

# Arctic, Antarctic, and Alpine Research

An Interdisciplinary Journal

ISSN: (Print) (Online) Journal homepage: [www.tandfonline.com/journals/uaar20](http://www.tandfonline.com/journals/uaar20)

## Activity of predators in seabird colonies decreases during the darkest compared to the brightest phase of the diel cycle below, but not above, the Arctic Circle

Nicholas P. Huffeldt, Floris M. van Beest, Haley L. Kenyon, Jóhannis Danielsen & Tim Guilford

To cite this article: Nicholas P. Huffeldt, Floris M. van Beest, Haley L. Kenyon, Jóhannis Danielsen & Tim Guilford (2024) Activity of predators in seabird colonies decreases during the darkest compared to the brightest phase of the diel cycle below, but not above, the Arctic Circle, Arctic, Antarctic, and Alpine Research, 56:1, 2367262, DOI: [10.1080/15230430.2024.2367262](https://doi.org/10.1080/15230430.2024.2367262)

To link to this article: <https://doi.org/10.1080/15230430.2024.2367262>



© 2024 The Author(s). Published with license by Taylor & Francis Group, LLC.



[View supplementary material](#)



Published online: 22 Jul 2024.



[Submit your article to this journal](#)



Article views: 142




[View related articles](#)



[View Crossmark data](#)



## Activity of predators in seabird colonies decreases during the darkest compared to the brightest phase of the diel cycle below, but not above, the Arctic Circle

Nicholas P. Huffeldt <sup>a,b</sup>, Floris M. van Beest <sup>b</sup>, Haley L. Kenyon <sup>c</sup>, Jóhannis Danielsen <sup>d</sup>, and Tim Guilford<sup>e</sup>

<sup>a</sup>Department of Birds and Mammals, Greenland Institute of Natural Resources, Nuuk, Greenland; <sup>b</sup>Arctic Ecosystem Ecology, Department of Ecoscience, Aarhus University, Roskilde, Denmark; <sup>c</sup>Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, Colorado, USA; <sup>d</sup>Seabird Ecology Department, Faroe Marine Research Institute, Tórshavn, Faroe Islands; <sup>e</sup>Department of Zoology, University of Oxford, Oxford, UK

### ABSTRACT

Predator activity can structure communities temporally and influence the spatial distribution of prey. Yet, despite the influence this may have on prey species' activity or geographic persistence, our understanding of whether diel predator activity changes geographically remains limited. Here, we conduct a case study to test whether predator activity during the darkest phase of the diel cycle increases with the duration of daylight (i.e. photoperiod) at high latitudes during summer, aligning with the photoperiod constraint hypothesis. Using both observations and experiments at one seabird colony above and one below the northern polar (Arctic) circle, we compared predator activity between the brightest and darkest phases of the diel cycle. Avian predator counts were greater and nest predation events were more common during the brightest phase of the diel cycle below the Arctic Circle (i.e. where the sun goes below the horizon) but similar across phases during polar summer (i.e. above the Arctic Circle when the sun does not set). Our results highlight the potential influence of light on activity of predator communities and suggest a possible latitudinal limit to the advantage gained by dark-active strategies for avoidance of visually hunting predators.

### ARTICLE HISTORY

Received 26 January 2024  
Revised 31 May 2024  
Accepted 4 June 2024

### KEYWORDS




Chronoecology; diel activity; light–dark cycle; photoperiod constraint hypothesis; polar latitude; predator activity


### Introduction

Predator activity can influence where and when prey are active (Kronfeld-Schor and Dayan 2003; Vallejo-Vargas et al. 2022). On a global scale, overall increased predation pressure at lower latitudes is thought to place strong limitations on the composition of prey communities (e.g., Schemske et al. 2009; Freestone et al. 2021; Zvereva and Kozlov 2021), whereas at high latitudes a generally lower predation risk may alleviate these limitations for many groups (e.g., McKinnon et al. 2010; Roslin et al. 2017; Roesti et al. 2020; cf., e.g., Harper and Peck 2016 and Freeman et al. 2020 for differing latitudinal predation patterns). More locally, prey may maximize survival and fitness through behavioral modifications, scheduling mating, competitive interactions, and resource acquisition to phases of environmental cycles, in which risk is low (Kronfeld-Schor and Dayan 2003; Shima et al. 2020; Cox, Gardner, and Gaston 2021; Vallejo-Vargas et al. 2022; Ottmann et al.

2023). Specifically, the 24-hour light–dark cycle, which changes with latitude and date, is a primary environmental driver of animal activity patterns (Helm et al. 2017; Kumar 2017; Gilbert et al. 2022; Vallejo-Vargas et al. 2022). If variation in diel predation risk changes concurrently with a change in amplitude of the environmental light–dark cycle, then the population ranges of prey species that schedule activity to a specific phase of this cycle to avoid predation may be restricted (Kaartvedt 2008; Poloczanska et al. 2016; Huffeldt 2020; Ljungström, Langbehn, and Jørgensen 2021; Gilbert et al. 2022; Langbehn et al. 2022; cf. McKinnon et al. 2010; Roslin et al. 2017; Roesti et al. 2020). However, our understanding of whether geographic variation in the diel light–dark cycle influences predator activity remains limited and, in particular, lacks empirical insight (Gilbert et al. 2022; cf. Ljungström, Langbehn, and Jørgensen 2021; Langbehn et al. 2022).

Extreme photoperiods at the highest latitudes can have strong effects on animal activity patterns

**CONTACT** Nicholas P. Huffeldt  [nph@natur.gl](mailto:nph@natur.gl)  Department of Birds and Mammals, Greenland Institute of Natural Resources,  P.O. Box 570, Nuuk 3900, Greenland

 Supplemental data for this article can be accessed online at <https://doi.org/10.1080/15230430.2024.2367262>.

© 2024 The Author(s). Published with license by Taylor & Francis Group, LLC.

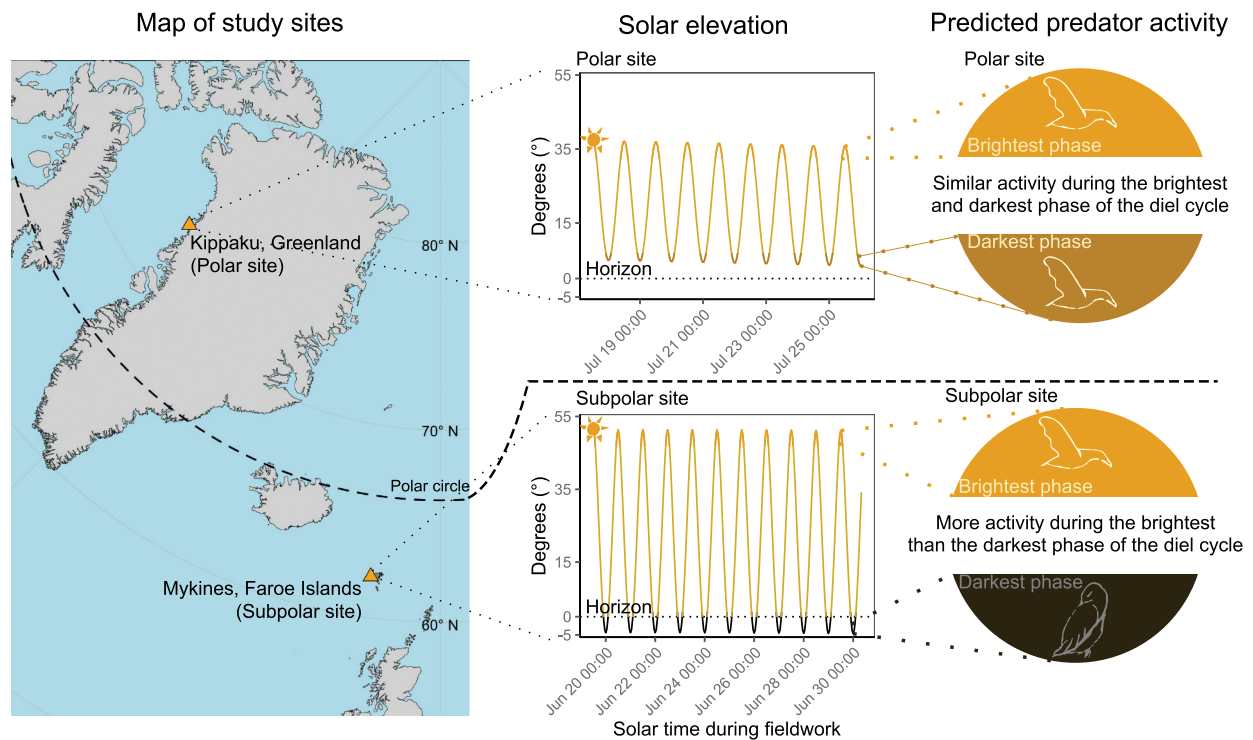
This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (<http://creativecommons.org/licenses/by-nc/4.0/>), which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited. The terms on which this article has been published allow the posting of the Accepted Manuscript in a repository by the author(s) or with their consent.

(Williams, Barnes, and Buck 2015; Bulla et al. 2016; Gilbert et al. 2022; Langbehn et al. 2022), and the increased illumination of the continuous light of polar summer may increase visual encounters between predators and prey across the diel cycle (Watanuki 1986; Langbehn et al. 2022). The occurrence of prey that rely on darkness to escape visual predators could be limited by diminished differences in the temporal variation in visual search efficiency (i.e., the photoperiod constraint hypothesis; Kaartvedt 2008; Langbehn et al. 2022) and/or continuous activity of light-active predators during polar summer. This chronoecological influence of predators may challenge some prey taxa as they track environmental change poleward by eliminating phases of the diel cycle with reduced predation risk (Kaartvedt 2008; Ljungström, Langbehn, and Jørgensen 2021).

Specifically, the interaction between photoperiod and visual predation may affect high-latitude range edges and poleward range shifts of prey species that schedule activity to the darkest phase of the diel and lunar cycles, putatively to buffer against predation (Kaartvedt 2008; Poloczanska et al. 2016; Ljungström, Langbehn, and Jørgensen 2021; Langbehn et al. 2022). These prey species include some insects (Seifert et al. 2016), fishes (Langbehn et al. 2022), birds (Watanuki 1986), and

small mammals (Jones and Rydell 1994; Prugh and Golden 2014). Empirical investigations of the diel variation in predation risk or predator activity aligning with the photoperiod constraint hypothesis are scarce (cf. Ljungström, Langbehn, and Jørgensen 2021; Langbehn et al. 2022 for modeling exercises) but necessary to provide insight into the biogeographic change in activity patterns, top-down control by predators of the temporal organization of communities, and whether predation risk across the diel cycle counteracts the lower overall predation risk at high latitude.

Here, we conduct a restricted case study using observations and nest depredation experiments at two seabird colonies (one polar and one subpolar) with mainly visually hunting predators to ask whether predator activity differs between the darkest and brightest phases of the diel cycle. We define *brightest phase* as the phase surrounding the highest solar elevation (solar noon) and *darkest phase* as the phase surrounding the lowest solar elevation (solar midnight). We predict that predator activity will be greater at the brightest phase in the subpolar colony but will not differ between the brightest and darkest phases at the polar colony, where light is more homogenous across the diel cycle (Figure 1). This case study specifically tests whether predator activity decreases



**Figure 1.** A summary of the prediction and photic environment at the study sites above and below the Arctic Circle.

The dashed line represents the northern polar (Arctic) circle (66.6° N). Yellow indicates that the sun was above the horizon, and black indicates that the sun was below the horizon. We predicted that predator activity would not differ between the brightest and darkest phases of the diel cycle at the polar site but that predator activity would be greater during the brightest phase compared to the darkest phase of the diel cycle at the subpolar site. We illustrated this by depicting avian predators that were active (a flying bird) or inactive (a sleeping bird).

during the darkest phase, compared to the brightest phase, of the diel cycle and does not assess homogenization of diel predation risk or visual search efficiency. These preliminary insights lay an empirical proof of concept to guide future research into the chrono-ecology influence of the photic environment and the top-down effects of predator activity across latitudes, which may have implications for species' range limits.

## Methods

### Study system

Fieldwork occurred at a seabird colony just below the Arctic Circle (62.10° N, 7.64° W; Mykines, Faroe Islands; *subpolar site*) from 18 to 30 June 2021 and a polar seabird colony (73.72° N, 56.62° W; Kippaku, Greenland; *polar site*) from 17 to 26 July 2021 (Figure 1). During fieldwork, the sun went below the horizon for  $4.25 \pm 0.051$  hours (mean  $\pm$  SD) per 24-hour cycle at the subpolar site and never went below the horizon at the polar site (Figure 1). At the subpolar site, all fieldwork occurred in the main seabird breeding areas approximately  $\geq 500$  m west of the settlement on Mykines (including Mykineshólmer) and approximately  $\geq 200$  m east-southeast of the unlit helicopter pad. The areas of Mykines used were mainly grassy hills bordered by sea cliffs. At the polar site, fieldwork occurred across the entire approximately five hectare island, and the island is a mix of rocky grass slopes bordered by sea cliffs on three sides of the island. The polar site was  $>20$  km, mostly over water during summer, from the nearest human settlement.

We conducted the work at seabird colonies, which enabled us to assess the predator community within the colonies with a high degree of certainty. Seabird colonies are fairly isolated on remote islands and have relatively few species of mostly avian predators that depredate other adult and juvenile birds and their nests. Additionally, birds are good models because they are comparably easy to observe, hunt mainly by sight, and are generally more active and

forage more with increasing photoperiod (Pokrovsky et al. 2021).

The most common members of the predator and prey community at each site are different, with more diversity at the subpolar site (Table 1). Briefly, the subpolar site had thirteen species of regularly breeding seabirds (up to seventeen species), including three species of seabirds that only visit the colony during the darkest phase. Domestic sheep and, nearer the settlement, domestic fowl also occurred at the subpolar site. The polar site had five species of breeding seabird, and the glaucous gull (*Larus hyperboreus*), a seabird, was the primary predator observed (Supplementary Material). For the first time since contemporary field campaigns began in 2008, an arctic fox (*Vulpes lagopus*) occurred at the polar site. In addition to the prey listed in Table 1, nests of predatory gulls can be depredated at each site. Each predator species was observed depredating nests, chicks, adults, or a combination thereof of the breeding seabirds at the subpolar and polar sites. Primarily, predators depredated eggs or chicks from open nests, but avian predators also depredated adult gulls, adult auks, and eggs of crevice nesting birds. At both sites, seabirds nested on cliff ledges, on the ground, and in cavities.

### Observations

A single observer counted predators within 300 m of their location every 10 minutes during an *observation block* beginning 30 minutes before and ending 30 minutes after solar noon or solar midnight (seven scans per observation block). The observer conducted one observation block at solar noon or midnight and another observation block at the opposite phase of the diel cycle at the same location (i.e., an *observation replicate*). The observer recorded all predators, usually to species level but always to genus level, and noted whether the predator was active (walking or flying) or inactive (standing or sitting). We excluded inactive predators from further analyses because we observed very few inactive predators at the subpolar site (seven predators). Although when we included all observed predators, the

**Table 1.** Common predators and prey at each study site.

Site	Common predators	Common prey
Subpolar site	Herring gull ( <i>Larus argentatus</i> ), great black-backed gull ( <i>Larus marinus</i> ), lesser black-backed gull ( <i>Larus fuscus</i> ), parasitic jaeger ( <i>Stercorarius parasiticus</i> ), great skua ( <i>Stercorarius skua</i> ), hooded crow ( <i>Corvus cornix</i> ), and northern raven ( <i>Corvus corax</i> )	Arctic tern ( <i>Sterna paradisaea</i> ), black-legged kittiwake ( <i>Rissa tridactyla</i> ), Atlantic puffin ( <i>Fratercula arctica</i> ), black guillemot ( <i>Cepphus grylle</i> ), razorbill ( <i>Alca torda</i> ), common murre ( <i>Uria aalge</i> ), European storm petrel ( <i>Hydrobates pelagicus</i> ), Leach's storm petrel ( <i>Hydrobates leucorhous</i> ), northern fulmar ( <i>Fulmarus glacialis</i> ), and Manx shearwater ( <i>Puffinus puffinus</i> )
Polar site	Glaucous gull ( <i>Larus hyperboreus</i> ), gyrfalcon ( <i>Falco rusticolus</i> ), peregrine falcon ( <i>Falco peregrinus</i> ), northern raven, and arctic fox ( <i>Vulpes lagopus</i> )	Black-legged kittiwake, black guillemot, razorbill, and thick-billed murre ( <i>Uria lomvia</i> )

direction and significance of the results did not change for either site (Supplementary Material).

All observations were made in or directly adjacent to the main breeding areas of prey seabirds. The observer scanned for 45 seconds from ground level to directly above them, starting from behind them and working right until ending at the starting position. Binoculars were used to identify predators spotted during scans, when necessary, but scans were otherwise conducted by naked eye. If visibility was <300 m, then the observer abandoned the observation block (one observation block). Despite the sun being below the horizon during darkest-phase observation blocks at the subpolar site, the lower light intensity did not negatively affect the data collection, and predators were clearly visible and identifiable to at least genus without binoculars. We counted a similar maximum number of predators during observation blocks during each phase (see Results), supporting that our ability to observe and identify predators was not systematically reduced during the darkest phase at the subpolar site. The observer conducted predator observations at six locations at the subpolar site and four locations at the polar site. A minimum of 48 hours elapsed between the beginning of observation replicates at a location at each site. One observation block at the subpolar site was significantly compromised because many individual gulls would consistently take off and make alarm calls when a red light on video equipment was blinking. This observation block was therefore conducted again later. Lights on cameras were otherwise turned off or covered before and after this incident. Another observation block at the subpolar site was compromised by poor weather and humans walking multiple times through the observation area, and this observation replicate was abandoned. In total, there were  $N = 7$  observation replicates at each study site.

## Experiments

We placed an egg in an empty nest that was visible from at least two sides by flying predators. Because we were interested in measuring the general activity and predation by predators, not the reproductive success of prey species, we used a combination of natural and simulated empty nests. Additionally, because we used a paired design (described below) in which a placement generally occurred in a nest during both the brightest and darkest phases of the diel cycle, bias attributed to one nest type should be accounted for in the data collected.

In most cases, a placement occurred during the brightest and darkest phases at the same nest within

a diel cycle. We alternated the first placement between the darkest phase and the brightest phase, unless prohibited, for example, by adverse weather. At the subpolar site, the mean time of placement during the *darkest phase* was 23:54 (95 percent confidence interval [CI] = 23:43 to 00:05) local time (UTC + 1 h), which was approximately 20 minutes after sunset, and during the *brightest phase* it was 12:20 (95 percent CI = 12:03 to 12:38) local time. At the polar site, the mean time of placement during the *darkest phase* was 00:30 (95 percent CI = 00:17 to 00:42) local time (UTC - 2 h), which was approximately 1 hour before solar midnight, and during the *brightest phase* it was 12:50 (95 percent CI = 12:32 to 13:08) local time. In all but one case at the subpolar site, a minimum of 48 hours elapsed before another placement in a location. If predators were active during a placement, we covered the placement with an opaque cloth tied to a string. We then moved approximately 20 m from the placement and waited for 15 minutes or until the predator(s) disappeared before pulling the cloth off the placement. If a placement was covered, the time of the placement was the time of day in which the placement was uncovered. We had placements at twenty-three nests in twelve locations and twelve nests in seven locations at the subpolar and polar sites, respectively. Trail cameras (Reconyx Hyperfire 2) took one photograph every 15 minutes and ten photographs when triggered by motion at a nest. Time of predation was the timestamp of the first photograph where either the placement was missing or a predator was photographed depredate the placement.

A placement was excluded from analysis if it was not in the camera's frame of view (subpolar site: four placement, polar site: one placement); was rolled out of the frame of view by a nonpredatory seabird, such as an auk species (subpolar site: one placement, polar site: two placements); or was not depredated within approximately 24 hours (subpolar site: four placements, polar site: two placements). At one nest at the subpolar site, multiple gulls were still disturbed and active after placements were uncovered and the experimenter began walking away. We therefore excluded these placements from analyses because the investigator's presence appeared to cause the activity (two placements). In total, there were  $N = 45$  placements for the subpolar site and  $N = 28$  placements for the polar site. All eggs were sourced from domestic fowl, bought locally, similar in size, and the same color. Eggs were hard-boiled  $\geq 12$  minutes before placement in areas in which contact with domestic livestock, domestic fowl, or human activity and rubbish was unlikely.



## Statistical analyses

### Observations

We calculated the mean and maximum count recorded during the scans within an observation block. We calculated the mean count for each observation block by taking the mean of the number of predators that were active across all seven scans. We used this as a general representation of predator activity. The maximum count for an observation block was the number of individual predators (regardless of species) that were active during a single scan of that observation block. We used this number of simultaneously observed individual predators as a conservative estimate of the minimum number of individual predators active in an area. We tested whether the means and maxima from each study site met the assumptions for normality and homogeneity of variance between the two phases. We then used two-tailed parametric paired *t*-tests or nonparametric paired Wilcoxon signed-rank tests and Hedges' *g* to calculate effect sizes (R package *effectsize*; Ben-Shachar, Ludecke, and Makowski 2020).

### Experiments

We analyzed experimental egg placement results using a binary response variable that described whether eggs were depredated within three hours of placement (1 = depredated within 3 hours; 0 = not depredated within 3 hours). We examined the 3 hours following placements because this corresponded to the approximate amount of time that the sun remained below the horizon after placement during the darkest phase at the subpolar site (Figure 1). This approach allowed us to compare the likelihood of eggs placed a night being depredated during this phase of darkness to the likelihood of eggs placed during the day being depredated after the same amount of time. We repeated this comparison for the polar site and asked whether these sites differed. We used a limited window because we only placed eggs during two time points of the diel cycle, which resulted in us not being able to distinguish between depredation due to random chance from increased exposure durations and timepoints of the diel cycle. Our aim was to test whether the darkest or brightest phase influenced the likelihood of predation over equivalent amounts of time, depending on latitude.

We used a generalized linear mixed-effects model with a binary response, binomial error structure, and the categorical predictor *phase* (brightest, darkest) using *lme4* and R (Bates et al. 2015). We used placement number in a nest within trial number at a location as nested random intercepts and placement number in a nest as a separate random intercept to

control for variation associated with the possibility that predators depredated placements in a specific order or frequented certain locations more often during the investigation. If a random effect accounted for little or no variance (e.g., resulted in a singular fit) in the model, we dropped the random effect and reran the model. We checked model assumptions visually by plotting residuals and fitted versus observed values. We compared the final model to a nested null model (i.e., excluding the phase predictor) by using a likelihood ratio test (Tredennick et al. 2021). The phase predictor was significant if the model containing it was significantly different from the null model ( $\alpha = .05$ ). We used estimated marginal means and 95 percent confidence intervals obtained with the R package *emmeans* when plotting model results (Lenth 2023). We conducted all statistical analyses using the R language and environment v4.2.2 (R Core Team 2022).

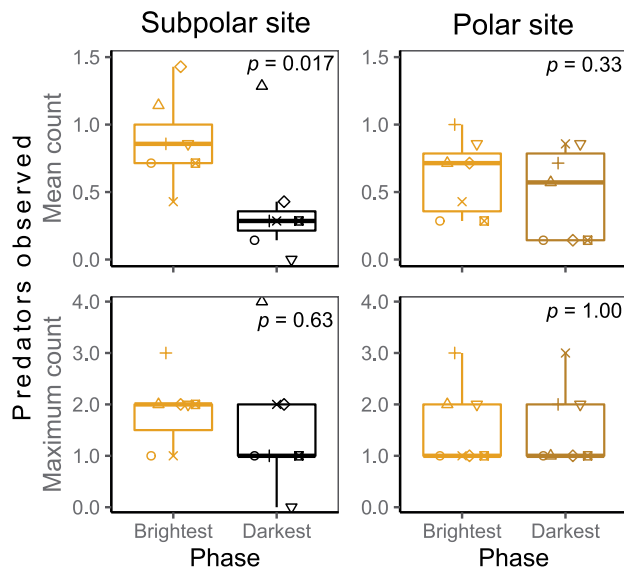
## Results

### Observations: Are more active predators observed during the brightest than the darkest phase?

We observed predators in an equal number of observation replicates at each study site ( $N = 7$  per study site). All predators observed during scans at both sites were birds (Supplementary Material). At the subpolar site, the same maximum number of predators were counted during both phases of the diel cycle (maximum count:  $t_6 = 0.51$ ,  $p = .63$ ,  $N = 7$ , Hedges' *g* [95 percent CI] = .17 [−0.49 to 0.81]; Figure 2), but on average more predators were counted during the brightest phase compared to the darkest phase (mean count:  $t_6 = 3.29$ ,  $p = .017$ ,  $N = 7$ , Hedges' *g* [95 percent CI] = 10.8 [0.18 to 1.93]; Figure 2; Supplementary Material). Within replicates at the subpolar site, the mean count of predators was consistently lower during the darkest phase (Figure 2). At the polar site, the same maximum and mean number of predators were counted during the brightest and darkest phases of the diel cycle (maximum count:  $V_{7,7} = 3.0$ ,  $p = 1.00$ , Hedges' *g* [95 percent CI] = 0.00 [−0.64 to 0.64]; mean count:  $t_6 = 1.07$ ,  $p = 0.33$ ,  $N = 7$ , Hedges' *g* [95 percent CI] = 0.35 [−0.33 to 1.01]; Figure 2; Supplementary Material).

### Experiments: Does predation occur more often during the brightest than the darkest phase?

Predation was more likely during the brightest phase than during the darkest phase at the subpolar site ( $\chi^2_1 = 4.14$ ,  $p = .042$ ,  $N = 45$  placements; Figure 3;



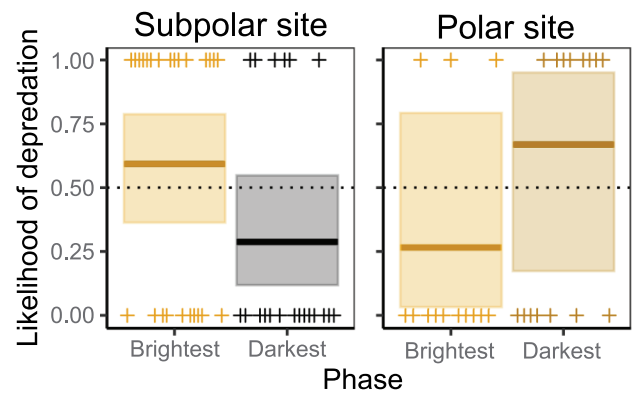
**Figure 2.** The mean and maximum number of predators observed at the subpolar and polar sites during the brightest and darkest phases of the diel cycle.

Yellow indicates that the sun was above the horizon, and black indicates that the sun was below the horizon. We calculated the mean count by averaging the number of predators that were active across all seven scans in an observation block; we used this as a general representation of predator activity. The maximum count for an observation block was the number of predators that were active during the scan with the most active predators; we used this number of simultaneously observed predators as a conservative estimate of the minimum number of individual predators active in an area. Within each panel, the boxes are bounded by the first and third quartiles, horizontal bars are at the median, and whiskers indicate the smallest or largest measurement within  $1.5\times$  the interquartile range. Individual points represent the mean or maximum count, respectively, in an observation block. Individual shapes represent different observation replicates at each study site.

Supplementary Material). At the polar site, however, phase did not influence the likelihood of predation ( $\chi^2_1 = 2.87$ ,  $p = .09$ ,  $N = 28$  placements; Supplementary Material). These results did not change when we reran the analyses excluding confirmed predation by an arctic fox ( $\chi^2_1 = 0.14$ ,  $p = .70$ ,  $N = 14$  placements).

## Discussion

We found that counts of predators and the likelihood of nest depredation in a seabird colony were similar during the brightest and darkest phases of the diel cycle above the Arctic Circle but differed between these phases at a subpolar site, decreasing when the sun was below the horizon (Figures 2 and 3). This is consistent with predictions of the photoperiod constraint hypothesis, because the observed lack of change in predator activity above the polar circle



**Figure 3.** Predation within 3 hours of placement at the polar and subpolar sites during the brightest and darkest phases of the diel cycle. Yellow indicates that the sun was above the horizon, and black indicates that the sun was below the horizon. Solid lines are reverse-transformed model estimates, and shaded boxes are the reverse-transformed 95 percent confidence intervals. Crosses represent the raw data (0 = not depredated, 1 = depredated). The model producing the plotted estimates for the subpolar site explained significantly more variation than a null model without phase as a predictor ( $\chi^2_1 = 4.14$ ,  $p = .042$ ), whereas the model for the polar site did not explain significantly more variation than a null model ( $\chi^2_1 = 2.87$ ,  $p = .09$ ).

may challenge prey species that rely on phases of reduced predator activity or foraging efficiency for survival. Additionally, the proximity of the subpolar site to the Arctic Circle provided an indication that a diel change in light intensity equivalent to a change from full daylight to just civil twilight (civil twilight = solar elevation between  $0^\circ$  and  $-6^\circ$ ; Figure 1) at the subpolar site may influence the activity of a predator community just below the Arctic Circle (Figures 2 and 3).

Despite the change in light intensity at the subpolar site, an observer could still clearly identify individuals to genus level within 300 m of themselves during the darkest phase, which suggests that predators may also be able to detect prey visually within the same distance. However, we know very little about the visual acuity or detection distances of predators and prey in the seabird colonies investigated. Additionally, predators that do not search for prey visually may continue to have the same search efficiency across the diel cycle, and prey in communities with predators that hunt during the light and dark phase of the diel cycle, such as many inland areas with predatory mammals, may experience similar predation risk across the 24-hour day even when darkness occurs. Therefore, our results provide only preliminary support for the photoperiod constraint hypothesis in two communities with mainly visual predators. Our results highlight the need for large-scale,

global comparisons of predation rates and search efficiencies across the diel cycle at many sites above and below the polar circles and for further investigation of confounding factors that also change with the diel cycle that may influence when animals are active. This includes temperature, which often changes across the diel cycle and may affect activity via thermoregulation (Alonso, Salgado, and Palacín 2016; Choy et al. 2021).

Our results provide a coarse comparison of the activity of the predator community between only two sites around solar noon and solar midnight for the observations and during a restricted 3-hour window during the darkest and brightest phases of the diel cycle for the experiments. Our results can therefore neither capture nuanced characteristics of predation risk across the full diel cycle nor be extrapolated across a large geographic scale. We still do not know whether the similar predator activity during the brightest and darkest phases of continuous light documented here translates to a change in cumulative predation risk over a 24-hour period.

Despite some differences between the predator communities at our polar and subpolar sites, however, we believe that the differences in predator activity at these sites (Figures 2 and 3) are driven by diel differences in the environment, potentially reflecting general latitudinal associations, rather than site-specific activity patterns. For instance, the gulls (*Larus* spp., the majority of predators) at the subpolar site also occur in polar Greenland (Boertmann and Hufferdt 2013; Boertmann and Frederiksen 2016) and can be active during the darkest phase of the diel cycle at higher latitudes (Sjöberg 1989; pers. obs.). Additionally, glaucous gulls (the species observed most at the polar site; Supplementary Material) have been reported to not forage in a seabird colony when darkness occurred during summer at a similar latitude as the subpolar site (62.5° N; figure 2 in Gilchrist, Gaston, and Smith 1998), and charadriiforms, which include gulls, show much variation in activity patterns across the diel cycle above the polar circle (Steiger et al. 2013; Bulla et al. 2016; Hufferdt and Merkel 2016; Hufferdt et al. 2021). This evidence in combination suggests that the pattern of reduced activity under darkness and the population-level pattern of similar activity during phases of the polar day in this group of avian predators is widespread. Nonetheless, because our case study did not incorporate observations across the full diel cycle, we cannot exclude that different predator communities and individuals with different activity patterns may underlie a geographic change of the diel activity of the predator

communities investigated. Further investigation using either individual tracking with high temporal resolution or a data collection schedule spanning the full diel cycle is warranted.

Though some evidence indicates that predation rates are lower at the highest latitudes (McKinnon et al. 2010; Roslin et al. 2017; Roesti et al. 2020), other work suggests that birds, the primary predators observed here, increase activity with increasing photoperiod, presumably due to increased foraging opportunities (Pokrovsky et al. 2021). Indeed, in some seabird colonies, predation risk links tightly and positively to light intensity (Watanuki 1986; Gilchrist, Gaston, and Smith 1998; Keitt, Tershy, and Croll 2004; Riou and Hamer 2008). Thus, under the continuous light of polar summer, a less risky phase of the diel cycle may attenuate or disappear, requiring prey to allocate more time to predator avoidance and less time to other behaviors across the diel cycle. Nonetheless, the continuous photoperiod of polar summer may also present benefits to prey by allowing for earlier visual detection of predators. This could confound the importance of similar predator activity during the darkest and brightest phases at high latitudes via a trade-off between cumulative predation risk, predator detection, and other behaviors. The outcome of this trade-off is probably species or taxon specific. These potential scenarios, however, highlight the importance for understanding whether cumulative predation risk across the diel cycle differs between subpolar and polar regions, whether these risk profiles are a function of diel activity patterns of predators, and how diel risk profiles may change as species shift ranges polewards due to climate change.

## Conclusions

We found preliminary evidence that predator activity is similar during the brightest and darkest phases of the diel cycle above the Arctic Circle but not below it where activity is reduced under darkness. Our case study provides an empirical foundation for future research examining how the activity patterns of predator communities can change latitudinally with environmental variation associated with the diel cycle. Our results emphasize the need to better understand the interplay among the diel cycle, activity, photoperiod, and latitude and elucidate the causes and consequences of activity patterns (Gilbert et al. 2022).

Open questions include the following:



- Do bottom-up processes determined by prey or top-down processes determined by predators shape activity patterns more often at low latitude compared to high latitude?
- How does seasonality in temperature and the annual transition in photoperiod affect biogeographical patterns in activity?
- Does community complexity affect the diversity of activity patterns (Gilbert et al. 2022) or their underlying mechanisms?
- How does predation risk across the diel cycle change as different species immigrate to climate refugia above the polar circles?

With global change, chronoecological processes may either hinder or facilitate adaptation (Bradshaw and Holzapfel 2010; Cox, Gardner, and Gaston 2021; Ljungström, Langbehn, and Jørgensen 2021; Gilbert et al. 2022). The evolutionary capacity to adapt to new temporal interactions across the diel cycle may be either population or taxon specific and may be challenged by the pace of rapid environmental change (Huffeldt 2020, 2021). The interplay between the photic environment and species interactions (Kronfeld-Schor and Dayan 2003; Kehoe et al. 2018, 2020; Häfker and Tessmar-Raible 2020), including diel activity interactions (Langbehn et al. 2022; Vallejo-Vargas et al. 2022), may have important implications for forecasts of species' ranges and their persistence, but more research is needed to confirm whether this could occur and whether our preliminary findings represent a generalized phenomenon across latitudes and communities.

## Acknowledgments

We thank P.J. Huffeldt for assistance on Mykines, F.R. Merkel and M. Frederiksen for assistance on Kippaku, and R. Guldborg Hansen for use of the trail cameras.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

## Funding

This work and any supplementary material were supported by the Danish Ministry of Environment (Miljøministeriet) to NPH via the program for Environmental Support for the Arctic (Miljøstøtte til Arktisk) grant J.nr. 2020-64727, and the article's results and conclusions do not necessarily reflect the position of the Danish Ministry of Environment or the Government of Greenland. The funders had no role in study

design, data collection and analysis, decision to publish, or preparation of the manuscript.

## ORCID

Nicholas P. Huffeldt  <http://orcid.org/0000-0002-0154-2536>  
 Floris M. van Beest  <http://orcid.org/0000-0002-5701-4927>  
 Haley L. Kenyon  <http://orcid.org/0000-0001-5497-4052>  
 Jóhannis Danielsen  <http://orcid.org/0000-0002-9775-4786>

## Data and code availability statement

The data and R script used to obtain the results presented are available on Zenodo (Huffeldt 2024).

## Ethics statement

All fieldwork investigations aligned with the "Guidelines for the Treatment of Animals in Behavioural Research and Teaching" (ABS/ASAB 2021) and occurred with the relevant permissions from the Faroese landowners and the Government of Greenland (Dok. nr.: 7976563).

## Author contributions (CRediT Taxonomy)

NPH: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, visualization, writing—original draft preparation, writing—review and editing. FMvB: formal analysis, methodology, visualization, writing—original draft preparation, writing—review and editing. HLK: methodology, writing—original draft preparation, writing—review and editing. JD: resources, writing—review and editing. TG: conceptualization, writing—review and editing.

## References

- ABS/ASAB. 2021. Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour* 171: I–XI. doi:10.1016/S0003-3472(20)30373-0.
- Alonso, J. C., I. Salgado, and C. Palacín. 2016. Thermal tolerance may cause sexual segregation in sexually dimorphic species living in hot environments. *Behavioral Ecology* 27, no. 3: 717–24. doi:10.1093/beheco/arv211.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using *lme4*. *Journal of Statistical Software* 67, no. 1: 1–48. doi:10.3929/ethz-b-000105397.
- Ben-Shachar, M., D. Lüdtke, and D. Makowski. 2020. Effectsize: Estimation of effect size indices and standardized parameters. *Journal of Open Source Software* 5, no. 56: 2815. doi:10.21105/joss.02815.
- Boertmann, D., and M. Frederiksen. 2016. Status of Greenland populations of Great Black-backed Gull (*Larus marinus*), Lesser Black-backed Gull (*Larus fuscus*) and Herring Gull (*Larus argentatus*). *Waterbirds* 39, no. sp1: 29–35. doi:10.1675/063.039.sp109.
- Boertmann, D., and N. P. Huffeldt. 2013. *Seabird colonies in the Melville Bay, Northwest Greenland*. Denmark: Aarhus

- University, DCE - Danish Centre for Environment and Energy.
- Bradshaw, W. E., and C. M. Holzapfel. 2010. Light, time, and the physiology of biotic response to rapid climate change in animals. *Annual Review of Physiology* 72, no. 1: 147–66. doi:10.1146/annurev-physiol-021909-135837.
- Bulla, M., M. Valcu, A. M. Dokter, A. G. Dondua, A. Kosztolányi, A. L. Rutten, B. Helm, et al. 2016. Unexpected diversity in socially synchronized rhythms of shorebirds. *Nature* 540, no. 7631: 109–13. doi:10.1038/nature20563.
- Choy, E. S., R. S. O'Connor, H. G. Gilchrist, A. L. Hargreaves, O. P. Love, F. Vézina, K. H. Elliott, et al. 2021. Limited heat tolerance in a cold-adapted seabird: Implications of a warming Arctic. *Journal of Experimental Biology* 224, no. 13. doi:10.1242/jeb.242168.
- Cox, D. T. C., A. S. Gardner, and K. J. Gaston. 2021. Diel niche variation in mammals associated with expanded trait space. *Nature Communications* 12, no. 1: 1753. doi:10.1038/s41467-021-22023-4.
- Freeman, B. G., M. N. Scholer, M. M. A. Boehm, J. Heavyside, D. Schluter, M. Bonfim, D. P. López, M. F. Repetto, C. Schlöder, B. J. Sewall, and G. M. Ruiz. 2020. Adaptation and latitudinal gradients in species interactions: Nest predation in birds. *The American Naturalist* 196, no. 6: E160–E166. doi:10.1086/711415.
- Freestone, A. L., M. E. Torchin, L. J. Jurgens, M. Bonfim, D. P. López, M. F. Repetto, C. Schlöder, et al. 2021. Stronger predation intensity and impact on prey communities in the tropics. *Ecology* 102, no. 8: e03428. doi:10.1002/ecy.3428.
- Gilbert, N. A., K. A. McGinn, L. A. Nunes, A. A. Shipley, J. Bernath-Plaisted, J. D. J. Clare, P. W. Murphy, et al. 2022. Daily activity timing in the Anthropocene. *Trends in Ecology & Evolution* 38, no. 4: 324–36. doi:10.1016/j.tree.2022.10.008.
- Gilchrist, H. G., A. J. Gaston, and J. N. M. Smith. 1998. Wind and prey nest sites as foraging constraints on an avian predator, the Glaucous Gull. *Ecology* 79, no. 7: 2403–14. doi:10.1890/0012-9658(1998)079[2403:WAPNSA]2.0.CO;2.
- Häfker, N. S., and K. Tessmar-Raible. 2020. Rhythms of behavior: Are the times changin'? *Current Opinion in Neurobiology* 60: 55–66. doi:10.1016/j.conb.2019.10.005.
- Harper, E. M., and L. S. Peck. 2016. Latitudinal and depth gradients in marine predation pressure. *Global Ecology and Biogeography* 25, no. 6: 670–8. doi:10.1111/geb.12444.
- Helm, B., M. E. Visser, W. Schwartz, N. Kronfeld-Schor, M. Gerkema, T. Piersma, G. Bloch, et al. 2017. Two sides of a coin: Ecological and chronobiological perspectives of timing in the wild. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372, no. 1734: 20160246. doi:10.1098/rstb.2016.0246.
- Huffeldt, N. P. 2020. Photoc barriers to poleward range-shifts. *Trends in Ecology & Evolution* 35, no. 8: 652–5. doi:10.1016/j.tree.2020.04.011.
- Huffeldt, N. P. 2021. Importance of photic constraints depends on the population. *Trends in Ecology & Evolution* 36, no. 6: 480–1. doi:10.1016/j.tree.2021.03.008.
- Huffeldt, N. P. 2024. Data for: Activity of predators in seabird colonies decreases during the darkest compared to the brightest phase of the diel cycle below, but not above, the Arctic Circle (version 1) [data set]. *Zenodo*. doi:10.5281/zenodo.12706940.
- Huffeldt, N. P., and F. R. Merkel. 2016. Sex-specific, inverted rhythms of breeding-site attendance in an Arctic seabird. *Biology Letters* 12, no. 9: 20160289. doi:10.1098/rsbl.2016.0289.
- Huffeldt, N. P., A. Tigano, K. E. Erikstad, W. Goymann, S. Jenni-Eiermann, T. Moum, T. K. Reiertsen, et al. 2021. The relationship between daily behavior, hormones, and a color dimorphism in a seabird under natural continuous light. *Hormones and Behavior* 130: 104930. doi:10.1016/j.yhbeh.2021.104930.
- Jones, G., and J. Rydell. 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 346: 445–55. doi:10.1098/rstb.1994.0161.
- Kaartvedt, S. 2008. Photoperiod may constrain the effect of global warming in Arctic marine systems. *Journal of Plankton Research* 30, no. 11: 1203–6. doi:10.1093/plankt/fbn075.
- Kehoe, R. C., D. Cruse, D. Sanders, K. J. Gaston, F. J. F. van Veen. 2018. Shifting daylength regimes associated with range shifts alter aphid-parasitoid community dynamics. *Ecology and Evolution* 8, no. 17: 8761–9. doi:10.1002/ece3.4401.
- Kehoe, R. C., D. Sanders, D. Cruse, M. Silk, K. J. Gaston, J. R. Bridle, F. van Veen, et al. 2020. Longer photoperiods through range shifts and artificial light lead to a destabilizing increase in host-parasitoid interaction strength. *Journal of Animal Ecology* 89, no. 11: 2508–16. doi:10.1111/1365-2656.13328.
- Keitt, B. S., B. R. Tershy, and D. A. Croll. 2004. Nocturnal behavior reduces predation pressure on Black-vented Shearwaters. *Marine Ornithology* 32: 173–8.
- Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics* 34, no. 1: 153–81. doi:10.1146/annurev.ecolsys.34.011802.132435.
- Kumar, V., ed. 2017. *Biological timekeeping: Clocks, rhythms and behaviour*. New Delhi: Springer India.
- Langbehn, T. J., D. L. Aksnes, S. Kaartvedt, Ø. Fiksen, G. Ljungström, C. Jørgensen. 2022. Poleward distribution of mesopelagic fishes is constrained by seasonality in light. *Global Ecology and Biogeography* 31, no. 3: 546–61. doi:10.1111/geb.13446.
- Lenth, R. V. (2023) *Emmeans*: Estimated marginal means, aka least-squares means. R Package Version 1.8.9 <https://CRAN.R-project.org/package=emmeans>
- Ljungström, G., T. J. Langbehn, and C. Jørgensen. 2021. Light and energetics at seasonal extremes limit poleward range shifts. *Nature Climate Change* 11, no. 6: 530–6. doi:10.1038/s41558-021-01045-2.
- McKinnon, L., P. A. Smith, E. Nol, J. L. Martin, F. I. Doyle, K. F. Abraham, H. G. Gilchrist, et al. 2010. Lower predation risk for migratory birds at high latitudes. *Science* 327, no. 5963: 326–7. doi:10.1126/science.1183010.
- Ottmann, D., T. J. Langbehn, P. Reglero, D. Alvarez-Berastegui, and Ø. Fiksen. 2023. Model of mesopelagic fish predation on eggs and larvae shows benefits of tuna spawning under full moon. *Limnology and Oceanography* 68, no. 12: 2632–41. doi:10.1002/lno.12465.
- Pokrovsky, I., A. Kölzsch, S. Sherub, W. Fiedler, P. Glazov, O. Kulikova, M. Wikelski, et al. 2021. Longer days enable higher diurnal activity for migratory birds. *Journal of Animal Ecology* 90, no. 9: 2161–71. doi:10.1111/1365-2656.13484.

- Poloczanska, E. S., M. T. Burrows, C. J. Brown, J. García Molinos, B. S. Halpern, O. Hoegh-Guldberg, C. V. Kappel, et al. 2016. Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science* 3:62. doi:10.3389/fmars.2016.00062.
- Prugh, L. R., and C. D. Golden. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology* 83, no. 2: 504–14. doi:10.1111/1365-2656.12148.
- R Core Team. 2022. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>
- Riou, S., and K. C. Hamer. 2008. Predation risk and reproductive effort: Impacts of moonlight on food provisioning and chick growth in Manx shearwaters. *Animal Behaviour* 76, no. 5: 1743–8. doi:10.1016/j.anbehav.2008.08.012.
- Roesti, M., D. N. Anstett, B. G. Freeman, J. A. Lee-Yaw, D. Schluter, L. Chavarie, J. Rolland, et al. 2020. Pelagic fish predation is stronger at temperate latitudes than near the equator. *Nature Communications* 11, no. 1: 1527. doi:10.1038/s41467-020-15335-4.
- Roslin, T., B. Hardwick, V. Novotny, W. K. Petry, N. R. Andrew, A. Asmus, I. C. Barrio, et al. 2017. Higher predation risk for insect prey at low latitudes and elevations. *Science* 356, no. 6339: 742. doi:10.1126/science.aaj1631.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics* 40, no. 1: 245–69. doi:10.1146/annurev.ecolsys.39.110707.173430.
- Seifert, C. L., C. H. Schulze, T. C. T. Dreschke, H. Frötscher, and K. Fiedler. 2016. Day vs. night predation on artificial caterpillars in primary rainforest habitats – An experimental approach. *Entomologia Experimentalis Et Applicata* 158, no. 1: 54–9. doi:10.1111/eea.12379.
- Shima, J. S., C. W. Osenberg, S. H. Alonzo, E. G. Noonburg, P. Mitterwallner, and S. E. Swearer. 2020. Reproductive phenology across the lunar cycle: Parental decisions, offspring responses, and consequences for reef fish. *Ecology* 101, no. 8: e03086. doi:10.1002/ecy.3086.
- Sjöberg, K. 1989. Time-related predator/prey interactions between birds and fish in a northern Swedish river. *Oecologia* 80, no. 1: 1–10. doi:10.1007/BF00789924.
- Steiger, S. S., M. Valcu, K. Spoelstra, B. Helm, M. Wikelski, and B. Kempenaers. 2013. When the sun never sets: Diverse activity rhythms under continuous daylight in free-living Arctic-breeding birds. *Proceedings of the Royal Society B: Biological Sciences* 280, no. 1764: 20131016. doi:10.1098/rspb.2013.1016.
- Tredennick, A. T., G. Hooker, S. P. Ellner, and P. B. Adler. 2021. A practical guide to selecting models for exploration, inference, and prediction in ecology. *Ecology* 102, no. 6: e03336. doi:10.1002/ecy.3336.
- Vallejo-Vargas, A. F., D. Sheil, A. Semper-Pascual, L. Beaudrot, J. A. Ahumada, E. Akampurira, R. Bitariho, et al. 2022. Consistent diel activity patterns of forest mammals among tropical regions. *Nature Communications* 13, no. 1: 7102. doi:10.1038/s41467-022-34825-1.
- Watanuki, Y. 1986. Moonlight avoidance behavior in Leach's Storm-Petrels as a defense against Slaty-backed Gulls. *The Auk* 103, no. 1: 14–22. doi:10.1093/auk/103.1.14.
- Williams, C. T., B. M. Barnes, and C. L. Buck. 2015. Persistence, entrainment, and function of circadian rhythms in polar vertebrates. *Physiology* 30, no. 2: 86–96. doi:10.1152/physiol.00045.2014.
- Zvereva, E. L., and M. V. Kozlov. 2021. Latitudinal gradient in the intensity of biotic interactions in terrestrial ecosystems: Sources of variation and differences from the diversity gradient revealed by meta-analysis. *Ecology Letters* 24, no. 11: 2506–20. doi:10.1111/ele.13851.