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Article:

Davies, RD, Wanless, S, Lewis, S et al. (1 more author) (2013) Density-dependent foraging and colony growth in a pelagic seabird species under varying environmental conditions. *Marine Ecology Progress Series*, 485. 287 - 294. ISSN 0171-8630

<https://doi.org/10.3354/meps10348>

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1 **Density-dependent foraging and colony growth under varying**
2 **environmental conditions in a pelagic seabird**

3

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24 **ABSTRACT**

25 Intra-specific competition for food resources affects both foraging behaviour and population
26 growth rates in many species, highlighting a need to understand better how changing
27 environmental conditions affect individuals in populations of different sizes. Using chick-
28 rearing northern gannets as a model, we examined the influence of colony size on per capita
29 population growth rates over two time-periods (1994-2000 and 2000-2009) and on foraging
30 trip durations in each of two years (2000 and 2009) at 10 colonies in two separate regions of
31 the UK and Ireland (the North Sea and the Celtic/Irish Sea). The slope of the relationship
32 between population size and foraging trip duration in 2009 was less than one quarter of that
33 in 2000, suggesting a much weaker influence of population size in 2009, presumably due to
34 less intense intra-specific competition for prey resources at sea. There was also regional
35 variation, with colonies in the Celtic/Irish Sea growing substantially slower for their size over
36 the period between 2000 and 2009 than did colonies bordering the North Sea, whilst observed
37 trip durations in 2009 were on average 13% shorter than predicted from population size at
38 colonies bordering the North Sea but 32% longer than predicted at colonies in the Celtic and
39 Irish Seas. These data suggest less favourable conditions for gannets in the latter region in
40 recent years, and that annual variation in trip durations will be particularly marked at large
41 colonies, making them especially vulnerable to adverse effects of low prey availability at sea.

42

43 **Key-words:**

44 Competition; Climate change; Northern gannets; *Morus bassanus*; North Sea; Populations

45

46

47 INTRODUCTION

48 There is growing concern over impacts of climate change on animal populations (Pearce-
49 Higgins et al. 2010, Rolland et al. 2010, Davey et al. 2011). Recent studies have highlighted
50 that in many cases, climate-related changes are also affected by population density (Rotella et
51 al. 2009, Votier et al. 2009, Smallegange et al. 2011), but the mechanisms underlying such
52 density-dependence are often unclear (Ahola et al. 2009, Laws & Belovsky 2010, Linares et
53 al. 2010). In marine environments, the pace and direction of changes in climate over the past
54 five decades have shown marked geographical variation (Burrows et al. 2011) but net
55 warming has had a net negative impact on primary production (Behrenfeld et al. 2006, Boyce
56 et al. 2010). There is also growing evidence that such decreases in production have been
57 propagated to other trophic levels (Beaugrand et al. 2002, Behrenfeld et al. 2006), extending
58 in some cases to higher marine predators such as seabirds (Wanless et al. 2007, Dorresteijn et
59 al. 2012, Satterthwaite et al. 2012). Intense fishing pressure can also have cascading effects
60 on marine food webs (Baum & Worm 2009) and the greatest threat to fish stocks is likely to
61 be the combined effects of climate change and overfishing (Brander 2007). Recent studies
62 have suggested that these combined effects can also have important consequences for seabird
63 breeding success, survival and population stability (Frederiksen et al. 2004, Ainley & Blight
64 2009).

65

66 Many seabird species breed in dense colonies, making them potentially powerful models to
67 examine density-dependent responses to changes in prey availability (Kitaysky et al. 2000,
68 Ashbrook et al. 2010). In particular, foraging trip durations of many species are longer under
69 poorer conditions (Hamer et al. 1993, Lewis et al. 2006, Riou et al. 2011) and also increase as
70 a function of colony size, providing strong evidence of intra-specific competition for prey
71 resources at sea (Lewis et al. 2001, Forero et al. 2002, Ainley et al. 2003). Changes in

72 foraging conditions may thus be expected to have greater impacts on trip durations in larger
73 populations (Hamer et al. 2006), but there are few data to test this prediction.

74

75 Within the British Isles, northern gannets *Morus bassanus* (hereafter gannets) breed at
76 colonies differing in size from tens to tens of thousands of pairs (Wanless et al. 2005). They
77 are generalist predators, able to exploit a wide variety of species and sizes of prey, including
78 lipid-rich fish such as mackerel (*Scomber scomber*) and sandeels (mainly *Ammodytes*
79 *marinus*) in addition to discards from fishing vessels (Hamer et al. 2000, Lewis et al. 2003).
80 Most British colonies are increasing in size, with smaller colonies having higher per capita
81 growth rates (Wanless et al. 2005). In addition, direct observations of nest attendance have
82 revealed a positive relationship between colony size and the mean foraging trip durations of
83 breeding birds, both among colonies of different sizes in the same year and, from the limited
84 longitudinal data available, within individual colonies as they grow (Lewis et al. 2001).
85 However, trip durations and foraging ranges at one of the largest gannet colonies in the UK
86 were found to be much longer in years when sandeel stocks around the colony were low
87 (Hamer et al. 2007a), suggesting that impacts of changes in prey availability may outweigh
88 those of changes in population size. Yet it is not known whether birds at colonies of different
89 sizes were similarly affected. Lewis et al. (2006) found that chronically poor conditions
90 resulted in greater foraging effort by Cape gannets *Morus capensis* even at small colonies,
91 highlighting a need to understand better how changing environmental conditions affect birds
92 in populations of varying size.

93

94 Here we resampled the same colonies as those studied in 2000 by Lewis et al. (2001), after a
95 further nine years of population growth. Lewis et al. (2001) found no evidence of any spatial
96 variation in the effects of population size, but since then, several studies have identified

97 strong regional structure in breeding productivity and population trends of seabirds within
98 Britain and Ireland (Frederiksen et al. 2007, Cook et al. 2011). In particular, for gannets, the
99 Celtic and Irish Sea region was considered ecologically distinct from the North Sea region,
100 including Fair Isle and Shetland, on the basis of consistent variation in abundance at breeding
101 colonies (Fig 3 in Cook et al. 2011). In the North Sea region, several species of seabird have
102 experienced declining breeding success since the mid 1980s (Burthe et al. 2012), but
103 breeding productivity in 2009 was higher than it had been for a number of years including
104 2000, possibly due to increased availability of sandeels in 2009 (JNCC 2011). Stocks of
105 mackerel in the southern, western and northern North Sea were also 30% higher in 2009 than
106 in 2000 (4.0×10^3 tonnes and 3.1×10^3 tonnes, respectively; data from ICES 2010). Hence
107 we predicted less intense competition, i.e. a smaller influence of population size on foraging
108 trip durations, at North Sea colonies in 2009 compared to 2000.

109

110 In contrast to the North Sea, there was little evidence for any increases in prey availability or
111 quality within the Celtic or Irish Seas in 2009 and some evidence of recent declines in prey
112 biomass in this region (JNCC 2011, Riou et al. 2011). As a result of this difference between
113 the two regions in 2009, we predicted less difference between years in the relationship
114 between population size and trip duration at colonies in the Celtic and Irish Seas than in the
115 North Sea, resulting in significant interactions between the effects of population size, year
116 and region on trip duration. We also examined the per capita growth rates of our study
117 colonies over the periods 1994-2000 and 2000-2009. We assessed whether the relationship
118 between population size and growth rate was similar in each time-period or whether it was
119 affected by changing environmental conditions, resulting in significant two-way or three-way
120 interactions between the effects of population size, time-period and region on per capita
121 growth rate.

122

123 **METHODS**

124 Fieldwork took place from June to August 2000 and 2009 at nine gannet colonies around the
125 coast of Britain and Ireland. A tenth colony (Lambay, established in 2007) was also sampled
126 in 2009 (Fig 1). Counts of Apparently Occupied Sites (AOS), made from aerial photographs
127 combined with visits to colonies, both with a maximum sampling error of around 5-10%
128 (Wanless et al. 2005), were obtained from the literature (Murray & Wanless 1997, Wanless et
129 al. 2005, Murray 2011), together with more recent unpublished data for some colonies (see
130 acknowledgements). Five of the nine colonies sampled in 2000 were counted that year.
131 Population sizes for the other four colonies (two counted in 1999, one in 1998 and one in
132 1995) were adjusted using colony-specific per capita growth rates recorded between 1994 and
133 2004 (Murray & Wanless 1997, Lewis et al. 2001, Wanless et al. 2005) to estimate the
134 additional increase in population size since the most recent count (in practice these
135 increments were < 3% of population size). Six of the 10 colonies sampled in 2009 were
136 counted that year. The other four were last counted in 2004 (n=2) or 2008 (n=2) and
137 population sizes for these colonies in 2009 were estimated by assuming that per capita growth
138 rates recorded between 1994 and 2004 or 2008 were maintained until 2009. The remaining
139 colony (Ailsa Craig) decreased slightly in size between 1994 and 2004 (Wanless et al. 2005)
140 but has shown no further decreases since then (B. Zonfrillo pers comm.) and so we assumed
141 the same size in 2009 as in 2004.

142

143 To determine foraging trip durations, around 20 chick-rearing pairs at each colony (2000, 18-
144 24 pairs; 2009, 19-30 pairs) were observed during daylight hours (sunrise to sunset) for an
145 average of 41 hours each (2000, 16-60hrs; 2009, 16-64hrs). Following Hamer et al. (1993)
146 and Lewis et al. (2001), the arrival and departure times of foraging adults were recorded to

147 the nearest minute and used to calculate a daily changeover rate at each colony (number of
148 changeovers observed divided by the nest-days of observation). The mean trip duration at
149 each colony was then calculated by dividing the time available per day for undertaking
150 foraging trips (24 hours minus the mean time adults spent together at the nest) by the
151 estimated changeover rate. To account for possible changes in trip durations as chicks grew,
152 chicks were aged using a combination of observed hatch dates and plumage characteristics
153 (Nelson 2002). The median age of all chicks observed was 7 weeks in 2000 and 5 weeks
154 2009.

155
156 All statistical analyses were carried out using R version 2.12.1 (R-Development-Core-Team
157 2010). We used a linear mixed effects model (LME) (Pinheiro & Bates 2000) using the
158 package ‘nlme’ to examine whether the relationship between natural log (Log_e) population
159 size (log-transformed to normalize the data and because population growth is a multiplicative
160 rather than additive effect) and per capita growth rate differed over the periods 1994-2000
161 and 2000-2009. This model included region (North Sea or Celtic/Irish Sea, as defined by
162 Cook et al. 2011) as a fixed effect and colony identity as a random effect to account for
163 repeated measures (see Fig 1 for locations of colonies; the model had the form: per capita
164 growth rate \sim initial log_e colony size + (initial log_e colony size * time period) + (initial log_e
165 colony size * time period * region) + random $\text{=(}\sim 1 | \text{colony)}$, with a Gaussian error
166 distribution). We then used an additional LME to examine how the relationship between
167 square root colony size and foraging trip duration differed between years. This model also
168 included two potential confounding effects (median chick age and total number of nest-hours
169 of observation at each colony) and had the form: trip duration (hours) = square-root colony
170 size + (square-root colony size * year) + (square-root colony size * region) + chick age +
171 nest-hours + random $\text{=(}1 | \text{colony)}$, with a Gaussian error distribution. Colony size was

172 square-root transformed for this second analysis, following Lewis et al. (2001), because the
173 area covered by birds at sea increases with the square of the mean foraging radius. To check
174 the robustness of our analyses, we compared each full model with the minimum adequate
175 model (Crawley 2007) following serial deletion of non-significant terms (Mundry & Nunn
176 2009). To check that our analysis was not affected by errors in estimating population sizes,
177 we also re-ran each model using extreme population sizes, assuming no further growth of any
178 colonies since the most recent counts. This had no qualitative effect on our results in either
179 case, and so we are confident that any errors in estimating population sizes did not affect our
180 conclusions.

181 In contrast to foraging trip durations, mean travel speeds at sea show remarkable
182 consistency between different colonies and years (Grémillet et al. 2006, Hamer et al. 2007,
183 Votier et al. 2010). Hence, in addition to trip durations, we also estimated foraging ranges
184 each year, using telemetry data to calibrate foraging range against trip duration, following
185 Hamer et al. (2001).

186

187 **RESULTS**

188 **Population sizes and per capita growth rates**

189 Study colonies differed in size from 188 AOS (Ireland's Eye) to 45,569 AOS (Bass Rock) in
190 2000 and from 158 AOS (Lambay) to 52,292 AOS (Bass Rock) in 2009. With the exception
191 of Ailsa Craig (see Methods), all colonies increased in size between 2000 and 2009 (Fig 1).

192 Per capita population growth rates between 1994 and 2000 and between 2000 and 2009 were
193 significantly negatively related to population size in 1994 and 2000, respectively (LME; $F_{1,7}$
194 = 27.3, $P = 0.001$) with no difference in this relationship over the two time-periods (two-way
195 interaction; $F_{1,7} = 1.0$, $P > 0.05$; 1994-2000: $b = -1.953$, 2000-2009: $b = -3.675$; Fig 2).

196 However, colonies in the Celtic/Irish Sea region (I, G and A) grew substantially and

197 significantly more slowly for their size over the period between 2000 and 2009 than did
198 colonies bordering the North Sea (three-way interaction; $F_{2,6} = 9.2$, $P < 0.05$; Fig 2).

199

200 **Foraging trip durations**

201 There was a significant positive relationship between current population size (square root
202 transformed AOS) and mean trip duration (TD) during chick rearing in both 2000 and 2009
203 (LME; $F_{1,5} = 28.97$, $P = 0.01$) but with a much steeper slope, indicating a much stronger
204 influence of population size, in 2000 (TD (hours) = $[0.069 * \text{Sqrt colony size(AOS)}] + 6.39$)
205 than in 2009 (TD (hours) = $[0.011 * \text{Sqrt colony size(AOS)}] + 8.08$); two-way interaction
206 between square-root colony size and year; $F_{1,5} = 8.73$, $P < 0.05$; Fig 3). Population size also
207 explained much more of the variation in trip duration among colonies in 2000 ($R^2 = 0.76$)
208 than in 2009 ($R^2 = 0.43$). Despite the increases in population sizes over the study period, birds
209 at all but the two smallest colonies studied in 2000 (Ireland's Eye and Troup Head) made
210 shorter trips in 2009 than in 2000 (Fig 3), suggesting that in most cases, changes in
211 environmental conditions had a stronger effect on trip durations than did the increases in
212 colony size.

213

214 There was also a significant effect of region in the model ($F_{1,8} = 7.36$, $P < 0.05$), with
215 observed trip durations in 2009 on average 32% longer than predicted from colony size (i.e.
216 above the fitted regression line for 2009) at colonies in the Celtic and Irish Seas, but 13%
217 shorter than predicted (i.e. below the regression line) at colonies bordering the North Sea (Fig
218 3). This difference between regions was confirmed by running separate linear models for
219 each year; there was a significant two-way interaction between square-root colony size and
220 region in 2009 ($F_{2,7} = 7.56$, $P < 0.05$) but not in 2000 ($F_{2,6} = 2.82$, $P = 0.1$). There was a small

221 but significant additional effect of chick age ($F = 13.83$, $P = 0.03$) but no effect of the number
222 of nest-hours of observation (ns).

223 To assess further the difference between years and regions in the influence of colony size, we
224 used the relationship between colony size and trip durations found in 2000 to predict trip
225 durations from colony sizes in 2009. Observed trip durations in 2009 were shorter than
226 predicted at all six colonies bordering the North Sea but longer than predicted at three of the
227 four study colonies in the Celtic and Irish Sea, the exception being the colony on Ailsa Craig
228 (Fig 4).

229

230 **DISCUSSION**

231 The slope of the relationship between population size and foraging trip duration in 2009 was
232 less than one quarter of that in 2000 (Fig 3), suggesting a much weaker influence of
233 population size in 2009, presumably due to less intense intra-specific competition for prey
234 resources at sea. Gannets compete mainly through passive interference due to prey
235 disturbance rather than by depleting prey (Lewis et al. 2001, Camphuysen 2011), but lower
236 prey abundance can nonetheless lead to greater competition through fewer, smaller and/or
237 shorter-lasting occurrences of prey close to the surface within the vertical foraging ranges of
238 birds (Lewis et al. 2002). Gannets may also compete directly for discards from fishing
239 vessels, which comprise about 15% of the diet at colonies in the UK (Hamer et al. 2007;
240 Votier et al. 2010). Changes in prey availability can result in birds altering their activity at sea
241 (e.g. the proportion of time spent resting on the water; Monaghan et al. 1994, Litzow & Piatt
242 2003) without any effect on trip durations (Lescroël & Bost 2005, Garthe et al. 2011), but
243 large reductions in prey availability are likely to exceed this buffering capacity, resulting in
244 longer trips, especially at large colonies where birds have less flexibility in their time/activity
245 budgets owing to their greater foraging effort (Lewis et al. 2004, Hamer et al. 2007a).

246

247 Trips at most colonies were shorter in 2009 than in 2000, despite all but one of these colonies
248 increasing in size since 2000. Hence the impact of changes in prey availability between years
249 exceeded that of changes in colony sizes in most cases. However, trips at the two smallest
250 colonies studied in 2000 (Troup Head and Ireland's Eye) were longer in 2009, because
251 annual variation in density-dependence had little effect on trip durations at these small
252 colonies (Fig 3). Hence the main influence on trip duration in these two cases was from
253 colony growth. This has important implications for the use of trip durations to monitor
254 marine environments (Furness & Camphuysen 1997, Hamer et al. 2006), because even large
255 changes in prey availability will have relatively little effect on trip durations at small
256 colonies.

257

258 A recent analysis of seabird monitoring data for the UK identified two separate ecologically
259 coherent regions for gannets, corresponding with the North Sea and the Celtic/Irish Sea,
260 within which trends in abundance varied in a consistent fashion (Cook et al. 2011). In support
261 of this distinction, we found that colonies in the Celtic/Irish Sea region grew significantly
262 more slowly for their size over the period between 2000 and 2009 than did colonies bordering
263 the North Sea. We also found that observed trip durations in 2009 were shorter than predicted
264 at colonies bordering the North Sea, but longer than predicted at colonies in the Celtic and
265 Irish Seas. These data suggest less favourable environmental conditions in the latter region
266 over recent years, similar to the impacts of low food availability on trip durations and
267 population trajectories of Cape gannets *Morus capensis* in southern Africa (Lewis et al.
268 2006). This suggestion is also supported by recent data showing longer trips than expected
269 from population size at a gannet colony in Brittany (Grémillet et al. 2006), long foraging trips
270 and poor chick growth of Manx shearwaters *Puffinus puffinus* since 2007 at a colony in SW

271 Wales (Riou et al. 2011) and decreases in overwinter survival of adult guillemots *Uria aalge*
272 and razorbills *Alca torda* breeding in Wales (Votier et al. 2005).

273

274 At Ailsa Craig, in the northern Irish Sea, population size decreased slightly between 1995 and
275 2000 (Wanless et al. 2005) but mean trip duration in relation to population size was lower in
276 2009 than at more southerly colonies (Fig 4). We have no data on diets of birds or prey
277 biomasses in this region but this difference suggests more favourable environmental
278 conditions within the northern Irish Sea in more recent years. This corresponds with both a
279 suspected northerly shift in the foraging areas of Manx shearwaters from the south of the
280 region (Guilford et al. 2008) and large increases in populations of guillemots and razorbills at
281 nearby Rathlin Island, following steep declines between 1999 and 2007 (Allen et al. 2011).

282

283 In contrast to gannets, which have maintained consistently high breeding success over this
284 period (Hamer et al. 2007a, JNCC 2011), several species of seabird at colonies in the North
285 Sea have experienced declining breeding success since the mid 1980s (Burthe et al. 2012)
286 and greatly reduced adult survival since the mid-2000s (Lahoz-Monfort et al. 2011). This
287 difference partly reflects the greater flexibility of gannets in terms of diet and foraging ranges
288 (Hamer et al. 2007a, Hamer et al. 2009) and may also be linked to recent increases in North
289 Sea stocks of mackerel (ICES 2010), which are too large to be taken by most other seabirds
290 in the region and may compete with them for prey species such as sandeels (Furness 2002,
291 Frederiksen et al. 2007, Langoy et al. 2012), but have been the main component in the diet of
292 gannets at the large colony on Bass Rock in recent years (> 80% by frequency; R.D. Davies
293 et al. unpubl.data).

294

295 The consistency between different colonies and years in the mean travel speeds of gannets at
296 sea (Grémillet et al. 2006, Hamer et al. 2007a, Votier et al. 2010b) can be used in conjunction
297 with the relationship between colony size and trip duration to project foraging ranges and
298 hence at-sea distributions for additional colonies (Grecian et al. 2012; Fig 3). However, the
299 results of this study highlight the importance of accounting for temporal variation in the latter
300 relationship to avoid mismatches between observed and predicted foraging ranges.

301

302 The observed difference between years in the effect of population size on gannet foraging
303 behaviour means that annual variation in trip durations will be particularly marked at large
304 colonies, making them especially vulnerable to adverse effects of low prey availability. Long
305 foraging trips result in chicks receiving less food per unit time, assuming food loads are no
306 larger after long trips (Lewis et al. 2006), and also increase the likelihood of adults leaving
307 chicks unattended and at risk of being washed from the nest during poor weather, exposed to
308 cold temperatures or attacked by conspecifics (Nelson 2002, Lewis et al. 2004). There is no
309 evidence to date of a relationship between colony size and breeding success in gannets
310 (Lewis et al. 2001), but such a relationship has been observed in some other species (Hunt et
311 al. 1986, Kitaysky et al. 2000) and evidence from one large gannet colony suggests that in
312 years of poor food availability, adults have very little leeway to increase foraging effort any
313 further without likely adverse effects on chick survival (Hamer et al. 2007a).

314

315 Finally, there is evidence that gannets from large colonies recruit into smaller colonies (Moss
316 et al. 2002, Votier et al. 2011), so it is possible that trip durations and provisioning rates play
317 a role in influencing where birds choose to breed for the first time (Lewis et al. 2001). Our
318 data indicate that the difference in trip durations between large and small colonies is most
319 marked during adverse foraging conditions, and so differences in recruitment rate may have

320 contributed towards both the observed negative density-dependent growth of populations and
321 the lower per capita growth rates since 2000 at colonies in the Celtic and Irish Sea (Fig 2).

322

323

324 **ACKNOWLEDGMENTS**

325 We thank the Royal Society for the Protection of Birds, Scottish Natural Heritage, Sir Hew
326 Hamilton-Dalrymple, Julian Gaisford-St. Lawrence, the Neale family and Lord Revelstoke
327 for granting access to study colonies. We are also grateful to Stephen Newton, Deryk Shaw,
328 Scottish Natural Heritage and Ruth Porter (RSPB) for recent colony counts (Ireland's Eye;
329 Fair Isle; Noss and Hermaness; and Bempton Cliffs, respectively). We thank the Scottish
330 Seabird Centre, Stephen Newton, Oscar Merne, Alyn Walsh and Bernie Zonfrillo for logistic
331 support and advice. Many thanks also to Mike Harris, Helen Kimbell and Amy Leedale for
332 their help in the field. The project was funded by a PhD studentship from the Natural
333 Environment Research Council.

334

335

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511

512 **FIGURES**

513 **Figure 1.** Locations and sizes of the ten gannet colonies studied in 2000 and 2009 (A, Ailsa
514 Craig; BR, Bass Rock; B, Bempton Cliffs; F, Fair Isle; G, Great Saltee; H, Hermaness; I,

515 Ireland's Eye; L, Lambay; N, Noss; T, Troup Head). Colony sizes (number of apparently
516 occupied sites, square-root transformed) are shown for 2000 (grey bars) and 2009 (black
517 bars). The area of each circle is proportional to colony size in 2009. Scales on the y axes
518 differ among colonies.

519

520 **Figure 2.** The relationship between \log_e population size (AOS) and percentage per capita
521 population growth rate from 1994 to 2000 (A) and from 2000 to 2009 (B). North Sea
522 colonies: filled circles, Celtic/Irish Sea colonies: open circles. In 2000-2009, there was a
523 significant difference between colonies in the North Sea (solid regression line) and the
524 Celtic/Irish Sea (dashed regression line).

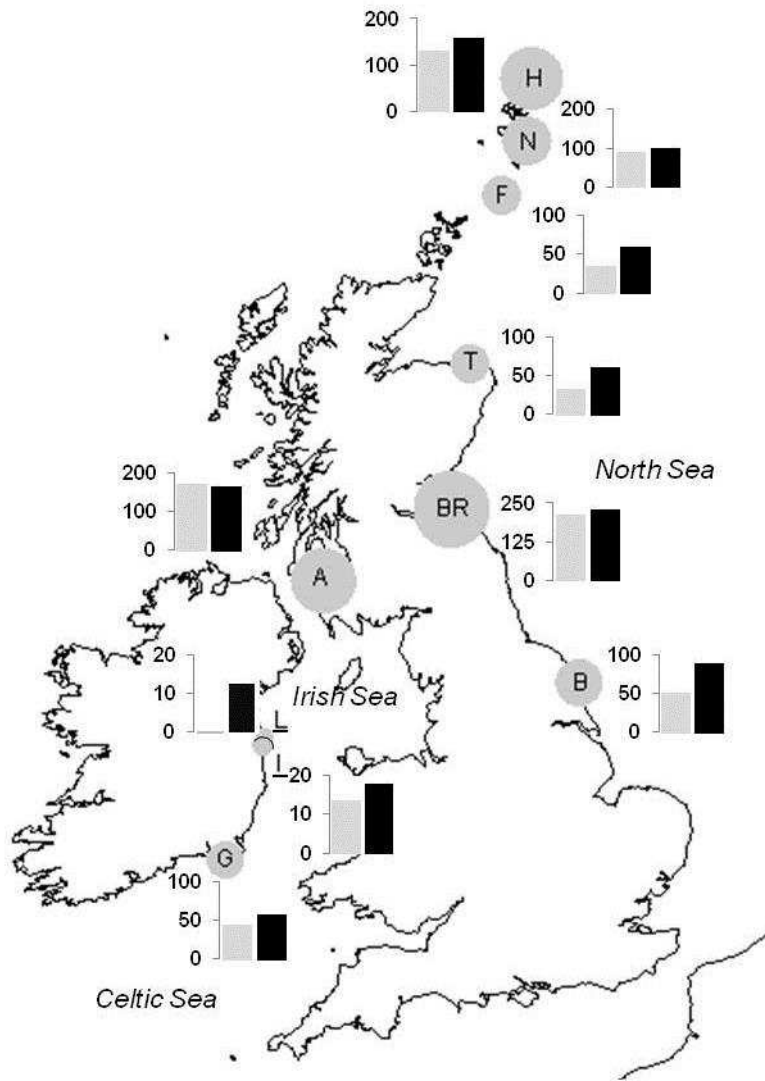
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526 **Figure 3.** The relationship between mean foraging trip duration (hours) and population size
527 (square-root transformed to be proportional to the number of birds at sea) in 2000 (triangles)
528 and 2009 (circles). Open symbols, Irish/Celtic Sea colonies; Filled symbols, North Sea
529 colonies (A, Ailsa Craig; BR, Bass Rock; B, Bempton Cliffs; F, Fair Isle; G, Great Saltee; H,
530 Hermaness; I, Ireland's Eye; L, Lambay; N, Noss; T, Troup Head).

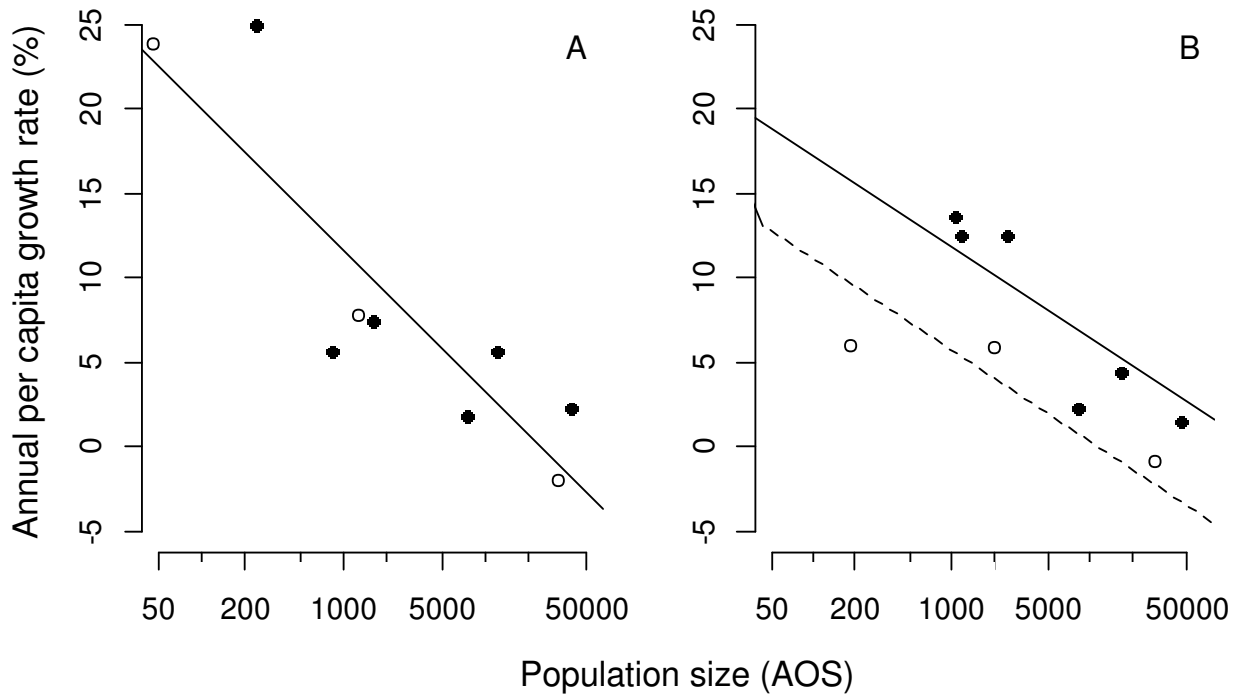
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532 **Figure 4.** Observed (O) and predicted (P) trip durations (hours), with associated standard
533 errors, at different colonies in 2009. Predictions were based on population sizes in 2009,
534 using the relationship between square-root population size and trip duration that was
535 observed in 2000 (A, Ailsa Craig; BR, Bass Rock; B, Bempton Cliffs; F, Fair Isle; G, Great
536 Saltee; H, Hermaness; I, Ireland's Eye; L, Lambay; N, Noss; T, Troup Head).

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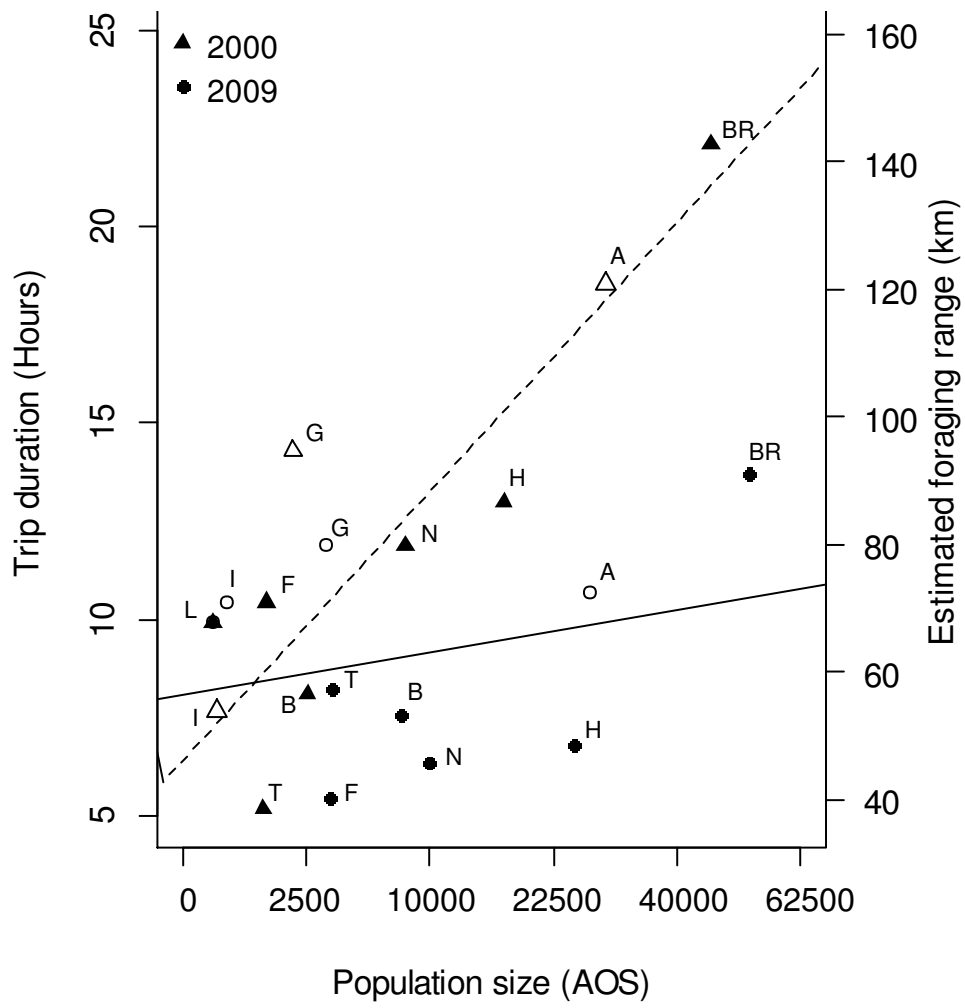
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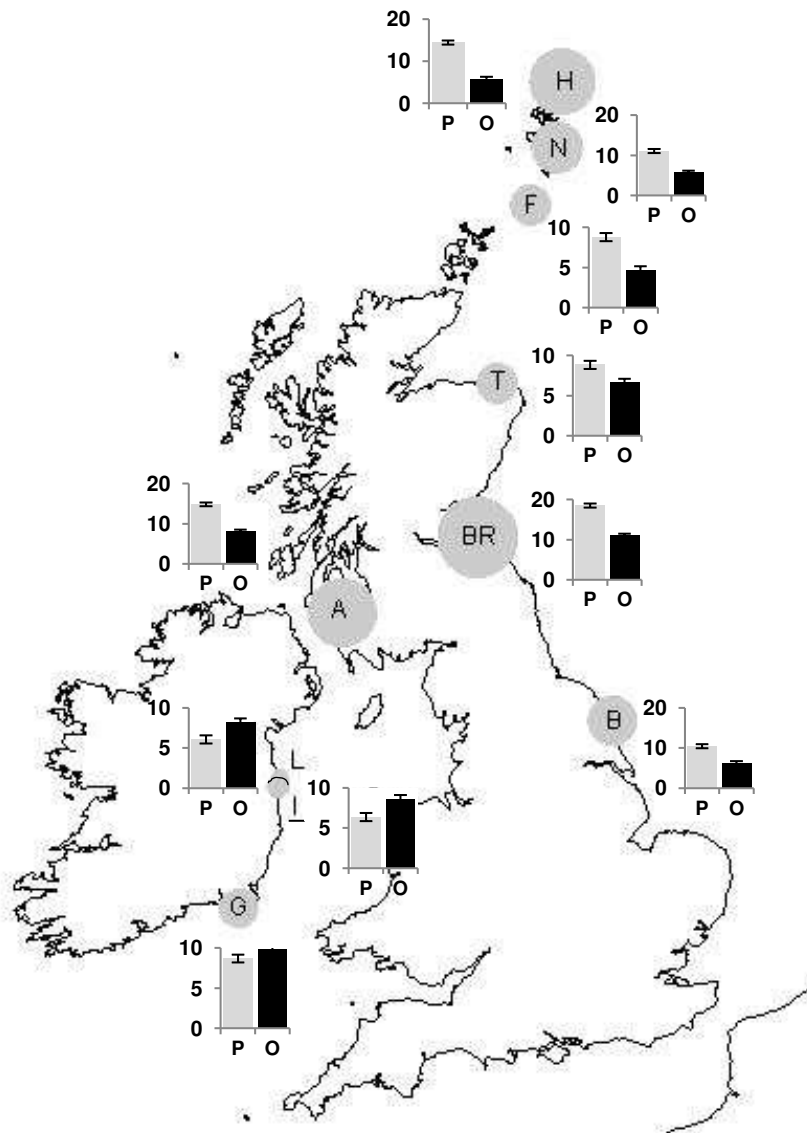
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548 Figure 3.

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