

# JOURNAL OF AVIAN BIOLOGY

## Article

### Spatial and temporal variation in foraging of breeding red-throated divers

J. Duckworth, S. O'Brien, I. K. Petersen, A. Petersen, G. Benediktsson, L. Johnson, P. Lehikoinen, D. Okill, R. Väisänen, J. Williams, S. Williams, F. Daunt and J. A. Green

J. Duckworth (<https://orcid.org/0000-0002-4715-2189>)  (james.duckworth@liverpool.ac.uk) and J. A. Green, Univ. of Liverpool, Brownlow Hill, Liverpool, UK. – S. O'Brien, Joint Nature Conservation Committee, Inverdee House, Aberdeen, UK. – I. K. Petersen, Dept of Bioscience, Aarhus Univ., Denmark. – A. Petersen, G. Benediktsson, Independent Researcher, Reykjavik, Iceland. – L. Johnson, D. Okill, J. Williams and S. Williams, Independent Researcher, Scotland, UK. – P. Lehikoinen, Finnish Museum of Natural History, Univ. of Helsinki, Finland. – PL and R. Väisänen, Avescapes Oy, Helsinki, Finland. – F. Daunt, Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian, UK.

**Journal of Avian Biology**

2021: e02702

doi: 10.1111/jav.02702

Subject Editor: Judith Morales

Editor-in-Chief: Thomas Alerstam

Accepted 25 March 2021



Differing environmental conditions can have profound effects on many behaviours in animals, especially where species have large geographic ranges. Seasonal changes or progression through life history stages impose differential constraints, leading to changes in behaviours. Furthermore, species which show flexibility in behaviours, may have a higher capacity to adapt to anthropogenic-induced changes to their environment. The red-throated diver (RTD) is an aquatic bird, that is able to forage in both freshwater and marine environments, though little else is known about its behaviours and its capacity to adapt to different environmental conditions. Here, we use time-depth recorders and saltwater immersion loggers to examine the foraging behaviour of RTDs from three regions across northwest Europe. We found that in the breeding season, birds from two regions (Iceland and Scotland) foraged in the marine environment, while birds from Finland, foraged predominantly in freshwater. Most of the differences in diving characteristics were at least partly explained by differences in foraging habitat. Additionally, while time spent foraging did not change through the breeding season, dives generally became more pelagic and less benthic over the season, suggesting RTDs either switched prey or followed vertical prey movements, rather than increasing foraging effort. There was a preference for foraging in daylight over crepuscular hours, with a stronger effect at two of the three sites. Overall, we provide the first investigation of RTD foraging and diving behaviour from multiple geographic regions and demonstrate variation in foraging strategies in this generalist aquatic predator, most likely due to differences in their local environment.

Keywords: behaviour, diving, foraging ecology, *Gavia*, loon



[www.avianbiology.org](http://www.avianbiology.org)

© 2021 The Authors. Journal of Avian Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

## Introduction

Many species and animal populations are dealing with reduced fecundity and survival from a plethora of anthropogenic pressures, such as marine debris (Horn et al. 2020), pollution (Erikstad et al. 2013, Amelineau et al. 2019) and habitat loss (Harper et al. 2008). These threats can vary widely across geographic landscapes, leading to differential pressures affecting populations (Plumpton and Andersen 1998, Hovick et al. 2014). Additionally, the pressures experienced by populations vary temporally; across annual cycles and between years (Salamolard and Weimerskirch 1993, Shaffer et al. 2001). For example, during the breeding season, some animals must provide parental care and be geographically constrained as central place foragers, which contrasts with non-breeding periods such as migration. Even within a period, demands over time and pressures experienced may not be constant. For example, the behavioural budgets of an individual can change with demands of the growing offspring (Tulp et al. 2009) which might alter their exposure to anthropogenic pressures and/or exacerbate any constraints that they may impose (Thaxter et al. 2015). Understanding the fundamental biology of species and changes in their behaviour and ecology over temporal and spatial gradients is thus key to making informed management decisions to minimise current and future threats (Grémillet and Boulinier 2009).

Foraging behaviour is closely linked to demographic rates, as energy intake plays a vital role in both survival and reproduction (Boggs 1992). Therefore, changes to foraging characteristics that affect energy intake, such as distance to foraging site (Bost et al. 2015), foraging success (Crocker et al. 2006) and prey selection (Peckham et al. 2011) can be linked to changes in population demographic rates. For species which have some flexibility in how and where they forage, then the nature of the environment and ecosystems that they inhabit can have a major influence on foraging behaviour (Maynard and Davoren 2020). Furthermore, for species foraging in areas influenced by humans, anthropogenic activity has the potential to affect foraging characteristics (Senzaki et al. 2016, Scrafford et al. 2017, Millon et al. 2018). This makes the acquisition of knowledge on the foraging behaviour of species vital to understand, in order to know whether conservation efforts or interventions are required (Grémillet and Boulinier 2009).

Red-throated divers (RTDs; *Gavia stellata*) are a northerly distributed species of aquatic bird, generally occupying latitudes above 50°N (Carboneras et al. 2020). This species faces many of the threats previously mentioned (Schmutz et al. 2009, Burger et al. 2019) and is known to be vulnerable to anthropogenic presence (Schwemmer et al. 2011, Nummi et al. 2013, Uher-Koch et al. 2015) and structures (Furness et al. 2013, Mendel et al. 2019, Heinänen et al. 2020). This aversion to anthropogenic presence could be detrimental to demographic rates, through displacement effects (Drewitt and Langston 2006), but these effects are hard to observe and measure directly, as the birds are often in inaccessible locations. Some information exists on aspects

of the behaviour and ecology of this species at the nest during the breeding season, such as descriptions of chick rearing and nesting success (Eriksson et al. 1990, Rizzolo et al. 2015, Uher-Koch et al. 2018). However, there is a lack of information on foraging behaviour and water depth usage compared to other, better studied species (Grémillet et al. 1998, Linnebjerg et al. 2014, Amelineau et al. 2019, Poupart et al. 2019).

To build on this limited body of knowledge, we used biologging technology to examine the breeding season foraging behaviour of RTDs from three geographically distinct regions in northern Europe: Scotland, Finland and Iceland. By looking across multiple sites, we were able to both describe the foraging behaviour of the sampled individuals and examine how local environment may drive foraging behaviour differences between regions. The limited information available on RTD foraging allowed us to generate broad predictions on how foraging behaviour could differ between regions. Surveys of non-breeding season distribution show RTDs tend to favour habitats with water depths less than 20 m (Petersen et al. 2010, O'Brien et al. 2012), but can also be found in deeper waters (Heinänen et al. 2020). Biologging data from a single RTD in the breeding season provided some evidence to support this shallow depth usage, with the individual showing few dives reaching depths deeper than 20 m (Duckworth et al. 2020b).

RTDs in Finland breed at a much greater distance from the coast than the majority of those breeding in Scotland and Iceland, and previous evidence from populations breeding in similar environments further from the coast show RTDs to be likely to forage in freshwater habitats (Eriksson et al. 1990, Eriksson and Sundberg 1991, Duckworth et al. 2020b). In contrast, birds breeding close to the coast, tend to forage in marine environments (Reimchen and Douglas 1984, Black et al. 2015, Rizzolo et al. 2015). Therefore, we predicted that the recorded foraging metrics of birds from Scotland and Iceland, which were all breeding close to the coasts, should be the most similar, while birds breeding inland in Finland should be less so. Overall, we expect RTDs across all regions to be diving to shallow depths, < 20 m and demonstrate a mixture of benthic and pelagic foraging strategies (Kleinschmidt et al. 2019). We also predict that foraging effort would increase as the breeding season progresses, due to the increasing energetic demands of breeding over time (Dunn et al. 2018). The proportion of benthic dives was predicted to decrease over the breeding season, as previous study has shown adults sometimes provide small benthic prey when chicks are young and a wider array of larger benthic and pelagic prey as the chicks grows (Reimchen and Douglas 1984). This was based on the single-prey loading constraint on divers and therefore a need to maximise the energy that can be delivered per foraging trip, while not exceeding the maximum swallowing capacity of a chick at a given age. Among aquatic prey, benthic invertebrates can form a large part of chick diet, due to the small prey size required by young divers during their first days of growth (Jackson 2003). Spatial and temporal drivers may also interact with each other since

divers are opportunistic foragers (Kleinschmidt et al. 2019) and have demonstrated an ability to forage in different aquatic habitats. Thus, temporal effects during the breeding season may vary between locations, most likely driven by local prey accessibility. Previous evidence has also suggested RTDs may forage based on light conditions, with crepuscular foraging patterns (Duckworth et al. 2020a).

Our overall goal was to provide the first detailed information on breeding season foraging behaviour from multiple individual RTDs and begin to quantify spatial and temporal variation in this behaviour. To achieve this, we addressed three specific objectives: 1) Describe the foraging and diving behaviour of RTDs from three geographically distinct regions. 2) Investigate variation in foraging behaviour and strategies across these three regions. 3) Look at variation in foraging ecology over long (breeding season) and short (daily light levels) time scales.

## Methods

### Sampling birds

From May-2018 to July-2018, 74 RTDs were caught at nesting sites across three distinct geographical regions in southern

Finland ( $n=31$ ), north-eastern Iceland ( $n=12$ ) and the Scottish archipelagos of Orkney and Shetland ( $n=31$ ) (Fig. 1). Birds were caught using nest traps, mist nets or walk-in traps (O'Brien et al. 2018). Accurate assessment of the sex of each bird through molecular assessment was not possible. Both time-depth recorders (TDR; Cefas G5 Standard TDR, dimensions:  $8 \times 31$  mm, weight: 2.7 g) and light-based geolocators (GLS; Biotrack MK4083 Geolocator, dimensions:  $17 \times 10 \times 6.5$  mm, weight: 1.8 g) were attached to the legs of each captured RTD. In total 27 birds were recaptured in 2019, using the same capture methods. We recovered 8, 8 and 7 functioning TDRs and 7.7 and 5 functioning GLS tags from Finland, Iceland and Scotland, respectively (Supporting information). Due to the inaccessibility of nests and to avoid undue disturbance to breeding RTDs, it was not possible to observe the fate of breeding attempts or breeding chronology of each sampled birds in terms of nest initiation, laying, hatching, fledging and departure for migration.

### Logger regimes

TDRs recorded pressure, as a proxy for water depth, at six second intervals and temperature every ten minutes. The TDR measured with a precision of 0.03 m and 0.03°C for depth and temperature, respectively. To preserve battery

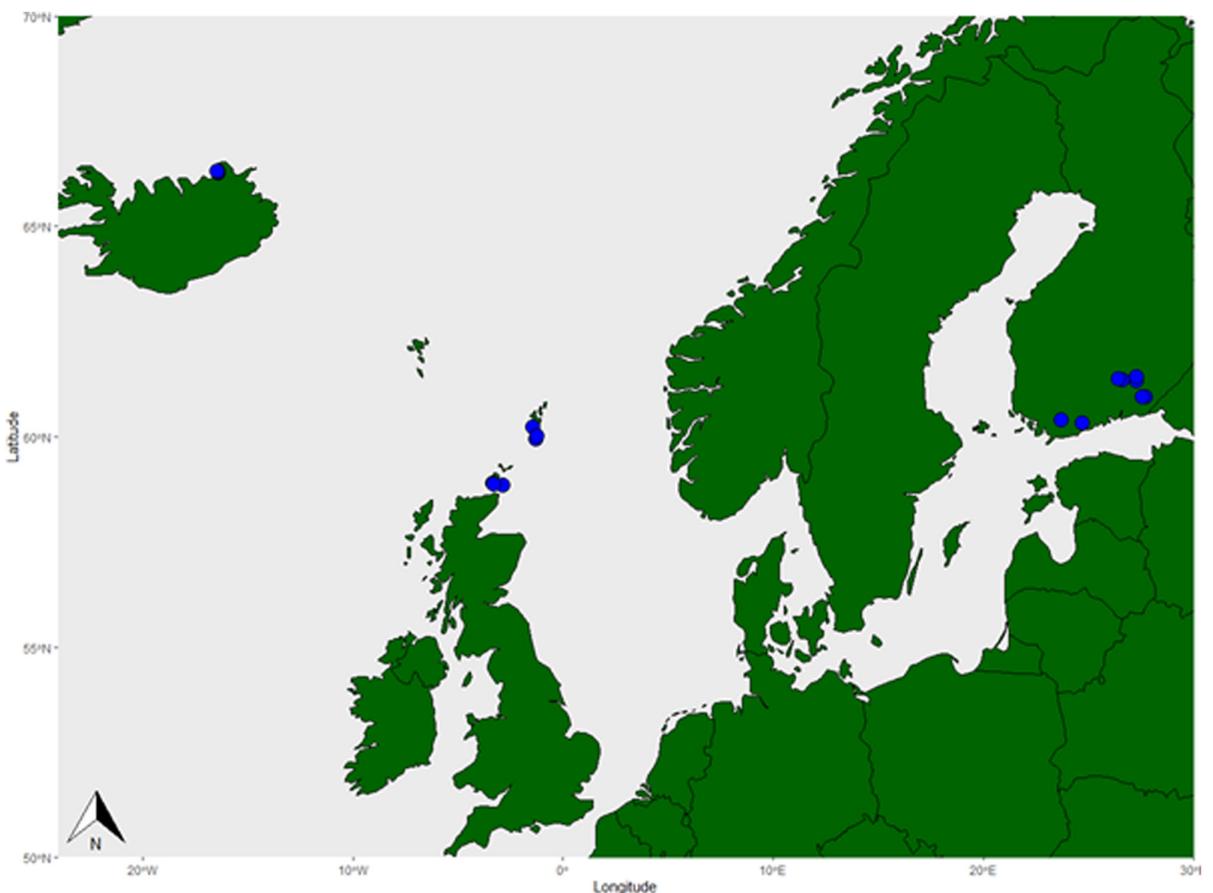


Figure 1. Capture locations for the studied *Gavia stellata* across northern Europe. Blue points represent capture and recovery locations.

life, the TDRs only recorded data every fifth day. GLS tags recorded maximum light levels for each five-minute period, every day. Additionally, the GLS tags had a salt-water immersion switch, which recorded immersion every three seconds and stored the information as a proportion of each ten-minute period that the tag was immersed in saltwater.

## Defining dives and foraging bouts

TDR are subject to shifts in surface water baseline changes in pressure, due to varying environmental conditions experienced throughout the annual cycle (Hays et al. 2007, Luque and Fried 2011) and extreme temperature changes (Bagniewska et al. 2013). A modified script from Duckworth et al. (2020b) was used to correct the shifting baseline of the TDRs. Broadly, this script detects prolonged periods (180 s in this study) of time at values greater or less than 0 m, indicative of surface behaviour, and returns them and subsequent data to 0 m, to ensure all dives start and end at the water surface, while maintaining the integrity of the dive shape. Dives were then defined as any corrected TDR record of depth greater than 1 m. This excluded any noise leftover from the shifting baseline or small depth changes due to swimming on the surface of the water. Visual inspection of the data was then used to remove any remaining erroneous dive records.

Dives were defined using a slightly modified version of the approach from Duckworth et al. (2020b). For all dives, maximum dive depth, duration, bottom time and post-dive interval were recorded. The six second sampling regime used in this study was higher than 10% of the median dive duration (30 s across all dives recorded in this study), which slightly limits our ability to classify bottom time and dive efficiency (Wilson et al. 1995). Therefore, dive shapes were restricted to classification of either U or non-U, where U shaped dives were defined as having at least one recording of bottom time, between two depth records. The bottom time of a dive was defined by two conditions: 1) rate of depth change below  $0.2 \text{ m s}^{-1}$ ; 2) deeper than 85% of the maximum dive depth within the dive (Rodary et al. 2000, Zimmer et al. 2010). This calculation could not be carried out reliably on dives with a length of 12 s or less due to only having two or fewer records of depth, therefore these dives are always classified as non-U and are not included in any analysis of dive shape. The proportion of U-shaped dives was calculated for each day of data collection.

Groups of dives with post-dive interval less than 66 s (determined using the log-likelihood method from Sibly et al. 1990) were classified into foraging bouts and the duration and number of dives in each of these bouts was recorded (Supporting information). We defined bouts with more than two dives as foraging bouts (Halsey et al. 2007, Foo et al. 2016). Time spent in these foraging bouts was summed over a day to generate a metric of daily time spent foraging. Dives not within these bouts were excluded from further analysis. This enabled the exclusion of isolated dives, which were commonly very shallow, and other miscellaneous events associated

with sudden pressure or temperature changes, e.g. landing on water, preening, leg-tucking. Dives within foraging bouts accounted for 94% of all dives. To quantify benthic foraging, the proportion of inter depth zone (IDZ) dives (Tremblay and Cherel 2000, Halsey et al. 2007) was calculated per day as the number of dives where the maximum depth was within 10% of the previous dive's maximum dive depth, within a bout, divided by the total number of dives within a bout minus one. A higher proportion of IDZ dives is indicative of a benthic foraging strategy, since a bird exploiting a benthic environment will serially dive to a similar depth (Tremblay and Cherel 2000, Quillfeldt et al. 2011, Knox et al. 2018).

This process generated seven foraging and diving metrics for further analysis: 1) bout length, 2) number of dives per bout, 3) maximum dive depth, 4) proportion of U-shaped dives, 5) dive duration, 6) proportion of IDZ dives, 7) daily time spent foraging. The saltwater immersion data was used to describe use of salt and freshwater habitats across the three regions.

## Analysis

Only data from the second recording day (to remove any immediate effects that catching and handling the bird might have on diving behaviour) until the median departure date were analysed in this study. Since the focus of this study was the RTD breeding season, data were truncated to include only this period. Once RTDs from these regions leave their breeding grounds, they no longer commonly use freshwater habitats (Duckworth et al. 2020a). Therefore, in the absence of observation data, date of departure was determined using the saltwater immersion data to detect extended use of saltwater habitats, characteristic of the overwinter period for all three sites. The end of the breeding season was defined as the first day of 5 consecutive days that had at least 45% of records showing saltwater immersion (values calculated by inspection of known winter data) (Supporting information). To account for not all birds having both a functional TDR and GLS (Supporting information), a single date of departure was derived for each region, based on the median departure date across all individuals with functioning tags from within that region.

We used generalised linear mixed effects models and linear mixed effect models, with each of the foraging metrics as response variables in separate models, to look at site level differences. We fitted random effects for bird ID and fixed effect for the three regions using the lme4 package (Bates et al. 2015). The model was compared to a null model, with only the random effects for individual ID included. Models were visually inspected for deviations from assumptions and as a result log transformation of the response variable was carried out on the models for bout duration and maximum dive depth within a dive (Supporting information). We included dive duration as a fixed effect since it was only recorded every six seconds, plus an interaction between site and dive duration, when looking at the proportion of U-shaped dives and only included dives with over 2 data points in analysis of U-shaped

dives. This accounted for longer dives having a higher probability of being detected as U-shaped dives, due to having a higher number of data points within the dive. For the two metrics (daily time spent foraging and proportion of IDZ dives) for which we predicted a temporal change we included three more candidate models, one which included date and time and one with only time (as a continuous variable for the days until breeding site departure) and finally a model with both date, time and an interaction term between date and site (Supporting information). AIC was used to determine the best performing model of the candidate models for all analyses, where the selected model was the most parsimonious model within 2 AIC units of the best model (Arnold 2010). Where the best performing model contained site as a fixed effect, site level differences were determined using pairwise Tukey tests in the R package 'emmeans' (Russell 2020). Details on error distributions used for each model can be found in Supporting information.

We calculated the proportion of time a bird spent in daylight and twilight by classifying each day in six minute intervals, based on light conditions at each nest location. Twilight was defined as a sun elevation angle between 0 and  $-12^{\circ}$  (nautical sunset/sunrise), while 'day' was defined as a sun elevation angle greater than or equal to 0 (Regular et al. 2011). Foraging dives were then classified in the same way as either occurring during the day or twilight (Duckworth et al. 2020b). For all foraging dives, both the proportion of available time which would be classified as night (sun elevation below  $-12^{\circ}$  degrees) and the proportion of foraging dives which occurred at night were less than 0.5% of the total, so were therefore removed from any analysis. To determine whether foraging behaviour was biased towards crepuscular hours, we used Chi-squared tests to compare the combined number of foraging dives in each light category (daylight and twilight) from all birds to the combined proportion of time each light category was available to all individuals. Separate tests were conducted for each site.

All statistical analysis and data processing was carried out in R (<[www.r-project.org](http://www.r-project.org)>). All means are shown with standard deviations, unless stated otherwise.

## Results

The median nest departure dates for Scotland ( $n=5$ ), Finland ( $n=7$ ) and Iceland ( $n=7$ ) were 15 August, 31 August and 10 August, respectively (Supporting information). Only one Finnish RTD, breeding  $\sim 15$  km from the coast, had records of saltwater immersion between deployment and nest departure. This bird recorded between 3 and 11 h in saltwater on ten consecutive days of 102 days of the breeding season. Otherwise saltwater immersion before the estimated date of departure from the breeding site was not detected for any Finnish birds, indicating that birds from this geographic region foraged nearly exclusively in freshwater. In contrast the Scottish and Icelandic RTDs recorded 8.1 ( $\pm 4.8$ ) and 7.7 ( $\pm 3.5$ ) hours a day immersed in saltwater, respectively.

The maximum dive depth observed across all sites was 29.3 m, which was performed by a bird in Iceland. In Scotland and Finland maximum depth recordings were 24.6 m and 27.4 m, respectively (Fig. 2). However, dives were typically shallow in nature with 94% of all foraging dives recorded being less than 15 m depth (Fig. 2). The longest dive recorded was 84 s, but 98% of all foraging dives were less than 60 s (Fig. 2). The longest foraging bout recorded overall was 215 min in Finland, while in Iceland and Scotland the maximum duration was 170 and 103 min, respectively. Foraging bouts of RTDs in Finland and Iceland were longer, on average, than those in Scotland (Table 1). Longer bouts were achieved by more dives within bouts (Table 1) although dive duration was significantly longer in Finland than Iceland and Scotland (Table 1). Maximum dive depth and dive duration were both greater, on average, in Finland than in Scotland and Iceland (Table 1). The proportion of U-shaped dives was high across all sites and both dive duration and the interaction between site and dive duration were included in the best model for the proportion of U-shaped dives. This showed that as dive duration increased the likelihood of detecting a U-shaped dive increased with a slightly steeper increase in Iceland (Supporting information). In addition to these effects, Iceland showed a higher proportion of U-shaped dives than Scotland and Finland, which were similar (Table 1). Results for all model fits and AIC values used for model selection can be found in the Supporting information.

The best performing model for daily time spent foraging contained only site as a fixed effect and did not include an interaction term. Finnish birds were shown to spend longer foraging than Scottish birds, with Icelandic birds being intermediate and not different from birds at either of the other two sites (Fig. 3). The Akaike weight of this model was low ( $w_i = 0.36$ ), however the model with only time did not outperform the null model (Supporting information), while the three other models did. We therefore decided against model averaging, to avoid overrepresenting the important of time, and instead discuss only the top preforming model and the effects of site level differences.

The best performing model for the proportion of IDZ dives included time, site and an interaction term between site and time. The model showed the proportion of IDZ dives decreased through the season, with the steepest decline in IDZ dives observed in the birds in Scotland (Fig. 4). Birds breeding in Scotland showed the lowest overall proportion of IDZ dives, while birds from Finland showed the highest and Iceland was intermediate, with all pairwise differences being significant ( $p < 0.05$ ) (Fig. 4).

At each site, dives were not distributed evenly between the two light regimes. In Finland, birds showed a bias towards diving during daylight (available daylight: 71%, dives during daylight: 85%) ( $p < 0.001$ ,  $df = 1$ ,  $\chi^2 = 3720$ ). In Scotland, dives were biased towards daylight (available daylight: 72%, dives during daylight: 87%) ( $p < 0.001$ ,  $df = 1$ ,  $\chi^2 = 2355$ ). In Iceland, birds also showed a slight bias towards diving in the daylight (available daylight: 86%, dives during daylight: 88%) ( $p < 0.001$ ,  $df = 1$ ,  $\chi^2 = 54$ ).

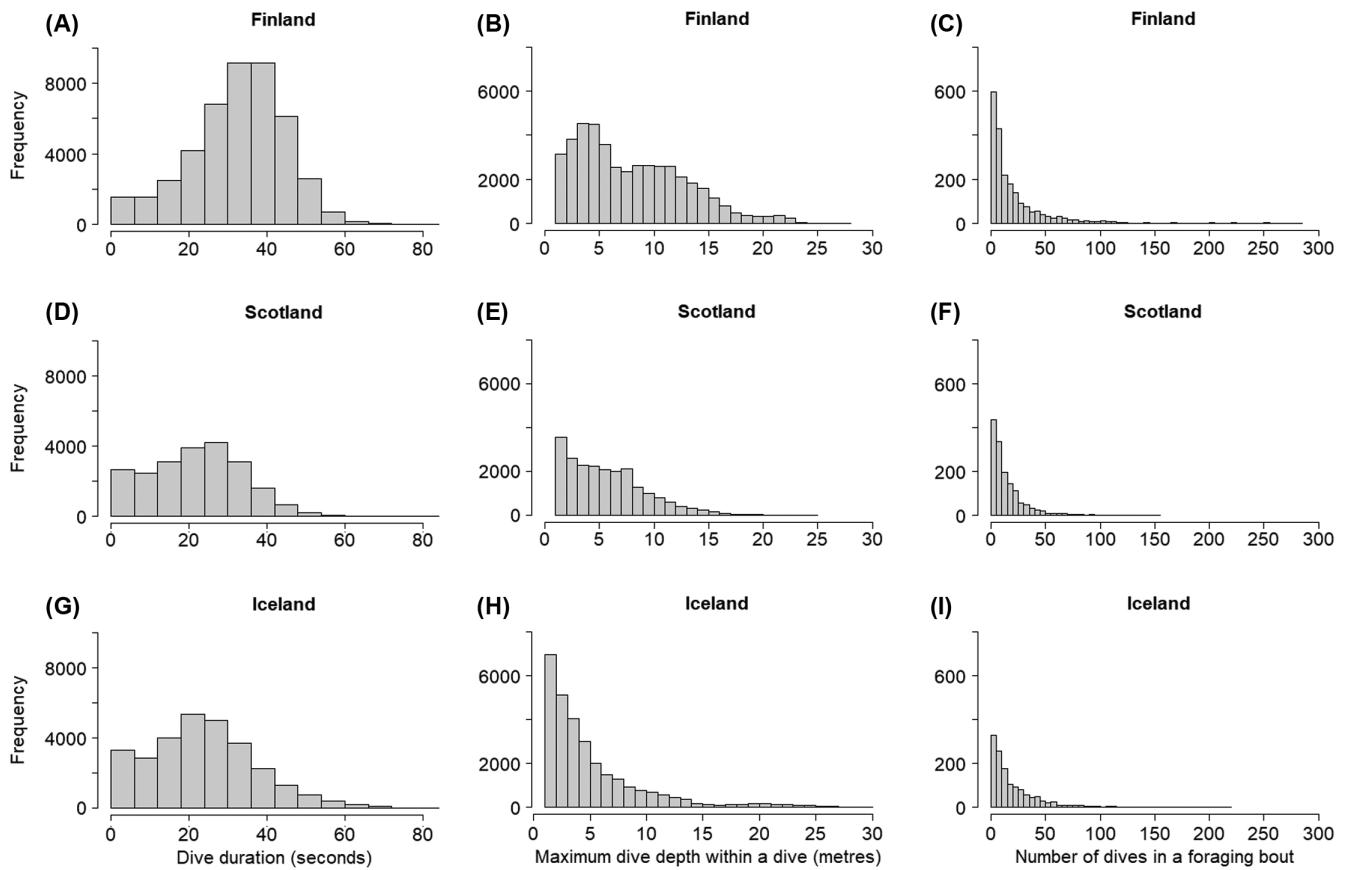


Figure 2. Histograms showing the dive duration (panel A, D and G), maximum dive depth within a dive (B, E and H) and number of dives within a foraging bout (C, F and I) at three sites: Finland (A, B and C), Scotland (D, E and F) and Iceland (G, H and I).

## Discussion

Our study provides the first description of foraging behaviour of RTDs across three geographically distinct regions in northern Europe. We found RTDs predominantly engaged in short, shallow dives of less than 10 m, in foraging bouts ranging from a few minutes to hours. Among the three regions examined here, there were differences between at least two of them in all of the metrics we tested. In the case of diving metrics, differences were largely between freshwater and marine foraging habitats. With RTDs in Finland undertaking longer deeper dives during longer bouts comprising more dives, compared with birds breeding in Iceland and Scotland.

Furthermore, we analysed two of these traits, proportion of IDZ dives and daily time spent foraging, for temporal patterns and found that while the time spent foraging varied between sites, it did not change over time. In contrast, the proportion of benthic dives undertaken decreased as the breeding season progressed. These findings suggest a capability for both spatial and temporal variation in RTD foraging in response to environmental differences. This could indicate RTDs have a high degree of foraging flexibility, which may act as a buffer to anthropogenic change in the breeding grounds for individuals where alternate habitat is available.

Unusually for a diving bird that overwinters in marine environments, RTDs have been shown to forage in both

Table 1. Foraging bout and diving characteristics and tag samples sizes of red-throated divers from three breeding locations. Breeding sites sharing a subscripted letter were not significantly different from each other. Values given are the predicted mean, with ranges in brackets denoting 95% confidence intervals generated by GLMMs. \*Adjusted for the effect of dive duration.

	Scotland	Finland	Iceland
Number of individuals with TDRs	8	8	7
Number of individuals with viable GLSs	5	7	7
Bout length (minutes)	7.2 <sup>a</sup> (6.1–8.5)	10.8 <sup>b</sup> (9.1–12.8)	10.2 <sup>b</sup> (8.5–12.2)
Number of dives in a bout	15 <sup>a</sup> (13–17)	21 <sup>b</sup> (18–25)	22 <sup>b</sup> (18–25)
Mean maximum dive depth within a dive (Metres)	4.5 <sup>a</sup> (3.8–5.3)	6.4 <sup>b</sup> (5.4–7.6)	3.8 <sup>a</sup> (3.2–4.6)
Proportion of U-shaped dives*	0.90 <sup>a</sup> (0.87–0.92)	0.91 <sup>a</sup> (0.88–0.93)	0.97 <sup>b</sup> (0.96–0.98)
Dive duration (seconds)	25 <sup>a</sup> (22–27)	36 <sup>b</sup> (33–38)	26 <sup>a</sup> (23–29)



Figure 3. The predicted mean time spent foraging per day generated from the best fitting model for *Gavia stellata*. Breeding sites sharing a letter were not significantly different from each other. Error bars show the 95% upper and lower confidence intervals.

freshwater (Eriksson et al. 1990, Eriksson and Sundberg 1991, Duckworth et al. 2020b) and marine environments during the breeding season (Reimchen and Douglas 1984, Black et al. 2015, Rizzolo et al. 2015). As predicted, all diving metrics (dive depth and dive duration) differed between Finland and at least one of the other two sites (Table 1). This is likely due to differences in foraging habitat, with Finnish birds foraging almost exclusively in freshwater habitats, while birds breeding at the other two sites regularly used marine habitat. The distance of the nests from the coast was greater at all nests in Finland ( $> 10$  km) than for birds at the other two

sites (always  $< 10$  km). Distance from the coast was likely driving these differences in diving metrics, as the energetic cost of flying to the marine environment was presumably not worth the energetic payoff in terms of prey items gained (Lihoreau et al. 2011). At nest sites in Scotland, many of the local acidic lochans were devoid of prey, so marine prey was the only option. RTDs in Finland instead foraged in local lakes, where freshwater prey species provided a much more spatially convenient option. However, one Finnish RTD that bred ~15 km from the coast did forage in the marine environment for several days at the start of the study period, before

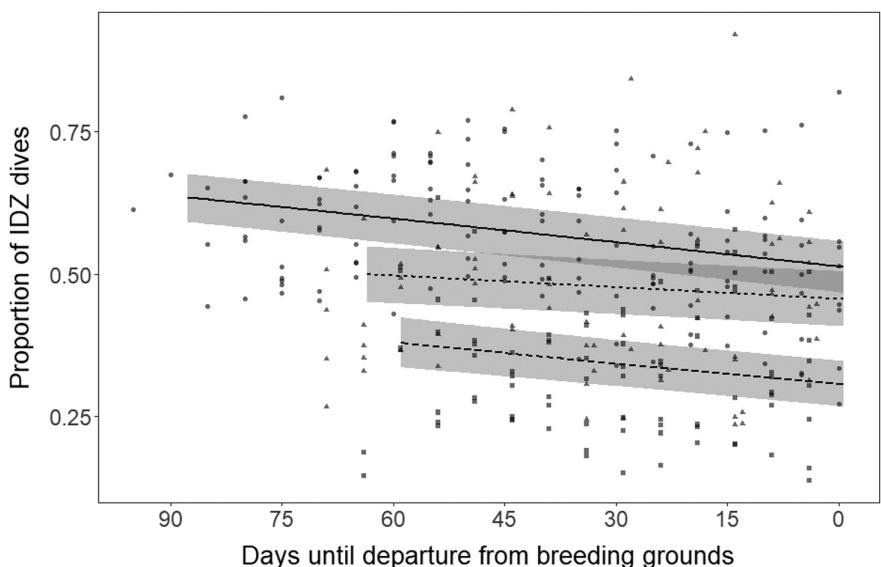


Figure 4. The proportion of *Gavia stellata* inter-depth zone (IDZ) dives per day across RTDs breeding in Finland (solid line), Iceland (dotted line) and Scotland (dashed line). Lines show the predicted values from the model, with 95% confidence intervals (grey shading). Points represent the observed proportions of IDZ dives for each individual on each day sampling occurred with circles, triangles and squares representing Finland, Iceland and Scotland, respectively.

returning to entirely freshwater habitat for the remainder of the breeding season. Unfortunately, the exact conditions that lead to this change in habitat use are unknown, but this observation suggests that RTDs may be able to buffer against poor foraging success in local freshwater habitats.

Large-scale differences in foraging habitats are clearly not the only driver of foraging behaviour in this species. Unexpectedly, number of dives within a bout and bout length, the two foraging metrics that represented how bouts were organised (Table 1), differed between Scotland and the other two sites. Specifically, foraging bouts in Scotland were shorter and had fewer dives. This difference could be related to foraging success and food availability, as fewer dives and a shorter time in each foraging bout suggests the time required to meet the energy demand of each foraging bout is lower. This is also partly demonstrated in other aquatic birds, such as kittiwakes (Chivers et al. 2012) and guillemots (Davoren and Montevecchi 2003), through birds increasing the duration of foraging bouts in years where food availability is lower. This suggests foraging success could have been higher at Scotland than the other two sites, which is supported by the lower daily time spent foraging (Fig. 3). However, this did not appear to affect breeding success, with only 38% of monitored RTD pairs in Scotland producing at least one chick in 2018, compared with 62% of monitored RTD pairs in Finland (O'Brien et al. 2018).

Animals foraging during a breeding season have to adapt their foraging effort temporally in order to accommodate the demands of growing young (Tulp et al. 2009, Sotillo et al. 2019). However, at all three sites, the foraging effort for RTDs did not change through the season as we expected. Instead it appears that the tracked divers may have adapted their foraging strategy via prey selection, rather than increasing the number of foraging trips or foraging intensity through time. This is suggested by earlier observations of RTDs from Sweden, where it was found that the number of foraging trips did not change as the breeding season progressed, but instead the size of the prey brought back by the parents changed (Eriksson et al. 1990). This effect was particularly noticeable when the chicks were very young (Reimchen and Douglas 1984). The proportion of IDZ (benthic) dives decreased during the breeding season across all sites. Such changes have previously been linked to differences in prey selection in diving predators, where higher resolution data on location and bathymetry has been available (Kuhn et al. 2010). RTDs are single prey loaders, therefore they may maximise the energy gain per foraging trip by ensuring they bring back food items with maximum energy returns, rather than increasing foraging effort and delivering the same prey items throughout the season. This strategy will avoid the costs of an increased number of flights, which would be exacerbated by the high wing loading of RTDs (Lovvorn and Jones 1994).

The RTDs at the three sites also displayed some evidence of flexibility between regions in how they altered their foraging behaviour as the season progressed. Though the progressive decrease in the proportion of IDZ (benthic) dives was common across sites, the degree of change in the proportion of

IDZ dives was not the same, with Iceland showing little biologically meaningful change (a change of 4% over the 65 days) in foraging strategy through the season (Fig. 4). Diet changes within a breeding season are common for several aquatic bird species in the northern Japanese sea, as the influx of warm water changes the prey availability (Watanuki et al. 2009, Watanuki and Ito 2012). Similar events could affect RTDs in Iceland foraging consistently in the same habitat through the season, but targeting different prey as the season progressed. On the other hand, RTDs in Finland and Scotland showed a more notable decrease in proportion of IDZ dives. This could relate to following vertical prey movement, foraging in different habitat or switching to prey occupying a different area of the water column (Sotillo et al. 2019), to fulfil the food size demand of the chicks (Reimchen and Douglas 1984). The latter could especially be true in Finland, as evidence suggests black-throated divers *Gavia arctica* foraging in freshwater can provision benthic invertebrates to chicks in the early stages of rearing (Jackson 2003). Furthermore, the closed nature of lake systems makes it unlikely that there will be temporal changes in prey availability. This use of invertebrate prey may also explain why RTDs in Finland had the highest proportion of IDZ dives and therefore the most benthic dives, especially early in the season. Conversely, RTDs in Scotland showed a low proportion of IDZ dives overall. Tremblay and Cherel (2000) visually classified groups of dives as either pelagic or benthic and found that groups of pelagic dives had less than 40.3% of IDZ dives within these groups. In our study, the model showed birds from Scotland generally had a proportion of IDZ dives below this threshold. Therefore, it is likely that RTDs in Scotland are mostly foraging pelagically in the marine environment. While this does not preclude the occurrence of benthic dives, it strongly suggests pelagic foraging is more important in Scotland than in Finland and Iceland. These results have demonstrated that local environment has an effect on the foraging behaviour of RTDs, but in order to confirm the prey switching hypothesis, further analysis is required to create a direct link between diet and foraging behaviour, perhaps through the use of stable isotope analysis (Hobson and Clark 1992, Gómez et al. 2018).

Many pursuit divers are dependent on high light levels to target and catch their prey, though nocturnal activity can be observed in some cases (Wilson et al. 1993, Cannell and Cullen 2008, Dunn et al. 2019). Preliminary evidence suggested that RTDs are crepuscular when foraging (Duckworth et al. 2020b), but data collection from this study does not support that suggestion. Birds breeding at Scotland and Finland showed differences in the proportion of dives across light conditions, with a preference for foraging in daylight. However, while the same was found in Iceland, the difference in foraging effort between the two light conditions was much smaller. Overall, this preference for diving in daylight would be expected for pursuit diving, visually orientated birds, as high light conditions provide the perfect conditions to track and capture prey (Wilson et al. 1993). However, these findings could be a product of high individual difference and a low sample size. Therefore, further investigation

into RTD behaviour is required to determine whether there is a capacity for nocturnal foraging.

This paper provides the first multi-individual descriptions of RTD diving, from three distinct regions and thus form the current best understanding of summer foraging behaviour of this species. As such our results are also necessarily limited and provoke ideas for further study. We considered temporal change, however, RTDs are not synchronous breeders and can relay clutches, with many breeding pairs at different breeding stages at any given point during the breeding season. Therefore, using days since egg laying or hatching would give a better picture of how the activity budgets differ at each of the breeding stages. Due to the remote locations of many of the nests and the extreme sensitivity of the species to disturbance, we were not able to regularly monitor RTD nests across all sites, both to minimise the effect our attendance had on behaviour and minimise ethical concerns arising from disturbance. Future study could deploy remote camera traps to maximise information on nest attendance while minimising human presence (Edney and Wood 2020). In addition, the lack of precise foraging locations of birds meant we were unable to link foraging to local environmental conditions, so could not relate foraging behaviour to environmental influences such as tidal cycles and hydrographic features (Skov and Prins 2001) and future studies should try to also track birds with GPS if this can be achieved without additional disturbance. Additionally, the TDR pressure sampling frequency was relatively low, prohibiting more detailed analysis of dive characteristics such as bottom activity, ascent rate and descent rate. As the logger resolution is < 10% of the median dive duration, it is likely that some of the parameters may be imperfect estimations (Wilson et al. 1995). However, this resolution of data allows for valid comparisons between our geographically distinct groups and will still provide accurate values for the proportion of time spent foraging and estimates for other parameters are unlikely to have a substantial error at our resolution (Dunn et al. 2019). We also acknowledge the small sample size of this study limits our ability to make true large-scale comparisons across sites. Instead, our study focusses on description of foraging behaviours and highlights differences between regions. As technology and methodologies develop it may be possible to increase our understanding of this important species, up to the level of better understood aquatic birds (Soanes et al. 2014) but our study is an important first step in this process.

Having demonstrated some degree of spatial and temporal variation in foraging behaviour, our study suggests RTDs have some flexibility in foraging strategies. This could further suggest breeding RTDs are have some capacity to resist anthropogenic effects, as the species as a whole is capable of exploiting a range of niches (Devictor et al. 2008, Wilson et al. 2008). However, the two commonalities across all RTDs is their necessity to build nests by freshwater lakes (Rizzolo et al. 2014) and their migration to mostly marine habitats (Polak and Ciach 2007, McCloskey et al. 2018). Therefore, while foraging can vary both within and

between individuals, these two fundamental aspects of RTD ecology remain constraints in their annual cycle. Therefore, work must also be done to improve the understanding of the potential effects of climate change on nesting habitat suitability and RTD foraging behaviour during the winter.

**Acknowledgements** – The PhD studentship was funded by a NERC (Natural Environment Research Council) CASE PhD studentship in collaboration with JNCC, as part of the ACCE Doctoral Training Partnership. Fieldwork was managed by JNCC and funded by: The Crown Estate, Ørsted, Equinor, Vattenfall and Hartley Anderson Ltd (BEIS Offshore Energy SEA Research Fund). Thanks to the Ministry for the Environment and Natural Resources in Iceland for support during the study in Iceland. The authors declare no other conflict of interest. All applicable institutional and/or national guidelines for the care and use of animals were followed. We are also grateful to all those involved with giving permission to undertake this work including the Centre for Economic Development, Transport and the Environment in Finland, the National Parks, Finland, the British Trust for Ornithology, Scottish Natural Heritage and the Royal Society for the Protection of Birds.

## Author contributions

**James Duckworth:** Conceptualization (equal); Data curation (supporting); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Susan O'Brien:** Conceptualization (equal); Data curation (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (equal); Supervision (supporting); Writing – review and editing (equal). **Ib Petersen:** Conceptualization (equal); Investigation (equal); Resources (equal); Supervision (supporting); Writing – review and editing (equal). **Aivar Petersen:** Funding acquisition (supporting); Methodology (equal); Resources (equal); Writing – review and editing (equal). **Guðmundur Benediktsson:** Methodology (equal); Resources (equal); Writing – review and editing (equal). **Logan Johnson:** Methodology (equal); Resources (equal); Writing – review and editing (equal). **Petteri Lehikoinen:** Methodology (equal); Resources (equal); Writing – review and editing (equal). **David Okill:** Methodology (equal); Resources (equal); Writing – review and editing (equal). **Jim Williams:** Methodology (equal); Resources (equal); Writing – review and editing (equal). **Stuart Williams:** Methodology (equal); Resources (equal); Writing – review and editing (equal). **Roni Väistänen:** Methodology (equal); Resources (equal); Writing – review and editing (equal). **Francis Daunt:** Investigation (supporting); Supervision (supporting); Writing – review and editing (equal). **Jonathan Green:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Project administration (supporting); Supervision (lead); Writing – review and editing (equal).

## Transparent Peer Review

The peer review history for this article is available at <https://publons.com/publon/10.1111/jav.02702>.

## Data availability statement

Data will be held at the public JNCC repository at <https://hub.jncc.gov.uk/> email enquiries can be sent to [data@jncc.gov.uk](mailto:data@jncc.gov.uk).

## References

Amelineau, F., Gremillet, D., Harding, A. M. A., Walkusz, W., Choquet, R. and Fort, J. 2019. Arctic climate change and pollution impact little auk foraging and fitness across a decade. – *Sci. Rep.* 9: 15.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. – *J. Wildl. Manage.* 74: 1175–1178.

Bagniewska, J. M., Hart, T., Harrington, L. A. and Macdonald, D. W. 2013. Hidden Markov analysis describes dive patterns in semiaquatic animals. – *Behav. Ecol.* 24: 659–667.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.

Black, J., Dean, B. J., Webb, A., Lewis, M., Okill, D. and Reid, J. B. 2015. Identification of important marine areas in the UK for red-throated divers *Gavia stellata* during the breeding season. – JNCC, Peterborough, UK.

Boggs, C. L. 1992. Resource allocation: exploring connections between foraging and life history. – *Funct. Ecol.* 6: 508–518.

Bost, C. A., Cotté, C., Terray, P., Barbraud, C., Bon, C., Delord, K., Gimenez, O., Handrich, Y., Naito, Y., Guinet, C. and Weimerskirch, H. 2015. Large-scale climatic anomalies affect marine predator foraging behaviour and demography. – *Nat. Comm.* 6: 8220.

Burger, C., Schubert, A., Heinänen, S., Dorsch, M., Kleinschmidt, B., Žydelis, R., Morkūnas, J., Quillfeldt, P. and Nehls, G. 2019. A novel approach for assessing effects of ship traffic on distributions and movements of seabirds. – *J. Environ. Manage.* 251: 109511.

Cannell, B. and Cullen, J. 2008. The foraging behaviour of little penguins *Eudyptula minor* at different light levels. – *Ibis* 140: 467–471.

Carboneras, C., Christie, D. A. and Garcia, E. F. J. 2020. Red-throated loon *Gavia stellata*. – In: Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. and De Juana, E. (eds), *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona.

Chivers, L. S., Lundy, M. G., Colhoun, K., Newton, S. F., Houghton, J. D. R. and Reid, N. 2012. Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake. – *Mar. Ecol. Prog. Ser.* 456: 269–277.

Crocker, D. E., Costa, D. P., Le Boeuf, B. J., Webb, P. M. and Houser, D. S. 2006. Impact of El Niño on the foraging behavior of female northern elephant seals. – *Mar. Ecol. Prog. Ser.* 309: 1–10.

Davoren, G. K. and Montevecchi, W. A. 2003. Consequences of foraging trip duration on provisioning behaviour and fledging condition of common murres *Uria aalge*. – *J. Avian Biol.* 34: 44–53.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A. and Couvet, D. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. – *Global Ecol. Biogeogr.* 17: 252–261.

Drewitt, A. L. and Langston, R. H. W. 2006. Assessing the impacts of wind farms on birds. – *Ibis* 148: 29–42.

Duckworth, J., Green, J., Daunt, F., Johnson, L., Lehikoinen, P., Okill, D., Petersen, A., Petersen, I. K., Väistönen, R., Williams, J., Williams, S. and O'Brien, S. 2020a. Red-throated diver energetics project: preliminary results from 2018/19. – JNCC, Peterborough, UK.

Duckworth, J., O'Brien, S., Väistönen, R., Lehikoinen, P., Petersen, I. K., Daunt, F. and Green, J. A. 2020b. First biologging record of a foraging red-throated loon *Gavia stellata* shows shallow and efficient diving in freshwater environments. – *Mar. Ornithol.* 48: 17–22.

Dunn, R. E., Wanless, S., Green, J. A., Harris, M. P. and Daunt, F. 2019. Effects of body size, sex, parental care and moult strategies on auk diving behaviour outside the breeding season. – *J. Avian Biol.* 50: e02012.

Dunn, R. E., White, C. R. and Green, J. A. 2018. A model to estimate seabird field metabolic rates. – *Biol. Lett.* 14: 20180190.

Edney, A. J. and Wood, M. J. 2020. Applications of digital imaging and analysis in seabird monitoring and research. – *Ibis* 163: 317–337.

Eriksson, M. O. G. and Sundberg, P. 1991. The choice of fishing lakes by the red-throated diver *Gavia stellata* and black-throated diver *G. arctica* during the breeding season in south-west Sweden. – *Bird Study* 38: 135–144.

Eriksson, M. O. G., Blomqvist, D., Hake, M. and Johansson, O. C. 1990. Parental feeding in the red-throated diver *Gavia stellata*. – *Ibis* 132: 1–13.

Erikstad, K. E., Sandvik, H., Reiertsen, T. K., Bustnes, J. O. and Strom, H. 2013. Persistent organic pollution in a high-Arctic top predator: sex-dependent thresholds in adult survival. – *Proc. R. Soc. B* 280: 7.

Foo, D., Semmens, J. M., Arnould, J. P. Y., Dorville, N., Hoskins, A. J., Abernathy, K., Marshall, G. J. and Hindell, M. A. 2016. Testing optimal foraging theory models on benthic divers. – *Anim. Behav.* 112: 127–138.

Furness, R. W., Wade, H. M. and Masden, E. A. 2013. Assessing vulnerability of marine bird populations to offshore wind farms. – *J. Environ. Manage.* 119: 56–66.

Gómez, C., Larsen, T., Popp, B., Hobson, K. A. and Cadena, C. D. 2018. Assessing seasonal changes in animal diets with stable-isotope analysis of amino acids: a migratory boreal songbird switches diet over its annual cycle. – *Oecologia* 187: 1–13.

Grémillet, D. and Boulinier, T. 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. – *Mar. Ecol. Prog. Ser.* 391: 121–137.

Grémillet, D., Argentin, G., Schulte, B. and Culik, B. M. 1998. Flexible foraging techniques in breeding cormorants *Phalacrocorax carbo* and shags *Phalacrocorax aristotelis*: benthic or pelagic feeding? – *Ibis* 140: 113–119.

Halsey, L. G., Bost, C. A. and Handrich, Y. 2007. A thorough and quantified method for classifying seabird diving behaviour. – *Polar Biol.* 30: 991–1004.

Harper, E. B., Rittenhouse, T. A. G. and Semlitsch, R. D. 2008. Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: predicting extinction risks associated with inadequate size of buffer zones. – *Conserv. Biol.* 22: 1205–1215.

Hays, G. C., Forman, D. W., Harrington, L. A., Andrew, L. H., Macdonald, D. W. and Righton, D. 2007. Recording the free-living behaviour of small-bodied, shallow-diving animals with data loggers. – *J. Anim. Ecol.* 76: 183–190.

Heinänen, S., Žydelis, R., Kleinschmidt, B., Dorsch, M., Burger, C., Morkūnas, J., Quillfeldt, P. and Nehls, G. 2020. Satellite telemetry and digital aerial surveys show strong displacement of red-throated divers *Gavia stellata* from offshore wind farms. – *Mar. Environ. Res.* 160: 104989.

Hobson, K. A. and Clark, R. G. 1992. Assessing avian diets using stable isotopes I: turnover of  $^{13}\text{C}$  in tissues. – *Condor* 94: 181–188.

Horn, D. A., Granek, E. F. and Steele, C. L. 2020. Effects of environmentally relevant concentrations of microplastic fibers on Pacific mole crab *Emerita analoga* mortality and reproduction. – *Limnol. Oceanogr. Lett.* 5: 74–83.

Hovick, T. J., Elmore, R. D., Dahlgren, D. K., Fuhlendorf, S. D. and Engle, D. M. 2014. Review: Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. – *J. Appl. Ecol.* 51: 1680–1689.

Jackson, D. B. 2003. Between-lake differences in the diet and provisioning behaviour of black-throated divers *Gavia arctica* breeding in Scotland. – *Ibis* 145: 30–44.

Kleinschmidt, B., Burger, C., Dorsch, M., Nehls, G., Heinänen, S., Morkūnas, J., Žydelis, R., Moorhouse-Gann, R. J., Hipperson, H., Symondson, W. O. C. and Quillfeldt, P. 2019. The diet of red-throated divers *Gavia stellata* overwintering in the German Bight (North Sea) analysed using molecular diagnostics. – *Mar. Biol.* 166: 77.

Knox, T. C., Baylis, A. M. M. and Arnould, J. P. Y. 2018. Foraging site fidelity in male Australian fur seals. – *Mar. Biol.* 165: 108.

Kuhn, C. E., Tremblay, Y., Ream, R. R. and Gelatt, T. S. 2010. Coupling GPS tracking with dive behavior to examine the relationship between foraging strategy and fine-scale movements of northern fur seals. – *Endangered Species Res.* 12: 125–139.

Lihoreau, M., Chittka, L., Raine, N. E. and Kudo, G. 2011. Trade-off between travel distance and prioritization of high-reward sites in traplining bumblebees. – *Funct. Ecol.* 25: 1284–1292.

Linneberg, J. F., Huffeldt, N. P., Falk, K., Merkel, F. R., Mosbech, A. and Frederiksen, M. 2014. Inferring seabird activity budgets from leg-mounted time-depth recorders. – *J. Ornithol.* 155: 301–306.

Lovvold, J. R. and Jones, D. R. 1994. Biomechanical conflicts between adaptations for diving and aerial flight in estuarine birds. – *Estuaries* 17: 62–75.

Luque, S. P. and Fried, R. 2011. Recursive filtering for zero offset correction of diving depth time series with GNU R package diveMove. – *PLoS One* 6: e15850.

Maynard, L. and Davoren, G. 2020. Inter-colony and interspecific differences in the isotopic niche of two sympatric gull species in Newfoundland. – *Mar. Ornithol.* 48: 103–109.

McCloskey, S. E., Uher-Koch, B. D., Schmutz, J. A. and Fondell, T. F. 2018. International migration patterns of red-throated loons *Gavia stellata* from four breeding populations in Alaska. – *PLoS One* 13: 1–15.

Mendel, B., Schwemmer, P., Peschko, V., Müller, S., Schwemmer, H., Garthe, S. and Mercker, M. 2019. Operational offshore wind farms and associated ship traffic cause profound changes in distribution patterns of loons (*Gavia* spp.). – *J. Environ. Manage.* 231: 429–438.

Millon, L., Colin, C., Brescia, F. and Kerbiriou, C. 2018. Wind turbines impact bat activity, leading to high losses of habitat use in a biodiversity hotspot. – *Ecol. Eng.* 112: 51–54.

Nummi, P., Väänänen, V., Pakarinen, R. and Pienmuunne, E. 2013. The red-throated diver *Gavia stellata* in human-disturbed habitats – building up a local population with the aid of artificial rafts. – *Ornis Fenn.* 90: 16–22.

O'Brien, S. H., Webb, A., Brewer, M. J. and Reid, J. B. 2012. Use of kernel density estimation and maximum curvature to set marine protected area boundaries: identifying a special protection area for wintering red-throated divers in the UK. – *Biol. Conserv.* 156: 15–21.

O'Brien, S., Ruffino, L., Lehikoinen, P., Johnson, L., Lewis, M., Petersen, A., Petersen, I. K., Okill, D., Väisänen, R., Williams, J. and Williams, S. 2018. Red-throated diver energetics project – 2018 field season report. JNCC Report No. 627. – JNCC, Peterborough, UK.

Peckham, S. H., Maldonado Diaz, D., Tremblay, Y., Ochoa, R., Polovina, J., Balazs, G., Dutton, P. H. and Nichols, W. J. 2011. Demographic implications of alternative foraging strategies in juvenile loggerhead turtles *Caretta caretta* of the North Pacific Ocean. – *Mar. Ecol. Prog. Ser.* 425: 269–280.

Petersen, I. K., Nielsen, R. D., Pihl, S., Clausen, P., Therkildsen, O., Christensen, T. K., Kahlert, J. and Hounisen, J. P. 2010. Landsdakkende optalling av vandfugle i Danmark, vinteren 2007/2008. Working Report from DMU. – The Danish Environmental Research Inst., Aarhus Univ., Denmark.

Plumpton, D. L. and Andersen, D. E. 1998. Anthropogenic effects on winter behavior of ferruginous hawks. – *J. Wildl. Manage.* 62: 340–346.

Polak, M. and Ciach, M. 2007. Behaviour of black-throated diver *Gavia arctica* and red-throated diver *Gavia stellata* during autumn migration stopover. – *Ornis Svec.* 17: 90–94.

Poupart, T. A., Waugh, S. M., Bost, C. A., Kato, A., Miskelly, C. M., Rogers, K. M. and Arnould, J. P. Y. 2019. Foraging ecology of a winter breeder, the Fiordland penguin. – *Mar. Ecol. Prog. Ser.* 614: 183–197.

Quillfeldt, P., Schroff, S., Van Noordwijk, H. J., Michalik, A., Ludynia, K. and Masello, J. F. 2011. Flexible foraging behaviour of a sexually dimorphic seabird: large males do not always dive deep. – *Mar. Ecol. Prog. Ser.* 428: 271–287.

Regular, P. M., Hedd, A. and Montevecchi, W. A. 2011. Fishing in the dark: a pursuit-diving seabird modifies foraging behaviour in response to nocturnal light levels. – *PLoS One* 6: e26763.

Reimchen, T. E. and Douglas, S. 1984. Feeding schedule and daily food consumption in red-throated loons *Gavia stellata* over the pre fledgling period. – *Auk* 101: 593–599.

Rizzolo, D. J., Schmutz, J. A. and Speakman, J. R. 2015. Fast and efficient: postnatal growth and energy expenditure in an Arctic-breeding waterbird, the red-throated loon *Gavia stellata*. – *Auk* 132: 657–670.

Rizzolo, D. J., Schmutz, J. A., McCloskey, S. E. and Fondell, T. F. 2014. Factors influencing nest survival and productivity of red-throated loons *Gavia stellata* in Alaska. – *Condor* 116: 574–587.

Rodary, D., Wienecke, B. C. and Bost, C. A. 2000. Diving behaviour of Adélie penguins *Pygoscelis adeliae* at Dumont D'Urville, Antarctica: nocturnal patterns of diving and rapid adaptations to changes in sea-ice condition. – *Polar Biol.* 23: 113–120.

Russell, L. 2020. emmeans: estimated marginal means, aka least-squares means. – <<https://github.com/rvlenth/emmeans>>.

Salamolard, M. and Weimerskirch, H. 1993. Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. – *Funct. Ecol.* 7: 643–652.

Schmutz, J. A., Trust, K. A. and Matz, A. C. 2009. Red-throated loons *Gavia stellata* breeding in Alaska, USA, are exposed to PCBs while on their Asian wintering grounds. – *Environ. Pollut.* 157: 2386–2393.

Schwemmer, P., Mendel, B., Sonntag, N., Dierschke, V. and Garthe, S. 2011. Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. – *Ecol. Appl.* 21: 1851–1860.

Scrafford, M. A., Avgar, T., Abercrombie, B., Tigner, J. and Boyce, M. S. 2017. Wolverine habitat selection in response to anthropogenic disturbance in the western Canadian boreal forest. – *For. Ecol. Manage.* 395: 27–36.

Senzaki, M., Yamaura, Y., Francis, C. D. and Nakamura, F. 2016. Traffic noise reduces foraging efficiency in wild owls. – *Sci. Rep.* 6: 30602.

Shaffer, S. A., Costa, D. P. and Weimerskirch, H. 2001. Behavioural factors affecting foraging effort of breeding wandering albatrosses. – *J. Anim. Ecol.* 70: 864–874.

Sibly, R. M., Nott, H. M. R. and Fletcher, D. J. 1990. Splitting behaviour into bouts. – *Anim. Behav.* 39: 63–69.

Skov, H. and Prins, E. 2001. Impact of estuarine fronts on the dispersal of piscivorous birds in the German Bight. – *Mar. Ecol. Prog. Ser.* 214: 279–287.

Soanes, L. M., Arnould, J. P. Y., Dodd, S. G., Milligan, G. and Green, J. A. 2014. Factors affecting the foraging behaviour of the European shag: implications for seabird tracking studies. – *Mar. Biol.* 161: 1335–1348.

Sotillo, A., Baert, J. M., Müller, W., Stienen, E. W. M., Soares, A. M. V. M. and Lens, L. 2019. Time and energy costs of different foraging choices in an avian generalist species. – *Mov. Ecol.* 7: 41.

Thaxter, C. B., Ross-Smith, V. H., Bouten, W., Clark, N. A., Conway, G. J., Rehfisch, M. M. and Burton, N. H. K. 2015. Seabird–wind farm interactions during the breeding season vary within and between years: a case study of lesser black-backed gull *Larus fuscus* in the UK. – *Biol. Conserv.* 186: 347–358.

Tremblay, Y. and Cherel, Y. 2000. Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. – *Mar. Ecol. Prog. Ser.* 204: 257–267.

Tulp, I., Schekkerman, H., Bruinzeel, L. W., Jukema, J., Visser, G. H. and Piersma, T. 2009. Energetic demands during incubation and chick rearing in a uniparental and a biparental shorebird breeding in the high arctic. – *Auk* 126: 155–164.

Uher-Koch, B. D., Koch, J. C., Wright, K. G. and Schmutz, J. A. 2018. Comparative nest survival of three sympatric loon species breeding in the Arctic. – *J. Avian Biol.* 49: e01671.

Uher-Koch, B. D., Schmutz, J. A. and Wright, K. G. 2015. Nest visits and capture events affect breeding success of yellow-billed and Pacific loons. – *Condor* 117: 121–129.

Watanuki, Y. and Ito, M. 2012. Climatic effects on breeding seabirds of the northern Japan Sea. – *Mar. Ecol. Prog. Ser.* 454: 183–196.

Watanuki, Y., Ito, M., Deguchi, T. and Minobe, S. 2009. Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. – *Mar. Ecol. Prog. Ser.* 393: 259–271.

Wilson, R. P., Pütz, K., Charrassin, J.-B. and Lage, J. 1995. Artifacts arising from sampling interval in dive depth studies of marine endotherms. – *Polar Biol.* 15: 575–581.

Wilson, R., Pütz, K., Bost, C., Culik, B., Bannasch, R., Reins, T. and Adelung, D. 1993. Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? – *Mar. Ecol. Prog. Ser.* 94: 101–104.

Wilson, S. K., Burgess, S. C., Cheal, A. J., Emslie, M., Fisher, R., Miller, I., Polunin, N. V. and Sweatman, H. P. 2008. Habitat utilization by coral reef fish: implications for specialists vs generalists in a changing environment. – *J. Anim. Ecol.* 77: 220–228.

Zimmer, I., Wilson, R. P., Beaulieu, M., Ropert-Coudert, Y., Kato, A., Ancel, A. and Ploetz, J. 2010. Dive efficiency versus depth in foraging emperor penguins. – *Aquat. Biol.* 8: 269–277.