

1 Colony size and foraging range in seabirds

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24

25 **Abstract**

26 The reasons for variation in group size among animal species remain poorly understood. Using  
27 “Ashmole’s halo” hypothesis of food depletion around colonies, we predict that foraging range  
28 imposes a ceiling on the maximum colony size of seabird species. We tested this with a  
29 phylogenetic comparative study of 43 species of seabirds (28,262 colonies), and investigated the  
30 interspecific correlation between colony size and foraging ranges. Foraging range showed weak  
31 relationships with the low percentiles of colony size of species, but the strength of the association  
32 increased for larger percentiles, peaking at the maximum colony sizes. To model constraints on  
33 the functional relationship between the focal traits, we applied a quantile regression based on  
34 maximum colony size. This showed that foraging range imposes a constraint to species'  
35 maximum colony sizes with a slope around 2. This second-order relationship is expected from  
36 the equation of the area of a circle. Thus, our large dataset and innovative statistical approach  
37 shows that foraging range imposes a ceiling on seabird colony sizes, providing strong support to  
38 the hypothesis that food availability is an important regulator of seabird populations.

39

40 Key-words: birds, food, group living, marine, sociality, phylogenetic comparative analysis.

41 **Introduction**

42 Colonial living shapes the ecology of 13% of extant bird species (Wittenberger and Hunt 1985,  
43 Rolland et al. 1998). Colony size can range from a few pairs up to millions of birds breeding  
44 together. Understanding the causes (e.g. conspecific attraction, food availability) and  
45 consequences (e.g. negative density dependence, parasitism) of such colony size variation is not  
46 only important to understand the ecology of colonial birds (Lack 1954, 1967, Wittenberger &  
47 Hunt 1985, Brown et al. 1990, Siegel-Causey & Kharitonov 1990, Rolland et al. 1998, Brown &  
48 Brown 2000, 2001, Coulson 2002, Safran 2004, Serrano and Tella 2007), but is also relevant for  
49 our interpretations about group living in general (Krause & Ruxton 2002), and to inform  
50 conservation policies (Mitchell et al. 2004). This is especially true in seabirds, where most  
51 species breed in colonies (Rolland et al. 1998). Accordingly, understanding colony size variation  
52 and its implications has been the driver of much research in seabird ecology (Ashmole 1963,  
53 Cairns 1989, Furness and Birkhead 1984, Lewis et al. 2001, Coulson 2002, Forero et al. 2002,  
54 Ainley et al. 2004, Ballance et al. 2009). However, while much research has been devoted to  
55 intraspecific patterns in colony size variation, less has been done at the interspecific level.

56 In two previous studies, analyzing thousands of colonies of varying sizes for tens of  
57 species, we showed (1) a huge variation in colony size within and between seabird species,  
58 showing colony size frequency distributions from log-normal to power laws, often spanning  
59 from very small to very large colony sizes within species (Jovani et al. 2008). (2) This  
60 intraspecific variation does not blur interspecific differences, and some species consistently show  
61 much larger median (repeatability analysis:  $R=0.73$ , 95% CI=0.46-0.93), 95th percentile (0.88  
62 (0.77-0.97)), and maximum (0.80 (0.61-0.95)) colony sizes than others, when comparing  
63 populations of the same seabird species in different geographic areas (Jovani et al. 2012). That is,

64 typical and maximum colony sizes are species-specific traits despite high intraspecific variation.  
65 The question we address here is why the colony sizes of seabirds differ so widely between  
66 species. To answer this, we focused on foraging distances of seabirds around breeding colonies,  
67 and their impact on seabird colony sizes, thus extending the consequences of Ashmole's halo  
68 (1963, see below) at an interspecific level.

69         Seabirds are “central place foragers”; they travel back and forth to the sea (or terrestrial  
70 habitats) constrained by the need to regularly gather and deliver food for their nestlings. As  
71 happens with colony sizes (Jovani et al. 2008, 2012), foraging distances differ between colonies  
72 within species (e.g. Lewis et al. 2001), but also between species (see below). This led to an early  
73 classification of seabirds as inshore, offshore and pelagic species (Lack 1954). Over millions of  
74 years species have evolved life-history (e.g. small clutch size), morphological (e.g. wing  
75 loading), physiological (e.g. oil feeding to chicks), and behavioural (e.g. flight style) adaptations  
76 to allow them to exploit food resources most effectively within their available foraging ranges.  
77 These characteristics vary across species and set different maximum distances from the breeding  
78 colony which species can travel while still allowing effective reproduction. Some species  
79 typically exploit resources close to the colony while others may travel hundreds or thousands of  
80 kilometers to gather food (Nelson 1980, Coulson 2002, Gaston 2004). Moreover, Gaston et al.  
81 (2007) recently showed through a modeling approach that seabird traits such as wing shape or  
82 the kind of parental care explain the energetic constraints (of flight and food provisioning) that  
83 lead to the formation of Ashmole's halos, and how these species traits lead to interspecific  
84 variation on the size of the halo (i.e. the foraging range of species). Thus, while the foraging  
85 distance of birds of a given colony is highly dependent on environmental (e.g. distance to the  
86 continental shelf; Mitchell et al. 2004), and social factors (e.g. the position of close conspecific

87 colonies, Wakefield et al. 2013), species differ a lot in their potential maximum foraging ranges  
88 due to other species traits such as wing loading or flight speed. In other words, individuals of all  
89 species can forage close to their colonies, but only individuals of some species could forage  
90 hundreds of kilometers away from the colony and still successfully feed their chicks.

91         The foraging range (maximum foraging distance) of species and the size of their colonies  
92 have been proposed to be mechanistically linked. Storer (1952) and Ashmole (1963) suggested  
93 that food availability around colonies (rather than non-reproductive survival; Lack 1967) is the  
94 main regulator of seabird populations. They suggested that colony members gradually deplete  
95 food around colonies, thus creating a “halo” with low food availability. Intraspecific studies have  
96 shown that breeding adults from larger colonies forage farther than from smaller colonies (Lewis  
97 et al. 2001, Ainley et al. 2004, Ballance et al. 2009), supporting the idea that food resources are  
98 depleted (or prey escape, Hamerik et al. 2014) around colonies (Birt et al. 1987, Elliott et al.  
99 2009).

100         Interspecifically, early anecdotic research into seabird ecology showed that pelagic  
101 species have larger colonies than species that feed inshore (Lack 1967, Nelson 1980). For  
102 instance, in six inshore tern (*Sterna*) species a positive correlation was shown between the  
103 typical foraging movements and the median colony size of the different species (Erwin 1978).  
104 Similarly, studying population size of different species in nine tropical oceanic islands, Diamond  
105 (1978) found that pelagic feeders outnumbered inshore feeders. Götmark (1982) also provided  
106 anecdotal evidence of a correlation between foraging distance and colony sizes in five gull  
107 species. Coulson (1985; cited in Coulson 2002) assessed 15 European seabird species and found  
108 that those with larger colonies were the ones with larger foraging distances. Despite these  
109 anecdotic data, no study has quantitatively tested the hypothesis of a correlation between the

110 foraging range of species and their colony sizes. This interspecific correlation is predicted by the  
111 Ashmole's halo hypothesis, despite the many factors potentially disrupting it (e.g. patchiness of  
112 food abundance, differences in species diet, number of chicks, foraging style). Here we test this  
113 hypothesis, grounded on our previous analyses of a large dataset of seabird colony size  
114 frequency distributions (Jovani et al. 2008, 2012), taking advantage of unprecedented  
115 information on seabird foraging ranges thanks to current telemetry tools, and applying a novel  
116 statistical approach using quantile regression under a comparative phylogenetic framework.

117         Our hypothesis centers on the scenario that foraging range is a constraint for the  
118 maximum colony size of species, but not necessarily for their smaller colony sizes. In other  
119 words, a species with the potential to conduct long foraging trips could nest in both small and  
120 large colonies, but species with a short maximum foraging distance could not nest in large  
121 colonies (i.e. successful breeding could not be achieved in a colony of hundreds of thousands of  
122 birds if the species could only forage within one kilometer of the colony, as food availability  
123 would become a limiting factor). However, it is expected that many species would not achieve  
124 the maximum colony sizes that their foraging ranges would potentially allow due to other  
125 potential constraints that can limit colony sizes (e.g. low food availability, pollution, nest site  
126 availability, disease, predators). Therefore no single model may explain the correlation between  
127 a species foraging range and their colony sizes, but several models depending on the additional  
128 factors that may constrain colony sizes. An ordinary least-squares (OLS) and the phylogenetic  
129 generalized least squares regression (PGLS) would capture the mean conditional effect,  $E(y/X)$ ,  
130 where the expected value of the response variable  $y$  is conditional on the value of the predictor  
131 variable  $X$ . However, this mean effect would not determine whether the foraging range of the  
132 species imposes a ceiling to the maximum colony size the species can achieve. This is a common

133 problem in ecology when (as happens here) more than one factor could constrain the response  
134 variable. Quantile regression is a straightforward statistical approach in these cases, being  
135 increasingly used in ecology and behavioural studies (Koenker and Bassett 1978, Cade and Noon  
136 2003, Chamaillé-Jammes and Blumstein 2012).

137         In this study we used, under a comparative phylogenetic approach, two statistical tools to  
138 test our hypothesis under this biological scenario. First, we correlated the foraging range of  
139 species with their minimum and maximum colony sizes, as well as different colony size  
140 percentiles. Then, we used quantile regression between foraging distance and the maximum  
141 colony sizes of species.

142

## 143 **Methods**

### 144 *Dataset-Colony sizes*

145         We gathered data from 28,262 colonies (a total of 16,602,080 breeding pairs) of 43  
146 colonial nesting seabird species in four distinct geographic regions of the Northern Hemisphere  
147 (see Jovani et al. 2008 for a discussion on the concept of colony and analyses on how this does  
148 not affect colony size estimates for the purpose of these comparative studies). Data from Britain  
149 and Ireland came from the Seabird 2000 project, a collaboration between the Joint Nature  
150 Conservation Committee, Royal Society for the Protection of Birds, BirdWatch Ireland, The  
151 Seabird Group, Scottish National Heritage, Environment and Heritage Service, English Nature,  
152 Countryside Council for Wales, SOTEAG, Department of the Environment, Heritage and Local  
153 Government and INTERREG II C (unpublished raw data; details and aggregated data in Mitchell  
154 et al. 2004 and Jovani et al. 2008). Data from Western Greenland came from a database  
155 maintained by the Department of Arctic Environment, National Environmental Research

156 Institute (obtained 1 March 2006). Data from the St Lawrence gulf and estuary, Canada, came  
157 from the Canadian Wildlife Service (obtained in 19 April 2005; Chapdelaine et al. 2005). Data  
158 from Alaska came from the Seabird Colonies 2000 of the Beringian Seabird Colony Catalog,  
159 maintained by the United States Fish and Wildlife Service USFWS (obtained in 6 June 2005;  
160 Stephensen and Irons 2003).

161 For each species, we calculated multiple percentile bins: the minimum and maximum  
162 colony size and 19 percentiles from 5th to 95th percentile. The 50th percentile is the median of  
163 the distribution, the 5th percentile is close to the minimum colony size, and the 95th percentile is  
164 closer to the maximum colony size (data available in Supplementary material Appendix 1).

165

#### 166 *Dataset-Foraging distances*

167 For this study, we retrieved an estimate of the maximum potential foraging distances  
168 from the colony (foraging range) of breeding adults for each species. For 22 species, this was  
169 sourced from Table 1 from the recent review by Thaxter et al. (2012). Data was updated for five  
170 of these species for which we found more recent and better quality data. For our study species  
171 not reviewed by Thaxter et al. (2012), we followed their protocol, reviewing a total of 68 studies  
172 for 21 species (see Supplementary material Appendix 2 for a detailed account of each study and  
173 species). In Thaxter et al. (2012), authors classified data in four quality categories: “Direct” (e.g.  
174 radio-tracking VHF devices and GPS tags), “Indirect” (e.g. estimations of travel distance from  
175 time away from the colony), “Survey” (e.g. sea line-transects from boats), and “Speculative”  
176 (e.g. diet, anecdotal observations). To test the reliability of foraging ranges at the species level,  
177 we built a mixed model, in which maximum foraging distance was the response variable and the  
178 species identity was used as random effect term, and from which we calculated repeatability



179 from the estimated inter- and intra-specific variance components (Nakagawa and Schielzeth  
180 2010). Using species for which more than one quality categories provided an estimate, we found  
181 that the maximum foraging distance was highly repeatable at the species level ( $R=0.731$ , 95% CI  
182  $= 0.570-0.847$ ,  $P<0.001$ ; confidence interval and significance level were estimated based on  
183 parametric bootstrap and by the randomization of data, respectively). To test for potential biases  
184 that can emerge when estimating species-specific foraging distance through data of different  
185 quality, we built a mixed model that included the underlying method of estimation (i.e. whether  
186 estimates came from direct or indirect observation, survey or speculation) as a fixed factor. With  
187 the whole dataset (Thaxter et al. 2012 and our new review), this model revealed no significant  
188 evidence for data quality biasing estimates of maximum foraging distances ( $\text{Chi}^2=2.060$ ,  $df = 3$ ,  
189  $P = 0.560$ ; statistical significance was determined by likelihood ratio test comparing the models  
190 with and without the categorical predictor). Moreover, repeatability estimates for maximum  
191 foraging distance from the model controlling for the underlying methodology was similar to that  
192 we obtained above from the null model containing no fixed effect term ( $R = 0.720$ , 95% CI =  
193  $0.528-0.836$ ,  $P < 0.001$ ). Finally, we found no bias when comparing multiple estimates within  
194 species across different methods in paired t-tests (e.g. Direct vs. Indirect; all  $P>0.2$ ).  
195 Consequently, following the method used in Thaxter et al. (2012), we selected best quality data  
196 available for each species and we used this value as our estimate of the maximum foraging range  
197 of species.

198

### 199 *Phylogenetic modeling*

200 Interspecific datasets rely on observations that cannot be considered as statistically  
201 independent data points, because the focal units of interest, i.e. species, are hierarchically

202 structured through the underlying common descent. Therefore, when testing for the interspecific  
203 relationship between traits, it is necessary to consider the phylogenetic history of species in the  
204 statistical analyses. To achieve an appropriate control for the phylogenetic relatedness of species,  
205 we used a regression technique based on PGLS (Symonds and Blomberg 2014). For these  
206 phylogenetic regressions, we extracted information on the phylogenetic relationship of seabirds  
207 from the BirdTree database (Jetz et al., 2012, <http://birdtree.org>). We could not obtain an  
208 overwhelmingly supported single phylogenetic tree from this resource, but we could download  
209 several equally likely candidate trees. Hence, to account for phylogenetic uncertainty, we fitted  
210 models to each available tree and subsequently applied multi-model inference to derive the  
211 regression parameters of interest across them (Garamszegi and Mundry 2014, Rubolini et al.  
212 2015). Specifically, we used 1,000 alternative trees for our list of species to calculate  
213 phylogenetic regressions based on identical model definition. To define our models we used  
214 maximum foraging distance as a predictor and the given percentile bin for colony size as a  
215 response. Furthermore, in each model we allowed the phylogenetic signal in the residuals (i.e.  
216 lambda,  $\lambda$ ) being optimized towards its maximum likelihood value. We derived mean and  
217 confidence estimates for the intercept and the slope of the regression at hand over the pool of  
218 phylogenies via model averaging, in which parameter estimates from each model were weighted  
219 based on their relative fit to the data. We repeated this procedure for each percentile bin for  
220 colony size, i.e. we fitted and averaged 1,000 models by sequentially using species-specific  
221 estimates of colony size from different percentile categories. These exercises were undertaken  
222 using the R package ‘caper’ (Orme et al. 2012) for the PGLS modelling, and by following the  
223 example codes on <http://www.mpcm-evolution.org/practice/online-practical-material-chapter-12>  
224 for the model averaging routines. We opted to handle phylogenetic uncertainty based on

225 multimodel inference within the information theoretic framework instead of adopting Bayesian  
226 approaches, because the latter introduces a considerable uncertainty in parameter estimates when  
227 non-informative priors are used (Garamszegi and Mundry 2014).

228

### 229 *Quantile regression*

230 Quantile regression allows a generalization of OLS regressions by using conditional  
231 quantiles,  $Q_y(\tau|X)$ , where  $\tau \in [0, 1]$  denote the quantiles, such as 100 $\tau$ % of the values of the  
232 response variable (e.g. maximum colony size) is less or equal to the estimate at the  $X$  value (e.g.  
233 of foraging ranges). In this way, the fit of the quantile regression at different  $\tau$  values allows  
234 testing of the effect of the predictor variable along different subsets of the response variable for  
235 particular  $X$  values. Here, we used the ‘quantreg’ R package (Koenker 2015) to analyze the effect  
236 of the foraging range of the species and its effect upon the maximum colony sizes of the species  
237 (as this was the colony size statistic with higher correlation with foraging range; Table 1). We  
238 did so by assessing the slope of the regression model for different values of  $\tau$  from 0.05 to 0.95.

239 Unfortunately, ‘quantreg’ has been developed for OLS regressions and thus is unable to  
240 incorporate information on the phylogenetic relatedness of species and handle PGLS models.  
241 Therefore, to deal with the phylogenetic structure of the data, we developed the following  
242 solution. We randomly took 100 phylogenetic trees from the available pool of 1000 trees, and  
243 performed the following analyses on each of them. We first rescaled the phylogeny at hand by  
244 using a  $\lambda$  transformation to a degree that was estimated by the best-fit PGLS model of maximum  
245 colony size (see Fig. 1B; we detected that the phylogenetic signal in the residuals of this model  
246 was  $\lambda=0.759$ ). As a next step, we calculated phylogenetic independent contrasts (Felsenstein  
247 1985) in ‘caper’ for both variables under the rescaled phylogeny. Phylogenetic contrasts are

248 phylogenetically transformed, independent variables that can be supplied to standard regression  
249 methods, and when forced through the origin the OLS regression of these contrasts provide  
250 equivalent slope estimates with the PGLS results (under certain assumptions). Therefore, by  
251 using the independent contrasts (that were thus independent of the phylogeny that were scaled to  
252 the best-fit  $\lambda$ ), we were able to submit an OLS regression through an origin to the quantile  
253 regression analysis that can be considered as a phylogenetically controlled approach. We  
254 detected that ‘quantreg’ does not provide estimates for 95% CI when the OLS regression forced  
255 through the origin, thus we were unable to obtain such confidence range around our phylogenetic  
256 slopes in the quantile regression framework. However, by repeating this series of analyses on  
257 100 phylogenetic trees, we could derive a summary statistics and confidence estimates on them  
258 over the pool of results corresponding to different phylogenetic hypotheses. Therefore, we  
259 calculated the mean and the 95% CI of the 100 slope estimates over trees to present the  
260 phylogenetically controlled results. The 95% CI in this case can be interpreted as the uncertainty  
261 in the parameter estimate that is caused by the uncertainty in the phylogenetic hypothesis.

262

## 263 **Results**

264 The interspecific correlation between foraging range and colony size changed across the  
265 different percentile bins used to describe the within-species frequency distribution of colony  
266 sizes (Figure 1, Table 1). While the minimum or the lower percentiles of the distribution were  
267 moderately correlated, the strength of the correlation monotonically increased towards the higher  
268 percentiles, whereby the median, the 95th percentile, and the maximum colony size of the  
269 species strongly correlated with their foraging range (Figure 1, Table 1). Moreover, the

270 phylogenetic signal in the model residuals ( $\lambda$ ) also changed, being zero for lower percentiles of  
271 colony sizes but increasing up to a maximum of 0.926 for the 95th percentile (Table 1).

272 The slope of the regression increased from values below 0.5 for lower percentile colony  
273 sizes of the species to a slope of 1.096 (CI = 0.529-1.662) for the maximum colony sizes (Figure  
274 1). A further analysis of the relationship between foraging range and the maximum colony size  
275 by using a quantile regression (Figure 2A) showed that the effect of foraging range was not  
276 homogeneous for different portions of the response variable (maximum colony size). Instead, the  
277 slope of the model increased at increasing  $\tau$  values, from values below 1 to values around 2  
278 (Figure 2B). The quantile regression with phylogenetic correction showed an even clearer shift in  
279 the slope along  $\tau$ , with values around 2 for  $\tau > 0.7$ , and reaching slopes of 3 for largest  $\tau$ . This  
280 pattern was highly consistent across different phylogenetic trees considered for the analysis.

281

## 282 **Discussion**

283 The colony size frequency distribution of seabirds was contrastingly shaped by the foraging  
284 range of the species. While the minimum colony sizes of species was little affected by foraging  
285 range, larger percentile bins for colony sizes were strongly correlated with the maximum  
286 foraging distances. The slope of the regression was largest at larger percentiles of the within-  
287 species frequency distribution of colony size with values around 1 for the maximum colony size.  
288 Note, however, that this slope refers to the rates of change in the mean of the distribution of  
289 colony size as a function of foraging distance. Interestingly, a quantile regression of the  
290 relationship between the maximum colony size and their foraging range (investigating other parts  
291 of the distribution in the response variable) showed that the foraging range imposed a ceiling to

292 colony size. In particular, the slope of the regression for species with larger colony sizes relative  
293 to their foraging ranges was close to 2.

294 The slope being close to 2 is interesting because it is the slope expected according to the  
295 equation of the area ( $A$ ) of a circle ( $A=\pi r^2$ ). Taking logarithms at both sides of the equation,  
296  $\log(A)=\log(\pi r^2)$ , then  $\log(A)=2\log(r)+\log(\pi)$ , resulting in a lineal relationship with a slope of 2  
297 between the logarithm of maximum foraging radius (foraging range, hereafter) of species and the  
298 logarithm of foraging area, and thus, of potential maximum colony size. Thus, our results show  
299 that the maximum colony size of seabird species increases lineally with the potential sea area  
300 available for foraging for each species.

301 Interestingly, similar claims have been made previously. For instance, Storer (1952)  
302 stated “Thus, in an area suitable to the existence of murre and guillemots, the limiting factor for  
303 the guillemots, nesting sites, is a linear one; and that for the murre, food supply, is two-  
304 dimensional. Consequently, the size of a population of murre in such an area is roughly the  
305 square of that of the guillemots”. Within species, Gaston et al. (2007) predicted “Because the  
306 potential foraging area ( $A$ ) increases as the square of foraging range ( $A=\pi r^2$ ), foraging range  
307 should be proportional to the square root of the [colony] population size.”. Indeed, this has been  
308 reported in northern gannets (Lewis et al. 2001). Here we report that this also holds at the  
309 interspecific level as a constraint to maximum colony size of species.

310 Many seabirds do not breed in locations with foraging areas equally available all around  
311 the colony, meaning a simple circle may be not the best model for mapping the foraging area of  
312 many species. In fact, Birkhead and Furness (1985) showed for Alaskan seabird colonies that  
313 those on isolated islands were larger than those in the mainland. Also, it could be argued that  
314 conspecific birds breeding in neighbouring colonies do not overlap in their foraging areas

315 (Masello et al. 2010; Wakefield et al. 2013), or that seabirds could share their colonies with other  
316 seabird species with similar diets (Croxall et al. 1980, Ballance et al. 1997), and thus that  
317 foraging radius misleadingly suggests larger foraging areas than those really available. However,  
318 the slope of the relationship between  $A$  and  $r$  holds for any portion of a circle. For instance, the  
319 area of a semicircle (something more acceptable for many seabirds breeding along the  
320 continental coastlines) would be  $\log(A)=1/2\log(\pi r^2)$ , and thus  $\log(A)=2\log(r)+\log(\pi)+\log(1/2)$ ,  
321 i.e.  $\log(A)=2\log(r)+0.197$ , thus only affecting the intercept but not the scaling slope of the  
322 relationship. Hence, from a pure mathematical point of view, any circumstance consistently  
323 shaping the foraging area available for a species given a certain foraging range would introduce  
324 noise to the correlation between foraging range and foraging area available, but the same slope of  
325 2 would hold.

326         The much lower mean slope for lower  $\tau$  values suggests that there are other factors that  
327 constrain colony growth. These could be due to both external factors (e.g. pollution, nest site  
328 availability, disease, predators) and species traits such as preferred diet (with varying calorific  
329 values of different prey items), feeding methods, and digestive capabilities (capacity to digest  
330 food at sea and deliver a nutritive stomach oil to chicks). These factors could depart species from  
331 showing the same/expected response to foraging distance.

332         Our data show that short-distance foraging species never have large colonies, and that the  
333 maximum colony sizes a species could potentially achieve scale as the square root of their  
334 foraging radius around colonies. This also supports Ashmole's (1963) hypothesis because no  
335 species could hold large colonies without a large foraging range.

336 *Evolutionary considerations*

337 Colony size and foraging distance are both dynamic patterns that highly depend on the  
338 prevailing social and environmental conditions in any given location, thus justifying the  
339 ecological approach adopted in this study (while statistically controlling for phylogenetic non-  
340 independence of species). However, these traits could be seen, at least partially, as evolutionary  
341 adaptations of species, thus our correlative findings could also support a causal evolutionary  
342 scenario in which colony size and foraging distance affect each other.

343 Different scenarios could be at play. First, larger foraging ranges could be adaptive per se  
344 (e.g. allowing the exploitation of a larger amount of food resources), or could be a by-product of  
345 other adaptations such as particular wing shapes used for long-distance migration. Large colony  
346 sizes could then be the ecological consequence of having the potential to forage far from  
347 colonies, and thus increasing the carrying capacity of colonies. An alternative scenario could be  
348 that some species favour breeding in larger colonies to reduce the chances of predation. This  
349 would impose a selective pressure to increase foraging distances of individuals, leading to the  
350 evolution of the morphological, behavioural, and physiological traits needed to increase foraging  
351 range and leading to the foraging range-colony size correlation reported here.

352 Finally, a mixed scenario would include a positive evolutionary feedback (Crespi 2004)  
353 between foraging range and colony size where larger colony sizes select for traits favoring larger  
354 foraging ranges (e.g. because food depletion around colonies select for individuals able to find  
355 more distance foraging areas) and larger foraging ranges increase the adaptive value of larger  
356 colony sizes (e.g. reduced risk of predation). Unfortunately, based on the correlative nature of  
357 our data, it is impossible to discriminate between these causal alternatives.

358 Why species differ so much in their group sizes is still little understood. Here, we have  
359 shown that 26% of the variance in maximum colony sizes is explained by foraging range (Table



360 1). Thus, we have shown that key individual behaviours (foraging distance) of species could be a  
361 simple yet powerful mechanistic explanation of why species from different bird families and  
362 with contrasting natural histories differ so widely in their collective patterns (colony sizes) at  
363 broad geographic scales.

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488

489 **Table 1.** Phylogenetic correlation coefficients (r) and their low (r.lb) and high (r.ub) 95%CI, and  
 490 phylogenetic signals ( $\lambda$ ) as estimated from the PGLS models for different percentile bins for  
 491 colony size (see also Figure 1A that presents the regression slopes from the same models).

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Quantile	$\lambda$	r	r.lb	r.ub	P
min	0	0.230	-0.076	0.496	0.139
Q5	0.584	0.401	0.115	0.626	0.008
Q10	0	0.466	0.192	0.672	0.002
Q15	0	0.374	0.083	0.607	0.013
Q20	0	0.362	0.069	0.597	0.017
Q25	0	0.350	0.056	0.589	0.021
Q30	0	0.346	0.051	0.586	0.023
Q35	0	0.353	0.059	0.590	0.020
Q40	0	0.352	0.058	0.590	0.021
Q45	0	0.348	0.053	0.587	0.022
Q50	0	0.356	0.062	0.593	0.019
Q55	0	0.370	0.079	0.604	0.015
Q60	0	0.381	0.091	0.611	0.012
Q65	0	0.409	0.124	0.632	0.006
Q70	0	0.415	0.130	0.636	0.006
Q75	0	0.418	0.135	0.638	0.005
Q80	0	0.431	0.150	0.648	0.004
Q85	0.044	0.432	0.151	0.648	0.004
Q90	0.45	0.429	0.148	0.646	0.004
Q95	0.926	0.402	0.115	0.627	0.008
max	0.759	0.509	0.247	0.702	0.000

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497 **Figure Legends**

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499 **Figure 1.** (A) Slopes (with 95% confidence limits) of the relationship between the  
500  $\log_{10}$ (maximum foraging distance) and the  $\log_{10}$ (Xth percentile) of the colony size frequency  
501 distribution of the species as estimated from the most appropriate PGLS models. (B-D)  
502 Examples of the relationship between the  $\log_{10}$ (maximum foraging distance) and different the  
503  $\log_{10}$ (Xth percentile). Solid lines are estimated regression lines, while dashed lines correspond to  
504 slope = 2.

505

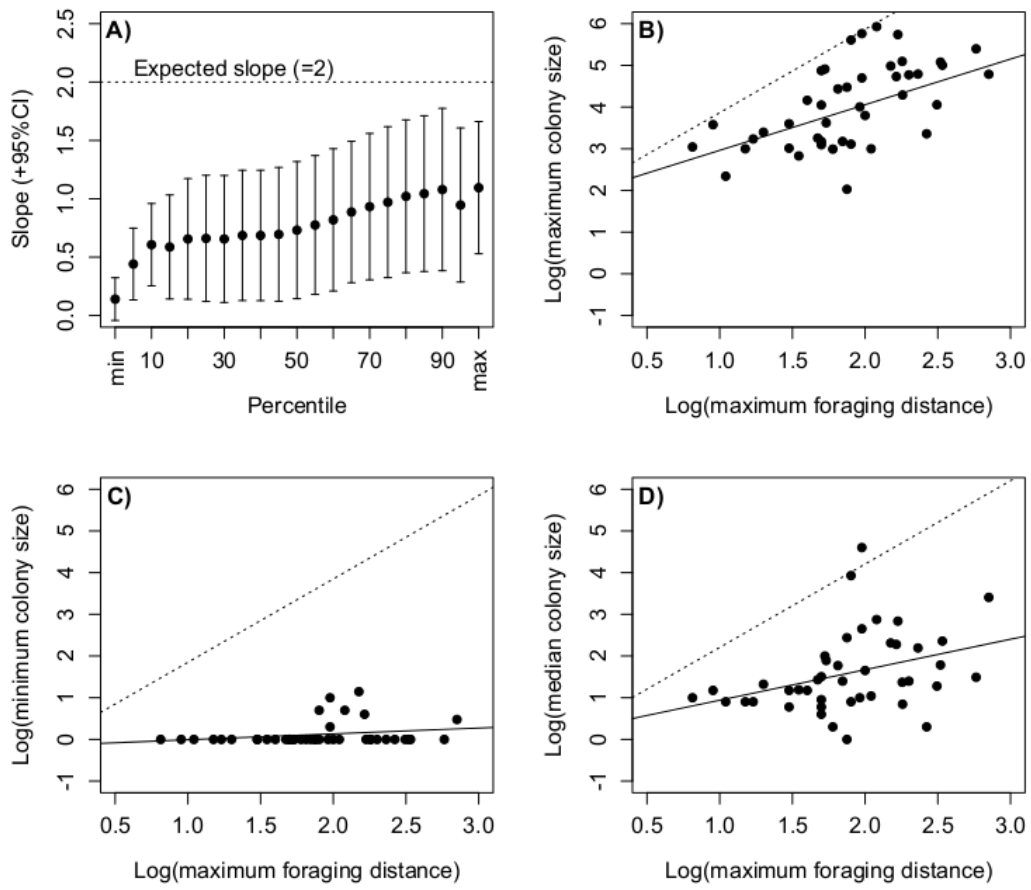
506 **Figure 2.** (A) Slopes of the quantile regression for different  $\tau$ 's without phylogenetic control  
507 based on the species-specific raw data (black dots, grey area for 95% CI) and quantile regression  
508 with phylogenetic control based on phylogenetically independent contrasts (white dots, area  
509 bounded with dashed lines for 95% CI over 100 phylogenetic trees). (B) The relationship  
510 between maximum colony size and maximum foraging distance (see Figure 1B) when  
511 investigated with quantile regressions for  $\tau$  from 0.05 to 0.95 (without phylogenetically  
512 independent contrasts).

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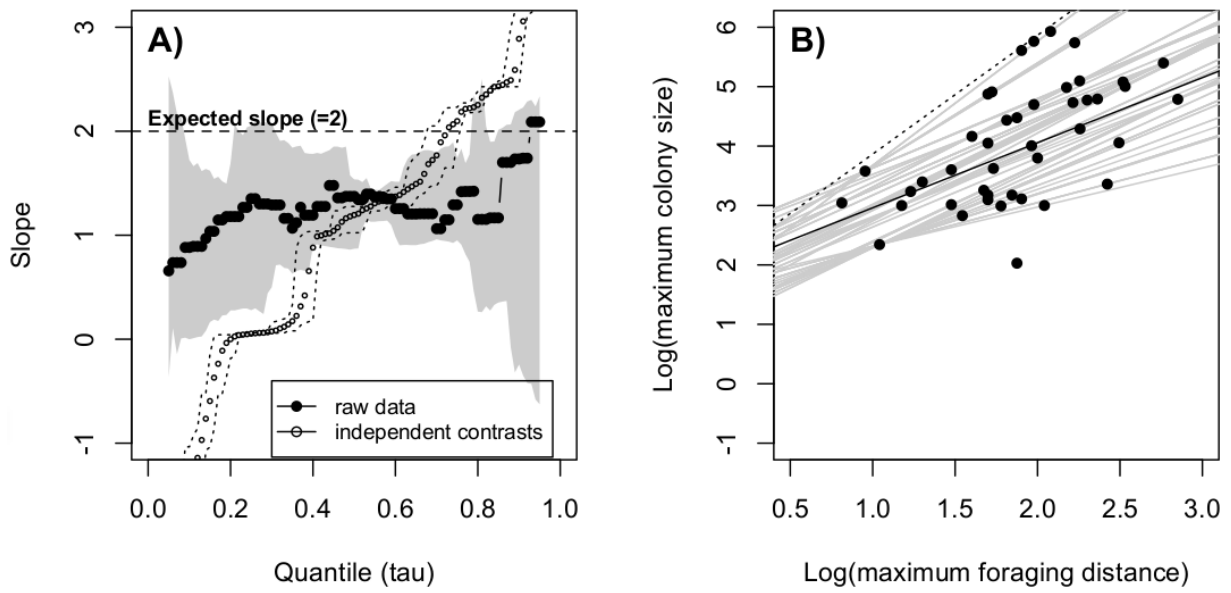


514 Figure 1

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516 Figure 2



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## Appendix 1. Summary table for foraging distance and colony size statistics for each species.

F.R.= foraging range (the maximum foraging distance, in Km, of breeding birds from the colony). N\_col = number of colonies. N\_nests = number of nests. Min. and Max. = minimum and maximum colony sizes. Percentiles of the colony size frequency distribution from percentiles 5<sup>th</sup> to 95<sup>th</sup> are also shown.

Species	F.R.	N_col	N_nests	min.	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	max.
<i>Aethia cristatella</i>	80	39	1,449,004	5	12	55	129	1,150	1,563	1,800	2,500	2,550	5,018	8,500	10,950	14,900	15,000	22,332	48,193	61,110	82,886	104,610	154,300	407,195
<i>Aethia psittacula</i>	50	172	203,566	1	2	4	5	8	13	15	20	24	25	32	40	50	64	84	150	252	525	1,000	5,000	75,000
<i>Aethia pusilla</i>	95	33	2,764,382	10	20	50	533	1,899	6,875	8,063	11,025	13,373	20,227	40,000	41,625	50,902	69,150	116,400	147,496	150,000	180,785	208,215	293,137	580,000
<i>Aethia pygmaea</i>	50	31	3,357	1	1	1	1	2	2	2	2	3	3	4	5	5	8	10	11	25	93	160	1,200	1,500
<i>Alca torda</i>	312 <sup>b</sup>	1,143	169,674	1	1	2	3	4	5	7	9	12	15	19	25	34	46	60	81	121	174	295	596	11,384
<i>Alle alle</i>	110	12	1,123	1	1	1	1	1	2	2	4	6	9	11	13	13	15	18	22	26	32	325	904	1,000
<i>Catharacta skua</i>	265 <sup>c</sup>	726	9,635	1	1	1	1	1	1	1	1	1	1	2	2	3	4	5	7	10	15	30	2,293	
<i>Cepphus columba</i>	50	753	24,110	1	1	2	3	3	4	5	5	6	8	9	10	13	18	23	28	40	50	85	138	1,250
<i>Cepphus grylle</i>	7	2,282	54,101	1	1	1	2	3	3	4	5	6	8	10	11	14	16	20	24	30	39	50	85	1,107
<i>Cerorhinca monocerata</i>	164	16	85,048	4	7	15	15	15	18	22	25	25	64	190	330	420	580	705	875	1,450	4,780	23,019	45,390	54,000
<i>Fraterecula arctica</i>	200 <sup>a</sup>	557	620,285	1	1	2	3	4	6	8	11	17	20	25	33	44	73	99	131	215	444	739	3,068	59,471
<i>Fraterecula cirrhata</i>	53	647	1,157,691	1	3	5	10	14	17	25	30	50	62	100	127	150	240	400	568	1,000	1,945	3,246	7,659	81,658
<i>Fraterecula corniculata</i>	180	568	469,925	1	1	2	3	4	5	7	10	15	18	24	30	40	50	80	100	160	252	576	2,000	125,000
<i>Fulmarus glacialis</i>	580 <sup>a</sup>	3,041	1,345,829	1	2	3	4	6	8	11	14	19	24	31	40	52	69	93	125	173	248	389	823	250,000
<i>Hydrobates pelagicus</i>	65 <sup>a</sup>	98	82,818	1	2	2	5	7	12	17	23	36	52	59	79	100	111	160	288	487	866	1,742	4,866	27,297
<i>Larus argentatus</i>	92 <sup>a</sup>	3,030	191,411	1	1	1	1	2	3	4	5	6	8	10	14	17	22	29	37	51	74	114	225	10,129
<i>Larus canus</i>	50 <sup>a</sup>	1,620	56,890	1	1	1	1	2	2	3	3	4	5	6	7	9	11	14	18	22	30	43	84	11,219
<i>Larus fuscus</i>	181 <sup>a</sup>	1,165	124,925	1	1	1	1	1	2	2	3	4	5	7	9	13	17	24	33	44	64	108	210	19,487
<i>Larus glaucescens</i>	100	757	128,242	1	3	5	9	12	15	20	25	30	35	45	56	70	88	107	150	184	250	400	726	6,300
<i>Larus hyperboreus</i>	15	733	20,003	1	1	1	1	1	2	3	3	5	6	8	10	10	14	20	25	28	40	50	100	1,000
<i>Larus marinus</i>	60	2,224	20,597	1	1	1	1	1	1	1	1	1	2	2	3	4	5	6	9	13	20	37	983	
<i>Larus ridibundus</i>	40 <sup>a</sup>	681	141,888	1	1	1	2	3	4	6	7	10	12	15	21	29	37	50	70	100	175	300	800	14,575
<i>Morus bassanus</i>	709 <sup>d</sup>	25	336,628	3	91	147	317	844	1,114	1,244	1,722	1,905	2,358	2,552	3,872	6,577	10,032	16,386	24,796	29,744	34,541	44,110	55,561	61,340
<i>Oceanodroma leucorhoa</i>	120 <sup>a</sup>	80	1,824,388	5	19	50	100	131	175	250	380	500	584	750	1,000	1,191	1,750	2,391	3,678	5,375	10,000	31,352	75,866	850,000
<i>Phalacrocorax aristotelis</i>	17 <sup>a</sup>	1,392	32,222	1	1	1	2	2	3	4	5	6	7	8	10	12	14	17	21	26	34	48	84	1,720
<i>Phalacrocorax auritus</i>	47	168	27,006	1	1	3	4	6	8	10	12	16	22	27	36	55	75	112	147	250	347	509	750	1,806
<i>Phalacrocorax carbo</i>	35 <sup>a</sup>	432	17,356	1	1	1	2	3	5	7	9	10	12	16	20	24	29	36	43	52	66	96	160	675
<i>Phalacrocorax pelagicus</i>	9	381	22,219	1	1	2	3	4	5	7	8	10	13	15	18	21	25	34	42	50	64	101	226	3,790
<i>Phalacrocorax urile</i>	20	193	24,440	1	1	2	4	5	8	10	12	15	18	21	30	31	42	51	77	107	174	321	692	2,500
<i>Ptychoramphus aleuticus</i>	95	36	236,472	2	22	25	30	50	63	115	200	200	250	450	500	1,000	1,450	1,750	3,100	6,500	12,503	22,700	50,000	50,000
<i>Puffinus puffinus</i>	330 <sup>e</sup>	53	332,272	1	2	5	5	7	10	19	25	33	40	61	141	230	628	1,006	1,815	2,987	3,521	7,002	41,697	120,000
<i>Rissa brevirostris</i>	150	7	104,426	14	14	40	86	131	150	159	168	180	193	206	340	473	876	2,889	4,902	15,403	47,121	78,840	96,965	96,965
<i>Rissa tridactyla</i>	231 <sup>f</sup>	1,262	1,264,848	1	5	12	20	30	45	55	75	100	124	156	200	250	345	430	600	854	1,214	2,190	4,907	61,960
<i>Somateria mollissima</i>	80 <sup>a</sup>	332	13,700	1	1	1	1	2	3	3	4	5	6	8	10	13	15	19	24	31	51	77	166	1,293
<i>Stercorarius parasiticus</i>	75 <sup>a</sup>	667	2,327	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	3	3	4	6	12	107
<i>Sterna albifrons</i>	11 <sup>a</sup>	119	2,093	1	1	1	2	2	2	3	4	4	5	8	10	12	13	15	19	20	29	47	85	220
<i>Sterna aleutica</i>	70	57	6,457	1	2	3	4	6	10	12	13	19	20	25	25	30	36	40	56	91	148	235	808	1,500
<i>Sterna hirundo</i>	30 <sup>a</sup>	424	13,859	1	1	1	1	1	2	2	3	4	5	6	8	11	14	17	22	31	42	68	122	1,033
<i>Sterna paradisaea</i>	30 <sup>a</sup>	1,277	73,899	1	1	2	2	3	4	6	8	10	12	15	18	23	28	34	44	54	75	100	200	4,000
<i>Sterna sandvicensis</i>	54 <sup>a</sup>	38	13,977	1	1	2	5	7	12	17	27	52	72	78	89	140	274	316	340	440	517	929	1,844	4,200
<i>Synthliboramphus antiquus</i>	75	57	109,386	1	2	9	50	63	100	100	150	200	250	275	350	500	500	850	1,250	1,500	1,500	4,500	11,500	30,000
<i>Uria aalge</i>	340 <sup>g</sup>	834	1,904,969	1	4	9	17	26	41	60	87	111	154	229	306	409	626	877	1,269	1,778	3,024	5,021	10,284	100,957
<i>Uria lomvia</i>	168	100	1,114,632	1	6	16	27	66	91	157	195	326	525	688	884	1,240	1,693	2,078	3,068	4,959	8,078	15,742	32,817	549,300

<sup>a</sup>Foraging range as in Thaxter et al. (2012)

<sup>b</sup>Species with data on foraging range in Thaxter et al. (2012), but updated with “Direct” quality data from <http://atlanticarea.ccdr-n.pt/news/docs/fame-article>

<sup>c</sup>Species with data on foraging range in Thaxter et al. (2012), but updated with “Direct” quality data from Thaxter et al. (2013).

<sup>d</sup>Species with data on foraging range in Thaxter et al. (2012), but updated with “Direct” quality data from Wakefield et al. (2013)

<sup>e</sup>Species with two potential foraging ranges in Thaxter et al. (2012). Here we selected the 330Km foraging range instead of the 32Km foraging range because, as explained in Thaxter et al. (2012), the 32Km estimate was for maintenance rafting behaviour around colonies, and the 330Km estimate was obtained by tracking individuals with GPS while on foraging trips from the colony.

<sup>f</sup>Species with data on foraging range in Thaxter et al. (2012), but updated with “Direct” quality data from <http://atlanticarea.ccdr-n.pt/news/docs/fame-article>

<sup>g</sup>Species with data on foraging range in Thaxter et al. (2012), but updated with “Direct” quality data from <http://atlanticarea.ccdr-n.pt/news/docs/fame-article>

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**Appendix 2. Review on the foraging ranges of species not reviewed in Thaxter et al. (2012)**

Scientific name	Max foraging distance (Km)	Data quality	Area	Ref.
<i>Aethia cristatella</i>	80	Survey	St. Lawrence Island, Alaska	57
<i>Aethia cristatella</i>	75	Survey	Shelikhov Gulf, Yamskiye Islands, Russia	64
<i>Aethia psittacula</i>	50	Survey	Kuril Islands, Russia	6
<i>Aethia pusilla</i>	65	Survey	St. Lawrence Island, Alaska, US	32
<i>Aethia pusilla</i>	75	Survey	King Island, Alaska, US	32
<i>Aethia pusilla</i>	10	Survey	St. George Island, Alaska, US	33
<i>Aethia pusilla</i>	56	Survey	St. Lawrence Island, Alaska, US	51
<i>Aethia pusilla</i>	5	Survey	St. Matthew Island, Alaska, US	51
<i>Aethia pusilla</i>	95	Survey	St. Lawrence Island, Alaska, US	57
<i>Aethia pygmaea</i>	50	Survey	Kuril Islands, Russia	6
<i>Aethia pygmaea</i>	43	Survey	Commander Islands, Russia	7
<i>Aethia pygmaea</i>	16	Survey	Alaska, US	12
<i>Aethia pygmaea</i>	10	Survey	Alaska, US	17
<i>Alle alle</i>	150	Survey	Spitsbergen, Norway	13
<i>Alle alle</i>	32	Survey	Horse Head Island, Greenland	20
<i>Alle alle</i>	76	Indirect	East Greenland, Greenland	27
<i>Alle alle</i>	110	Direct	Spitsbergen, Norway	35
<i>Alle alle</i>	100	Survey	Spitsbergen, Norway	39
<i>Cepphus columba</i>	2	Survey	Santa Barbara Island, California, US	10
<i>Cepphus columba</i>	5	Survey	California, US	10
<i>Cepphus columba</i>	6	Speculative	Mandarte Island, British Columbia, Canada	18
<i>Cepphus columba</i>	7	Survey	General	21
<i>Cepphus columba</i>	4	Speculative	Prince William Sound, Alaska, US	31
<i>Cepphus columba</i>	2	Survey	Santa Barbara Island, California, US	42
<i>Cepphus columba</i>	50	Indirect	Commander Islands, Russia	44
<i>Cepphus grylle</i>	4	Survey	Papa Westray, Scotland, UK	9
<i>Cepphus grylle</i>	7	Survey	Rockabill, Ireland	9
<i>Cepphus grylle</i>	15	Survey	Eastern Canadian Arctic, Canada	9

<i>Cepphus grylle</i>	13	Survey	Hudson Bay, Canada	11
<i>Cepphus grylle</i>	5	Survey	Hudson Bay, Canada	14
<i>Cepphus grylle</i>	10	Speculative	UK	24
<i>Cepphus grylle</i>	5	Survey	Caithness, Scotland, UK	46
<i>Cepphus grylle</i>	7	Survey	Atlantic (Northwest)	49
<i>Cepphus grylle</i>	55	Survey	North West Territories, Canada	50
<i>Cepphus grylle</i>	1	Direct	Bay of Fundy, Canada	56
<i>Cepphus grylle</i>	6.5	Direct	Papa Westray, UK	60
<i>Cerorhinca monocerata</i>	164	Indirect	Teuri Island, Japan	36
<i>Cerorhinca monocerata</i>	50	Survey	Strait of Juan de Fuca, Washington, US	67
<i>Fratercula cirrhata</i>	30	Survey	Kuril Islands, Antsiferova Island, Russia	6
<i>Fratercula cirrhata</i>	20	Survey	Kuril Islands, Ekarma Island, Russia	6
<i>Fratercula cirrhata</i>	50	Survey	Commander Islands, Russia	7
<i>Fratercula cirrhata</i>	50	Speculative	Tauyskaya Bay, Russia	26
<i>Fratercula cirrhata</i>	52.9	Direct	Middleton Island, Gulf of Alaska, US	40
<i>Fratercula cirrhata</i>	100	Speculative	General	54
<i>Fratercula corniculata</i>	150	Survey	General	26
<i>Fratercula corniculata</i>	110	Survey	Chisik Island, Lower Cook Inlet, Alaska, US	52
<i>Fratercula corniculata</i>	50	Survey	Bering Shelf and Alaska Coast	53
<i>Fratercula corniculata</i>	120	Survey	Cape Thompson, Chukchi Sea, Alaska, US	55
<i>Fratercula corniculata</i>	180	Survey	Sea of Okhotsk, Russia	65
<i>Fratercula corniculata</i>	60	Survey	Buldir Island, Canada	68
<i>Larus glaucescens</i>	25	Survey	Commander Islands, Russia	7
<i>Larus glaucescens</i>	100	Survey	British Columbia, Canada	45
<i>Larus hyperboreus</i>	15	Speculative	Karrak Lake, Canada	59
<i>Larus marinus</i>	10	Speculative	UK	24
<i>Larus marinus</i>	60	Survey	Belgium	63
<i>Phalacrocorax auritus</i>	70	Speculative	Farallon Islands, US	3
<i>Phalacrocorax auritus</i>	47.2	Direct	East Sand Island, Columbia River Estuary, US	5
<i>Phalacrocorax auritus</i>	14.2	Direct	Oneida Lake, New York, US	15
<i>Phalacrocorax auritus</i>	40	Direct	Cat Island, Green Bay, US	16
<i>Phalacrocorax auritus</i>	30	Speculative	Massachusetts, US	29
<i>Phalacrocorax auritus</i>	6.7	Direct	Beaver Archipelago, Lake Michigan, US	62

<i>Phalacrocorax pelagicus</i>	15	Speculative	Farallon Islands, US	4
<i>Phalacrocorax pelagicus</i>	9	Direct	Middleton Island, Gulf of Alaska, US	41
<i>Phalacrocorax urile</i>	20	Survey	Pribilof Islands, Alaska	61
<i>Ptychoramphus aleuticus</i>	95	Direct	Channel Islands, California, US	1
<i>Ptychoramphus aleuticus</i>	137	Survey	Farallon Islands, US	2
<i>Ptychoramphus aleuticus</i>	90	Direct	Triangle Island, British Columbia	58
<i>Rissa brevirostris</i>	110	Survey	Pribilof Islands, Alaska	30
<i>Rissa brevirostris</i>	150	Survey	Pribilof Islands, Alaska	34
<i>Sterna aleutica</i>	11	Survey	Seward Peninsula, Alaska, US	37
<i>Sterna aleutica</i>	50	Survey	Alaska, US	38
<i>Sterna aleutica</i>	30	Indirect	Sakhalin Island, Russia	47
<i>Sterna aleutica</i>	70	Indirect	Russia	48
<i>Synthliboramphus antiquus</i>	60	Survey	Raikoke islands, Russia	6
<i>Synthliboramphus antiquus</i>	75	Survey	Matua Island, Russia	6
<i>Uria lomvia</i>	168	Direct	Latrabjarg, Iceland	8
<i>Uria lomvia</i>	95	Indirect	Coats Island, Nunavut, Canada	19
<i>Uria lomvia</i>	119.9	Indirect	Hakluyt Island, Greenland	22
<i>Uria lomvia</i>	62.3	Indirect	Hakluyt Island, Greenland	22
<i>Uria lomvia</i>	137.8	Indirect	Coburg Island, Canada	22
<i>Uria lomvia</i>	47	Direct	Hakluyt Island, Greenland	23
<i>Uria lomvia</i>	150	Direct	Digges Island, Nunavut, Canada	25
<i>Uria lomvia</i>	120	Direct	St. George, Bering Sea, Alaska, US	28
<i>Uria lomvia</i>	60	Direct	St. Paul, Bering Sea, Alaska, US	28
<i>Uria lomvia</i>	50	Direct	Bogoslof, Bering Sea, Alaska	28
<i>Uria lomvia</i>	126	Survey	Svalbard, Norway	43
<i>Uria lomvia</i>	110	Survey	Shelikhov Gulf, Russia	64
<i>Uria lomvia</i>	150	Indirect	Wrangel Island, Russia	66

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