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1 Influence of sea-ice-related features and anthropogenic subsidies on the foraging behaviour of a
2 high-Arctic seabird, the ivory gull (*Pagophila eburnea*)

3

4 Keyvan Dumas^{1,3} *, Olivier Gilg^{2,3}, Nicolas Courbin¹, Alejandro Corregidor-Castro^{4a}, Guillaume
5 Evanno^{3,5}, Hallvard Strøm⁶, Anders Mosbech⁴, Morten Frederiksen⁴, and Glenn Yannic^{1,3}

6

7 ¹Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, 38000 Grenoble, France

8 ²Université de Bourgogne Franche Comté, UMR 6249 Chrono-environnement, 25000 Besançon,
9 France

10 ³Groupe de Recherche en Ecologie Arctique, 21440 Francheville, France

11 ⁴Department of Ecoscience, Aarhus University, 4000, Roskilde, Denmark

12 ⁵DECOD (Ecosystem Dynamics and Sustainability), INRAE, Institut Agro, IFREMER, Rennes,
13 France

14 ⁶Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway

15 ^aCurrent Address: Department of Biology, University of Padova, 35131 Padova, Italy

16

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18 *Corresponding author: Keyvan Dumas, dumaskeyvan@gmail.com

19

20 **ABSTRACT**

21

22 The Arctic region is currently experiencing major modifications in sea ice extent and phenology due
23 to global climate and anthropogenic changes. As Arctic marine ecosystems rely greatly on the
24 presence of sea ice and its seasonal dynamics, these changes could have major impacts on Arctic
25 biota. The ivory gull (*Pagophila eburnea*) is an endemic Arctic seabird whose populations are
26 declining in Canada and Svalbard. Its affinity for sea ice makes it a good sentinel species of current
27 changes in the high Arctic. We explored the influence of sea-ice-related features and anthropogenic
28 subsidies on the foraging behaviour of ivory gulls during the breeding season. To this end, we
29 analysed the movement of adult ivory gulls in north-east Greenland. We confirmed that ivory gulls
30 use a dual foraging strategy, with birds faithful to their foraging areas at short distances from the
31 colony, but used individual-specific areas during long-distance foraging trips. We highlight that
32 ivory gulls are spatially specialised individuals within a generalist species. We demonstrated that
33 human settlements attracted foraging birds, which shows that human presence in such a remote
34 place may influence seabird behaviour. Finally, by combining hidden Markov models and resource-
35 selection functions, we showed that ivory gulls selected highly concentrated sea ice for foraging
36 during the breeding season. Our study provides key information on the use of space and foraging
37 strategies of ivory gulls during the breeding season, and more broadly, how Arctic seabirds use ice
38 features.

39

40 **KEYWORDS:** Seabirds · Arctic ice fauna · GPS tracking · Dual foraging · Site fidelity · Greenland

41 1. INTRODUCTION

42 Global climate and anthropogenic changes have profound impacts on the Arctic, where warming is
43 occurring at least twice as rapidly as elsewhere on Earth (Miller et al. 2010; Box et al. 2019). The
44 increase in temperature is pressuring the cryosphere by melting sea ice and glaciers. The Arctic
45 region is expected to be free of sea ice in summer by the mid-21st century (IPCC, 2021). The
46 thinning and retreat of sea ice profoundly change trophic interactions at high latitudes by changing
47 landscapes (Post et al. 2013), animal interactions (Eamer et al. 2013; Macias-Fauria and Post 2018;
48 Clairbaux et al. 2019), and resource availability (Søreide et al. 2010). Sea ice can be divided into
49 two large-scale components: pack ice (sea ice concentration (SIC) > 80%) and the marginal ice
50 zone (MIZ), which is the area of sea ice between the ice edge (SIC = 15%) and the edge of the pack
51 ice (Strong and Rigor 2013). The high density of fractured sea ice in the MIZ supports development
52 of ice algae and phytoplankton, which are key primary producers whose blooms are triggered by the
53 breakup of sea ice in spring and summer (Søreide et al. 2010). Primary producer blooms structure
54 the entire trophic network, from zooplankton community growth (Kohlbach et al. 2016) to the
55 timing of seabird reproduction (Ramírez et al. 2017). However, thinning of sea ice causes it to break
56 up early in the season, which can result in a phenological mismatch between bloom production and
57 predator requirements, especially for reproduction (Søreide et al. 2010; Arrigo and van Dijken
58 2015; Ramírez et al. 2017).

59 Seabirds are widely recognised as good indicators of marine ecosystem health (Furness and
60 Camphuysen 1997; Dunphy et al. 2020; Grémillet et al. 2020; Wojczulanis-Jakubas et al. 2021).
61 Due to their high mobility and high trophic position, seabirds rely on large ocean areas for feeding.
62 They thus aggregate effects from multiple marine ecosystems phenomena (Durant et al. 2009).
63 The rapid response of their population fitness enables monitoring of environmental changes related
64 to ecosystem dynamics, prey availability, or the climate (Furness and Camphuysen 1997; Durant et
65 al. 2009; Grémillet and Charmantier 2010). In rapidly changing sea-ice landscapes, seabirds thus
66 seem to be excellent sentinel species to investigate the influence of changes in sea ice on marine

67 trophic networks. The global retreat of sea ice and a longer ice-free period each year could disrupt
68 prey availability around seabird breeding grounds, as shown, for example, for the Adelie penguin
69 (*Pygoscelis adeliae*; Michelot et al. 2020). Changes in sea ice could also provide new resources for
70 seabirds (Korczak-Abshire et al. 2021). For example, in the absence of sea ice, little auks (*Alle alle*)
71 can switch to foraging at nearby glacier meltwater fronts or at the shelf break (Grémillet et al. 2015;
72 Amélineau et al. 2016), at the cost of relying on lower-quality prey (Steen et al. 2007).

73 Additionally, climate-induced behavioural changes explain most of the decrease in fitness reported
74 for several Arctic specialists, including little auks (Amélineau et al. 2019).

75 The ivory gull (*Pagophila eburnea*) is an endemic Arctic seabird that is closely associated with sea
76 ice throughout the year (Spencer et al. 2014; Gilg et al. 2016). Ivory gulls breed on the ground or on
77 cliffs, in colonies of a few to hundreds of individuals in Greenland, Svalbard, Russia, and Canada.
78 Considered a generalist predator or opportunistic scavenger, ivory gulls concentrate on prey related
79 to sea ice (Divoky 1976; Mehlum and Gabrielsen 1993; Karnovsky et al. 2009), leftovers from
80 humans and large predators such as polar bears (*Ursus maritimus*) (Renaud and McLaren 1982),
81 and occasionally small mammals (Karnovsky et al. 2009). The ivory gull is classified as “Near
82 Threatened” on the IUCN Red List (BirdLife International, 2020). Reports suggest that its
83 populations have declined by 70% since the 1980s in Canada (Gilchrist and Mallory 2005) and by
84 40% in Svalbard (Norway) from 2009 to 2019 (Strøm et al. 2020), while trends are unclear in other
85 breeding regions (Gilg et al. 2009; Gavriilo and Martynova 2017; Boertmann et al. 2020). These
86 major declines highlight the fragile situation of these populations. The main threats identified for
87 ivory gulls are related to (i) a decrease in sea ice (*i.e.* ivory gulls’ main habitat) due to global
88 warming (Gilg et al. 2016; Spencer et al. 2016), (ii) contamination from persistent organic
89 pollutants and heavy metals through environmental exposure and bio-magnification (Braune et al.
90 2006; Miljeteig et al. 2009, 2012; Gaston et al. 2012; Bond et al. 2015; Lucia et al. 2015), (iii)
91 extensive development of human activities and associated pollution (e.g. oil or pollution spills from
92 resource extraction (oil, gas, mineral) and shipping routes in the Arctic) (Gilg et al. 2012;

93 Yurkowski et al. 2019), and (iv) extreme climatic events that decrease chick survival (Yannic et al.
94 2014).

95

96 The availability of miniaturised GPS trackers has helped understand the behaviour of seabirds
97 (Wilmers et al. 2015; Brisson-Curadeau et al. 2017). Methodological frameworks that combine GPS
98 data and advanced statistical methods to distinguish behavioural phases (e.g. resting, foraging,
99 transiting) provide detailed information on the movement behaviour of seabirds. During the
100 breeding season, the movement of breeding seabirds is strongly limited because they need to move
101 back and forth to the nest continually (i.e. “central place foraging”; Orians and Pearson 1979).
102 Consequently, however, colonial seabirds are thus restricted to forage in the same locations. This
103 concentration of individuals results in sub-optimal foraging opportunities near the colony. In
104 response to this increased competition, and to meet the food requirements of their chicks,
105 individuals can adopt a dual foraging strategy (Weimerskirch et al. 1994; Steen et al. 2007). In this
106 strategy, seabirds make frequent short trips to provide a steady supply of food to their chicks, but
107 they feed themselves on longer trips by exploring areas far from the colonies, with more resources
108 (Jakubas et al. 2012; Tyson et al. 2017). Trip characteristics thus show a bimodal distribution. To
109 improve foraging efficiency, seabirds may also select areas where the availability of resources is
110 spatially and temporally predictable (Patrick and Weimerskirch 2017; Courbin et al. 2018).

111

112 In environments with highly variable resources, seabirds often adopt a win-stay/lose-shift strategy
113 to optimise their energy gain when foraging (Kamil 1983; Davoren et al. 2003; Weimerskirch
114 2007), whereas in areas with predictable resources, seabirds appear to know the productive
115 locations and tend to feed preferentially in them to optimise their energy budget (Weimerskirch
116 2007). In the latter case, seabirds return regularly to the same foraging areas and therefore appear
117 site-faithful to them (Wakefield et al. 2015). Colonial seabirds must also compete for access to
118 resources. In a high-Arctic environment, snow and ice cover may hinder seabirds’ access to marine
119 resources, which makes them likely to develop site fidelity to the few favourable foraging areas.

120

121 In the present study, we sought to understand the foraging strategies of Arctic seabirds in relation to
122 ice features and human settlement, using ivory gulls as an example. To this end, we used high-
123 frequency GPS transmitters to track the movements of ivory gulls in north-east Greenland. Because
124 foraging opportunities in the Arctic are influenced by the availability of open water, distance to sea
125 ice, and the potential presence of anthropogenic food, we made three hypotheses. First, we
126 investigated the spatial strategies of ivory gulls by combining behavioural segmentation based on
127 hidden Markov models (HMMs) with site-fidelity analysis. We hypothesised that during short trips,
128 individual ivory gulls repeatedly forage in the same areas due to limited resource availability and
129 predictability around the colonies. Thus, we expected high site fidelity and overlap among birds
130 during short trips. Conversely, we hypothesised that longer trips have low site fidelity and overlap
131 (H1). Following previous fieldwork by members of our team, we hypothesised that the Station Nord
132 human settlement might affect ivory gulls- foraging behaviour . Due to the very predictable nature
133 of this food source, it should be regularly visited by ivory gulls (H2). Finally, we analysed habitat
134 selection to assess in more detail the foraging grounds used by ivory gulls. Based on previous
135 studies and expert knowledge, we hypothesised that ivory gulls select habitat within the MIZ and
136 near the sea ice edge when foraging (H3).

137

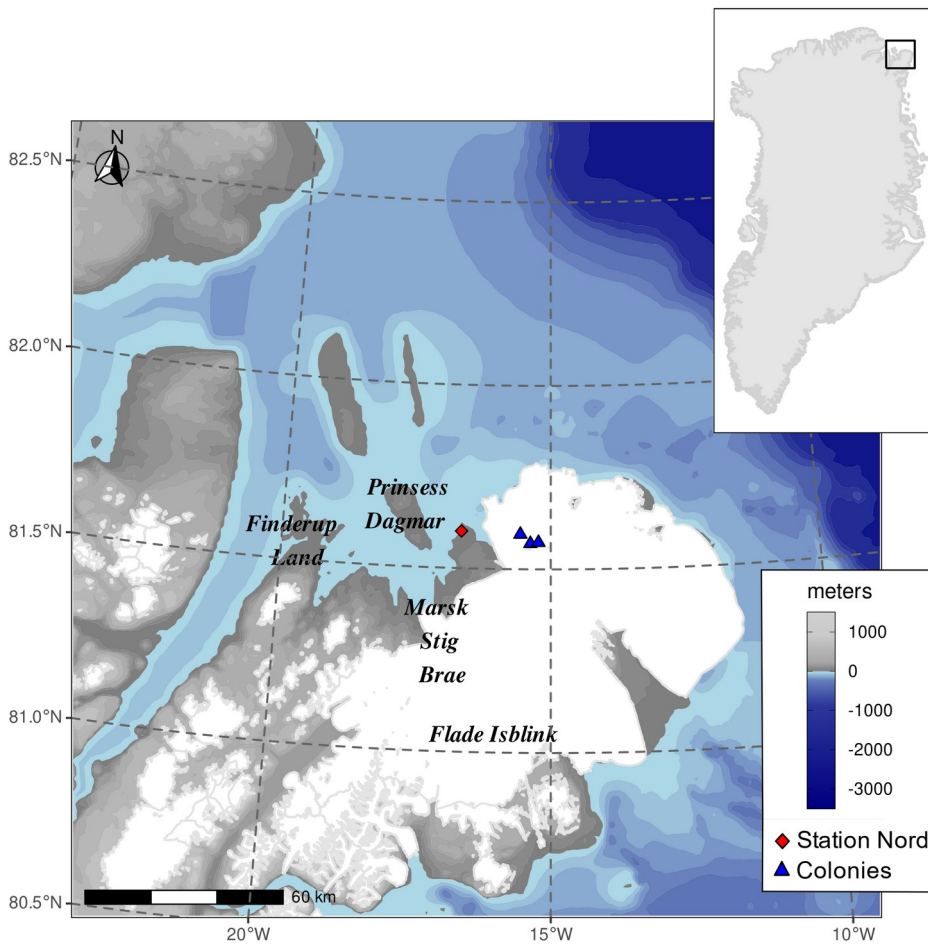
138 2. MATERIALS AND METHODS

139 2.1. FIELD SITE AND DATA COLLECTION

140

141 Adult ivory gulls were caught at Station Nord (STN, 81.60° N, 16.66° W), a Danish military and
142 research base in north-east Greenland, and at a nearby colony (81.60°N, 15.57°W; a complex of
143 three sub-colonies located 18-25 km east of STN) in July 2018 (n=22 birds) and July 2019 (n=5
144 birds) (Fig. 1). In 2018, 15 of the birds were caught near the STN kitchen building, while the other
145 7 were caught at the colony. In 2019, all five birds were captured near the STN kitchen building.
146 All birds were captured using baited traps or flap nets. Capture and handling procedures are fully
147 described by Frederiksen et al. (2019, 2021). In brief, each captured bird was weighed using a

148 Pesola spring scale (to the nearest 5 g), measured (the head, and for some birds, also the gonys,
149 tarsus, and wing, to the nearest mm; Yannic et al. 2016), and fitted with a metal ring (Zoological
150 Museum, Copenhagen, Denmark) and an engraved Darvic colour ring (white or yellow, with a two-
151 letter code in black). The combined mass of the two rings was 2.86 g. For birds caught at the
152 colony, the breeding status was inferred from the presence of a chick in the nest. For birds caught at
153 STN, the breeding status was unknown because all ivory gulls have a brood patch during the
154 breeding season. Feathers were sampled for molecular sexing (Table S1). All 27 ivory gulls were
155 tagged with RadioTag-14 solar GPS transmitters (Milsar Technologies SRL, Romania). They were
156 attached with a leg-loop harness made from Teflon ribbon (Bally Ribbon Mills, USA) that was
157 designed to fall off by itself after approximately one year. The combined mass of the GPS (10.4 g)
158 and harness was 12.2 g, which represented $2.2 \pm 0.1\%$ (mean ± 1 standard deviation) of the mean
159 body mass of tagged individuals. GPS data were remotely downloaded by a VHF base station when
160 birds were within a ca. 5 km radius around the device. Of the 27 ivory gulls tagged with a GPS
161 transmitter, only those whose GPS fixes were recorded at 5-min intervals were kept for analysis.
162



163
 164 Figure 1. Map of the study site and the surrounding region. Blue and grey shading refers to
 165 bathymetry and altitude, respectively (Jakobsson et al. 2012). White areas are glaciers and icecaps
 166 (Raup et al. 2007).

167

168 2.2. DATA PROCESSING

169 GPS fixes collected within 24 h of capture were removed to exclude altered movement behaviours
 170 (Gupte et al. 2021). All GPS tracks were checked for missing data, which never exceeded 1% of a
 171 track. All locations collected after 15 August were also removed, as we considered that birds started
 172 displaying post-breeding dispersal behaviour around this date (Gilg et al. 2010). As the interval
 173 between GPS fixes can sometimes vary by a few dozen sec, which can influence subsequent
 174 analyses, each GPS tracks were divided into 300 sec (5 min) intervals (Table S1). For each bird
 175 tagged at STN, its breeding sub-colony was inferred from its GPS track, whereas the sub-colony
 176 was known for birds tagged at the colony. One bird (ID 931013) transmitted data for two

177 consecutive years, but in the second year, it showed no attachment to any sub-colony and was thus
178 removed from all analyses except for habitat selection analysis. As only two of the seven birds
179 captured at the colony and equipped with a transmitter returned data, we could not investigate
180 differences between capture sites (i.e. STN vs. sub-colonies) (Fig. 1), which may represent a bias of
181 our study. The small sample size also precluded testing the influence of sex on foraging behaviours
182 and strategies.

183

184 2.3. FORAGING TRIPS

185 We defined trips as round trips of at least 1 h during which a bird flies further than 500 m from its
186 sub-colony. For each trip, we calculated the duration, Euclidean distance between the sub-colony
187 and the furthest point of the trip, and the total distance travelled during the entire trip. We used
188 piecewise linear regression (i.e. breakpoint analysis) to assess whether ivory gulls performed dual
189 foraging (i.e. the duration of short and long trips differs significantly). To this end, we used the
190 *segmented* package (Muggeo 2020) of R software (R Core Team 2019) to solve the following
191 equation: $furthestdistance = \alpha \times \log(tripduration)$, with α a constant whose value differed on either
192 side of the breakpoint. The duration threshold (D_{thresh}), at which α changed, was used in the analysis
193 as the threshold between short and long trips.

194

195 To investigate the potential influence of breeding phenology on trip duration, we modelled the
196 relationship between the duration of foraging trips and the day of year. We used a generalised
197 additive model to detect non-linear changes in trip duration, which likely happen when birds change
198 from incubation to chick rearing. Using the *gamm4* package (Wood and Scheipl 2020) of R, we fit
199 trip duration as a function of the day of year, with the individual as a random effect on the intercept
200 and slope to capture the influence of individual differences in phenology.

201

202 2.4. BEHAVIOURAL SEGMENTATION

203 We defined individuals' behavioural states by fitting HMMs of the step length and the change in
204 angle between steps (Morales et al. 2004) to the tracking data with the *moveHMM* package
205 (Michelot et al, 2016) of R. Based on studies of seabird behaviour (Zhang et al. 2019; Harris et al.
206 2020; Dunphy et al. 2020), we developed a three-state model. Firstly, we defined a low-movement
207 state that had a very short step length and, due to GPS error, a large change in angle between steps;
208 because it likely corresponded to rest or feeding, we defined it as “rest”. This state corresponded to
209 birds remaining at the same location for a given amount of time. Because these two behavioural
210 states have a similar movement signature, and the Arctic summer lacks a day/night cycle which
211 could help distinguish these states (rest at night vs feeding during the day), we grouped both of
212 them in the same state. Secondly, we defined a moderate-movement state with a moderate step
213 length and large change in angle between steps, which likely corresponded to an “area-restricted
214 search” (ARS) state, in which individuals were foraging. Finally, we defined a high-movement state
215 with a long step length and small change in angle between steps, in which individuals were moving
216 rapidly from one area to another (i.e. “transit”). We assumed gamma and von Mises distributions
217 for the step length and angle between steps, respectively (Michelot et al. 2016). Twenty sets of
218 random initial parameters were tested from a range of biologically plausible values (Table S2),
219 following the procedure described by Michelot et al. (2016). The best segmentation, based on the
220 maximum log-likelihood value, was selected for further analysis, and states were attributed using
221 the Viterbi algorithm.

222

223 2.5. INDIVIDUAL SITE FIDELITY AND INTER-INDIVIDUAL OVERLAP IN FORAGING AREAS

224 During the breeding season, colonial seabirds exist in a competitive space. To understand how they
225 share space and resources, we investigated individual site fidelity and the overlap among
226 individuals' foraging areas. These two metrics were calculated separately for short and long trips to
227 assess how dual foraging influenced the use of space. We included all GPS fixes of complete trips
228 in the analysis. Foraging areas were defined as zones in which birds displayed ARS. Individual site

229 fidelity is the tendency for an individual to forage in the same location repeatedly (Switzer 1993;
230 Piper 2011; Patrick and Weimerskirch 2017), whereas overlap among individuals' foraging areas
231 indicates how birds aggregate or segregate in favourable foraging grounds (Masello et al. 2010;
232 Sánchez et al. 2018). GPS fixes within a 2 km radius of each sub-colony were removed, as we
233 assumed that gulls were not likely to forage there (GY, pers. obs.). Only GPS fixes defined as ARS
234 by the HMM were kept in the analysis. We calculated the kernel utilisation distribution (UD) at a
235 1000 m resolution for (i) ARS locations of a single trip and (ii) all ARS locations visited by an
236 individual across trips. We used Bhattacharyya's affinity (BA) index (Fieberg and Kochanny 2005)
237 to assess UD overlap and site fidelity (Wakefield et al. 2015; Courbin et al. 2018). BA ranges from
238 0 (no overlap among UDs) to 1 (identical UDs). Based on Clapp and Beck (2015), BA indices were
239 calculated for both 95% and 50% isopleths to quantify site fidelity at different scales. To compare
240 overlap between the 95% and 50% UDs, their BA index values were rescaled to the [0, 1] interval
241 by dividing them by the highest possible value (0.95 and 0.50, respectively). Individual site fidelity
242 was the mean of the BA indices calculated for each pair of trips for the same individual. Overlap
243 was calculated as the BA index between each individual's foraging areas. In both cases, short and
244 long trips were compared separately.

245 To rigorously interpret BA index values for site fidelity and inter-individual foraging overlap, we
246 calculated BA index values under a null hypothesis (BA_{null}). We randomly reattributed foraging
247 trips to 15 individual tracks and calculated individual site fidelity and inter-individual foraging
248 overlap using the method described previously. This procedure was repeated 500 times. Site fidelity
249 and inter-individual overlap values were then compared to their BA_{null} values using a Wilcoxon
250 signed-rank test. The null hypothesis values and observed values were compared to assess whether
251 the birds' site fidelity and inter-individual overlap differed from that expected by chance.

252

253 2.6. INFLUENCE OF HUMAN SETTLEMENT ON THE USE OF SPACE

254 Ivory gulls are frequently observed at the STN settlement, either foraging or feeding on waste from

255 human activities. To better understand this behaviour, we estimated UDs of ivory gulls based on all
256 GPS fixes using the biased random bridges (BRB) method (Benhamou 2011) implemented in the
257 *adehabitatHR* package (Calenge, 2006) of R. BRB is based on sequential spatio-temporal
258 correlation of animal tracks, which provides mechanistic understanding of UDs. It can be separated
259 into an intensity distribution (i.e. the mean amount of time spent in a given area) and a recursion
260 distribution (i.e. the proportion of total visits to a given area) (Benhamou and Riotte-Lambert 2012).
261 The *maxt* parameter (i.e. the maximum amount of time a bird could spend outside a patch before
262 considering re-entry into the patch as a separate event) was set to 30 min. As we were interested in
263 foraging events, we wanted to avoid considering erratic movement around an area as multiple visits.
264 The *hmin* parameter (i.e. minimum smoothing) was set to 300 m. Intensity and recursion
265 distributions were calculated for each individual at a 1000 m resolution. The proportion of time
266 spent at STN per individual was determined using the intensity distribution. The proportion of
267 revisits within 500 m of STN was estimated using the recursion distribution. We determined
268 intensity and recursion distributions for each individual in a 500 m radius around STN. We
269 considered that potential attraction of ivory gulls to STN would be indicated by a large percentage
270 of the time budget spent at STN (intensity distribution) and many revisits (recursion distribution).
271 To investigate this, we used the *recurse* package (Bracis et al., 2018) of R to calculate revisits to
272 STN to forage and the time between them. Ivory gulls were assumed to forage at STN when they
273 were within 500 m of STN and in an ARS behavioural state.

274

275 Based on our hypothesis that STN is a focal point for foraging ivory gulls, we expected to find a
276 large percentage of rest and ARS behavioural states near STN. We calculated these percentages in a
277 500 m radius around STN and used a randomisation procedure to estimate the percentages of states
278 expected by chance in the population. For each GPS fix of the tracked gulls, we calculated the
279 percentage of states within 500 m of the fix. We then used the mean percentage of each step as the
280 sample mean and compared these means to those observed near STN.

281

282 2.7. MARINE HABITAT SELECTION

283 We used resource selection functions (RSF) to explore the marine habitat selection of ivory gulls at
284 sea (Manly et al. 2002, Muff et al. 2020). All GPS fixes on land (AMSR2 land mask, 10 km × 10
285 km grid) were excluded. Due to a lack of variables for land-based resource availability, we inferred
286 habitat selection at sea using the 44,875 GPS fixes obtained in 2018 and 2019. RSF compares the
287 environmental attributes of observed GPS fixes (“used”) to those of locations randomly sampled
288 within likely reachable areas (“available”). To obtain a comprehensive sample of available habitats,
289 we used a 1:10 ratio for used:available locations for each individual. According to this ratio, for
290 each observed location, 10 available locations were created with the same attributes as the observed
291 one (behavioural states, date, individual ID). We considered the non-random distribution of
292 available area due to the central place foraging behaviour of ivory gulls by applying a circular
293 bivariate exponential distribution centred on the centroid of the sub-colonies each year, with a
294 radius equal to the furthest GPS fix observed within the 95% UD isopleth (628.6 km) (Monsarrat et
295 al. 2013; Grémillet et al. 2020). Because ivory gulls ignored areas south-west of the sub-colonies,
296 the availability distribution was truncated to the 1st-99th percentiles for a circular distribution, using
297 the *circular* package (Agostinelli and Lund, 2022) of R.

298

299 Three continuous environmental variables were used to fit the RSF: (i) bathymetry (m) at a 500 m
300 resolution based on the International Bathymetric Chart of the Arctic Ocean (Jakobsson et al, 2012);
301 (ii) SIC (percentage per cell) at a 10 km resolution from the AMSR2 daily SIC product of the
302 EUMETSAT Ocean and Sea Ice Satellite Application Facility (<http://www.osi-saf.org>); and (iii)
303 distance to the edge of sea ice (km, dist2edge) (i.e. nearest cell with 15% SIC), also from the
304 AMSR2 SIC product (Pang et al. 2018). The dist2edge was positive when gulls were on ice and
305 negative when they were on open water (Gilg et al. 2016). To avoid having missing data when
306 exploiting the high temporal frequency of SIC maps, SIC and dist2edge were averaged over a 3-day

307 sliding window centred on the GPS fix date. All three variables were mean centred and divided by
308 their standard deviation to facilitate model convergence. RSFs were fitted with a generalised linear
309 mixed model with binomial errors using the *glmmTMB* package (Brooks et al, 2017) of R. The use-
310 availability likelihood of RSF was maximized fitting a logistic regression (McDonald, 2013).
311 Within a species, many characteristics are likely to vary among individuals. To represent individual
312 differences and bias in habitat selection, we used random intercepts for individuals and random
313 slopes for predictors, following statistical recommendations of Muff et al. (2020). To represent non-
314 linear responses, we used a spline with four degrees of freedom for all environmental predictors.
315 The variables for which we estimated a non-linear response were selected using the Akaike
316 information criterion.
317 To represent behaviour-specific habitat selection, we considered the behavioural states defined by
318 the HMM as a factor that interacted with all environmental variables. During the ca. 2-month study
319 period each year, the day of year may have influenced habitat selection through factors such as
320 breeding stage or weather. To consider temporal changes during the study period, the day of year
321 was thus considered a random effect nested within each year.

322

$$323 \quad \omega(x_{ij}) = \exp(\beta_0 + (\beta_{bathy} bathy_{ij} + \beta_{dist2edge} dist2edge_{ij} + \beta_{SIC} x_{SIC_{ij}}) \beta_s stateHMM_{ij} + \gamma_{0j} + \gamma_{0yd} + \gamma_{bathy,j} + \gamma_{dist2edge,j} + \gamma_{SIC,j}) \quad Eq. (1)$$

324

325 The RSF model estimated the relative probability of selection ($\omega(x_{ij})$), expressed as a binary vector
326 for the i^{th} location and j^{th} gull tracked (Eq. 1), where β_0 is the mean intercept; β_{bathy} , $\beta_{dist2edge}$, and β_{SIC}
327 are fixed-effect coefficients for *bathymetry*, *dist2edge*, and *SIC*, respectively; β_s is the coefficient
328 for *stateHMM* in state s ; γ_{0j} and γ_{0yd} are random intercepts for individual j and day of year yd ,
329 respectively; and $\gamma_{bathy,j}$, $\gamma_{dist2edge,j}$, and $\gamma_{SIC,j}$ are random slope coefficients for the corresponding
330 predictors for gull j .

331

332 Model robustness was assessed using 30 runs of k-fold cross-validation. For each run, the complete

333 dataset was randomly split into a training set (80% of the individuals) and a testing set (the
334 remaining 20%). We calculated RSF probabilities for the training dataset and split them into ten
335 bins (area-adjusted frequency). We then calculated the Spearman rank correlation between the rank
336 of the bins and the frequency of the RSF probabilities calculated for the testing set in each bin. A
337 mean Spearman rank correlation close to 1 indicated high capacity to predict ivory gull distribution
338 (Boyce et al. 2002).

339

340 All analyses were performed using R software 3.5.3 (R Core Team 2019). All results are presented
341 as mean \pm standard deviation, unless stated otherwise.

342 3. RESULTS

343

344 3.1. FORAGING TRIP DESCRIPTION

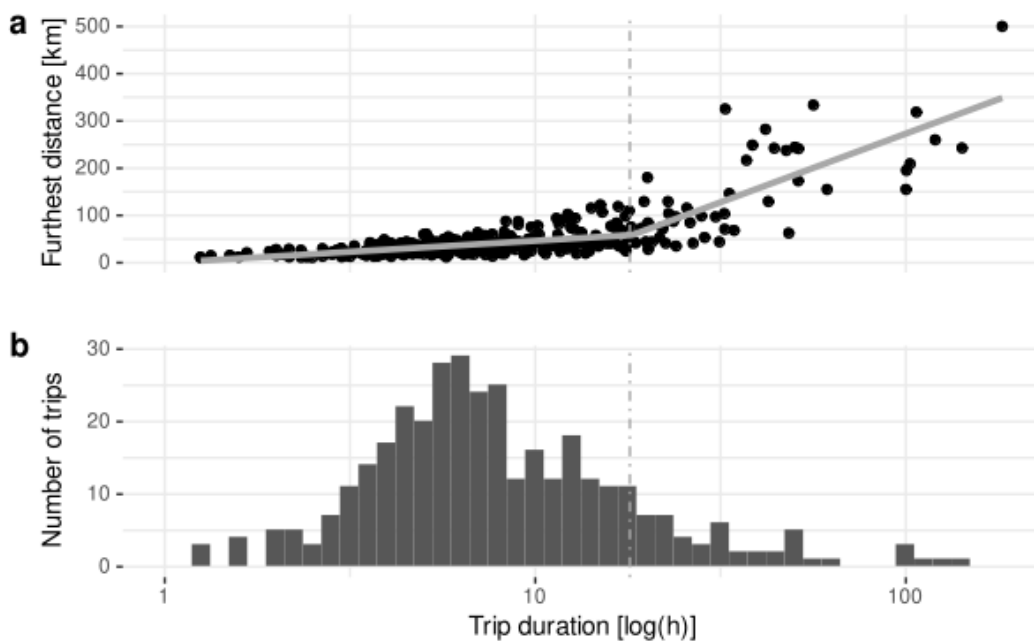
345 We tracked a total of 15 birds (13 only in 2018 and 2 only in 2019). One bird tagged in 2018 was
346 tracked in both 2018 and 2019, but the second year of tracking was used only for RSF analysis. This
347 yielded a total of 16 summer tracks. See Table S1 for information on the individuals tagged. Ivory
348 gulls made a total of 356 trips (23.7 ± 18.9 trips per bird) (306 in 2018 and 50 in 2019). The
349 piecewise linear regression yielded a D_{thresh} of 18.2 h (Fig. 2a). By rounding, we thus considered
350 trips shorter than 18 h as “short” and those longer than 18 h as “long”, regardless of the distance
351 travelled. The slope between trip duration and distance was five times as high for long trips as for
352 short trips (Fig. 2a), which showed that long trips had a longer maximum distance per unit of time.
353 See Table S3 for basic summary metrics, such as the duration, furthest distance reached, and total
354 distance of ivory gull trips. Of the 16 birds studied, 3 never took short trips (mean = 20.3 ± 18.0 ,
355 min = 0, and max = 50 short trips per individual), whereas all 16 took at least one long trip (mean =
356 3.4 ± 2.2 , min = 1, and max = 8 long trips per individual). The proportion of short and long trips
357 varied among individuals (Fig. S1), but the mean proportion of short or long trips for the 16 birds
358 was 0.85 and 0.15, respectively. Day of year influenced trip duration ($p < 0.05$), but explained only
359 a small part of it ($R^2 = 0.05$), with high variability among individuals. Thus, it is unlikely that

360 breeding stage had a significant effect.

361

362 We identified two main foraging areas that ivory gulls used during short trips: (i) the coasts of the
363 mainland (around STN) and islands and (ii) the Marsk Stig Bræ tidewater glacier front (Fig. 3a). A
364 large lead to the north-east between the fjord system and the open sea was also used for foraging,
365 but less intensively. During long trips, ivory gulls used multiple areas on the pack ice or in the MIZ
366 near the North-East Water Polynya (Fig. 3b).

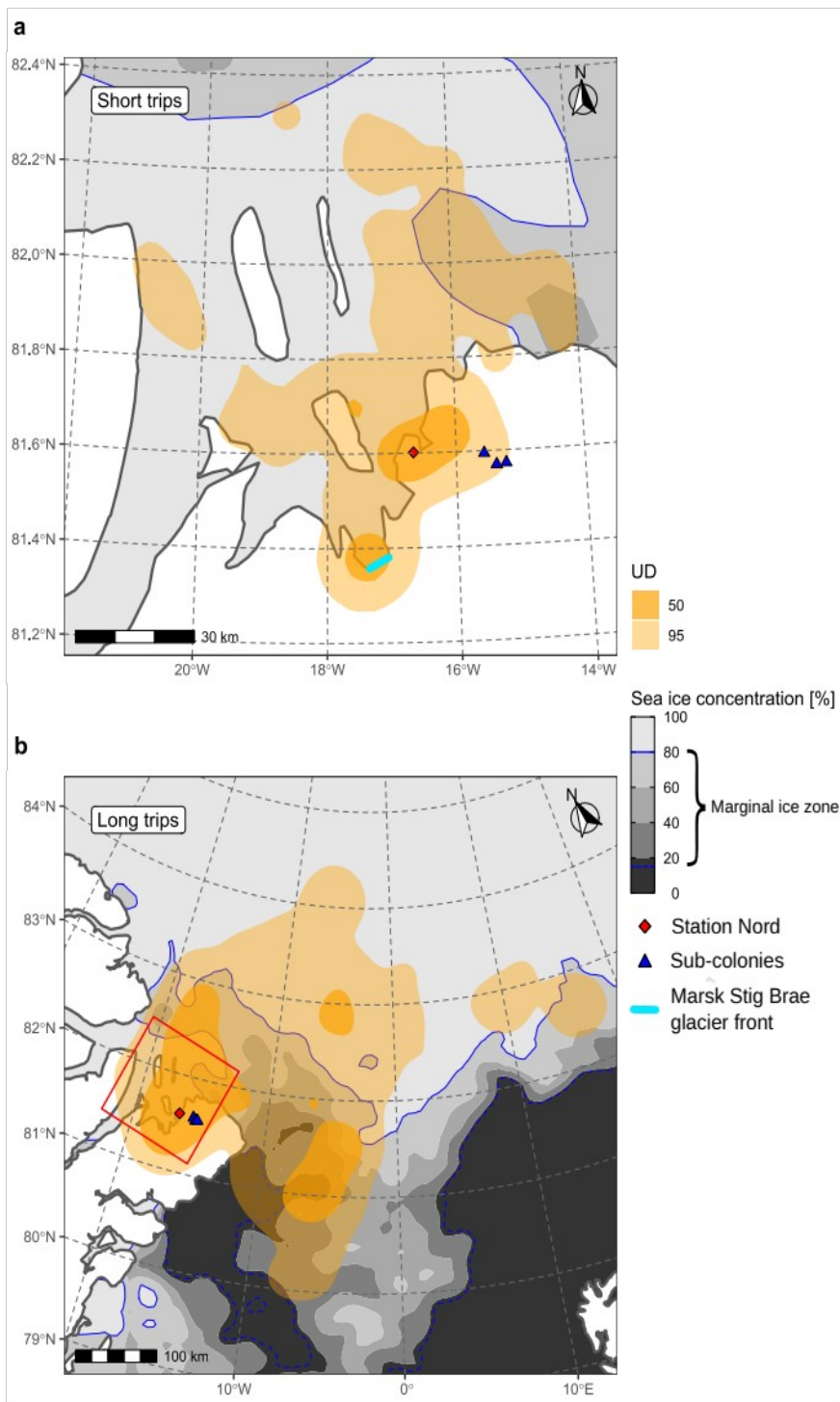
367



368

369 Figure 2. Characteristics of ivory gull trips as a function of trip duration. (a) Piecewise linear
370 regression of the furthest distance reached during a trip as a function of trip duration, for short trips
371 (left of the threshold of 18 h, vertical grey line) and long trips (right of the threshold). (b) Number
372 of trips as a function of trip duration.

373



374

375 Figure 3. Areas that ivory gulls used for foraging in north-east Greenland during (a) short (< 18 h)

376 and (b) long (>18 h) foraging trips. Short trips were concentrated at glacier fronts, coastal leads, or

377 nearby pack ice in areas of high sea ice concentration (SIC), whereas long trips were concentrated

378 on areas with variable SIC along the ice edge in the North-East Water Polynya, and over pack ice.

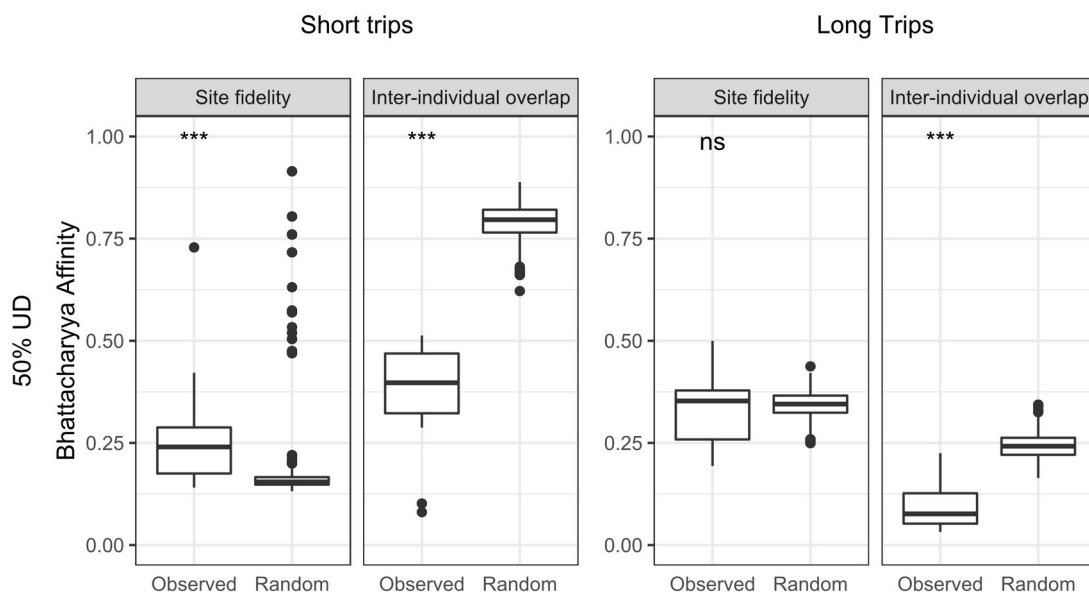
379 Dark and light yellow shading represents 50% and 95% UD of foraging areas, respectively. The
 380 map shows sea ice concentration for 31 July 2018. The red rectangle in (b) shows the extent of (a).
 381

382 3.2. INDIVIDUAL SITE FIDELITY

383 Ivory gulls showed site fidelity during short trips, with BA indices higher than those expected by
 384 chance (50% UD BA index = 0.28 ± 0.17 , $N_{\text{obs}} = 15$, $P < 0.001$, Fig. 4; 95% UD BA index = $0.44 \pm$
 385 0.24 , $N_{\text{obs}} = 15$, $P < 0.001$, Fig. ESM1). Conversely, ivory gulls did not show site fidelity during long
 386 trips (Fig. 4). This pattern was consistent for both the 50% and 95% UD.

387 3.3. INTER-INDIVIDUAL OVERLAP IN FORAGING AREAS

388 Suitable foraging areas around STN were rare and limited mainly by coastal ice, which restricted
 389 access to marine prey. During short trips, BA_{null} indices were high (50% UD BA_{null} index = $0.79 \pm$
 390 0.04 , Fig. 4; 95% UD BA_{null} index = 0.82 ± 0.03 , Fig. ESM1), indicating that under the null model,
 391 individuals were expected to share most of their foraging areas with each other. However,
 392 individual ivory gulls tended to use different foraging areas, as shown by lower observed BA
 393 indices (50% UD BA_{observed} index = 0.36 ± 0.26 , $N_{\text{obs}} = 12$, $P < 0.001$, Fig. 4; 95% UD BA_{observed}
 394 index = 0.56 ± 0.22 , $N_{\text{obs}} = 12$, $P < 0.001$; Fig. ESM1) than under the null hypothesis, which
 395 indicated spatial segregation between individuals during foraging (Fig. 4).



396

397 Figure 4. Bhattacharyya's Affinity (BA) index for individual site fidelity and utilisation distribution
398 (UD) overlap among individuals' foraging areas during (left) short (< 18 h) and (right) long (> 18 h)
399 trips into core foraging areas (50% UD). "Observed" refers to the BA index observed for individual
400 ivory gulls, whereas "Random" refers to the BA index based on random trips (BA_{null}). Observed and
401 random BA indices were compared using the Wilcoxon-signed-rank test (significance levels: ns =
402 non-significant, *** < 0.001). Whiskers equal 1.5 times the interquartile range.

403

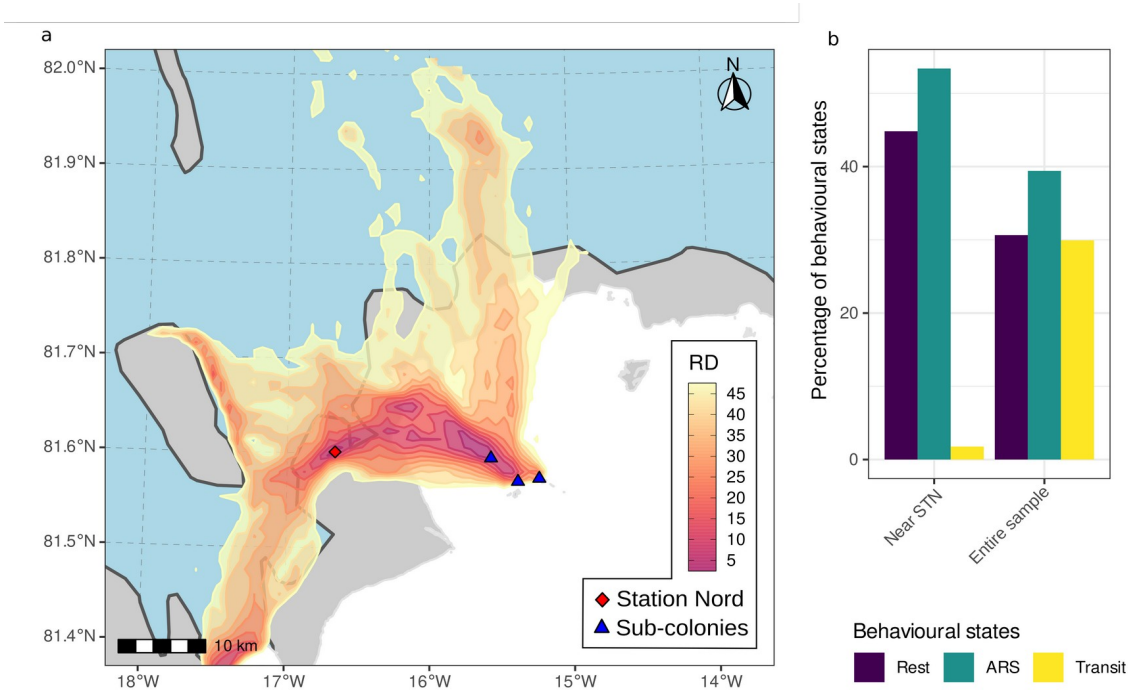
404 The larger areas explored by ivory gulls during long trips, mainly the ice edge north of the North-
405 East Water Polynya and the pack ice east of STN (Fig. 2b), led to a smaller spatial segregation of
406 individuals. A significant difference was observed during long trips between BA_{null} indices (50%
407 UD $BA_{null} = 0.24 \pm 0.03$, Fig. 4; 95% UD $BA_{null} = 0.41 \pm 0.04$, Fig. ESM1) and observed BA indices
408 (50% UD $BA_{observed} = 0.09 \pm 0.13$, min = 0, max = 0.53, $N_{obs} = 15$, $P < 0.001$, Fig. 4; 95% UD
409 $BA_{observed} = 0.34 \pm 0.24$, $N_{obs} = 15$, $P < 0.001$; Fig. ESM1). Thus, ivory gulls also showed spatial
410 segregation during long trips.

411

412 3.4. INFLUENCE OF HUMAN SETTLEMENT ON THE USE OF SPACE

413 Among the 16 tracked birds, 3 (including the 2 tagged at the colony) never came close enough to
414 STN (i.e. within 500 m) to be considered as visiting it. For the 13 birds tagged at STN, all but 1
415 spent time there. The gulls visited STN in 43% of the short trips and 45% of the long trips. A total
416 of 160 trips (45% of the total) were visits to STN. Ivory gulls spent $16.1\% \pm 24.4\%$ of their time at
417 STN (min = 3.2%, max = 100.0%) and frequently revisited it ($13.02\% \pm 26.90\%$ (min = 0.12%,
418 max = 100.00%) of revisits were to STN). Based on the recursion distribution of the population
419 (Fig. 5a), ivory gulls made 271 revisits to forage at STN (mean 18.1 ± 13.2 visits per individual),
420 which yielded a mean of 5.4 ± 3.4 visits per week of tracking per individual. Gulls remained at STN
421 a mean of 0.9 ± 1.1 h (min = 0.02 h, max = 6.2 h). In total, ivory gulls spent 192.9 h at STN. At
422 STN, the percentage of rest, ARS, and transit was 44.8%, 53.4%, and 1.8%, respectively. For rest

423 and ARS, these percentages at STN were much higher than those for all tracked gulls (31.0% and
 424 39.4%, respectively). Conversely, the transit state occurred only for 1.7% of the tracked gulls at
 425 STN, compared to 29.5% of the all tracked gulls (Fig. 5b). Thus, the birds displayed behavioural
 426 states related to feeding or foraging during most of their time at STN. Thus, compared to other
 427 areas, STN was more a location that ivory gulls visited to forage than to transit.



428 Figure 5. Use of space around Station Nord (STN) and its influence on ivory gull behaviour. (a) The
 429 0-50% recursion distribution (RD) interval for all foraging trips, which illustrates areas that ivory
 430 gulls frequently visited. White areas are glaciers (Raup et al. 2007). (b) The percentage of time that
 431 ivory gulls spent within 500 m of STN per behavioural state. ARS: area-restricted search
 432

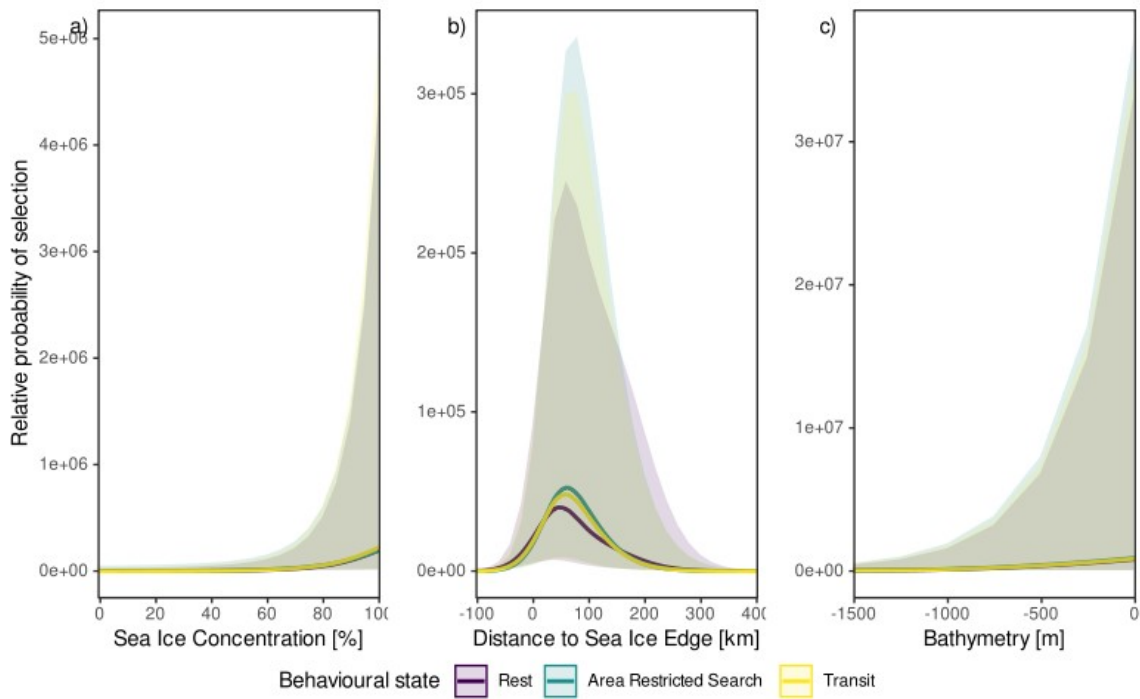
433

434 3.5 BEHAVIOUR-SPECIFIC MARINE HABITAT SELECTION

435 The RSF showed that bathymetry, distance to the sea ice edge, and SIC significantly influenced the
 436 marine habitat selection of ivory gulls. The distance to the sea ice edge was the only explanatory
 437 variable for which a non-linear effect was retained. The influence of behaviours on habitat selection
 438 was significant but often weak for all variables, except for SIC, for which no difference in selection
 439 was observed between the rest and transit states ($p = 0.09$). The influence of the ARS and transit

440 states on habitat selection was also weak, with almost no difference in selection between them,
441 whereas “rest” had a positive influence on bathymetry and SIC selection (Fig. 7). The model was
442 robust to cross-validation (mean Spearman rank correlation: 0.60 ± 0.07). Ivory gulls strongly
443 selected high SIC from the upper edge of the MIZ (SIC = 70-80%) to pack ice (> 80%), but they did
444 not select areas with SIC less than 60% (Fig. 6a). The gulls strongly selected areas over sea ice
445 rather than over the open sea, with a peak in the relative probability of selection over ice 50-60 km
446 from the ice edge (Fig. 6b). Conversely, the relative probability of selection decreased sharply over
447 the open sea, falling to zero 50 km from the ice edge. Ivory gulls selected coastal areas, with
448 increased relative probability of selection for areas with depths of 0-500 m (Fig. 6c). Gulls showed
449 no affinity for the deep sea and rarely selected areas deeper than 1000 m (Fig. 6c). Core foraging
450 areas for individuals during short trips were located mainly in coastal areas or over the Greenland
451 ice shelf, with high SIC and far from the ice edge (Fig. 3). Conversely, long trips focused on deeper
452 areas with a variety of SIC located in the Fram Strait and North-East Water Polynya, within the
453 MIZ and pack ice (Fig. 3).

454

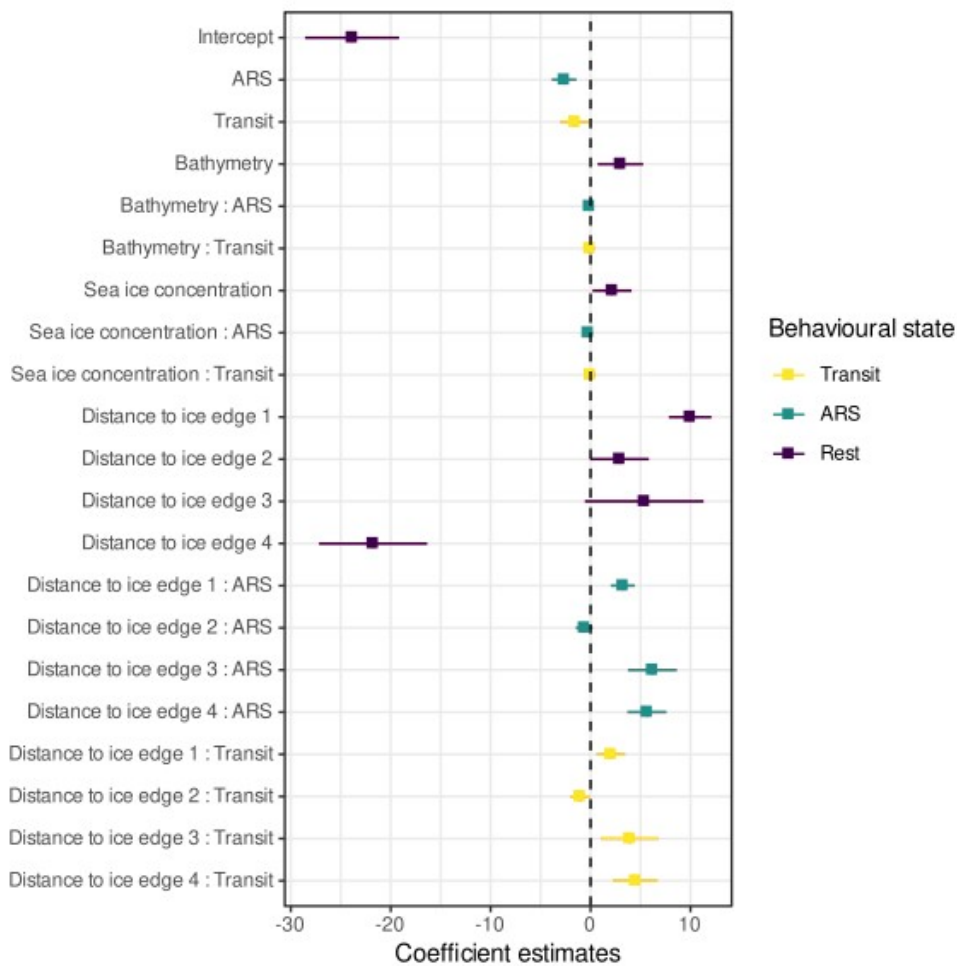


455

456 Figure 6. Relative probability of habitat selection as predicted by the resource selection function
 457 model for (a) sea ice concentration (percentage of ice at a 10 km resolution), (b) distance to the sea
 458 ice edge (negative = over open sea, positive = over sea ice), and (c) bathymetry. Colours indicate
 459 different behavioural states defined by a three-state hidden Markov model (rest, area-restricted
 460 search, and transit). Shaded area represent the 95% confidence interval.

461

462



463
 464 Figure 7. Mean and 95% confidence intervals of coefficients associated with the resource selection
 465 function. Colours indicate different behavioural states. ARS = area-restricted search

466

467 **4. DISCUSSION**

468 The present study provided rare insight into the foraging behaviour of seabirds at high latitudes. We
 469 confirmed that ivory gulls use a dual foraging strategy and highlighted their differing spatial
 470 strategies during short and long trips. When making short trips, ivory gulls appeared to be site
 471 faithful but segregated in space, with individual-specific foraging areas. This finding strengthens the
 472 hypothesis that dual foraging is also a strategy for decreasing competition among colonial seabirds.
 473 Furthermore, most birds in the study visited and regularly returned to STN to forage, which
 474 confirms that human settlement in the Arctic can provide food sources for seabirds. Finally, we
 475 provide additional details about habitat selection by ivory gulls while at sea that confirm their
 476 affinity for high-concentration patches in the pack ice.

478 4.1. IMPLICATION OF DUAL FORAGING FOR ARCTIC SEABIRDS

479 Many seabird populations use a dual foraging strategy, alternating short and long foraging trips in
480 response to the energetic cost of rearing chicks (Welcker et al. 2009; Wojczulanis-Jakubas et al.
481 2010). In the present study, we did not observe a clear bimodal distribution of trip duration, as
482 observed for little auks (Welcker et al. 2009) or Manx shearwaters (*Puffinus puffinus*; Shoji et al.
483 2015). However, ivory gulls did make short and long foraging trips during the breeding season. The
484 long trips were notable for their duration and destinations, which focused mainly on distant areas in
485 the pack ice and the MIZ, where overlap among individuals, and thus intra-colony competition, was
486 low.

487

488 For little auks, dual foraging enables individuals to gain mass during the breeding season, whereas
489 short trips focus mainly on delivering food to chicks (Welcker et al. 2012; Jakubas et al. 2014).
490 Little auks forage in distant areas regardless of local foraging conditions, which suggests that dual
491 foraging is unrelated to the local environment, but is likely related to local competition, resource
492 availability, and physiological constraints (Wojczulanis-Jakubas et al. 2010). In the harsh
493 environment around ivory gull colonies in north-east Greenland, favourable foraging areas are rare
494 and located mainly at the land-sea interface (coast and glacier fronts) and in the MIZ. The
495 availability of favourable foraging grounds is therefore limited, which increases competition among
496 individuals. Spatial segregation of individuals in different foraging areas is likely a response to the
497 limited access to resources that enables individuals to decrease competition. Ivory gulls were site-
498 faithful to the foraging grounds used during short trips. Competition for resources is not likely the
499 only explanation for site fidelity, however, because the latter is driven by several factors, including
500 previous foraging success, personality, and shared social information on the location of resources
501 (Carroll et al. 2018; Harris et al. 2020). Site fidelity of ivory gulls in north-east Greenland is
502 probably reinforced by the predictability and higher productivity of annual coastal cracks or

503 tidewater glacier fronts than of the offshore pack ice, which has thicker ice that makes accessing
504 marine resources more difficult (Lee et al. 2010). Coastal cracks and glacier fronts are major
505 features of the landscape in the Arctic and are spatially stable over several years. Conversely, ivory
506 gulls did not show site fidelity to foraging areas during long trips, for which ice features are more
507 likely less predictable, with locations that change each year or during the breeding season. Over
508 pack ice, ivory gulls are known to feed on polar bear kills, whose spatial and temporal distribution
509 is likely highly unpredictable. Foraging for unpredictable prey could explain why ivory gulls
510 explored larger areas during long foraging trips, as covering large area increases the chances of
511 finding resources. Thus, these long trips could be more exploratory than short trips, which agrees
512 with findings of Paiva et al. (2010).

513

514 4.2. FORAGING AREAS AND THE SPATIAL STRATEGY OF IVORY GULLS IN NORTH-EAST 515 GREENLAND

516 Using a null-model framework, we simulated which strategies ivory gulls would implement if they
517 behaved randomly. Surprisingly, under this framework, ivory gulls should have low site fidelity and
518 high overlap during short trips, and medium site fidelity and low overlap during long trips.
519 However, we observed that the gulls used different strategies. The gulls used mainly two foraging
520 areas during short trips. Although most foraged at least partially in one of the areas (*i.e.* the strait
521 between STN and Princess Dagmar Island), spatial segregation occurred within our sample, as
522 indicated by the lower foraging overlap observed than that of the null model. Individuals were
523 spatially specialised and used different areas than their conspecifics (*e.g.* individuals foraging
524 almost exclusively on a glacier front or along a large lead in the ice to the north-east of STN).
525 Moreover, individuals appeared to be site-faithful during short foraging trips, which reinforced their
526 spatial specialisation. These results partially support our second hypothesis. Although ivory gulls
527 did not aggregate during short trips, as was expected due to the local nature of the resources, but
528 tended to be spatially segregated, they did disperse during longer foraging trips (H2). Furthermore,

529 site fidelity was observed only during short trips, for which resources are likely more predictable
530 than during long trips. Whether these strategies are only a spatial phenomenon or are related to
531 individual diet specialisation remains unclear, as the ivory gull is usually considered a generalist
532 species, even though hypotheses about individual specialisation have emerged (Karnovsky et al.
533 2009). However, specialised individuals within a generalist population have been observed for other
534 seabirds, such as Antarctic petrels (*Thalassoica antarctica*; Tarroux et al. 2020) and Scopoli's
535 shearwaters (*Calonectris diomedea*; Courbin et al. 2018). Combining isotopic niche analysis and
536 spatial analysis of foraging strategies at population and individual levels could help distinguish
537 whether ivory gull site fidelity is related to prey specialisation and individual trophic niche
538 specialisation within a generalist species (Bonnet-Lebrun et al. 2018; Courbin et al. 2018).

539

540 4.3. INFLUENCE OF ANTHROPOGENIC SUBSIDIES ON ARCTIC SEABIRDS

541 Anthropogenic food resources modify the behaviour and foraging strategies of opportunistic
542 scavengers (Cama et al. 2012; Patrick et al. 2015), which may influence a population's long-term
543 survival (Fluhr et al. 2017). The few human settlements in the high Arctic could provide an
544 important source of anthropogenic food for some seabirds compared to the surrounding natural
545 habitats. This has been observed for ivory gulls in Canada (Thomas and MacDonald 1987; Mallory
546 et al. 2003). We found that STN is an attractive location for ivory gulls in north-east Greenland, as
547 they frequently return there to forage. Due to their high spatial and temporal predictability,
548 anthropogenic subsidies attract mammals and seabirds worldwide (Plaza and Lambertucci 2017),
549 especially gulls (Lenzi et al. 2019), and can represent a large part of an animal's diet in an
550 environment with low resource availability (Savory et al. 2014). However, the food available for
551 opportunistic birds at STN – garbage and sewage from the kitchen, as well as leftover dog food –
552 has decreased in the past few decades. A new sewer system and waste incinerator, as well as
553 changes in the management of dog food, reduced leftovers, which has reduced the amount of
554 anthropogenic subsidies in recent years (OG and GY, pers. obs.). Nevertheless, foraging birds

555 frequently visit STN, indicating that it remains an attractive place to forage, although the ivory gull
556 colony has moved a few km further from STN over the past decade (Gilg et al. 2009; Frederiksen et
557 al. 2019). We may have overestimated the influence of STN on ivory gulls, however, as birds
558 observed at STN tended to return regularly, whereas many birds from the colonies have likely never
559 visited STN. The few birds observed daily at STN during the breeding season ($n \ll 10$, with a high
560 proportion of resightings; authors, pers. obs) contrasts with the 120-130 ivory gull pairs that bred in
561 the sub-colonies in 2018 (Frederiksen et al., 2019) and 2019 (Boertmann et al., 2019). When
562 considering all of the birds tagged with GPS transmitters in 2018 and 2019, data from 16 of the 20
563 birds tagged at STN (80%) were retrieved, although we included only 14 of them in the study. For
564 gulls tagged in the colonies, only 30% of their transmitters (2 out of 7) transmitted data for more
565 than 24 h. Because the main base station used to collect GPS data was located mainly at STN, it is
566 likely that most birds tagged at the colony did not visit STN, or did so briefly.

567

568 4.4. RESOURCE SELECTION BY IVORY GULLS AT SEA

569 A high-frequency GPS dataset of ivory gull tracks and a robust validated RSF assessed in a
570 dynamic temporal framework provided strong evidence that ivory gulls select highly concentrated
571 sea ice (>60%) when foraging at sea during the breeding season. This was partially expected based
572 on the first hypothesis (H1); however, ivory gulls used a wider range of SIC than that hypothesised,
573 as they used areas with SIC that included the upper limit of MIZ (60-80%) to pack ice (>80%).
574 These results are consistent with those of Gilg et al (2016), which were similar for year-round
575 ARGOS tracking of ivory gulls from different colonies in the Arctic. However, we highlight that
576 birds in the present study selected marine habitats with a small but significant influence of certain
577 behavioural states (i.e. rest, ARS, and transit) during the time at sea. We also observed that ivory
578 gulls selected relatively shallow areas, which are common around STN.

579

580 4.5. SEABIRD USE OF TIDEWATER GLACIER FRONTS IN THE ARCTIC

581 Our study also highlighted that ivory gulls forage at tidewater glacier fronts, which agrees with
582 previous studies of ivory gulls (Renaud and McLaren 1982; Lydersen et al. 2014), black-legged
583 kittiwakes (*Rissa tridactyla*) (McLaren and Renaud 1982; Lydersen et al. 2014; Bertrand et al.
584 2021), or northern fulmars (*Fulmarus glacialis*) (McLaren and Renaud 1982; Nishizawa et al.
585 2020). High concentrations of surface-feeding seabirds foraging at glacier fronts have been
586 observed in the Arctic (Hartley and Fisher 1936; Irons 1998), including large flocks of ivory gulls
587 (Renaud and McLaren 1982). Tidewater glacier fronts usually provide more stable foraging habitats
588 for surface feeders than certain climate-induced ephemeral habitats (Grémillet et al. 2015). Foraging
589 in these areas is facilitated by the discharge of nutrient-rich freshwater from the bottom of the
590 glacier, which causes upwelling and forces zooplankton upward in the water column, which
591 increases productivity (Apollonio 1973; Arimitsu et al. 2016; Arrigo et al. 2017) and kills plankton
592 via osmotic shock (Hartley and Fisher 1936). Climate-induced continental glacier melt is likely to
593 maintain the attraction of tidewater glacier fronts for seabirds and even increase the discharge of
594 freshwater into the ocean (Mu et al. 2020; Nishizawa et al. 2020). However, climate change is a
595 long-term threat to this habitat, as continental glaciers are currently losing mass, and this loss is
596 amplified by the decrease in sea ice (Liu et al. 2016; Pedersen and Christensen 2019). Foraging at
597 tidewater glacier fronts is likely to remain stable in the short-to-medium term, and might allow
598 seabird populations to temporarily buffer the impact of climate change on sea ice, as Grémillet et al.
599 (2015) observed for little auks.

600

601 4.6. IMPORTANCE OF SEA ICE AND IMPACT OF CHANGES IN SEA ICE FOR SEABIRDS

602 Along with changes in glacier runoff, and despite rapid changes in the extent and thickness of
603 glaciers, sea ice remains the most attractive foraging area for most ivory gulls, which forage over
604 high-concentration patches of sea ice. The opening of cracks in previously dense, multiyear sea ice
605 provides new foraging opportunities for breeding birds, especially in coastal areas around colonies.

606 As mentioned, this is likely to temporarily delay the impact of climate change on Arctic marine
607 ecosystems. The main threats to breeding seabird populations in the Arctic will be changes in the
608 timing of the planktonic bloom and the continuous northward retreat of the MIZ (Rolph et al. 2020).
609 Due to climate change, sea ice breaks up earlier in many parts of the Arctic (Johnson and Eicken
610 2016; Kowal et al. 2017). This could result in a mismatch between breeding phenology (*e.g.* egg
611 laying, chick rearing) and the peak of the planktonic bloom, making it difficult for adults to feed
612 themselves and their chicks, which could decrease survival. The mismatch between the supply of
613 resources and the demand of breeding adults is a major threat of climate change, as it decreases
614 adult survival and influences population demographics (Thomas et al. 2001; Durant et al. 2007;
615 Gilg et al. 2012). Seabirds are already responding to changes in ice phenology, but earlier laying
616 dates are strongly influenced by individual experience and thus vary within a population (Descamps
617 et al. 2019; Sauve et al. 2019). Even if seabirds adapt their breeding phenology, stochastic changes
618 in climatic conditions in the Arctic, such as a switch from snowfall to rainfall in summer during the
619 breeding season, can have a dramatic influence on recruitment (*e.g.* [Yannic et al. 2014](#)). Ivory gulls
620 forage over high-concentration patches of sea ice, even around their colonies. In the context of
621 climate change, these areas may move northward, forcing the birds to switch to other foraging areas
622 (Grémillet et al. 2015) or to make longer trips, which increases the time, distance, and energetic cost
623 of travel between foraging grounds and colonies, whereas seabirds already struggle to balance an
624 increase in the duration of foraging trips without reducing the rate of feeding chicks (Welcker et al.
625 2009). An unbalanced energy budget may decrease adult fitness and chick survival (Kidawa et al.
626 2015; Kitaysky and Hunt 2018; Duffy-Anderson et al. 2019). This has likely contributed to the
627 decline observed in ivory gull colonies in south-east Greenland, Canada, and Svalbard (Strøm et al.
628 2019).

629 Despite our study of ivory gull habitat selection during foraging trips and previous studies of their
630 feeding habits (Karnovsky et al. 2009), there is a lack of precise knowledge about the pagophilic
631 organisms that ivory gulls prey upon and the importance of scavenging in their diet. Further

632 investigation using alternative approaches (e.g. isotopic analyses, meta-barcoding of the diet) is thus
633 required to better understand the role of sea ice habitats on ivory gulls' diet.

634

635 5. CONCLUSION

636 Using fine-scale spatial and temporal tracking of ivory gulls, we analysed the foraging strategies
637 and habitat selection of high-Arctic seabirds in relation to sea ice. Although our study was limited
638 to the breeding season of the ivory gull in north-east Greenland, we could not confirm whether the
639 tracked birds were actively breeding or the phenological influence of breeding on their behaviour.
640 This is a major caveat of our study, as breeding is most likely to influence seabirds' foraging
641 strategies due to the energy that it requires. We performed robust analysis of spatial strategies (site
642 fidelity and foraging area overlap) and habitat selection to provide relevant insight into Arctic
643 seabirds' foraging behaviour during the breeding season, which is a vital period for all species. Our
644 results highlight that human settlements and glacier fronts are attractive foraging grounds for this
645 Arctic seabird species. Opportunities for new temporary food subsidies will most likely increase in
646 the near future for opportunistic species such as the ivory gull, while its main natural habitat – sea
647 ice – will continue to shrink. Nonetheless, the relative contribution of anthropogenic and natural
648 subsidies in the ivory gull diet should be investigated to accurately assess the short- and long-term
649 influence of anthropogenic subsidies on bird fitness. We focused on ivory gulls from north-east
650 Greenland during the breeding season, and such studies should be extended to encompass the entire
651 Arctic breeding range of the species.

652

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661 COMPLIANCE WITH ETHICAL STANDARDS

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665 1210”].

666 CONFLICTS OF INTEREST

667 All authors declare that they have no conflict of interest.

668 AVAILABILITY OF DATA

669 Part of the dataset analysed in the present study is available in the MOVEBANK repository
670 (Movebank ID: 1123149708). The rest of the dataset is available on request, and will be made
671 available on MOVEBANK upon publication.

672 AUTHORS' CONTRIBUTIONS

673 KD and GY designed the study, with input from OG and MF. GE, MF, and GY performed
674 fieldwork and collected data. KD analysed the data with help from NC and input from ACC. KD
675 led the writing of the manuscript. All authors commented on previous drafts and approved the final
676 manuscript.

677 ETHICS APPROVAL

678 This project was approved by the Government of Greenland (Permits Nanoq - ID No. 7708144
679 (2018), Nanoq - ID No. 8246959 (2018), and Nanoq - ID No. 10615955 (2019)).

680 REFERENCES

- 681 Agostinelli C and Lund U (2022) R package 'circular': Circular Statistics (version 0.4-95). URL [https://r-](https://r-forge.r-project.org/projects/circular/)
682 [forge.r-project.org/projects/circular/](https://r-forge.r-project.org/projects/circular/)
- 683 Amélineau F, Grémillet D, Bonnet D, Bot TL, Fort J (2016) Where to Forage in the Absence of Sea Ice?
684 Bathymetry As a Key Factor for an Arctic Seabird. PLOS ONE 11:e0157764. doi:
685 10.1371/journal.pone.0157764
- 686 Amélineau F, Grémillet D, Harding AMA, Walkusz W, Choquet R, Fort J (2019) Arctic climate change and
687 pollution impact little auk foraging and fitness across a decade. Sci Rep 9:1014. doi: 10.1038/s41598-
688 018-38042-z
- 689 Apollonio S (1973) Glaciers and Nutrients in Arctic Seas. Science 180:491–493. doi:
690 10.1126/science.180.4085.491
- 691 Arimitsu ML, Piatt JF, Mueter F (2016) Influence of glacier runoff on ecosystem structure in Gulf of Alaska
692 fjords. Mar Ecol Prog Ser 560:19–40. doi: 10.3354/meps11888
- 693 Arrigo KR, van Dijken GL (2015) Continued increases in Arctic Ocean primary production. Prog Oceanogr
694 136:60–70. doi: 10.1016/j.pocean.2015.05.002
- 695 Arrigo KR, Dijken GL van, Castelao RM, Luo H, Rennermalm ÅK, Tedesco M, Mote TL, Oliver H, Yager
696 PL (2017) Melting glaciers stimulate large summer phytoplankton blooms in southwest Greenland
697 waters. Geophys Res Lett 44:6278–6285. doi: 10.1002/2017GL073583
- 698 Benhamou S (2011) Dynamic Approach to Space and Habitat Use Based on Biased Random Bridges. PLOS
699 ONE 6:e14592. doi: 10.1371/journal.pone.0014592
- 700 Benhamou S, Riotte-Lambert L (2012) Beyond the Utilization Distribution: Identifying home range areas
701 that are intensively exploited or repeatedly visited. Ecol Model 227:112–116. doi:
702 10.1016/j.ecolmodel.2011.12.015
- 703 Bertrand P, Bêty J, Yoccoz NG, Fortin M-J, Strøm H, Steen H, Kohler J, Harris SM, Patrick SC, Chastel O,
704 Blévin P, Hop H, Moholdt G, Maton J, Descamps S (2021) Fine-scale spatial segregation in a pelagic
705 seabird driven by differential use of tidewater glacier fronts. Sci Rep 11:22109. doi: 10.1038/s41598-021-
706 01404-1
- 707 BirdLife International (2018) *Pagophila eburnea*. The IUCN Red List of Threatened Species 2018.
708 <https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22694473A132555020.en>. Accessed 1 Sep 2020
- 709 Boertmann D, Petersen IK, Nielsen HH (2020) Ivory Gull population status in Greenland 2019. Dan Orn
710 Foren Tidsskr 114:141–150.
- 711 Bond AL, Hobson KA, Branfireun BA (2015) Rapidly increasing methyl mercury in endangered ivory gull
712 (*Pagophila eburnea*) feathers over a 130 year record. Proc R Soc B Biol Sci 282:20150032. doi:
713 10.1098/rspb.2015.0032
- 714 Bonnet-Lebrun A-S, Phillips RA, Manica A, Rodrigues ASL (2018) Quantifying individual specialization
715 using tracking data: a case study on two species of albatrosses. Mar Biol 165:152. doi: 10.1007/s00227-
716 018-3408-x
- 717 Box JE, Colgan WT, Christensen TR, Schmidt NM, Lund M, Parmentier F-JW, Brown R, Bhatt US,
718 Euskirchen ES, Romanovsky VE, Walsh JE, Overland JE, Wang M, Corell RW, Meier WN, Wouters B,
719 Mernild S, Maard J, Pawlak J, Olsen MS (2019) Key indicators of Arctic climate change: 1971–2017.
720 Environ Res Lett 14:045010. doi: 10.1088/1748-9326/aafc1b
- 721 Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. Ecol
722 Model 157:281–300. doi: 10.1016/S0304-3800(02)00200-4
- 723 Bracis C, Bildstein KL, Mueller T (2018) Revisitation analysis uncovers spatio-temporal patterns in animal
724 movement data. Ecography 41:1801–1811. doi: [10.1111/ecog.03618](https://doi.org/10.1111/ecog.03618)
- 725 Braune BM, Mallory ML, Gilchrist HG (2006) Elevated mercury levels in a declining population of ivory
726 gulls in the Canadian Arctic. Mar Pollut Bull 52:978–982.
- 727 Brisson-Curadeau E, Patterson A, Whelan S, Lazarus T, Elliott KH (2017) Tracking Cairns: Biologging
728 Improves the Use of Seabirds as Sentinels of the Sea. Front Mar Sci. doi: 10.3389/fmars.2017.00357
- 729 Brooks ME, Kristensen K, Benthem KJ van, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M,
730 Bolker BM (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated
731 Generalized Linear Mixed Modeling. The R Journal 9:378–400.

732 Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat
733 use by animals. *Ecological Modelling* 197:516–519. doi: 10.1016/j.ecolmodel.2006.03.017

734 Cama A, Abellana R, Christel I, Ferrer X, Vieites DR (2012) Living on predictability: modelling the density
735 distribution of efficient foraging seabirds. *Ecography* 35:912–921. doi: 10.1111/j.1600-
736 0587.2011.06756.x

737 Carroll G, Harcourt R, Pitcher BJ, Slip D, Jonsen I (2018) Recent prey capture experience and dynamic
738 habitat quality mediate short-term foraging site fidelity in a seabird. *Proc R Soc B Biol Sci*
739 285:20180788. doi: 10.1098/rspb.2018.0788

740 Clairbaux M, Fort J, Mathewson P, Porter W, Strøm H, Grémillet D (2019) Climate change could overturn
741 bird migration: Transarctic flights and high-latitude residency in a sea ice free Arctic. *Sci Rep* 9:17767.
742 doi: 10.1038/s41598-019-54228-5

743 Clapp JG, Beck JL (2015) Evaluating distributional shifts in home range estimates. *Ecol Evol* 5:3869–3878.
744 doi: 10.1002/ece3.1655

745 Courbin N, Besnard A, Péron C, Saraux C, Fort J, Perret S, Tornos J, Grémillet D (2018) Short-term prey
746 field lability constrains individual specialisation in resource selection and foraging site fidelity in a
747 marine predator. *Ecol Lett* 21:1043–1054. doi: 10.1111/ele.12970

748 Davoren GK, Montevecchi WA, Anderson JT (2003) Search strategies of a pursuit-diving marine bird and
749 the persistence of prey patches. *Ecol Monogr* 73:463–481. doi: <https://doi.org/10.1890/02-0208>

750 Descamps S, Ramírez F, Benjaminsen S, Anker-Nilssen T, Barrett RT, Burr Z, Christensen-Dalsgaard S,
751 Erikstad K-E, Irons DB, Lorentsen S-H, Mallory ML, Robertson GJ, Reiertsen TK, Strøm H, Varpe Ø,
752 Lavergne S (2019) Diverging phenological responses of Arctic seabirds to an earlier spring. *Glob Change*
753 *Biol* 25:4081–4091. doi: 10.1111/gcb.14780

754 Divoky GJ (1976) The Pelagic Feeding Habits of Ivory and Ross’ Gulls. *The Condor* 78:85–90. doi:
755 10.2307/1366919

756 Duffy-Anderson JT, Stabeno P, Andrews AG, Cieciel K, Deary A, Farley E, Fugate C, Harpold C, Heintz R,
757 Kimmel D, Kuletz K, Lamb J, Paquin M, Porter S, Rogers L, Spear A, Yasumiishi E (2019) Responses of
758 the Northern Bering Sea and Southeastern Bering Sea Pelagic Ecosystems Following Record-Breaking
759 Low Winter Sea Ice. *Geophys Res Lett* 46:9833–9842. doi: 10.1029/2019GL083396

760 Dunphy BJ, Vickers SI, Zhang J, Sagar RL, Landers TJ, Bury SJ, Hickey AJR, Rayner MJ (2020) Seabirds
761 as environmental indicators: foraging behaviour and ecophysiology of common diving petrels
762 (*Pelecanoides urinatrix*) reflect local-scale differences in prey availability. *Mar Biol* 167:53. doi:
763 10.1007/s00227-020-3672-4

764 Durant J, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator
765 requirements and resource availability. *Clim Res* 33:271–283. doi: 10.3354/cr033271

766 Durant JM, Hjernmann DØ, Frederiksen M, Charrassin J-B, Le Maho Y, Sabarros PS, Crawford RJM,
767 Stenseth NC (2009) Pros and cons of using seabirds as ecological indicators. *Clim Res* 39:115–129. doi:
768 10.3354/cr00798

769 Eamer J, Donaldson GM, Gaston AJ, Kosobokova KN, Lárusson KF, Melnikov IA, J. D. Reist, Evan
770 Richardson, L. Staples, C. H. von Quillfeldt (2013) Life Linked to Ice. A guide to sea-ice-associated
771 biodiversity in this time of rapid change.

772 Fieberg J, Kochanny CO (2005) Quantifying Home-Range Overlap: The Importance of the Utilization
773 Distribution. *J Wildl Manag* 69:1346–1359. doi: 10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2

774 Fluhr J, Benhamou S, Riotte-Lambert L, Duriez O (2017) Assessing the risk for an obligate scavenger to be
775 dependent on predictable feeding sources. *Biol Conserv* 215:92–98. doi: 10.1016/j.biocon.2017.07.030

776 Frederiksen M, Mosbech A, Andersson A, Corregidor Castro A, Egevang C, Fort, Grémillet D, Linnebjerg
777 JF, Lyngs P, Nielsen HH, Rømer JK (2019) Population size and habitat use of breeding seabirds in
778 Northeast Greenland. *Field studies* 2017-18. Aarhus University, DCE – Danish Centre for Environment
779 and Energy.

780 Frederiksen M, Gilg O, Yannic G (2021) Cross-icecap spring migration confirmed in a high-Arctic seabird,
781 the Ivory Gull *Pagophila eburnea*. *Ibis* 163:706–714. doi: <https://doi.org/10.1111/ibi.12903>

782 Furness RW, Camphuysen K (C J) (1997) Seabirds as monitors of the marine environment. *ICES J Mar Sci*
783 54:726–737. doi: 10.1006/jmsc.1997.0243

784 Gaston AJ, Mallory ML, Gilchrist HG (2012) Populations and trends of Canadian Arctic seabirds. *Polar Biol*
785 35:1221–1232. doi: 10.1007/s00300-012-1168-5

786 Gavrilov M, Martynova D (2017) Conservation of rare species of marine flora and fauna of the Russian Arctic
787 National Park, included in the Red Data Book of the Russian Federation and in the IUCN Red List. *Nat*
788 *Conserv Res* 2:10–42. doi: 10.24189/ncr.2017.017

789 Gilchrist HG, Mallory ML (2005) Declines in abundance and distribution of the ivory gull (*Pagophila*
790 *eburnea*) in Arctic Canada. *Biol Conserv* 121:303–309. doi: 10.1016/j.biocon.2004.04.021

791 Gilg O, Boertmann D, Merkel F, Aebischer A, Sabard B (2009) Status of the endangered ivory gull,
792 *Pagophila eburnea*, in Greenland. *Polar Biol* 32:1275–1286. doi: 10.1007/s00300-009-0623-4

793 Gilg O, Strøm H, Aebischer A, Gavrilov MV, Volkov AE, Miljeteig C, Sabard B (2010) Post-breeding
794 movements of northeast Atlantic ivory gull *Pagophila eburnea* populations. *J Avian Biol* 41:532–542. doi:
795 10.1111/j.1600-048X.2010.05125.x

796 Gilg O, Kovacs KM, Aars J, Fort J, Gauthier G, Grémillet D, Ims RA, Møltøfte H, Moreau J, Post E,
797 Schmidt NM, Yannic G, Bollache L (2012) Climate change and the ecology and evolution of Arctic
798 vertebrates. *Ann N Y Acad Sci* 1249:166–190. doi: 10.1111/j.1749-6632.2011.06412.x

799 Gilg O, Istomina L, Heygster G, Strøm H, Gavrilov MV, Mallory ML, Gilchrist G, Aebischer A, Sabard B,
800 Huntemann M, Mosbech A, Yannic G (2016) Living on the edge of a shrinking habitat: the ivory gull,
801 *Pagophila eburnea*, an endangered sea-ice specialist. *Biol Lett* 12:20160277. doi: 10.1098/rsbl.2016.0277

802 Grémillet D, Charmantier A (2010) Shifts in phenotypic plasticity constrain the value of seabirds as
803 ecological indicators of marine ecosystems. *Ecol Appl Publ Ecol Soc Am* 20:1498–1503. doi:
804 10.1890/09-1586.1

805 Grémillet D, Fort J, Amélineau F, Zakharova E, Bot TL, Sala E, Gavrilov M (2015) Arctic warming:
806 nonlinear impacts of sea-ice and glacier melt on seabird foraging. *Glob Change Biol* 21:1116–1123. doi:
807 10.1111/gcb.12811

808 Grémillet D, Gallien F, El Ksabi N, Courbin N (2020) Sentinels of coastal ecosystems: the spatial ecology of
809 European shags breeding in Normandy. *Mar Biol* 167:43. doi: 10.1007/s00227-020-3655-5

810 Gupte PR, Beardsworth CE, Spiegel O, Lourie E, Toledo S, Nathan R, Bijleveld AI (2021) A guide to pre-
811 processing high-throughput animal tracking data. *J Anim Ecol*. doi: 10.1111/1365-2656.13610

812 Harris SM, Descamps S, Sneddon LU, Bertrand P, Chastel O, Patrick SC (2020) Personality predicts
813 foraging site fidelity and trip repeatability in a marine predator. *J Anim Ecol* 89:68–79. doi:
814 10.1111/1365-2656.13106

815 Hartley CH, Fisher J (1936) The marine foods of birds in an inland fjord region in West Spitsbergen: Part 2.
816 *Birds. J Anim Ecol* 5:370–389. doi: 10.2307/1041

817 IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the
818 Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P.
819 Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang,
820 K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou
821 (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, In press,
822 doi:10.1017/9781009157896.

823 Irons DB (1998) Foraging area fidelity of individual seabirds in relation to Tidal cycles and flock feeding.
824 *Ecology* 79:647–655. doi: 10.1890/0012-9658(1998)079[0647:FAFOIS]2.0.CO;2

825 Jakobsson M, Mayer L, Coakley B, Dowdeswell JA, Forbes S, Fridman B, Hodnesdal H, Noormets R,
826 Pedersen R, Rebesco M, Schenke HW, Zarayskaya Y, Accettella D, Armstrong A, Anderson RM,
827 Bienhoff P, Camerlenghi A, Church I, Edwards M, Gardner JV, Hall JK, Hell B, Hestvik O, Kristoffersen
828 Y, Marcussen C, Mohammad R, Mosher D, Nghiem SV, Pedrosa MT, Travaglini PG, Weatherall P
829 (2012) The International Bathymetric Chart of the Arctic Ocean (IBCAO) Version 3.0. *Geophys Res Lett*.
830 doi: 10.1029/2012GL052219

831 Jakubas D, Iliszko L, Wojczulanis-Jakubas K, Stempniewicz L (2012) Foraging by little auks in the distant
832 marginal sea ice zone during the chick-rearing period. *Polar Biol* 35:73–81. doi: 10.1007/s00300-011-
833 1034-x

834 Jakubas D, Wojczulanis-Jakubas K, Iliszko L, Darecki M, Stempniewicz L (2014) Foraging strategy of the
835 little auk *Alle alle* throughout breeding season – switch from unimodal to bimodal pattern. *J Avian Biol*
836 45:551–560. doi: 10.1111/jav.00303

837 Johnson M, Eicken H (2016) Estimating Arctic sea-ice freeze-up and break-up from the satellite record: A
838 comparison of different approaches in the Chukchi and Beaufort Seas. *Elem Sci Anth* 4:000124. doi:
839 10.12952/journal.elementa.000124

840 Kamil AC (1983) Optimal foraging theory and the psychology of learning. *Am Zool* 23:291–302.

841 Karnovsky NJ, Hobson KA, Brown ZW, George L, Hunt J (2009) Distribution and Diet of Ivory Gulls
842 (*Pagophila eburnea*) in the North Water. *ARCTIC* 62:65–74. doi: 10.14430/arctic113

843 Kidawa D, Jakubas D, Wojczulanis-Jakubas K, Stempniewicz L, Trudnowska E, Boehnke R, Keslinka-
844 Nawrot L, Błachowiak-Samołyk K (2015) Parental efforts of an Arctic seabird, the little auk *Alle alle*,
845 under variable foraging conditions. *Mar Biol Res* 11:349–360. doi: 10.1080/17451000.2014.940974

846 Kitaysky AS, Hunt (2018) Seabird responses to a changing Bering Sea. *Mar Ecol Prog Ser* 593:189–194.
847 doi: 10.3354/meps12580

848 Kohlbach D, Graeve M, Lange BA, David C, Peeken I, Flores H (2016) The importance of ice algae-
849 produced carbon in the central Arctic Ocean ecosystem: Food web relationships revealed by lipid and
850 stable isotope analyses. *Limnol Oceanogr* 61:2027–2044. doi: 10.1002/lno.10351

851 Korczak-Abshire M, Hinke JT, Milinevsky G, Juárez MA, Watters GM (2021) Coastal regions of the
852 northern Antarctic Peninsula are key for gentoo populations. *Biol Lett* 17:20200708. doi:
853 10.1098/rsbl.2020.0708

854 Kowal S, Gough WA, Butler K (2017) Temporal evolution of Hudson Bay sea ice (1971–2011). *Theor Appl*
855 *Climatol* 127:753–760.

856 Lee SH, Jin M, Whitley TE (2010) Comparison of bottom sea-ice algal characteristics from coastal and
857 offshore regions in the Arctic Ocean. *Polar Biol* 33:1331–1337. doi: 10.1007/s00300-010-0820-1

858 Lenzi J, González-Bergonzoni I, Machín E, Pijanowski B, Flaherty E (2019) The impact of anthropogenic
859 food subsidies on a generalist seabird during nestling growth. *Sci Total Environ* 687:546–553. doi:
860 10.1016/j.scitotenv.2019.05.485

861 Liu J, Chen Z, Francis J, Song M, Mote T, Hu Y (2016) Has Arctic Sea Ice Loss Contributed to Increased
862 Surface Melting of the Greenland Ice Sheet? *J Clim* 29:3373–3386. doi: 10.1175/JCLI-D-15-0391.1

863 Lucia M, Verboven N, Strøm H, Miljeteig C, Gavrilo MV, Braune BM, Boertmann D, Gabrielsen GW
864 (2015) Circumpolar contamination in eggs of the high-Arctic ivory gull *Pagophila eburnea*. *Environ*
865 *Toxicol Chem* 34:1552–1561. doi: 10.1002/etc.2935

866 Lydersen C, Assmy P, Falk-Petersen S, Kohler J, Kovacs KM, Reigstad M, Steen H, Strøm H, Sundfjord A,
867 Varpe Ø, Walczowski W, Weslawski JM, Zajaczkowski M (2014) The importance of tidewater glaciers
868 for marine mammals and seabirds in Svalbard, Norway. *J Mar Syst* 129:452–471. doi:
869 10.1016/j.jmarsys.2013.09.006

870 Macias-Fauria M, Post E (2018) Effects of sea ice on Arctic biota: an emerging crisis discipline. *Biol Lett*
871 14:20170702. doi: 10.1098/rsbl.2017.0702

872 Mallory ML, Gilchrist HG, Fontaine AJ, Akearok JA (2003) Local Ecological Knowledge of Ivory Gull
873 Declines in Arctic Canada. *Arctic* 56:293–298.

874 Manly BF, McDonald L, Thomas D, McDonald TL, Erickson WP (2002) *Resource Selection by Animals:
875 Statistical Design and Analysis for Field Studies*, 2nd edn. Springer Netherlands

876 Masello JF, Mundry R, Poisbleau M, Demongin L, Voigt CC, Wikelski M, Quillfeldt P (2010) Diving
877 seabirds share foraging space and time within and among species. *Ecosphere* 1:art19. doi: 10.1890/ES10-
878 00103.1

879 McDonald TL (2013) The point process use-availability or presence-only likelihood and comments
880 on analysis. *Journal of Animal Ecology* 82:1174–1182. doi: [10.1111/1365-2656.12132](https://doi.org/10.1111/1365-2656.12132)

881 McLaren PL, Renaud WE (1982) Seabird Concentrations in Late Summer along the Coasts of Devon and
882 Ellesmere Islands, N. W. T. *Arctic* 35:112–117.

883 Mehlum F, Gabrielsen GW (1993) The diet of High-Arctic seabirds in coastal and ice-covered, pelagic areas
884 near the Svalbard archipelago. *Polar Res* 12:1–20. doi: 10.3402/polar.v12i1.6698

885 Michelot C, Kato A, Raclot T, Shiomi K, Goulet P, Bustamante P, Ropert-Coudert Y (2020) Sea-ice edge is
886 more important than closer open water access for foraging Adélie penguins: evidence from two colonies.
887 *Mar Ecol Prog Ser* 640:215–230. doi: 10.3354/meps13289

888 Michelot T, Langrock R, Patterson TA (2016) moveHMM: an R package for the statistical modelling of
889 animal movement data using hidden Markov models. *Methods in Ecology and Evolution* 7:1308–1315.
890 doi: 10.1111/2041-210X.12578

891 Miljeteig C, Strøm H, Gavrilo MV, Volkov A, Jenssen BM, Gabrielsen GW (2009) High Levels of
892 Contaminants in Ivory Gull *Pagophila eburnea* Eggs from the Russian and Norwegian Arctic. *Environ Sci*
893 *Technol* 43:5521–5528. doi: 10.1021/es900490n

894 Miljeteig C, Gabrielsen GW, Strøm H, Gavrilov MV, Lie E, Jenssen BM (2012) Eggshell thinning and
895 decreased concentrations of vitamin E are associated with contaminants in eggs of ivory gulls. *Sci Total*
896 *Environ* 431:92–99. doi: 10.1016/j.scitotenv.2012.05.018

897 Miller GH, Alley RB, Brigham-Grette J, Fitzpatrick JJ, Polyak L, Serreze MC, White JWC (2010) Arctic
898 amplification: can the past constrain the future? *Quat Sci Rev* 29:1779–1790. doi:
899 10.1016/j.quascirev.2010.02.008

900 Monsarrat S, Benhamou S, Sarrazin F, Bessa-Gomes C, Bouten W, Duriez O (2013) How Predictability of
901 Feeding Patches Affects Home Range and Foraging Habitat Selection in Avian Social Scavengers? *PLOS*
902 *ONE* 8:e53077. doi: 10.1371/journal.pone.0053077

903 Morales JM, Haydon DT, Frair J, Holsinger KE, Fryxell JM (2004) Extracting More Out of Relocation Data:
904 Building Movement Models as Mixtures of Random Walks. *Ecology* 85:2436–2445. doi: 10.1890/03-
905 0269

906 Mu Y, Wei Y, Wu J, Ding Y, Shangguan D, Zeng D (2020) Variations of Mass Balance of the Greenland Ice
907 Sheet from 2002 to 2019. *Remote Sens* 12:2609. doi: 10.3390/rs12162609

908 Muff S, Signer J, Fieberg J (2020) Accounting for individual-specific variation in habitat-selection studies:
909 Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *J Anim Ecol*
910 89:80–92. doi: 10.1111/1365-2656.13087

911 Muggeo VMR (2008) segmented: an R Package to Fit Regression Models with Broken-Line Relationships.
912 *R News*, 8/1, 20-25. <https://cran.r-project.org/doc/Rnews/>.

913 Nishizawa B, Kanna N, Abe Y, Ohashi Y, Sakakibara D, Asaji I, Sugiyama S, Yamaguchi A, Watanuki Y
914 (2020) Contrasting assemblages of seabirds in the subglacial meltwater plume and oceanic water of
915 Bowdoin Fjord, northwestern Greenland. *ICES J Mar Sci* 77:711–720. doi: 10.1093/icesjms/fsz213

916 Orians GH, Pearson NE (1979) On the theory of central place foraging. *Anal Ecol Syst Ohio State Univ*
917 *Press* 154–177.

918 Paiva VH, Geraldine P, Ramírez I, Garthe S, Ramos JA (2010) How area restricted search of a pelagic seabird
919 changes while performing a dual foraging strategy. *Oikos* 119:1423–1434. doi: 10.1111/j.1600-
920 0706.2010.18294.x

921 Pang X, Pu J, Zhao X, Ji Q, Qu M, Cheng Z (2018) Comparison between AMSR2 Sea Ice Concentration
922 Products and Pseudo-Ship Observations of the Arctic and Antarctic Sea Ice Edge on Cloud-Free Days.
923 *Remote Sens* 10:317. doi: 10.3390/rs10020317

924 Patrick SC, Weimerskirch H (2017) Reproductive success is driven by local site fidelity despite stronger
925 specialisation by individuals for large-scale habitat preference. *J Anim Ecol* 86:674–682. doi:
926 10.1111/1365-2656.12636

927 Patrick SC, Bearhop S, Bodey TW, Grecian WJ, Hamer KC, Lee J, Votier SC (2015) Individual seabirds
928 show consistent foraging strategies in response to predictable fisheries discards. *J Avian Biol* 46:431–
929 440. doi: 10.1111/jav.00660

930 Pedersen RA, Christensen JH (2019) Attributing Greenland Warming Patterns to Regional Arctic Sea Ice
931 Loss. *Geophys Res Lett* 46:10495–10503. doi: 10.1029/2019GL083828

932 Piper W (2011) Making habitat selection more “familiar”: a review. *Behav Ecol Sociobiol*. doi:
933 10.1007/s00265-011-1195-1

934 Plaza PI, Lambertucci SA (2017) How are garbage dumps impacting vertebrate demography, health, and
935 conservation? *Glob Ecol Conserv* 12:9–20. doi: 10.1016/j.gecco.2017.08.002

936 Post E, Bhatt US, Bitz CM, Brodie JF, Fulton TL, Hebblewhite M, Kerby J, Kutz SJ, Stirling I, Walker DA
937 (2013) Ecological Consequences of Sea-Ice Decline. *Science* 341:519–524. doi:
938 10.1126/science.1235225

939 Post E, Alley RB, Christensen TR, Macias-Fauria M, Forbes BC, Gooseff MN, Iler A, Kerby JT, Laidre KL,
940 Mann ME, Olofsson J, Stroeve JC, Ulmer F, Virginia RA, Wang M (2019) The polar regions in a 2°C
941 warmer world. *Sci Adv* 5:eaaw9883. doi: 10.1126/sciadv.aaw9883

942 R Core Team (2019) *Core R: A Language and Environment for Statistical Computing*, Version 3.5. 3.
943 Foundation for Statistical Computing, Vienna, Austria.

944 Ramírez F, Tarroux A, Hovinen J, Navarro J, Afán I, Forero MG, Descamps S (2017) Sea ice phenology and
945 primary productivity pulses shape breeding success in Arctic seabirds. *Sci Rep* 7:4500. doi:
946 10.1038/s41598-017-04775-6

- 947 Raup B, Racoviteanu A, Khalsa SJS, Helm C, Armstrong R, Arnaud Y (2007) The GLIMS geospatial glacier
 948 database: A new tool for studying glacier change. *Glob Planet Change* 56:101–110. doi:
 949 10.1016/j.gloplacha.2006.07.018
- 950 Renaud WE, McLaren PL (1982) Ivory Gull (*Pagophila eburnea*) Distribution in Late Summer and Autumn
 951 in Eastern Lancaster Sound and Western Baffin Bay. *Arctic* 35:141–148.
- 952 Rolph RJ, Feltham DL, Schröder D (2020) Changes of the Arctic marginal ice zone during the satellite era.
 953 *The Cryosphere* 14:1971–1984. doi: <https://doi.org/10.5194/tc-14-1971-2020>
- 954 Sánchez S, Reina RD, Kato A, Ropert-Coudert Y, Cavallo C, Hays GC, Chiaradia A (2018) Within-colony
 955 spatial segregation leads to foraging behaviour variation in a seabird. *Mar Ecol Prog Ser* 606:215–230.
 956 doi: 10.3354/meps12764
- 957 Sauve D, Divoky G, Friesen VL (2019) Phenotypic plasticity or evolutionary change? An examination of the
 958 phenological response of an arctic seabird to climate change. *Funct Ecol* 33:2180–2190. doi:
 959 10.1111/1365-2435.13406
- 960 Savory G, Hunter CM, Wooller M, O’Brien D (2014) Anthropogenic food use and diet overlap between red
 961 foxes (*Vulpes vulpes*) and arctic foxes (*Vulpes lagopus*) in Prudhoe Bay, Alaska. *Can J Zool* 92:657–663.
 962 doi: 10.1139/cjz-2013-0283
- 963 Shoji A, Aris-Brosou S, Fayet A, Padget O, Perrins C, Guilford T (2015) Dual foraging and pair
 964 coordination during chick provisioning by Manx shearwaters: empirical evidence supported by a simple
 965 model. *J Exp Biol* 218:2116–2123. doi: 10.1242/jeb.120626
- 966 Søreide JE, Leu E, Berge J, Graeve M, Falk-Petersen S (2010) Timing of blooms, algal food quality and
 967 *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob Change Biol* 16:3154–3163. doi:
 968 10.1111/j.1365-2486.2010.02175.x
- 969 Spencer NC, Gilchrist HG, Mallory ML (2014) Annual Movement Patterns of Endangered Ivory Gulls: The
 970 Importance of Sea Ice. *PLOS ONE* 9:e115231. doi: 10.1371/journal.pone.0115231
- 971 Spencer NC, Gilchrist HG, Strøm H, Allard KA, Mallory ML (2016) Key winter habitat of the ivory gull
 972 *Pagophila eburnea* in the Canadian Arctic. *Endanger Species Res* 31:33–45. doi: 10.3354/esr00747
- 973 Steen H, Vogedes D, Broms F, Falk-Petersen S, Berge J (2007) Little auks (*Alle alle*) breeding in a High
 974 Arctic fjord system: bimodal foraging strategies as a response to poor food quality? *Polar Res* 26:118–
 975 125. doi: 10.3402/polar.v26i2.6220
- 976 Stephen K (2018) Societal Impacts of a Rapidly Changing Arctic. *Curr Clim Change Rep* 4:223–237. doi:
 977 10.1007/s40641-018-0106-1
- 978 Strøm H, Boertmann D, Gavrilov MV, Gilchrist HG, Gilg O, Mallory M, Mosbech A, Yannic G (2019) Ivory
 979 Gull: Status, Trends and New Knowledge. *NOAA Arct Rep Card* 2019 66.
- 980 Strøm H, Bakken V, Skoglund, Descamps S, Fjeldheim VB, Steen H (2020) Population status and trend of
 981 the threatened ivory gull *Pagophila eburnea* in Svalbard. *Endanger Species Res* 43:435–445.
- 982 Switzer PV (1993) Site fidelity in predictable and unpredictable habitats. *Evol Ecol* 7:533–555. doi:
 983 10.1007/BF01237820
- 984 Tarrow A, Chérel Y, Fauchald P, Kato A, Love OP, Ropert-Coudert Y, Spreen G, Varpe Ø, Weimerskirch
 985 H, Yoccoz NG, Zahn S, Descamps S (2020) Foraging tactics in dynamic sea-ice habitats affect individual
 986 state in a long-ranging seabird. *Funct Ecol* 34:1839–1856. doi: 10.1111/1365-2435.13632
- 987 Thomas DW, Blondel J, Perret P, Lambrechts MM, Speakman JR (2001) Energetic and Fitness Costs of
 988 Mismatching Resource Supply and Demand in Seasonally Breeding Birds. *Science* 291:2598–2600. doi:
 989 10.1126/science.1057487
- 990 Thomas VG, MacDonald SD (1987) The breeding distribution and current population status of the ivory gull
 991 in Canada. *Arctic* 211–218.
- 992 Tyson C, Kirk H, Fayet A, Van Loon EE, Shoji A, Dean B, Perrins C, Freeman R, Guilford T (2017)
 993 Coordinated provisioning in a dual-foraging pelagic seabird. *Anim Behav* 132:73–79. doi:
 994 10.1016/j.anbehav.2017.07.022
- 995 Wakefield ED, Cleasby IR, Bearhop S, Bodey TW, Davies RD, Miller PI, Newton J, Votier SC, Hamer KC
 996 (2015) Long-term individual foraging site fidelity—why some gannets don’t change their spots. *Ecology*
 997 96:3058–3074. doi: <https://doi.org/10.1890/14-1300.1>
- 998 Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res Part II Top Stud*
 999 *Oceanogr* 54:211–223. doi: 10.1016/j.dsr2.2006.11.013

1000 Weimerskirch H, Chastel O, Ackermann L, Chaurand T, Cuenot-Chaillet F, Hindermeier X, Judas J (1994)
1001 Alternate long and short foraging trips in pelagic seabird parents. *Anim Behav* 47:472–476. doi:
1002 10.1006/anbe.1994.1065

1003 Welcker J, Harding AMA, Karnovsky NJ, Steen H, Strøm H, Gabrielsen GW (2009) Flexibility in the
1004 bimodal foraging strategy of a high Arctic alcid, the little auk *Alle alle*. *J Avian Biol* 40:388–399. doi:
1005 10.1111/j.1600-048X.2008.04620.x

1006 Welcker J, Beiersdorf A, Varpe Ø, Steen H (2012) Mass Fluctuations Suggest Different Functions of
1007 Bimodal Foraging Trips in a Central-place Forager. *Behav Ecol* 23:1372–1378. doi:
1008 10.1093/beheco/ars131

1009 Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V (2015) The golden age of bio-logging:
1010 how animal-borne sensors are advancing the frontiers of ecology. *Ecology* 96:1741–1753. doi:
1011 10.1890/14-1401.1

1012 Wojczulanis-Jakubas K, Jakubas D, Karnovsky NJ, Walkusz W (2010) Foraging strategy of little auks under
1013 divergent conditions on feeding grounds. *Polar Res* 29:22–29. doi: 10.1111/j.1751-8369.2009.00145.x

1014 Wojczulanis-Jakubas K, Jakubas D, Stempniewicz L (2021) The Little Auk *Alle alle*: an ecological indicator
1015 of a changing Arctic and a model organism. *Polar Biol*. doi: 10.1007/s00300-021-02981-7

1016 Wood S, Scheipl F (2020) gamm4: Generalized Additive Mixed Models using “mgcv” and “lme4.”

1017 Yannic G, Aebischer A, Sabard B, Gilg O (2014) Complete breeding failures in ivory gull following unusual
1018 rainy storms in North Greenland. *Polar Res* 33:22749. doi: 10.3402/polar.v33.22749

1019 Yurkowski DJ, Auger-Méthé M, Mallory ML, Wong SNP, Gilchrist G, Derocher AE, Richardson E, Lunn
1020 NJ, Hussey NE, Marcoux M, Togunov RR, Fisk AT, Harwood LA, Dietz R, Rosing-Asvid A, Born EW,
1021 Mosbech A, Fort J, Grémillet D, Loseto L, Richard PR, Iacozza J, Jean-Gagnon F, Brown TM, Westdal
1022 KH, Orr J, LeBlanc B, Hedges KJ, Treble MA, Kessel ST, Blanchfield PJ, Davis S, Maftai M, Spencer N,
1023 McFarlane-Tranquilla L, Montevecchi WA, Bartzen B, Dickson L, Anderson C, Ferguson SH (2019)
1024 Abundance and species diversity hotspots of tracked marine predators across the North American Arctic.
1025 *Divers Distrib* 25:328–345. doi: 10.1111/ddi.12860

1026 Zhang J, Rayner M, Vickers S, Landers T, Sagar R, Stewart J, Dunphy B (2019) GPS telemetry for small
1027 seabirds: using hidden Markov models to infer foraging behaviour of Common Diving Petrels
1028 (*Pelecanoides urinatrix urinatrix*). *Emu - Austral Ornithol* 119:126–137. doi:
1029 10.1080/01584197.2018.1558997

1030