Under Cover of Darkness: Refuge from Artificial Light at Night may Mitigate Risks to Stranded
Seabirds

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ABSTRACT

Artificial light at night is an anthropogenic pollutant that has wide-ranging effects on wildlife. Fledgling seabirds of the 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 risk of predation. Limited evidence suggests that 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 and exhibited no response toward one light type over another. This was consistent with results from the open field test, in which individuals were less active in darkness than when exposed to two out of three light conditions (Warm White Light-Emitting Diode and High Pressure Sodium). More than half of birds entered the hide box in light conditions, compared to none in the dark. Considered together, our results indicate 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 may be limited in spatial or temporal coverage. Hide boxes constitute a novel mitigation measure that merits future testing for its ability to reduce stranding-induced mortality, especially in imperiled procellariiform species.

Keywords: ALAN, behaviour, fledging, light attraction, phototaxis, procellariiform, sensory ecology

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, which is often considered synonymous with light attraction, has been observed in many 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). Phototaxis toward

ALAN sources can result in mortality through a variety of mechanisms including physiological

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, commonly referred to as tube-nosed seabirds,

constitute 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 species of

procellariiform, such as storm-petrels and shearwaters, are susceptible stranding in developed

coastal areas and at offshore 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, as they are susceptible to

predation, poaching, and vehicle collisions as well as dehydration and starvation (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, Burt et al. 2024, Brown et al. in press). At finer scales and in

ground-based contexts, however, behavioural patterns are more equivocal and vary among

species. For example, 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 (*Fratercula arctica*) fledglings similarly orient toward light over darkness in a Y-maze

(Brown et al. in press), but stranded Cory's shearwater (*Calonectris diomedea*) fledglings

consistently move toward darkness in a similar experiment (Atchoi et al. 2024). The latter result

may indicate a 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 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 orange light or between low- and high-CCT LED

light (Brown et al. in press). 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. in press). 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).

Globally, 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). Although they remain one of the

most abundant procellariiforms in the world, population declines have led to the species being

listed globally as Vulnerable on the IUCN Red List (BirdLife International 2018) and Threatened

in Canada (COSEWIC 2020). Breeding typically begins at 5 years of age (Morse and

Buchheister 1977), and pairs return to the same colony and usually the same burrow each May

and produce a one-egg clutch (Pollet et al. 2021). Adults are nocturnal in their transit to and from

the colony, presumably to reduce predation risk (Pollet et al. 2021). 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,

presumably due to light attraction (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, the hundreds to thousands of

Leach's storm-petrels found stranded each year are presumably the minimum number affected,

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 (e.g., an estimated 300 grounded birds perished in a one-month period in Bay de

Verde; 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

Leach's storm-petrels and other procellariiforms often seek shelter in concealed locations after

grounding (Reed et al. 1985, Rodríguez et al. 2017a).

Our objectives were to: 1) measure phototactic behavioural responses of grounded Leach's

storm-petrels (hereafter "storm-petrels") to artificial lights; and 2) measure their activity under

various lighting conditions. Our working hypothesis across both objectives was that storm-

petrels are attracted to artificial light, and their levels of phototactic behaviour and general

activity will vary across light spectra. We used a Y-maze to measure phototactic behaviour

(objective 1) and expected that fledglings would exhibit positive phototaxis by preferentially

orienting toward light over darkness when both were provided as options. We further expected

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). This reasoning is

based on the peak optical sensitivity of this species to 405 nm violet light (Ödeen and Håstad

2003). We addressed objective 2 using 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*. Lastly, and 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 and 2 to test a third objective: whether different

lighting conditions would influence an individual's propensity to seek shelter in a hide box

(termed a "Safe Haven" box). This latter objective has the potential to inform local-scale rescue

efforts and conservation measures.

METHODS

Study Sites and Species

Experiments were conducted with stranded Leach's 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. Bay de Verde is the northernmost community in

Conception Bay at the northern tip of the Bay de Verde Peninsula (Figure 1) and has a

population of approximately 400 people (Statistics Canada 2017). The seafood processing plant

is a 6,919 m^2 two-storey rectangular building situated on a wharf in a relatively protected

harbour (Marco Group 2023) and receives on an annual basis a relatively large number of

stranded storm-petrels (Wilhelm et al. 2021, Burt et al. 2023, 2024). Storm-petrels that become

stranded there likely originate from Baccalieu Island, located approximately 7 km northeast of

Bay de Verde (Figure 1). We conducted experiments in two sheds on the wharf between 21:00

and 04:30 on 2-11 October 2021 and 3-8 October 2023. In 2021, our experiments at the plant

were conducted at the same time as a light-modifying experiment (Burt et al. 2024). However,

the light-modifying experiment would not have impacted our results, as we were studying the

behaviour of petrels once they had already been grounded and captured.

Figure 1. Leach's storm-petrel colony location (Baccalieu Island), study location (Bay de

Verde), and release location (Witless Bay) with reference to the province's capital city (St.

John's) in the province of Newfoundland and Labrador, Canada.

Animal Collection, Housing, and Release

We collected stranded storm-petrels during opportunistic walking surveys (single "laps")

around the processing plant from approximately 20:00 to 24:00. Although it is possible that

stranded storm-petrel fledglings do not represent a truly random sample of the entire 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. We recorded the approximate time at which individuals were

collected and placed them in cardboard pet carriers, approximately 47 cm long by 25 cm wide by

30 cm tall and lined with disposable absorbent multipurpose pads (up to 25 individuals per

carrier). We kept the containers with rescued birds in darkness in a third, slightly heated shed

near the experiment sheds 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 at

ambient temperature (approximately 5-15°C) in a sheltered location for a minimum 10-minute

rest period. In 2021, we tested Objectives 1 and 2 (phototactic behaviour and activity levels):

following the experiment testing phototactic behaviour, we replaced the bird in its cardboard box

and provided another rest period of minimum 10 minutes before participating in the activity level

experiment. In 2023, we only addressed objective 3, which involved two trials in close

succession: storm-petrels used in this experiment rested for a minimum of 10 minutes before the

first trial, but for only approximately 5 minutes between the first and second trial. In both years,

once an individual had completed its trials, we placed it in a cardboard pet carrier with other

birds that had already completed experimental trials, until release.

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). After the experiments

were completed, we released birds either from a dark shoreline in Bay de Verde (on the same

night of capture and experimentation) or held them overnight and transported them by car to be

released the following evening near Witless Bay, Newfoundland and Labrador (47.262°N,

52.811°W; Figure 1) by Environment and Climate Change Canada personnel.

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. (in press). Briefly, the apparatus consisted of a dark, metal

"acclimation box" (34 × 15 × 15 cm) which opened into a plastic "main box" (40 × 55 × 22 cm)

via a vertical sliding door. From the main box, a pair of corrugated plastic pipes led to one of two

plastic choice boxes (36 × 27 × 18 cm). Each choice box had a 3 cm-diameter round hole in the

end, through which our experimental lights could shine into each choice arm. We used two

infrared baby monitor cameras (VTech, VM5262-2; British Columbia, Canada) to view the

doorway between each choice arm and its corresponding choice box, through small holes in the

walls of the choice boxes, allowing us to detect when an individual had made a response.

We used three different types of lights in combination with various filters to produce four

stimulus combinations (materials and spectra of all light-filter combinations used can be found in

Supplementary Material Table S1; see also Brown et al. in press). The lights used were: HPS

with a 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). The four stimulus

combinations (with number of trials each, in brackets) were: 1) HPS vs Darkness ($n = 19$); 2)

HPS vs Warm White LED ($n = 19$); 3) Warm White LED vs Cool White LED ($n = 17$); and 4)

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 (ePlastics;

California, USA) and glass (Table S1). Further details on the setup of lights and calibration of

irradiance across light spectra are detailed in Brown et al. (in press).

We randomly selected 76 stranded storm-petrel fledglings and divided them amongst the

four light stimulus combinations. 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).

Before each trial, we placed the light stimuli in their positions and turned them on. We

brought the storm-petrel into the choice experiment shed, removed it from its box, and placed it

in the acclimation box of the Y-maze. We set a timer for two minutes, after which we removed

the inner sliding door, and the bird was allowed 13 minutes to make a "response" (each trial was

a maximum of 15 minutes). If the bird did not voluntarily exit the acclimation box within 5

minutes after removal of the inner door, it was gently prodded with the experimenter's hand until

it entered the main box ($n = 53$ out of 76 storm-petrels, or 70%, were prodded). A response was

considered to have been made by the bird when it reached the end of the choice arm, and any

part of the body was visible on the baby monitor screen (even if it did not enter the choice box).

The bird was removed from the apparatus after making a response or after 15 minutes had

elapsed with no response ("No Response"), whichever came first, and returned to its cardboard

box in preparation for the activity level experiment. In most cases of "No Response," storm-

petrels sat still in the apparatus, but "No Response" also includes the few individuals that audibly

wandered around inside the apparatus without ever becoming visible on the monitor screen.

Between trials we cleaned the entirety of the 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

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. (in press). Briefly, 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 (i.e.,

5 squares × 5 squares) on the floor, cut an access door into the bottom edge 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.

In this experiment, the same 76 storm-petrel fledglings trialed in the Y-maze were divided

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

either 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: 1)

Darkness ($n = 21$); 2) HPS ($n = 18$); 3) Warm White (2700K) LED ($n = 16$); and 4) 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

not statistically different across the three light treatments (23 – 26 lux; Kruskal-Wallis $\chi^2(2) =$

1.3696, $p = 0.5$; as per Brown et al. in press) and was similar to that of a comparable recent study

(30 lux; Atchoi et al. 2023). 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 set up and turned on the appropriate light (except in the

Dark treatment, in which the light was in place but not turned on) and started a video recording

(with audio). We placed the storm-petrel just inside the access door of the arena and started an

electronic timer for 10 minutes, after which time the video and audio recording were stopped.

The storm-petrel was removed from the arena, replaced in its box, and returned to the heated

shed. The floor of the arena was not cleaned between trials unless a storm-petrel defecated

during its 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 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 (see Brown et al. in press). 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 (KB) did all visual

and audial scoring.

Safe Haven Test

We used the same polycarbonate arena for the Safe Haven test as we used for the open

field test; however, we removed the roof and its overlaying curtain. Inside the arena we placed an

empty black plastic rodent bait station (approximately 36 cm × 31 cm × 16 cm; Bell Laboratories

Protecta Evo Express; Wisconsin, USA) which we hereafter refer to as the "Safe Haven box"

(Figure 2). 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.

Figure 2. A) Floor layout of the Safe Haven test arena, including Safe Haven box and Leach's

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 against the wall of the arena.

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 ($n = 8$). 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). We then removed the storm-petrel from the arena (or from the Safe Haven

box, when applicable), replaced it in its cardboard holding box, and allowed it to rest for 5

minutes until the arena was ready for the second trial. The floor of the arena was not cleaned

between trials unless a storm-petrel defecated during its trial, in which case the affected area was

cleaned with 70% isopropyl alcohol and allowed to dry before the next 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

All analyses were performed in program R (ver. 4.3.0; R Core Team 2021). We report

results to a significance level of $\alpha = 0.05$.

Choice experiment to measure phototactic behaviour.

To test whether storm-petrels displayed phototactic responses toward certain light spectra

over others, we first excluded individuals who exhibited "No Response". We used the remaining

data to conduct exact two-tailed binomial tests (package "*stats*", v. 4.3.0; in program R, v. 4.3.0)

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. We report 95%

confidence intervals of the estimated true proportions.

Measuring activity levels under various light spectra.

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). The regression equation was statistically significant ($r^2 = 0.823$; $F(1, 8) = 37.12$; $p <$

0.001), and auditory scores predicted visual scores ($\beta = 0.6980$; $p < 0.001$; Figure S1). 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.

We conducted a Levene Test (package "*car*", v. 3.1-2) to test for homogeneity of variance

in time spent mobile across treatments, and a Shapiro-Wilk test (package "*stats*", v. 4.3.0) on the

residuals of a standard ANOVA of time spent mobile across treatments to test for normality.

Variance differed significantly across treatments ($F(3, 70) = 7.5594$; $p < 0.001$) but the there was

no evidence for deviation from normality ($W = 0.984$, $p = 0.5$). We therefore used a Welch's

one-way ANOVA (which does not assume equal variances) 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 (package "*rstatix*",

v. 0.7.2).

Safe haven test.

To test whether individual storm-petrel fledglings differed in their probability to enter the

Safe Haven box depending on the light treatment used (Light or Dark), we conducted a classical

version of McNemar's chi-squared test for paired data (Pembury Smith and Ruxton 2020).

RESULTS

Choice Experiment to Measure Phototactic Behaviour

Sixty-three percent ($n = 48$ of a total $n = 76$) of storm-petrels displayed "No Response"

(Table 1) and were excluded from subsequent binomial tests to evaluate light response. Of the

remaining $n = 28$ individuals that responded to one of the two provided light options, 43% ($n =$

12) were prodded out of the acclimation box into the main box after 5 minutes of inactivity,

while 57% ($n = 16$) voluntarily left the acclimation box (Table 1). Focusing on the 28 storm-

petrels that made a response, we found no significant response toward any light type in our

stimulus combinations (i.e., light type 1 vs. light type 2; Table 2). Among individuals that made

a response, there was also no statistical evidence for side bias, as storm-petrels chose Box 1 ($n =$

15) relatively equally to Box 2 ($n = 13$; binomial test $p = 0.9$; 95% CI of estimated true

proportion of Box 1: 0.34-0.72).

Table 1. 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. Also shown are totals in each

category and total experimental sample size ($n = 76$).

		Prodded		
		Yes	**No**	**Total**
Responded	**Yes**	12	16	28
	No	41	7	48
	Total	53	23	**76**

Table 2. Number of storm-petrels that responded to each of the two light options in each stimulus combination (columns 2 and 4) or exhibited no response for one light type over the other ("No Response"). We also report the 95% confidence intervals of the true proportion of "Light type 1" as a reference, and the *p*-value of the exact two-tailed binomial test on the quantities that responded to each light option.

Light type 1	Number	Light type 2	Number	95% CI	*p*-value	No response
HPS	3	Dark	6	0.07-0.70	0.5	10
HPS	5	Warm White	3	0.24-0.91	0.7	11
Warm White	4	Cool White	4	0.16-0.84	1.0	9
Blue	2	Orange	1	0.09-0.99	1.0	18

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 individuals spent significantly less time mobile in Darkness (mean time spent mobile = 84 seconds) than in Warm White LED light (mean time spent mobile = 210 seconds) and in HPS light (mean time spent mobile = 172 seconds; $p < 0.01$ and $p < 0.05$, respectively; Figure 3). None of the other light treatments differed significantly from each other in time spent mobile. Note that because of the conversion applied to scores of time spent mobile in Darkness using a linear equation with intercept $y = 56$, there are no scores of time spent mobile lower than 56 seconds in that group. Although this adds a degree of uncertainty to some scores in that group (some individuals were

almost certainly active for < 56 seconds), it results in a more conservative approach to estimating

differences in time spent mobile across groups.

Figure 3. Fledgling Leach's 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, with overlaid individual data points. 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.

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 (Figure 4). In contrast, when exposed to the Light

treatment, 8 of the same 14 storm-petrels entered the Safe Haven box while 6 did not enter

(Figure 4).

Figure 4. Zero Leach's storm-petrels entered the Safe Haven box in darkness, but more than half

did in light conditions. Note that each individual experienced both a light and a dark trial ($n = 14$

individuals).

DISCUSSION

We expected that Leach's storm-petrels would display evidence of positive phototaxis when tested in a laboratory setting. We based our expectations on the hypothesis that light attraction is the main driver of Leach's storm-petrel stranding (Miles et al. 2010, Wilhelm et al. 2021, Burt et al. 2024). In contrast to our expectation, most fledglings either displayed no response to light stimuli or displayed evidence of negative phototaxis (light avoidance). 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 acclimation box and, following prodding, in the main box of the Y-maze apparatus. Further, although there were no significant responses displayed in any stimulus combination, numerically more birds moved toward darkness in the HPS vs Darkness group (three and six, respectively). The apparent photophobic behaviour of storm-petrels in the choice experiment was consistent with the lower activity levels they exhibited in darkness in our open field test, and with the increased probability of storm-petrels 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.

Our findings are consistent with those of Atchoi et al. (2023, 2024), who found evidence for photophobic behaviour in fallout-susceptible Cory's shearwater (*Calonectris diomedea*) 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) at their colonies in the form of reduced

attendance levels and later arrival when light is at naturally high levels (Watanuki 1986, Riou

and Hamer 2008, Silva et al. 2011) or artificially introduced (Syposz et al. 2021, Austad et al.

2023).

However, the aforementioned photophobic responses are in contrast to the positively

phototactic behaviours observed in other contexts or in other burrow-nesting seabird taxa. Of

course, our initial (incorrect) prediction that Leach's storm-petrel fledglings would be positively

phototactic in our Y-maze choice experiment 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, Burt et

al. 2024, Brown et al. in press). Our results contrast with previous findings in Ancient Murrelet

chicks (Gaston et al. 1988), Atlantic Puffin fledglings (Brown et al. in press), and Common

Diving Petrel (*Pelecanoides urinatrix*) adults (Brooke 1989), all of which responded

significantly more to light than to darkness when provided with the two as options.

These similarities and differences among results reflect a handful of the many taxon-, age-,

and context-dependent differences that likely exist among stranding-prone seabirds in their

behavioural responses to ALAN. 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 apparatuses (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

through an innate drive to seek the safety of darkness. Our experiment cannot distinguish these

competing hypotheses; future studies might seek to test them by introducing artificial predator

cues into an open field or Y-maze experiment to determine if photophobic behaviour is increased

in the presence of a perceived predator or by experimentally manipulating light and darkness

within the Safe Haven box itself (i.e., whether birds still enter the box when it is illuminated

from inside).

In contrast to fledgling procellariiforms, which show negative phototaxis when on the

ground (Atchoi et al. 2024, this study), chicks and fledglings of burrow-nesting charadriiforms

display positive phototaxis (specifically those in the family Alcidae; Gaston et al. 1988, Brown et

al. in press). Functionally speaking, it is unclear why the two groups differ when at similar

developmental stages and in similar contexts, despite their shared tendency to 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). In general, burrow-nesting charadriiforms 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, differences in

abundance, distribution, and shape of rod photoreceptors (which are responsible for visual

sensitivity in low light levels) as well as differences in shape and absolute size of the eye itself

between primarily diurnal versus nocturnal species reflect differential sensitivities to light in dark

environments (Rojas et al. 1999, Hart 2001, Harmening and Wagner 2011, Martin 2022). It is

therefore possible that the largely nocturnal Leach's storm-petrel (Pollet et al. 2021) is more

sensitive to light than the primarily diurnal Atlantic Puffin, contributing to the differences in

behavioural responses we observed in Leach's storm-petrels when compared to previous studies

of puffins (Brown et al. in press). That said, still little is known about variation in ocular anatomy

and physiology across stranding-prone seabird species and how it may contribute to observed

differences in phototactic behaviour.

In addition to investigating phototactic responses to light versus darkness, our study sought

to explore the effects of various light spectra on phototactic behaviour of stranded Leach's

storm-petrel fledglings in a Y-maze experiment and found no significant responses among any

light combinations we provided. We expected storm-petrels to preferentially respond to short

wavelength-dominant spectra (e.g., Cool White LED; Blue LED) over those that are long

wavelength-dominant (e.g., Warm White LED; Orange LED) based on previous studies that

found procellariiform attraction and stranding numbers increased in the presence of short

wavelength-dominant light (Salamolard et al. 2001 as cited in Minatchy 2004, Rodríguez et al.

2017b). Our current results demonstrating no differences in response by Leach's storm-petrels to

different light types agree with those of our previous Y-maze experiment with Atlantic Puffin

fledglings (Brown et al. in press), 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. 2021). In comparison, few

Leach's 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. Most of our light stimuli were calibrated such that the amount of light irradiated at

the peak wavelength of each spectrum was relatively equal (Figure S2). We did this because the

calibration of spectra based on perceived "brightness", although valuable, 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. 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. in press). 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 presumably, mobile birds are more conspicuous than stationary birds,

all else being equal.

It is important to note that our study, which focused on small-scale behavioural responses

to light in a ground-based context, does not attempt to predict phototactic behaviour of birds in

flight or how it may relate to stranding. It should also be noted that the storm-petrels used in our

experiments were already grounded and therefore may have encountered any number of stressors

prior to capture that could have influenced their behaviour.

When fledging birds become grounded, they are vulnerable to increased predation risk

(Rodríguez et al. 2017a, Burt et al. 2024). To address our third objective, we tested the

propensity of Leach's storm-petrel fledglings to enter a provided dark hiding place under

different lighting conditions. We found that more than half of birds 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,

preliminary trials revealed that birds only entered the Safe Haven box when its doors were

oriented along the wall of the open field apparatus, so this needs to be considered when

deploying them. 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 in a

single night (TMB and SIW, 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 significant evidence for photophobic behaviour in fledgling Leach's storm-

petrels that have been grounded in areas illuminated by ALAN. Importantly, we have also

demonstrated that this behaviour tends to be exhibited regardless of the spectrum of light to

which birds are exposed, although these results may be applicable to ground-based contexts only

(i.e., after stranding). Our findings have implications for seabird rescue programs:

procellariiforms that become grounded in dark areas are likely to remain there, as evidenced by

their low activity levels and lack of hiding response in experimentally dark conditions. This is in

contrast to procellariiform fledglings grounded in light areas, which exhibit high activity levels

and seek out dark hiding places. Given that individuals become stranded in large numbers in

lighted areas and rescue efforts are typically focused there, our results emphasize the importance

that industry-led bird surveys and grassroots rescue programs specifically target concealed dark

locations where stranded birds may hide. We also used our results to 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. The extinguishing of ALAN is not always possible,

especially in industrial settings where human safety during nocturnal operations is a priority;

additionally, rescue programs can only employ the help of a limited number of rescuers over a

limited time and geographic area. The deployment of Safe Haven boxes in illuminated stranding

"hotspots" takes advantage of the negatively phototactic behaviour displayed by stranded

fledglings to assist in their safe rescue and provide an additional measure to help conserve

seabird populations affected by ALAN.

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Ethics statement

All handling and experimental procedures involving the use of animals were performed in

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