	Dark	2
Plant	C30	362090	5237779	0	0	Dark	4

Appendix – General

Permission from copyright holders

Chapter 1: A path forward in the investigation of seabird strandings attributed to light attraction.

Published in: *Conserv. Sci. Pract.* (2023) 5:e12852.

doi: 10.1111/csp2.12852

Chapter 2: Navigating the night: effects of artificial light on the behaviour of Atlantic puffin fledglings.

Published in: *Anim. Behav.* (2024) 218:135-148.

doi: 10.1016/j.anbehav.2024.09.008

Dear Dr. Taylor Brown,

Article reference: YANBE_22979
Article Title: Navigating the Night: Effects of Artificial Light on the Behaviour of Atlantic Puffin Fledglings.

Thank you for your email. I sincerely apologize for any inconvenience or delay this matter has caused.

Thank you for contacting us with your query regarding reusing your above ref article.

I want to let you know that authors can reuse their articles, in full or in part, for various scholarly, non-commercial purposes, including inclusion in a thesis or dissertation.

Dear Prof. Brown,

Thank you for contacting us.

As an Elsevier journal author, you retain the right to Include the article in a thesis or dissertation (provided that this is not to be published commercially) whether in full or in part, subject to proper acknowledgment; see https://www.elsevier.com/about/policies/copyright for more information. As this is a retained right, no written permission from Elsevier is necessary.

As outlined in our permissions licenses, this extends to the posting to your university's digital repository of the thesis provided that if you include the published journal article (PJA) version, it is embedded in your thesis only and not separately downloadable.

Note: Yes, as the author of the article, you could modify your work to better serve your thesis.

Thank you.

Kind regards,

Thomas Rexson Yesudoss
Copyrights Specialist
ELSEVIER | HCM - Health Content Management

Chapter 3: Under cover of darkness: refuge from artificial light at night may mitigate

risks to stranded seabirds.

Published in: *Ornithol. Appl.* (2025) duaf018

doi: 10.1093/ornithapp/duaf018

Good afternoon Mark,

I am writing in regards to my article accepted for publication by Ornithological Applications entitled "Under cover of darkness: Refuge from artificial light at night may mitigate risks to stranded seabirds" (https://doi.org/10.1093/ornithapp/duaf018). I would like to include this article as a chapter in my PhD dissertation. I believe the current Creative Commons license allows me to do so regardless of whether I modify the article (e.g., pending revisions by my defense committee) but I just wanted to check with you and make sure there is nothing else I need to do to in order to be allowed to do this.

Best wishes,
Taylor Brown

Kyle Burns <Kyle.Burns@oup.com>
to AOSPublications, me ▾

Tue, Mar 4, 3:55 PM (3 days ago)

Hello Taylor,

You are correct. This article is an open access article distributed under the terms of the Creative Commons CC BY license, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

You are not required to obtain permission to reuse this article.

Let me know if you have any questions!