Navigating the Night: Effects of Artificial Light on the Behaviour of Atlantic Puffin Fledglings

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Abstract

Every year in Newfoundland, young Atlantic Puffins 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 toward 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 several different light types. 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, indicating 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 High Pressure Sodium light than in LED light, potentially holding implications for rescue, rehabilitation, and husbandry programs. Overall, our findings demonstrate that the only evidence-based strategy for the reduction of Atlantic Puffin strandings remains to be the reduction of coastal artificial lighting; however, further research is needed to determine if aspects of artificial light besides bulb type may be altered to effectively reduce light attraction in this species.

Keywords: alcid, ALAN, light attraction, seabird, phototaxis, fledging, behaviour

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 lighting is expected to worsen the ecological impacts of ALAN through a variety of mechanisms (Pawson and Bader, 2014; Davies and Smyth, 2018). 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 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 point sources of ALAN (Rodríguez et al., 2017a; but there are other non-mutually exclusive hypotheses for stranding; Brown et al., 2023). 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; Wilhelm et al., 2021; Collins et al., 2023). 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., 2023). 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).

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 pufflings and have thus been deemed stranding “hotspots” (Canadian Parks and Wilderness Society, unpubl. 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 suggest that young birds become stranded because of their inexperience in navigating a new environment (Brown et al., 2023). 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).

At small geographic scales, the behavior 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. Collecting this type of information for more stranding-affected species would supplement our understanding of seabird phototaxis as well as aid rescue efforts in predicting where stranded seabirds are likely to

go and how they will behave following stranding. Such knowledge 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; Warm White LED; Orange LED). 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 scientific permit #SC4051.

Study Sites and Species

In Newfoundland, most stranded puffin fledglings (hereafter, "pufflings") are found along a ~15 km section of coastline between the communities of Bay Bulls and Bauline East. This section forms the focal search area for the "Puffin Patrol", a volunteer-based puffling rescue program that operates each year during the fledging (and stranding) season (Wilhelm et al., 2013, 2021; Figure 1). Stranded pufflings are thought to largely originate from the breeding colonies on Gull Island (47.262297°N, 52.773389°W) and Great Island (47.187182°N, 52.813495°W), both part of the Witless Bay Ecological Reserve and located less than 3 km from shore at their closest points (Wilhelm et al., 2013). Collectively, the reserve hosts some 304,000 breeding pairs (Wilhelm et al., 2021), forming the largest concentration in North America (Lowther et al. 2020).

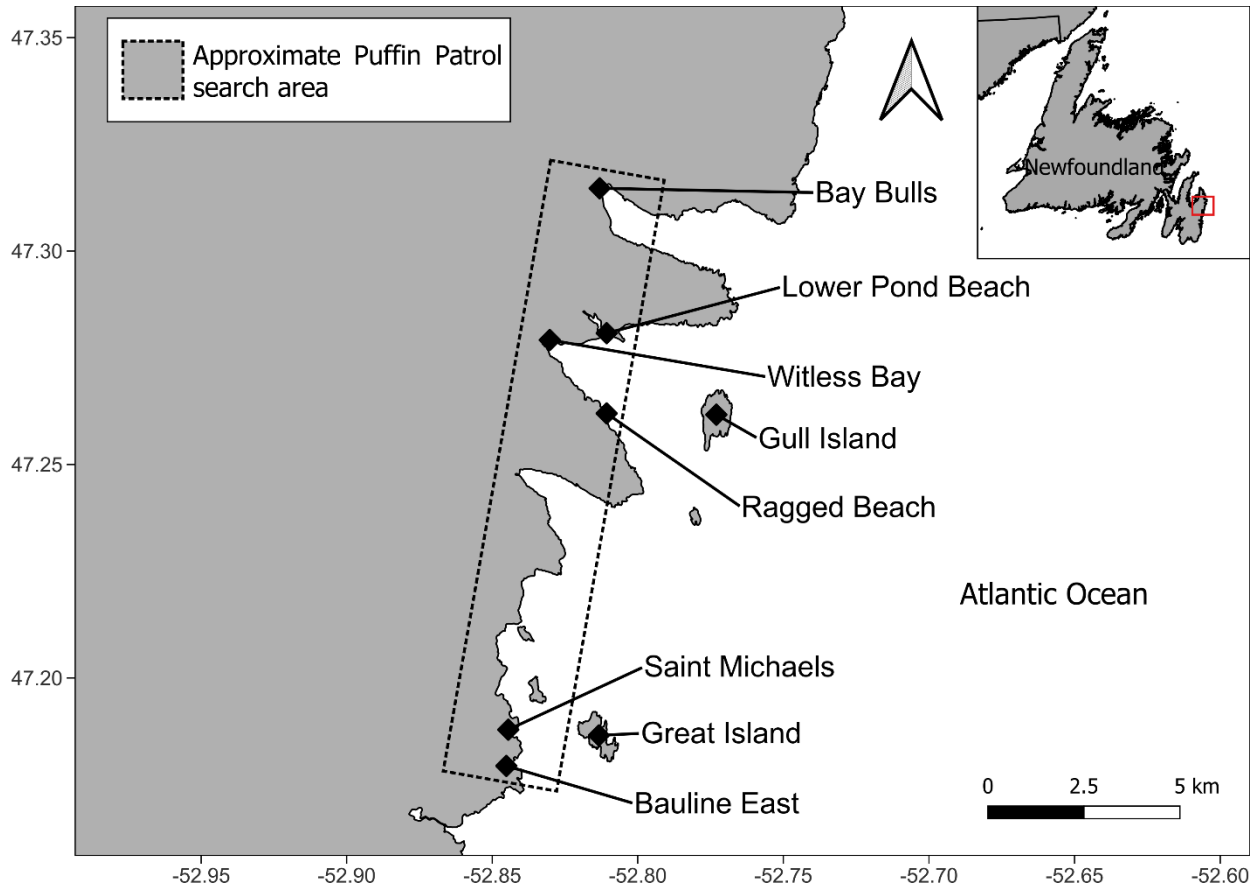

Figure 1. Map of Puffin Patrol search area in Newfoundland, Canada, including all relevant locations of research activities (Bay Bulls, Lower Pond Beach, Ragged Beach, Saint Michaels) and Atlantic Puffin breeding colonies (Gull Island, Great Island).

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 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 1). In 2021, we conducted the fine-scale experiments in one of two identical "field labs" (storage trailers, 2.4 x 1.4 x 2.1 m) located adjacent to the headquarters for the Canadian Parks and Wilderness Society'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 heated building in Saint Michaels (47.187247°N, -52.843990°W; Figure 1).

Response of pufflings to light at a coarse spatial scale

Equipment

We illuminated one of two beaches (Lower Pond beach or Ragged Beach; Figure 1) over 11 nights between 15-27 August 2022 (experiments were not conducted August 17 and 18 due to inclement weather). At both beaches, an LED light apparatus (Willpower 52-inch, 675-Watt LED light bar: Xalapa, Veracruz, Mexico) 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 metres above sea level). 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 apparatus and associated equipment was set up but not turned on.

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 21:30 and 00:30, depending on the night. On two nights there was an equipment malfunction in the middle of the trial, but by extending the 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 metres on either side of the light apparatus, to ensure no pufflings were already present on the beach prior to the start of the experiment. We then placed two reflective safety vests 25 metres 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 (~750 - 1000 m^2). This distance was chosen based on preliminary tests of the visual acuity and range of the night vision binoculars used (Bestguarder NV900 4.5-22.5 x 40 HD; Shenzhen, China) 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 50-metre-long and approximately 15- to 20-metre-wide focal beach observation area with night vision binoculars.

The remaining team members scanned the beach, water, and airspace with the unaided eye and recorded each puffling observation, as well as whether a puffling was suspected or known to be the same individual as one observed earlier. Observers took turns (of no set duration) using the night vision binoculars to avoid fatigue.

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 x 30 cm wide x 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. 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. We tabulated these three separate counts because, despite our best efforts in the field, it was not always possible to determine if an observed puffling was a "new" individual or one already observed earlier in the night. This was especially true for swimming individuals. *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. 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 (especially in the water and in the air, as they are able to quickly move in and out of view), 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. 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. Canadian Parks and Wilderness Society 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 ~20:00 and 21:00, we brought the first rescued pufflings in their crates to a grassy area next to our "field labs," approximately 25 metres 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.

Equipment 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; Figure S1). The metal "acclimation box" opened into the "main box", 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"). 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 x 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 threshold between each choice arm and its corresponding choice box, allowing us to detect when an individual had made a choice (Figure 2).

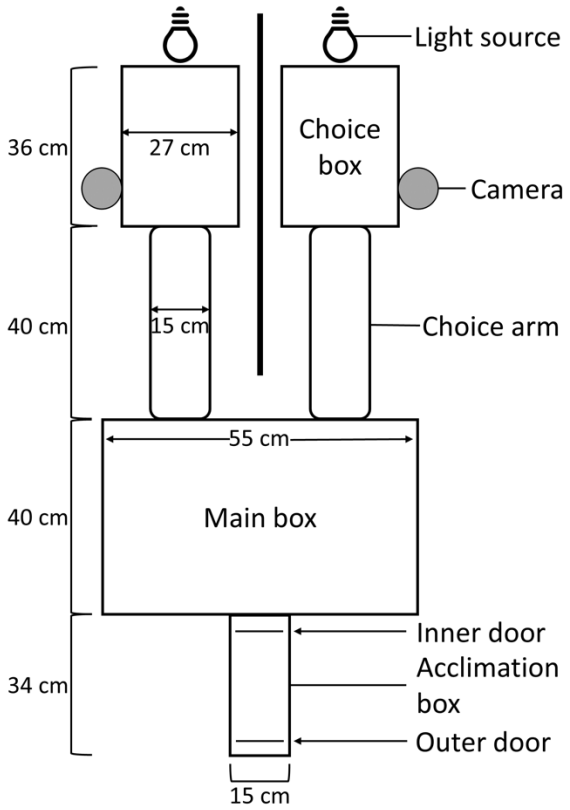

Figure 2. View from above the Y-maze apparatus used for our choice experiment. We placed an individual puffling inside the acclimation box prior to the start of a behavioural trial. The inner door was then opened, and the bird was allowed to enter and explore the main box, choice arms, and choice boxes. An infrared camera detected when an individual became visible at the threshold of a choice box. Note that the diagram is not to scale.

Three different types of lights were used in combination with various filters to produce six spectral choice combinations (spectra displayed in Figure S1): High Pressure Sodium with a

correlated colour temperature (CCT) of 2100 K ("HPS"; Light EnerG, 400 Watt; manufacturer location unknown); Warm White Light Emitting Diode (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 uniform and approximately equal across light types, as measured by a calibrated spectrometer (see Supplementary Material). 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 Supplementary Material). We tested pufflings in blue and orange LED light in an attempt to distinguish effects of "warm"- and

315 “cool”-coloured light on phototaxis, following distinctions reported in the literature for other
316 seabird species (Salamolard et al., 2001 as cited in Minatchy, 2004; Rodríguez et al., 2017b).

317

318 **Procedure of choice experiment to measure phototactic behaviour**

319 In 2021, 107 pufflings were randomly chosen from those that were stranded and rescued by
320 the Puffin Patrol and divided among five choice combinations. We tested only one combination
321 each night via selection out of a hat (i.e., it took five consecutive nights to conduct trials in all
322 five combinations, after which they were drawn nightly again in random order), except in the last
323 few days of the field season when we selected the choice combination each night to correct for
324 sample-size deficiencies. In 2022, 25 pufflings were tested in Bright Blue LED vs Orange LED,
325 resulting in a total choice experiment sample size of n = 132.

326 Before each trial, the light stimuli were put in their positions and turned on. Each puffling
327 was brought into the field lab, removed from its holding container, and placed in the acclimation
328 box of the Y-maze. After precisely 2 minutes the inner sliding door was removed and the puffling
329 was allowed 13 minutes to make a “choice”. If the puffling did not voluntarily exit the
330 acclimation box by 5 minutes after removal of the inner door, it was gently prodded with the
331 experimenter’s hand reaching through the outer sliding door until the puffling entered the main
332 box. In total, 20% (27 of 132) of pufflings needed prodding. A choice was considered to have
333 been made when a bird reached the end of a choice arm and any part of the body was visible on
334 the monitor (even if it did not fully enter the choice box). The bird was removed from the
335 apparatus after making a choice or after 15 minutes had elapsed (deemed “No Choice”),
336 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 preference on part of the birds.

Equipment 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 x 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 x 20 cm grid composed of 25 squares (i.e., 5 squares x 5 squares) was created on the floor using black electrical tape. A flap door (approximately 20 cm wide x 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 3cm 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 (qualitatively, this distance resulted in a relatively equal amount of light entering the arena).

360

361 **Experimental procedure to measure activity levels under various light spectra**

362 To determine whether puffling activity level was affected by light type, we performed an
363 open field test. In 2021, 96 of the 107 Atlantic Puffin fledglings used in the choice experiment
364 were used in the open field test, whereby we exposed them to either darkness or one of three
365 light spectra. Five individuals were removed from the final dataset due to camera malfunction,
366 resulting in a final sample size of $n = 91$. Treatments were: 1) Darkness ($n = 23$); 2) HPS ($n =$
367 19); 3) Warm White (2700 K) LED ($n = 24$); and 4) Cool White (5000 K) LED ($n = 25$). We did
368 not measure activity in response to blue or orange light. Each night, we used only two light
369 treatments in the open field test, and they were never the same as the two light types used in the
370 Y-maze on the same night. The initial treatment each night was chosen randomly, and treatments
371 were alternated for the rest of the night.

372 Prior to each open field trial, the appropriate light was set up and turned on (except in the
373 Dark treatment), and a video recording (with audio) was started. The puffling was placed just
374 inside the flap door of the arena, and an electronic timer started. After 10 minutes, the video and
375 audio recording were stopped. The puffling was removed from the arena, replaced in its holding
376 container, and returned to Puffin Patrol headquarters. The floor of the arena was not cleaned
377 between trials unless a puffling defecated during its trial, in which case the affected area was
378 cleaned with 70% isopropyl alcohol and allowed to dry before the next trial. As many trials as
379 possible were completed each night (median 10 trials; range 3-13 trials per night).

380

381 **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.

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, 2021). 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 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, obviating the need for formal statistical analysis.

Response of pufflings to light at fine spatial scales

<u>Phototactic behaviour</u>

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 Choice ($n = 23$). 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.

Activity levels

To determine if scoring videos aurally 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 ($\beta = 0.9228$; $p < 0.001$; Supplementary Figure S2). 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.

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 Supplementary Material). 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 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 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 (Supplementary Tables S1, S2). 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 3B). Focussing 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.

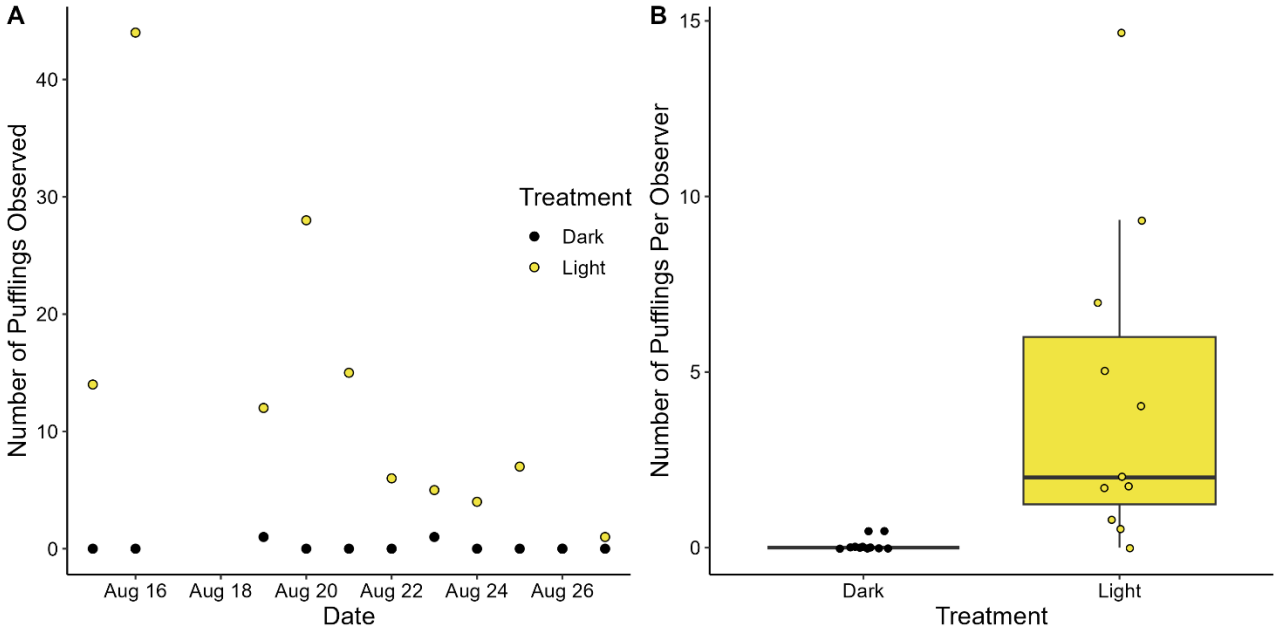

Figure 3. Number of fledgling puffins observed per night on artificially lit and dark beaches. A) Best-estimate total counts of pufflings seen each night during the Dark (black circle) and Light (yellow circle) treatments, 15-27 August 2022. Note that points overlap on August 26 due to zero birds being observed during either treatment. B) Observation rates (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.

Assessment of phototactic behaviour and light preferences

Significantly more individuals chose Bright HPS light than Dark ($p = 0.002$; estimated true proportion of Bright HPS, 95% CI: 0.69-1.00; Table 1) in the choice experiment. Although not statistically significant, more individuals chose Bright HPS over Dim HPS ($p = 0.1$; estimated true proportion of Bright HPS, 95% CI: 0.46-0.88). There was no significant preference of any

light type in any other remaining choice combination (Table 1). There was no statistical evidence for handedness, as pufflings chose Choice Box 1 (n = 57) relatively equally to Choice Box 2 (n = 52; binomial test p = 0.7; estimated true proportion of Choice Box 1, 95% CI: 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).

Table 1. Number of pufflings that chose each of the two light options in each choice combination. Individual binomial tests assessed evidence for a preference of one light type over the other in each choice combination (excluding "No choice" 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 made "No choice" in each combination.

Light type 1	Quantity	Light type 2	Quantity	95% CI	*p*-value	No choice
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 White	11	0.26-0.70	1.0	2
Warm White	10	Cool White	10	0.27-0.73	1.0	2
Dim Blue	13	Orange	9	0.36-0.79	0.5	2
Bright Blue	9	Orange	6	0.32-0.84	0.6	10

Assessment of activity levels in different light types

In our open field test, pufflings spent significantly more time mobile in at least one treatment group compared to the others (Kruskal-Wallis $\chi^2(3) = 18.396$; $p = 0.0004$). 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 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 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 Supplementary Material).

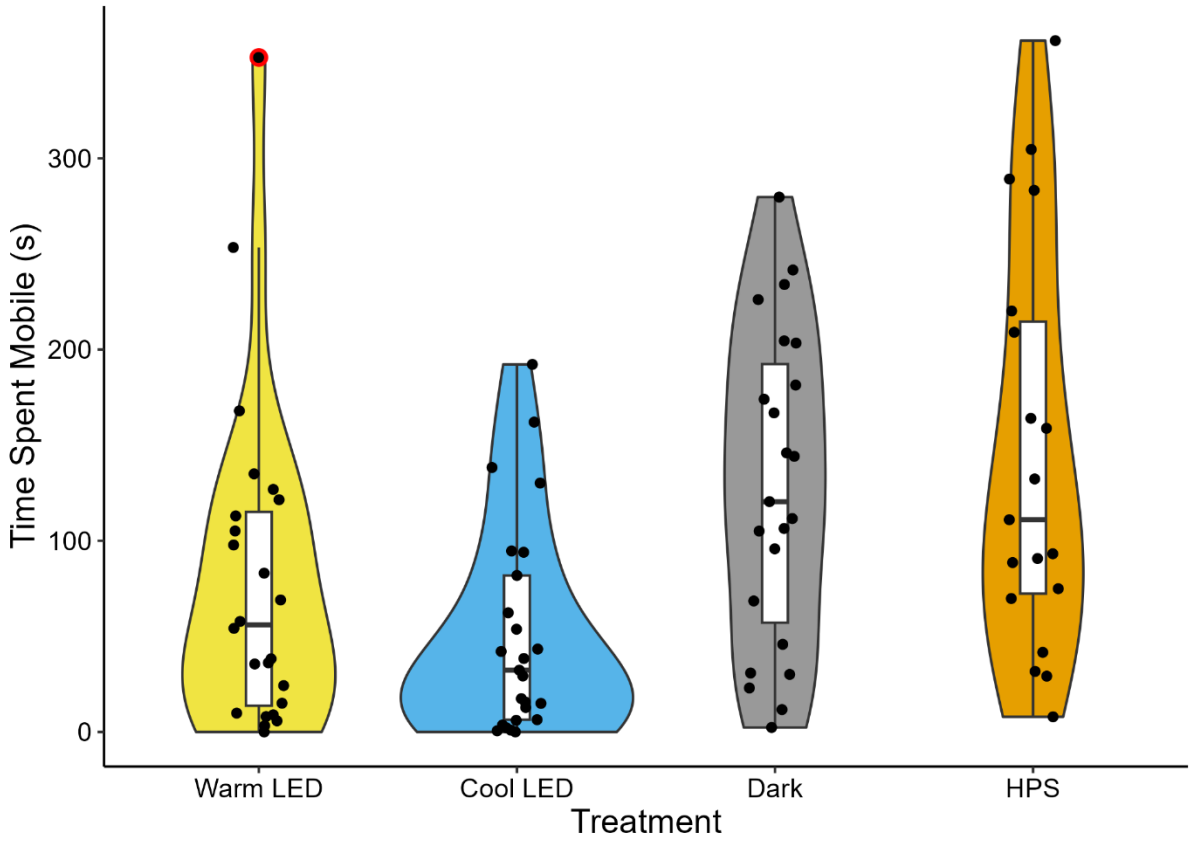

Figure 4. Time spent mobile by fledgling puffins when exposed to each of four light treatment groups. Figure combines a violin plot and boxplot with overlaid individual data points. Sample sizes: Warm White LED light ($n = 24$), Cool White LED light ($n = 25$), Darkness ("converted" data; $n = 23$, see 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 Cool White LED and Warm White LED than when exposed to Darkness, and also significantly less mobile in Cool White LED than in HPS.

Discussion

Our results form the first experimental evidence that light attraction behaviour is a causal mechanism behind the stranding of Atlantic Puffin fledglings (pufflings) in coastal areas during

521 their initial fledging flights. This evidence emerges at both coarse and fine spatial scales. Even
522 after controlling for search effort and size of the search area, in our coarse-scale beach
523 illumination experiment we found significantly more pufflings stranded during the Light
524 treatment than during the Dark treatment. Further, consistent with a light attraction hypothesis of
525 stranding, in our y-maze experiments pufflings significantly preferred light over darkness and
526 somewhat preferred bright HPS light over dim HPS light. Contrary to our expectation that
527 pufflings would prefer "cool" light spectra over "warm" light spectra (based on results of
528 Salamolard et al., 2001 as cited in Minatchy, 2004; Rodríguez et al., 2017b), we found no
529 preferences when pufflings were simultaneously presented with two different light spectra. Our
530 open field test experiment, in which we exposed pufflings to either darkness or one of three light
531 types, revealed that pufflings were more active in Darkness than in any LED light, and more
532 active in HPS light than under Cool White LED light. Pufflings also tended to be more active in
533 HPS light than in Warm White LED light, but this difference only bordered on statistical
534 significance.

535 We are first to demonstrate a reduction in stranding numbers of an alcid through the
536 experimental reduction of ALAN. Our finding that more pufflings became stranded at our two
537 beach sites during the Light treatment compared to the Dark treatment is consistent with similar
538 studies on procellariiforms (Reed et al., 1985; Miles et al., 2010; Rodríguez et al., 2014; Burt et
539 al., 2023). Our results therefore provide further support for recommendations to reduce or
540 eliminate sources of ALAN near breeding colonies of seabirds affected by stranding, especially
541 where populations are already in decline (e.g., Rodríguez et al., 2017a).

542 Previously, we expressed concern that human visual perception is more acute, and
543 therefore the detection of stranded birds is likely more efficient in light conditions compared to

544 darkness, potentially leading to a bias in detection probability (Brown et al., 2023). As such, in
545 our coarse-scale light attraction experiment we attempted to reduce the bias between our two
546 treatments by: 1) using identical night vision binoculars at each of our sites on each night of the
547 experiment; 2) clearly delineating a search area of the same size (area of approximately 50 m x
548 15-20 m) on both beaches that took into account the maximum visual range of the binoculars;
549 and 3) controlling for the number of observers present at each site in our data analysis. Even if
550 our Light treatment was still subject to bias toward elevated detection probability, it is highly
551 unlikely that the large difference in number of pufflings found (n = 54 in Light vs n = 1 in Dark)
552 is attributable to missing a significant number of pufflings in the Dark treatment. In fact, the
553 single puffling we detected within the search area during the Dark treatment was on a night with
554 very low lunar illumination (13.3%), after the moon had already set, and during overcast and
555 rainy conditions. That pufflings were visible to observers even in the worst of visibility
556 conditions suggests that if more individuals were indeed present in the Dark treatment, they
557 would have been detected. Additionally, by alternating each night the site location for Light
558 treatment, we simultaneously controlled for the potential effects of date, moon phase (see
559 Wilhelm et al., 2021) and site on the numbers of pufflings we observed.

560 In addition to the stark difference in number of pufflings observed within the delineated
561 beach search areas in the Light versus Dark treatment, more individuals were also observed
562 swimming and flying in the Light treatment (n = 77 and n = 78, respectively) than in the Dark
563 treatment (n = 1 and n = 1).

564 Support for the light attraction hypothesis of stranding in pufflings is bolstered by the
565 positive phototactic behaviour pufflings displayed in our choice experiment. Pufflings chose
566 Bright High Pressure Sodium (HPS) light significantly more often than darkness and chose

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

580 Contrary to our expectations, pufflings did not display any preferences for certain light
581 spectra over others when presented with a choice. We based our expectations on two premises:
582 first, previous studies have found that attraction behaviour and stranding numbers of fledgling
583 procellariiforms increase under exposure to short wavelength-dominant (i.e., high CCT) light
584 types like metal halide (~4500 K CCT) compared to long wavelength-dominant (low CCT) light
585 types like high pressure sodium (~2000 K CCT; Salamolard et al., 2001 as cited in Minatchy,
586 2004; Rodríguez et al., 2017b), although this is not always the case (e.g., shielding of long
587 wavelength light from radiating upward may negate the effect; Urmston et al., 2022; Atchoi et
588 al., 2024) and evidence is limited. Second, the procellariiform eye is quite sensitive to short
589 wavelengths (Reed, 1986; Bowmaker et al., 1997; Hart, 2004), implying a potential link between

590 the wavelengths of highest spectral sensitivity and those that induce the strongest phototactic
591 responses. Atlantic Puffins likely have similar spectral sensitivities given the similarities in
592 photoreceptor profiles between auks and procellariiforms (Ödeen and Håstad, 2003), which is
593 why we expected they would choose blue light over orange and cool white over warm white
594 LED light in our Y-maze. It is therefore unclear why these choice combinations did not elicit
595 differences in phototactic behaviour. Perhaps the spectrum of light presented simply has no effect
596 on the strength of the phototactic response, assuming the spectrum falls enough within the bird's
597 sensitivity range to be perceived as light at all. Another possible explanation is that the position
598 of the birds (i.e., standing and walking) in a small experimental apparatus is so contextually
599 different from flying that it elicits a completely different mode of behaviour as it relates to
600 lighting conditions. A coarse-scale beach illumination experiment that compares phototactic
601 responses and stranding numbers across several different light spectra may provide insight in a
602 more realistic context (as per Rodríguez et al., 2017b).

603 When we measured the activity levels of pufflings exposed to darkness and various spectra
604 of artificial light in our open field test, they spent significantly more time active in Darkness than
605 in Cool or Warm White LED light, and significantly more time active in High Pressure Sodium
606 (HPS) light than Cool White LED light. It is unclear what factors drove our results, especially in
607 Darkness. It is possible that in the HPS light treatment the low-level noise of the associated
608 ballast fan (unlike the LED lights which have no ballast fan) elicited an attractive response,
609 which has been anecdotally observed in stranded pufflings (Harris, 1982; Harris et al., 1998;
610 reviewed in Wilhelm et al., 2013). Conversely, it is worth considering the possibility that the
611 higher activity levels observed in Darkness and in HPS light were typical, and that LED spectra
612 (which emit more blue light than HPS, even in relatively warm-hued bulb types) have a calming

effect on pufflings that results in reduced activity. Indeed, ducklings reared under blue light are less active and exhibit a reduced fear response (i.e., tonic immobility) compared with individuals reared under other light colours (Sultana et al., 2013). Similarly, black-headed buntings (*Emberiza melanocephala*) experiencing periods of migratory restlessness are less active under blue light (λ_{peak} = 450 nm) than under red light (λ_{peak} = 640 nm), although these activity patterns are reversed outside of periods of migratory restlessness (Yadav et al., 2015). 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.

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. This implies that changes to street lighting from historically prevalent High

Pressure Sodium lamps to more energy-efficient Light Emitting Diode, 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. Contrary to what one might have intuitively expected, our open field test results imply that LED light exposure during captivity (i.e., post-stranding) may have a calming effect on stranded pufflings, even when compared with darkness. This latter result has potentially beneficial implications for rescue, rehabilitation, and even husbandry of puffins and other auks.

Data availability statement: Data are available as Supplementary Material.

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