

Behavioural responses of a trans-hemispheric migrant to climate oscillation

Abstract

Large scale climatic fluctuations, such as the El Niño-Southern Oscillation (ENSO), can have dramatic effects on ocean ecosystem productivity. Many mobile species breeding in temperate or higher latitudes escape the extremes of seasonal climate variation through long-distance, even trans-global migration, but how they deal with, or are affected by, such longer-phased climate fluctuations is less understood. To investigate how a long-lived migratory species might respond to such periodic environmental change we collected and analysed a 13-year biologging dataset for a trans-equatorial migrant, the Manx shearwater (*Puffinus puffinus*). Our primary finding was that in El Niño years, non-breeding birds were at more northerly (lower) latitudes than in La Niña years, a response attributable to individual flexibility in migratory destination. Daily time spent foraging varied in concert with this latitudinal shift, with birds foraging less in El Niño years. Secondly, we found that in subsequent breeding, a hemisphere away, El Niño years saw a reduction in foraging time and chick provisioning rates: effects that could not be attributed to conditions at their breeding grounds in the North Atlantic. Thus, in a highly migratory animal, individuals may adjust to fluctuating non-breeding conditions, but still experience cascading carry over effects on subsequent behaviour.

Key Words; Behaviour, Biologging, Climate, El Niño-Southern Oscillation, Migration, Seabird

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40 **Introduction**

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42 Migration can be a mechanism to escape the extremes of seasonal
43 climate variation through long-distance, trans-hemispheric movements
44 (1). How these movements respond to, or are affected by, longer-phased
45 climate fluctuations that affect environmental productivity at migratory
46 destinations is still poorly understood. One of the major drivers of climate
47 is the El Niño Southern Oscillation (ENSO), a climatic pattern that
48 alternates between an El Niño state, where Pacific trade winds weaken,
49 and the reverse, La Niña, both of which alter winds and temperatures
50 globally (2,3). With a periodicity of 3-7 years, both ENSO phases can
51 influence the distribution of food resources at foraging grounds (4). The
52 extent to which individual animals can adapt their foraging distributions
53 in response to shifting ENSO phases between years remains unclear,
54 necessitating the utilization of long-term datasets of highly mobile
55 species (5).

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57 Long distance migrants such as seabirds often spend non-breeding
58 periods in productive regions, far from their high latitude or temperate
59 breeding grounds. Breeding is energetically demanding for seabirds,
60 which invest large amounts of parental care into rearing a small number
61 of chicks, with breeding periods often lasting many months (6-8). Non-
62 breeding foraging is important for restoring condition and preparing for
63 the following breeding season (9,10). Both ENSO phases have been

64 shown to affect seabirds adversely during the breeding season, reducing
65 survival in Cory's shearwaters (*Calonectris borealis*) during La Niña (11)
66 causing an increase in birds skipping breeding in El Niño years for red-
67 footed boobies (*Sula sula*) (12) and changing the at-sea breeding
68 distribution of multiple species of tropical petrel (13). However, it is not
69 well understood how non-breeding ENSO conditions might impact
70 subsequent breeding across hemispheres, where a different set of
71 environmental conditions are encountered. Events in one season that
72 impact behaviour in the next are termed carry-over effects (14,15), and
73 can occur at any stage of the annual cycle. There are many documented
74 cases of carry-over effects in seabirds, including breeding success
75 affecting non-breeding phenology (8,16), and increased non-breeding
76 mass (10,17) and foraging success (18) improving breeding performance.

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78 The Manx shearwater (*Puffinus puffinus*), a small (400-gram)
79 Procellariiform seabird breeding mainly in northern Europe, is a species
80 particularly suited to studying individual responses to ENSO owing to its
81 high breeding site philopatry, high year-to-year survival and tolerance of
82 bird- and nest-borne instrumentation (19). In addition, carry-over effects
83 are thought to be especially important for migratory species such as
84 Manx shearwaters that undergo a long, and potentially costly trans-
85 equatorial migration to the Patagonian shelf (20,21), and link pelagic
86 ecology at a global scale. Manx shearwaters are long-lived with
87 protracted breeding seasons, so must balance reproductive and survival
88 decisions from year to year (19). Shearwaters that spent more time
89 foraging during the non-breeding period were found to be more likely to
90 skip breeding that year (22). This increased the likelihood of rearing a
91 chick successfully in the following breeding season. In turn, breeding
92 season conditions are known to carry-over to non-breeding behaviour and
93 future breeding success in this species, with experimentally shortened or
94 extended breeding seasons in Manx shearwaters having knock-on
95 consequences that can be measured using geolocators (10) .

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97 To understand individual responses to ENSO, and whether these
98 responses carry over into future seasons, long-term datasets of annual
99 movements are essential (23). To determine whether, and if so how,
100 ENSO phase predicts non-breeding latitude, we analyse a 13-year dataset
101 of geolocator logger-derived migratory positions and behavioural activity
102 in the Manx shearwater. We investigate the mechanistic drivers of
103 ENSO-related shifts by employing a mixed-effects model to assess
104 whether birds exhibit latitude shifts in tandem with peaks in chlorophyll
105 distribution, serving as an indicator of resource distribution. Further, we
106 take advantage of long-term tracking of individuals, parsing out within-
107 individual effects to investigate whether individuals are flexibly adjusting
108 their location between years with ENSO (24). Secondly, we predict
109 that effects of ENSO on shearwater non-breeding location and behaviour
110 will themselves carry-over into the subsequent breeding season's
111 foraging, chick provisioning behaviour and phenology. To explore how
112 ENSO affects shearwater north- and south-bound migration and breeding
113 behaviour we use a path analysis approach, allowing us to simultaneously
114 assess multiple temporally linked correlations between phenology, non-
115 breeding location, foraging behaviour and environmental covariates (25).
116 Lastly, to distinguish carry-over effects from correlations between local
117 conditions at the non-breeding and breeding sites, we construct a mixed
118 effects model to investigate variation in breeding season foraging with
119 the North Atlantic Oscillation, the major determinant of local conditions
120 in the northern hemisphere (26). To summarise a set of environmental
121 predictors (e.g. sea surface temperature, precipitation, sea surface level
122 etc) attributable to oscillations, we use large-scale climate indexes; the
123 Southern Oscillation Index (SOI) (an indicator of ENSO conditions) and
124 the North Atlantic Oscillation Index (NAO) (27,28).

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128 **Methods**

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130 **Fieldwork**

131 To determine the migratory timing, routes and destinations of individual
132 breeding birds, from 2007 to 2021, 770 geolocator (GLS) devices were
133 deployed and retrieved from Manx shearwaters breeding at multiple
134 colonies across the core breeding range of the species: Rum (Scotland)
135 (57.01°N, -6.33 °E); Skomer (Wales) (51.74°N, -5.29°E); Ramsey (Wales)
136 (51.74°N, 5.29°E); Copeland (Northern Ireland) (54.68°N, -5.53°E);
137 Nolsoy (Faroes) (61.98°N, -6.65°E), and Lundy (England) (51.18°N, -
138 4.67°E). To estimate daily foraging, resting and flight behaviour, we used
139 devices that incorporated a salt-water immersion logger. Models of GLS
140 included BAS Mk 6, 9, 15, 19 (2.5g), BAS Mk 13, 14, 18 (1.5g) and
141 MigrateTech intigeo C330, C250 (3.3g), C65, C65-Super (1g) combined
142 immersion and light loggers. With average bird mass being 400g (19), all
143 models weighed <1% of the birds' total body weight. GLS devices were
144 attached to a custom made darvic leg ring, using cable ties and a small
145 amount of super glue. Handling time was typically 5 to 10 minutes per
146 deployment. Although GLS devices typically can record 3 years of data,
147 most devices were retrieved, downloaded, and redeployed each year to
148 maximise data collection. For a subset of Skomer birds, chick peak
149 masses were obtained by daily chick weighing from 2012 to 2019 (n=63
150 chicks).

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152 **Processing Position Data**

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154 All processing and statistical analyses were carried out in RStudio
155 version 4.0.2 (R Core Team, 2021). Light data were processed using the
156 "geolight" package to calculate position from twilight events defined by a
157 light intensity threshold of 10 lux (30). Day length was used to estimate
158 latitude, and the timing of midday/midnight was used for longitude. As
159 light sensors may differ between geolocator models, the sun elevation
160 angle used to define twilight events was selected independently for each

161 individual track. Latitude versus time plots were analyzed across a range
162 of sun elevation angles to identify the one that best calculated latitudes
163 matching the accurate breeding latitude during the summer months
164 (31). The selected sun elevation angle ranged from -3 to -5. A rolling 3-
165 day mean was applied to both longitude and latitude to smooth out error
166 (32). Following the filtering of data to include only those that had
167 complete tracks of north and south-bound migration there were 423 bird-
168 years available from 222 individuals. Mean January position was used to
169 represent non-breeding foraging ground location, as it is a mid-point
170 month where position is least likely to be affected by birds arriving from
171 or departing on southbound and northbound migration, respectively (see
172 supplementary materials 3 for more information on shearwater
173 phenology). Given the noise associated with GLS position estimates,
174 latitude and longitude outliers were removed using the interquartile
175 range method, retaining the lower and upper bounds of data (33).
176 Migration phenology was determined using changes in longitude, rather
177 than changes in overall position, as it is not subject to equinox error.
178 Migration dates were determined from visual inspection of longitude (as
179 in supplementary figure 1).

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181 **Processing Immersion Data**

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183 Saltwater immersion data recorded at 10-minute intervals were used to
184 measure behavioural activity. Saltwater immersion was recorded every 3
185 seconds and summarised every 10 minutes to form an immersion score
186 from 0 (completely dry) to 200 (completely immersed). Geolocator
187 models that recorded immersion at alternate bin frequencies were
188 excluded from analysis of behaviours due to concerns over differences in
189 observed sensitivity between devices leaving 229 complete immersion
190 tracks, 89 of which had a consecutive year in which to assess carry over
191 effects due to limitations of the immersion logger memory. For the times
192 when the bird was at sea (see below for how colony visits were
193 determined during breeding), immersion bins were classified into three

194 states; a dry state (flying) where immersion score equalled zero, a wet
195 state (resting/preening) where immersion score equalled its maximum
196 and an intermediate score (foraging) that represented all values in-
197 between. Three behavioural states have previously been identified for
198 Manx shearwaters using immersion data in a number of different studies,
199 with the intermediate state representing foraging (20,34,35).
200 Simultaneously deployed dive logger, GPS and GLS devices validate
201 these behaviour states, showing foraging behaviours assigned from
202 immersion data do indeed contain most diving (36). Foraging effort
203 (proportion of daily time spent foraging) was obtained for non-breeding
204 birds during January and breeding birds during August (chick rearing
205 period). Chick rearing birds were included in the path analysis if there
206 was evidence that breeding was successfully attempted. When direct
207 evidence of breeding at the colony was not available, immersion data
208 were carefully reviewed for signs of regular incubation stints, identified
209 by characteristic extended dry periods (of at least 3 days) prior to chick
210 rearing excluding 9 non-breeding individuals. Of these, 4 had loggers
211 attached during the previous non-breeding season, and they were
212 included in a supplementary analysis exploring the relationship between
213 skipped breeding seasons and non-breeding foraging behaviour. Manx
214 shearwaters are known to primarily forage during daylight hours (37-
215 39). To standardise foraging effort for variation in day length, the
216 number of hours at sea spent foraging were divided by day length at each
217 bird's mean monthly position for January foraging, and per the mean
218 number of daylight hours at each breeding colony in August.

219

220 Colony visitation during August (a month when breeding adults across all
221 colonies will be chick-rearing) was obtained from the immersion data to
222 indicate chick provisioning rates. Manx shearwaters only arrive at or
223 depart from the colony during the night, when it is dark enough to avoid
224 predation (19,40). If they remain present in their burrow during daylight
225 hours, they are unlikely to depart until it is night. Therefore, during the
226 day if there was a continuous dry period for 6 hours or more, it was

227 assumed that the bird was in its burrow. Sunrise and sunset times were
228 derived from the R `suncalc` package (41). Determining night visits to the
229 colony required a different approach, as dark and dry periods at night
230 could be easily confused with night flight. For each night, immersion bins
231 were defined as 'wet' if any immersion was recorded and summed to
232 calculate the number of wet events per night (42,43);. A normal
233 Expectation Maximisation (EM) mixture model, a model used to identify
234 the distribution to which observations belong, was applied to distinguish
235 nights with colony visits from nights at sea using the `mixtools` package
236 (44). Two distinct distributions were identified and hence used to identify
237 colony visitation by assigning colony visits to nights that had higher
238 probability of belonging to the drier peak (see supplementary materials 2
239 for more details).

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242 **Environmental Variables**

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244 Non-breeding conditions were described using the Southern Oscillation
245 Index (SOI), whilst breeding conditions were described via the North
246 Atlantic Oscillation (NAO) index, both provided by NOAA (28). The SOI
247 describes a standardised difference between the barometric pressures at
248 observation sites in Darwin and Tahiti. When the pressure difference
249 weakens, El Niño conditions occur, indicated by negative index values.
250 For this analysis, the SOI index was taken as a mean for the months of
251 October, November and December. These months coincide with the peak
252 of an El Niño/ La Niña event and phytoplankton blooms in the
253 Southwestern Atlantic that dictate non-breeding conditions (45). The
254 NAO index describes the pressure difference between the Azores and
255 Iceland. NAO is most pronounced in winter and can have effects in
256 subsequent seasons (46). Summer NAO has an effect on European
257 climate but it is less understood (47). Therefore, in this analysis, winter
258 NAO (December-March) and summer NAO (June-August) were both
259 considered as drivers of climate around the breeding colony. We used

260 Aqua MODIS-derived chlorophyll a data provided by NASA to determine
261 which latitude in the Patagonian shelf area (a box of coordinates -35°N, -
262 63°E : -45°N, -59E°) had the maximum chlorophyll per January each year
263 (48).

264

265 **Statistical analysis**

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267 We implemented a path analysis model to link behavioural responses
268 from one season to the next via a path of correlated events (25,49). This
269 approach refines and expands on earlier work that described links across
270 the annual behavioural cycle of this species using structural equation
271 models, undertaken on a much smaller dataset (Kirk 2017, PhD thesis).
272 Path analysis was conducted via the r package Lavaan to investigate
273 links between the SOI and previous breeding season behaviour to non-
274 breeding latitude, phenology and foraging effort (50). These variables
275 were then linked to the following breeding season's behaviour via colony
276 visitation and foraging effort during August (figure 1). Significance levels
277 were Bonferroni adjusted for structural equation modelling (51);

278 $\alpha(\text{per test}) = \frac{0.05}{k^{1-\sqrt{|r|}}}$, where k is equal to the number of tests and r to the
279 correlation coefficient. To avoid model overfitting, and because our
280 analysis focuses on within individual changes between years, we did not
281 include colony as a factor. As we were interested in determining the
282 environmental factors causing latitudinal variation between years, and
283 these are confounded with time, the year itself was not included in the
284 path analysis model.

285

286 Path analysis relies on several, rather than a single statistical test to
287 assess model fit to the data. As chi squared (χ^2) p values are known to be
288 uninterpretable with large sample sizes, we instead used the
289 relative/normed chi-square (χ^2/df) to assess fit (52). The χ^2/df value was
290 2.49, which was suitably below the recommended maximum ratio of 5.
291 Both the comparative fit index (CFI) and the Tucker-Lewis Index (TLI) of

292 the path analysis were 0.9. The Root Mean Square Error of
293 Approximation (RMSEA) and the Standardized Root Mean Square
294 Residual (SRMR) which both relate to model residuals, were 0.05 and
295 0.07 respectively. All of the above statistics were, therefore, well within
296 the accepted thresholds for suitable model fit (53).

297

298 Separate to our path analysis, the relationship between August colony
299 visits and chick peak mass was tested. This was to validate whether GLS-
300 derived colony visits are indicative of chick provisioning rates in this
301 study, following previous validation in a study using mixture models to
302 indicate chick provisioning (42). Chick peak mass data were available
303 only for a subset of Skomer geolocator birds over the years of this study
304 ($n=63$), so all available August chick peak mass data on Skomer were
305 pooled to increase the sample size and analysed separately using a mixed
306 effects model in the *r* package *lme4* with burrow as a random effect (54).
307 The date the peak mass was taken was included as a fixed effect to
308 assure that any correlations between colony visitation and peak mass
309 were not occurring as a function of peak mass being obtained later in
310 some birds. We also implemented a binomial generalised linear model in
311 a supplementary analysis of whether January foraging increased the
312 likelihood of skipping breeding. Additionally, to test for local
313 environmental conditions during breeding, the relationship between the
314 North Atlantic Oscillation (NAO) and August foraging was tested in 2
315 mixed effects models: one for winter and one for summer NAO, with
316 individual as a random effect. A mixed effects model was also used to
317 test whether any variation in mean January non-breeding latitude with
318 changing ENSO conditions occurred as a result of individual adjustment.
319 Between-individual and within-individual responses to ENSO conditions
320 were separated using the Subject Centring Method from Van de Pol and
321 Wright, exact details of which can be found in (24). Finally, we
322 implemented a mixed effects model to assess whether birds adjusted
323 their non-breeding latitude to the latitude with the maximum chlorophyll
324 in the Patagonian shelf from that year, with individual as a random effect.

325 Significance was assessed in mixed effects models using Likelihood Ratio
326 Estimation and confidence intervals and effect sizes were obtained
327 through bootstrapping methods; where 1000 simulations of random and
328 fixed effects were implemented using the arm package (55).

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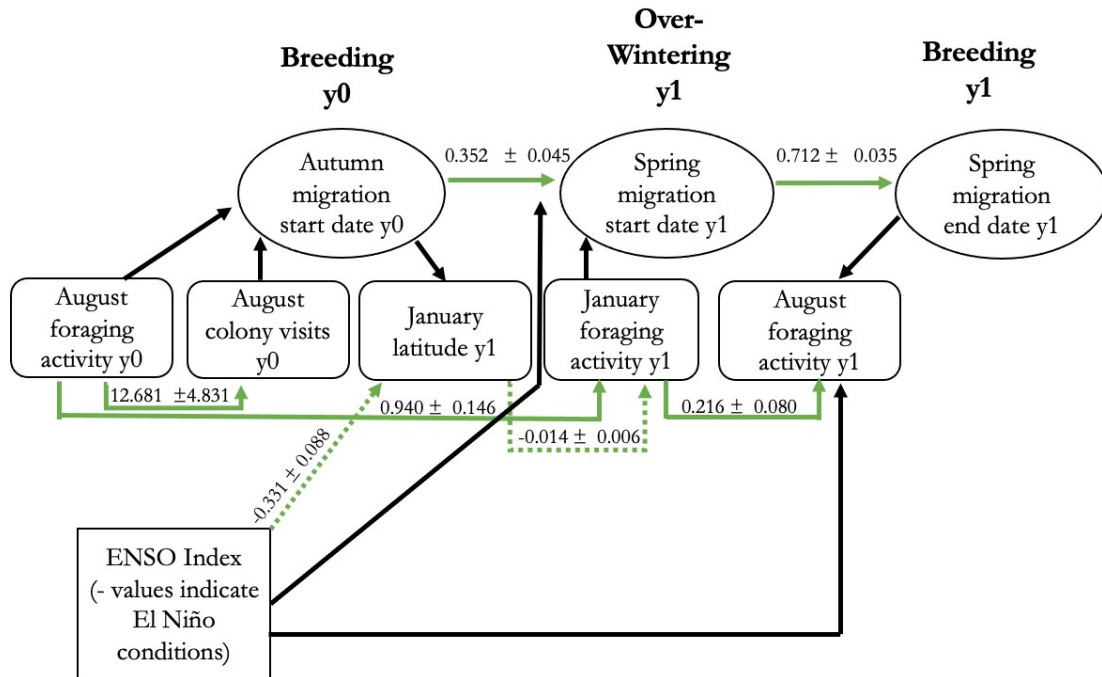
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350 **Figures**

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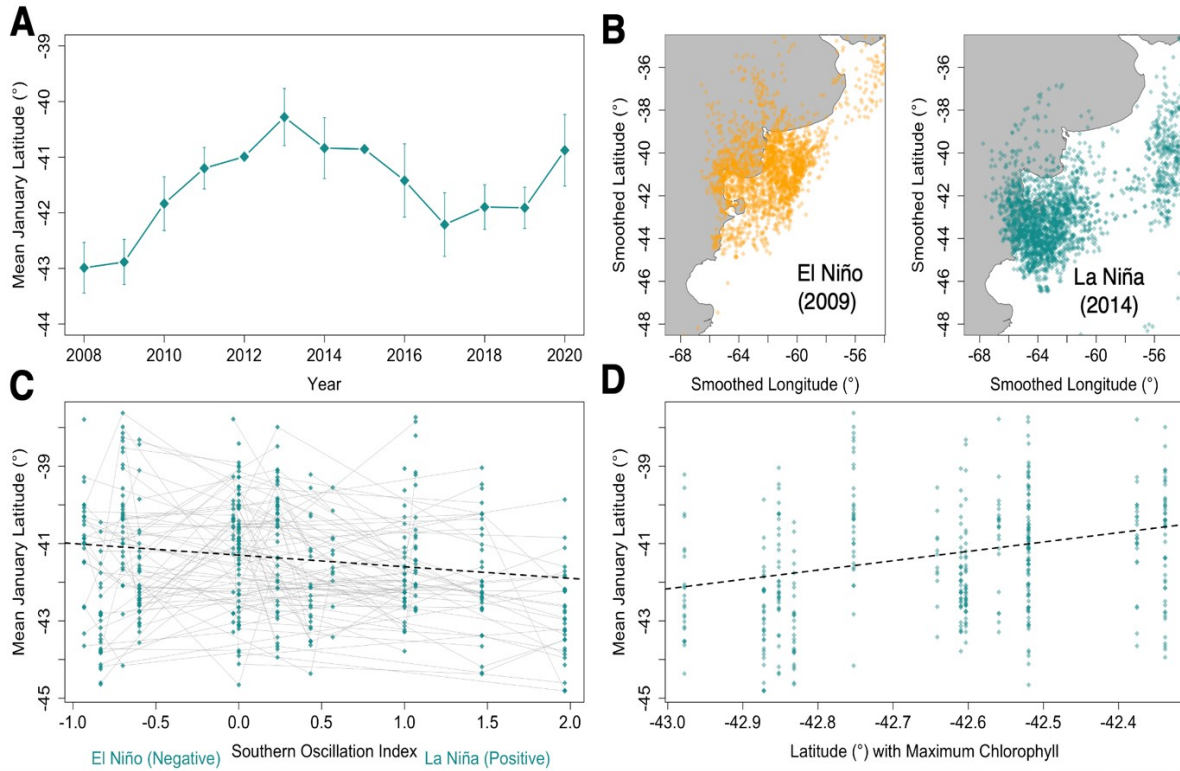
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355 **Figure 1.** A diagram illustrating path analysis correlations between
356 environmental, behavioural and phenological factors. All significant
357 effects are represented in green and non-significant paths in black.
358 Dotted lines indicate negative relationships and path estimates ($\beta \pm SE$)
359 are given for each significant path.

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371 **Figure 2.** The effect of the El Niño Southern Oscillation index on non-372 breeding latitude. **A)** Variation in mean non-breeding latitude (n=422)

373 between years with 95% confidence intervals, where each point

374 represents a mean of all individuals. **B)** Smoothed January latitude (°)

375 and longitude (°) for all individuals are plotted for a strong El Niño year

376 in orange (2009) (n=36) and a strong La Niña year in blue (2014) (n=37).

377 **C)** Variation in mean non-breeding latitude with the SOI index (NOAA,

378 2023). Grey lines connect individuals tracked in multiple years to

379 visualize individual adaptation to varying ENSO conditions. The

380 regression line is derived from the path analysis model. **D)** The

381 relationship between the latitude at which the maximum chlorophyll was

382 centred for a given year against mean January latitude. Chlorophyll data

383 were taken from the Aqua-MODIS project (48). The regression line is

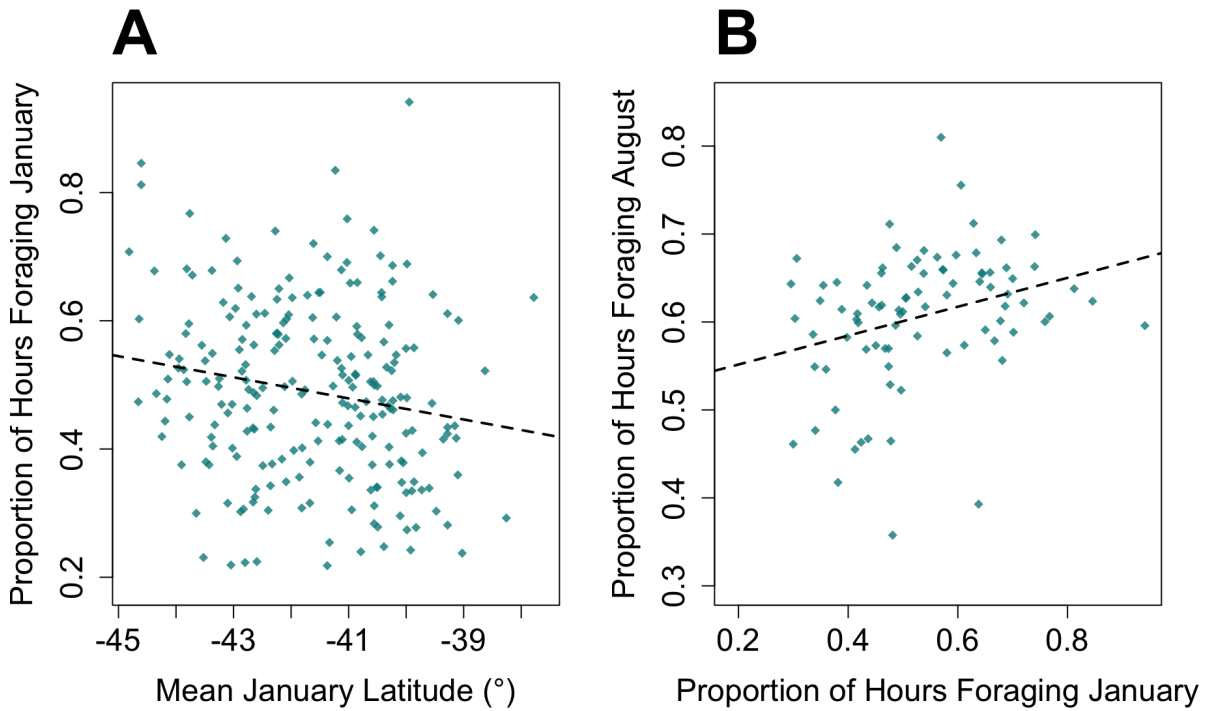
384 derived from the mixed effects model.

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391 **Figure 3.** The correlative effects of January latitude on non-breeding and
392 breeding foraging activity. **A)** The proportion of the day spent foraging
393 in January plotted against mean January latitude (n =226). **B)** The
394 proportion of the day spent foraging in August during chick rearing
395 plotted against the previous January's foraging time (n=87). For both,
396 proportions are derived from foraging hours divided by the available
397 daylight hours at the foraging site.

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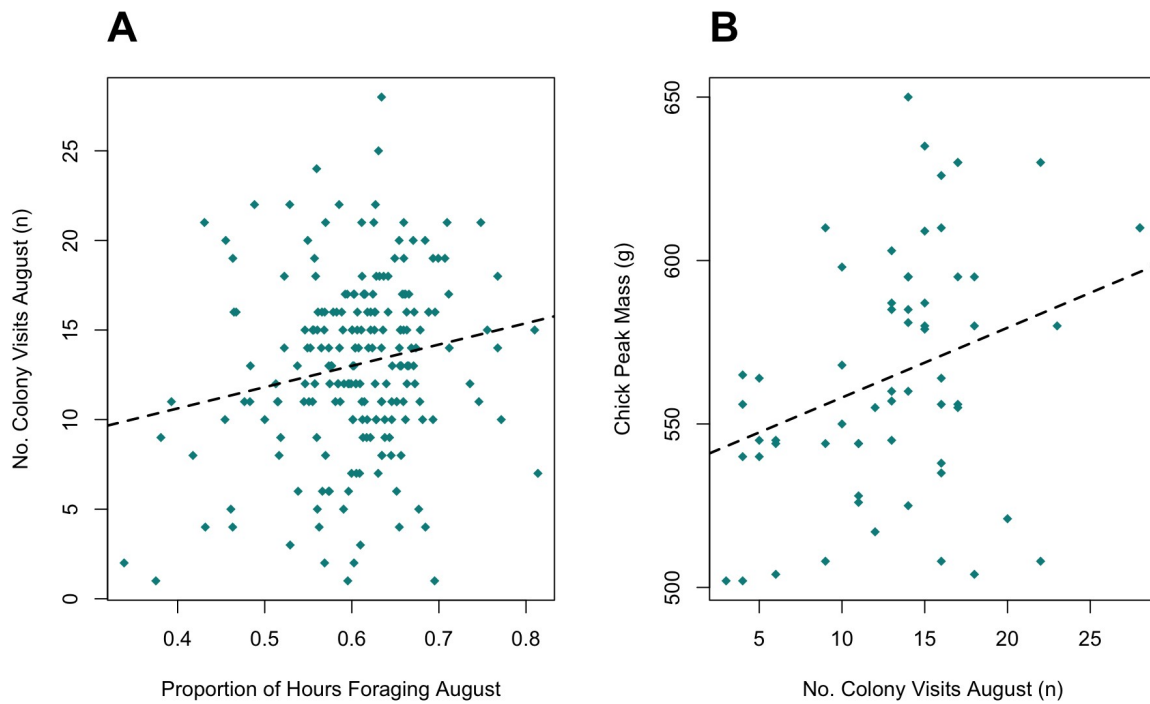
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407 **Figure 4.** The correlative effects of foraging activity on colony visitation408 and chick peak mass. **A)** The proportion of the day spent foraging in

409 August (foraging hours divided by the available daylight hours at the

410 foraging site) plotted against the number of colony visits in year 0 (n

411 =214). **B)** The number of colony visits plotted against chick peak mass

412 for Skomer birds only (n=63). Regression lines are derived from A) path

413 analysis and B) a mixed effects model.

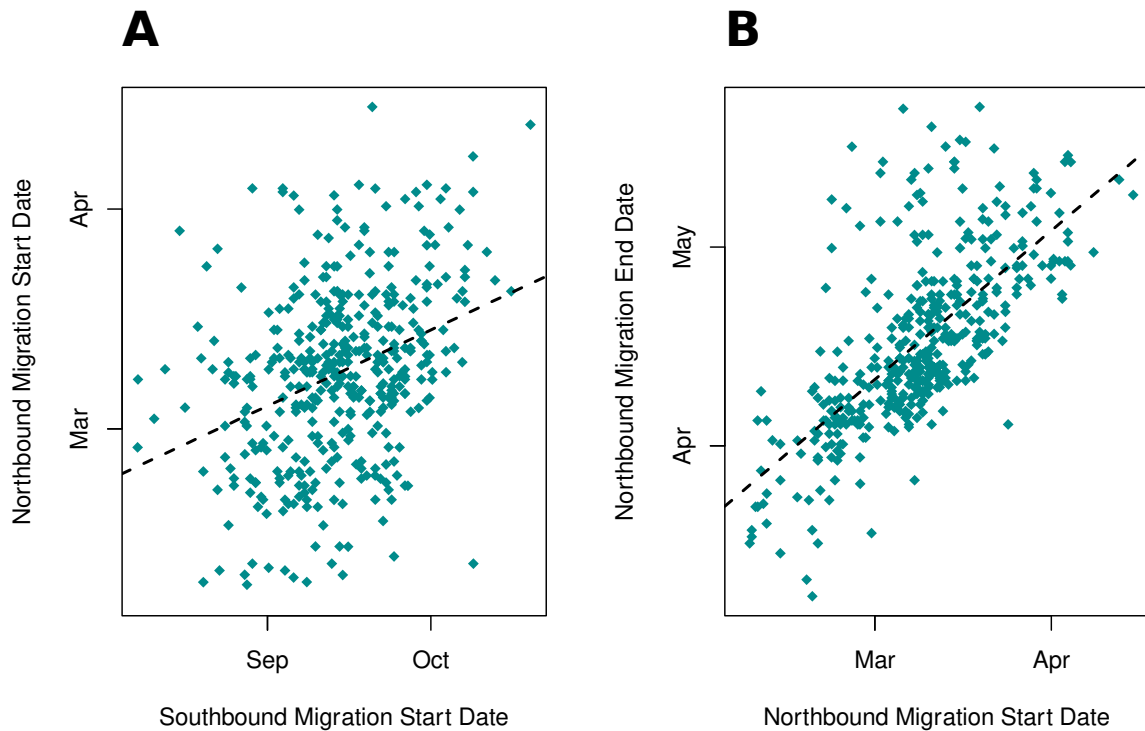
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Figure 5. Correlations between Southbound (Autumn) and subsequent Northbound migration (Spring). **A)** Northbound/spring migration start date plotted against previous southbound/autumn migration start date (n=421). **B)** Northbound/spring migration end date plotted against northbound/spring migration start date (n=419). Regression lines are derived from the path analysis model.

440 **Results**

441

442 The mean January latitude for non-breeding birds showed non-linear
443 variation between 2008 to 2020, oscillating in a wave-like pattern (figure
444 2). Consecutive years were more similar, with overlap between 95%
445 confidence intervals. This suggests that latitudinal shifts occur relative to
446 the previous year, and birds are responding to a periodic environmental
447 variable. Path analysis (figure 1) suggested this pattern may exist as a
448 result of changes in ENSO; where a significant correlation existed
449 between the SOI and non-breeding latitude ($\beta=-0.331$, $se=0.084$, $z=-$
450 3.944 , $p<0.001$). Birds were observed further north during non-breeding
451 in El Niño years (figure 2). To determine whether shifts occurred via
452 individual flexibility in foraging latitude with ENSO, we implemented a
453 mixed effects model via the Subject Centring Method, to find both
454 significant between ($\beta= -0.77$, 95%CI [-1.29, -0.28], $\chi^2_1=8.89$, $p<0.01$)
455 and within individual effects ($\beta= -0.30$, 95%CI[-0.49, -0.12], $\chi^2_1=10.00$,
456 $p< 0.01$) (24). There was, however, no significant difference in the
457 within- and between-individual latitudinal change (95%CI[-1.01, 0.05],
458 $p>0.05$), suggesting that the effect of El Niño on non-breeding latitude is
459 best explained by within-individual plasticity than between-individual
460 turnover. We also implemented a separate mixed effects model that
461 indicated birds adjust their non-breeding latitude to where the maximum
462 chlorophyll that year was centred ($\beta =2.41$, $\chi^2_1=47.24$, 95% CI[1.71,
463 3.06], $p < 0.0001$). Therefore, birds appear to adjust their non-breeding
464 latitude in response to shifting resource distributions.

465

466 Variation in non-breeding latitude had a significant effect on the
467 proportion of daylight hours spent foraging with foraging effort
468 decreasing at lower latitudes ($\beta=-0.0154$ $se=0.006$, $z=-2.517$,
469 $p<0.01$). Therefore, ENSO-induced changes in January latitude appear to
470 cause foraging effort to vary. When January foraging effort was higher, it
471 correlated with an increase in the proportion of time spent foraging in
472 the following August ($\beta=0.216$, $se=0.080$, $z=2.696$, $p<0.01$, figure 3). To

473 summarise, northward shifts in foraging latitude as a result of El Niño
474 conditions correlated with a reduction in non-breeding and subsequent
475 foraging behaviour during breeding. Additionally, although based on a
476 small sample size of non-breeders (n=4), supplementary analysis
477 indicated that reduced non-breeding (January) foraging effort may
478 increase the propensity of birds to skip breeding ($\beta= 12.87$, $se=5.67$,
479 $z=2.27$, $p<0.05$; supplementary 4). Foraging during August in year 0 had
480 a positive relationship with the following January's foraging ($\beta=0.940$,
481 $se=0.146$, $z= 6.450$, $p<0.001$). We found no evidence of environmental
482 conditions directly affecting foraging during breeding. We didn't detect
483 significant effects of ENSO on August foraging, nor winter ($\beta= 0.06$,
484 95%CI [-0.010, 0.018], $\chi^2_1=0.39$, $p>0.05$) or summer NAO ($\beta= 0.01$,
485 95%CI [-0.006, 0.03], $\chi^2_1=2.20$, $p> 0.05$).

486

487 An increase in foraging during August also increased the number of
488 colony visits during this time ($\beta =12.681$, $se=4.831$, $z=2.625$, $p<0.01$).
489 We implemented a separate mixed effects model using chick peak mass
490 measurements available from Skomer island (n=63), to validate that the
491 number of GLS derived colony visits appear indicative of chick
492 provisioning rates ($\beta= 2.13$, 95%CI [0.69, 3.60], $\chi^2_1= 8.82$, $p<0.01$).
493 There was no significant effect of the date peak mass was reached on the
494 peak mass measurement ($\beta= -9.52$, 95%CI [-26.04, 8.38], $\chi^2_1= 1.29$,
495 $p=0.2$), indicating that varying breeding phenologies were not biasing
496 August colony visitation rates. Therefore, increased colony visitation
497 rates over August are correlated with higher chick peak body mass.
498 Neither foraging effort nor the number of colony visits in August had a
499 significant effect on departure date from the colony (figure 1). Autumn
500 southbound migration start date was, however, significantly related to
501 the start date of the next spring's northbound migration ($\beta=0.352$,
502 $se=0.045$, $z=7.808$, $p<0.001$), which defined return date to the colony in
503 the following breeding season ($\beta=0.712$, $se=0.035$, $z=20.491$, $p<0.001$).
504 Therefore, individuals departing later on southbound migration from the
505 colony appeared to return later next year. Neither the SOI nor non-

506 breeding foraging effort had a significant effect on spring migration start
507 date (figure 1). Migratory phenology, therefore, appeared separate to the
508 effects of environmental variability via ENSO.

509

510 **Discussion**

511

512 Our main finding is that a long-distance migrant can adjust its non-
513 breeding destination in response to large scale oscillations in climate
514 (ENSO). During El Niño years, birds did not travel as far south or spend
515 as much time foraging during the non-breeding period as they did during
516 La Niña. As we tracked individual birds across multiple years, we were
517 able to demonstrate that this spatial response is primarily mediated by
518 individuals flexibly adjusting their position with environmental conditions
519 (and not the result of individual turn-over in our sample compounded by
520 some sampling bias propagating through the annual cycle). Nevertheless,
521 despite individual adjustments in position, reduced non-breeding
522 foraging went on to impact the subsequent breeding attempt 10,000 km
523 away, correlating with reduced foraging effort and colony visitation
524 during chick-rearing (figure 2). These results suggest that El Niño
525 conditions present losses in non-breeding foraging effort that may reduce
526 physical condition during chick provisioning. Reduced non-breeding
527 foraging effort may additionally increase the propensity of birds to skip
528 breeding (supplementary figure 4), a result contrary to previous work
529 that found the opposite effect in shearwaters (22), but examined data
530 over a smaller number of years (and therefore ENSO conditions).

531

532 Reduced non-breeding foraging effort may plausibly occur via several
533 mechanisms, for example El Niño conditions may lower resource
534 availability (56) or unfavourable environmental conditions may create
535 reduced opportunities for foraging (57). ENSO summarises pressure
536 differences that can equate to a range of environmental conditions
537 including changes in sea level, ocean acidification, storms, sea surface

538 temperature and precipitation; all known to impact seabird behaviour
539 (4,58). Such indices can allow ecologists to infer how seabirds might
540 respond to climate without multiple hypothesis testing, with potentially
541 more predictive power than local variables (59). However, a northward
542 shift in chlorophyll distribution has been documented along the
543 Patagonian shelf during El Niño years and thought to be partially driven
544 by wind anomalies (45). We therefore conducted a secondary analysis
545 (figure 2) using Aqua MODIS-derived chlorophyll a data that suggested
546 birds are significantly shifting their latitude with where the maximum
547 chlorophyll in the southwest Atlantic is centred (48). Despite the
548 limitations of using chlorophyll content as a proxy for prey distribution
549 (60), this suggests that observed shifts in latitude are driven by prey
550 availability (39). Understanding how birds vary their behaviour with
551 shifting resource distribution is important in terms of understanding
552 current and future climatic changes, with future ENSO events predicted
553 to become more extreme under greenhouse warming (61).

554

555 Many avian species are seeing changes in breeding phenology so as to
556 align breeding with peak prey availability (62). However, we did not find
557 any convincing effects of ENSO on migratory timings in Manx
558 shearwaters (figure 2). Interestingly, migratory dates were highly
559 correlated with one another (figure 5). We found that birds that leave
560 earlier on southbound autumn migration do not have longer non-
561 breeding periods, but instead returned to the colony earlier next year.
562 Breeding earlier is linked to higher success in many avian taxa, including
563 shearwaters (63), so migratory timing may already be under strong
564 directional selection (64–66).

565

566 Despite carry-over effects now being well documented in various taxa
567 (15,67–69), including Manx shearwaters, (22,34), the effects of global
568 shifting environmental conditions are not well understood (70–72). Here
569 we tie carry over effects to ENSO, yet do not find an influence of the
570 NAO, a major driver of European climate, on breeding season behaviour.

571 ENSO can influence northern hemisphere weather, and potentially even
572 the NAO (73), so further research is needed to understand how
573 environmental oscillations in different hemispheres, may interact across
574 the annual cycle of trans-global migrants.

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578 **References**

579

480 Pelletier D, Seyer Y, Garthe S, Bonnefoi S, Phillips RA, Guillemette M. So
581 far, so good. . . Similar fitness consequences and overall energetic costs
582 for short and long-distance migrants in a seabird. PLoS One.
583 2020;15(3):1-23.

584

585 Philander SGH. El Niño Southern Oscillation phenomena. Nature.
586 1983;302:295-301.

587

588 Ayarzagüena B, Ineson S, Dunstone NJ, Baldwin MP, Scaife AA.
589 Intraseasonal effects of El Niño-Southern Oscillation on North Atlantic
590 climate. J Clim. 2018;31(21):8861-73.

591

492 Quillfeldt P, Masello JF. Impacts of climate variation and potential effects
593 of climate change on South American seabirds - a review. Marine Biology
594 Research. 2013;9(4):337-57.

595

596 Bogdanova MI, Butler A, Wanless S, Moe B, Anker-nilssen T, Frederiksen
597 M, et al. Multi-colony tracking reveals spatio-temporal variation in carry-
598 over effects between breeding success and winter movements in a
599 pelagic seabird. Mar Ecol Prog Ser. 2017;578:167-81.

600

601 Kim Y, Priddel D, Carlile N. Incubation routine and associated changes in
602 body mass of gould's petrel (*Pterodroma leucoptera*). Emu.
603 2017;118(2):193-200.

604

705 Hunter S. Breeding biology and population dynamics of giant petrels
606 *Macronectes* at South Georgia (Aves: Procellariiformes). J Zool.
607 1984;203(4):441-60.

608

809 Gatt MC, Versteegh M, Bauch C, Tieleman BI, Granadeiro JP, Catry P.
610 Costs of reproduction and migration are paid in later return to the
611 colony, not in physical condition, in a long-lived seabird. Oecologia
612 [Internet]. 2020;195(2):287-97. Available from:
613 <https://doi.org/10.1007/s00442-020-04775-w>

614
~~615~~ Alerstam T, Hedenstrom A. The Development of Bird Migration Theory. *J*
616 *Avian Biol.* 1998;29(4):343-69.
617
~~618~~ Fayet AL, Freeman R, Shoji A, Kirk HL, Padget O, Perrins CM, et al.
619 Carry-over effects on the annual cycle of a migratory seabird: an
620 experimental study. *Journal of Animal Ecology.* 2016;85(6):1516-27.
621
~~622~~ Brichetti P, Foschi UF, Boano G. Does El Nino affect survival rate of
623 mediterranean populations of Cory's Shearwater? *Waterbirds.*
624 2000;23(2):147-54.
625
~~626~~ Cubaynes S, Doherty PF, Schreiber EA, Gimenez O. To breed or not to
627 breed: A seabird's response to extreme climatic events. *Biol Lett.*
628 2011;7(2):303-6.
629
~~630~~ Ballance LT, Pitman RL, Fiedler PC. Oceanographic influences on
631 seabirds and cetaceans of the eastern tropical Pacific: A review. *Prog*
632 *Oceanogr.* 2006;69(2-4):360-90.
633
~~634~~ O'connor CM, Norris DR, Crossin GT, Cooke SJ. Biological carryover
635 effects: Linking common concepts and mechanisms in ecology and
636 evolution. *Ecosphere.* 2014;5(3).
637
~~638~~ Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S. Carry-over
639 effects as drivers of fitness differences in animals. *Journal of Animal*
640 *Ecology.* 2011;80(1):4-18.
641
~~642~~ Bogdanova MI, Daunt F, Newell M, Phillips RA, Harris MP, Wanless S.
643 Seasonal interactions in the black-legged kittiwake, *rissa tridactyla*:
644 Links between breeding performance and winter distribution.
645 *Proceedings of the Royal Society B: Biological Sciences.*
646 2011;278(1717):2412-8.
647
~~648~~ Whelan S, Hatch SA, Irons DB, McKnight A, Elliott KH. Increased
649 summer food supply decreases non-breeding movement in black-legged
650 kittiwakes. *Biol Lett.* 2020;16(1).
651
~~652~~ Desprez M, Jenouvrier S, Barbraud C, Delord K, Weimerskirch H. Linking
653 oceanographic conditions, migratory schedules and foraging behaviour
654 during the non-breeding season to reproductive performance in a long-
655 lived seabird. *Funct Ecol.* 2018;32(8):2040-53.
656
~~657~~ Storey A, Brooke M. *The Manx Shearwater.* Vol. 14, Colonial Waterbirds.
658 1991. p. 66.
659
~~660~~ Guilford T, Meade J, Willis J, Phillips RA, Boyle D, Roberts S, et al.
661 Migration and stopover in a small pelagic seabird, the Manx shearwater

662 Puffinus puffinus: Insights from machine learning. Proceedings of the
663 Royal Society B: Biological Sciences. 2009;276(1660):1215–23.
664
~~245~~ Norris DR, Taylor CM. Predicting the consequences of carry-over effects
666 for migratory populations. Biol Lett. 2006;2(1):148–51.
667
~~268~~ Shoji A, Aris-Brosou S, Culina A, Fayet A, Kirk H, Padget O, et al.
669 Breeding phenology and winter activity predict subsequent breeding
670 success in a trans-global migratory seabird. Biol Lett. 2015;11(10).
671
~~272~~ Moe B, Frederiksen M, Steen H, Bogdanova MI, Butler A, Wanless S, et
673 al. Multi-colony tracking reveals spatio-temporal variation in carry-over
674 effects between breeding success and winter movements in a pelagic
675 seabird. Mar Ecol Prog Ser. 2017;578:167–81.
676
~~277~~ van de Pol M, Wright J. A simple method for distinguishing within- versus
678 between-subject effects using mixed models. Anim Behav.
679 2009;77(3):753–8.
680
~~251~~ Shipley B. Cause and correlation in biology: A user’s guide to path
682 analysis, structural equations and causal inference with R. 2016.
683
~~264~~ Forchhammer MC, Post E, Stenseth NC, Forchhammer MC, Postf E,
685 Stensethi NCHR. North Atlantic Oscillation Timing of Long- and Short-
686 Distance Migration. British Ecological Society. 2019;71(6):1002–14.
687
~~258~~ Forchhammer MC, Post E. Using large-scale climate indices in climate
689 change ecology studies. Popul Ecol. 2004;46(1):1–12.
690
~~281~~ NOAA. NOAA [Internet]. 2023. Available from:
692 <https://www.ncei.noaa.gov/access/monitoring/products/>
693
~~294~~ Team RC. R: A language and environment for statistical computing. R
695 Foundation for Statistical Computing,. Vienna, Austria: R Core Team;
696 2021.
697
~~308~~ Lisovski S, Hahn S. GeoLight - processing and analysing light-based
699 geolocator data in R. Methods Ecol Evol. 2012;3(6):1055–9.
700
~~311~~ Bråthen VS, Moe B, Amélineau F, Ekker M, Fauchald P, Helgason HH, et
702 al. An automated procedure (v2.0) to obtain positions from light-level
703 geolocators in large-scale tracking of seabirds A method description for
704 the SEATRACK project. 2021. 1–51 p.
705
~~306~~ Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR. Accuracy of
707 geolocation estimates for flying seabirds. Mar Ecol Prog Ser.
708 2004;266:265–72.
709

~~710~~ Liechti F, Bauer S, Dhanjal-Adams KL, Emmenegger T, Zehtindjiev P,
711 Hahn S. Miniaturized multi-sensor loggers provide new insight into year-
712 round flight behaviour of small trans-Saharan avian migrants. *Mov Ecol.*
713 2018;6(1):1-10.
714
~~715~~ Fayet AL, Freeman R, Shoji A, Kirk HL, Padget O, Perrins CM, et al.
716 Carry-over effects on the annual cycle of a migratory seabird: an
717 experimental study. *Journal of Animal Ecology.* 2016;85(6):1516-27.
718
~~719~~ Freeman R, Dean B, Kirk H, Leonard K, Phillips RA, Perrins CM, et al.
720 Predictive ethoinformatics reveals the complex migratory behaviour of a
721 pelagic seabird, the Manx Shearwater. *J R Soc Interface.* 2013;10(84).
722
~~723~~ Dean B, Freeman R, Kirk H, Leonard K, Phillips RA, Perrins CM, et al.
724 Behavioural mapping of a pelagic seabird: Combining multiple sensors
725 and a hidden Markov model reveals the distribution of at-sea behaviour. *J*
726 *R Soc Interface.* 2013;10(78).
727
~~728~~ Darby J, Clairbaux M, Bennison A, Quinn JL, Jessopp MJ. Underwater
729 visibility constrains the foraging behaviour of a diving pelagic seabird.
730 *Proceedings of the Royal Society B: Biological Sciences.* 2022;289(1978).
731
~~732~~ Shoji A, Dean B, Kirk H, Freeman R, Perrins CM, Guilford T. The diving
733 behaviour of the Manx Shearwater *Puffinus puffinus*. *Ibis.*
734 2016;158(3):598-606.
735
~~736~~ Kane A, Pirota E, Wischniewski S, Critchley EJ, Bennison A, Jessopp M,
737 et al. Spatio-Temporal patterns of foraging behaviour in a wide-ranging
738 seabird reveal the role of primary productivity in locating prey. *Mar Ecol*
739 *Prog Ser.* 2020;646:175-88.
740
~~741~~ Riou S, Hamer KC. Predation risk and reproductive effort: impacts of
742 moonlight on food provisioning and chick growth in Manx shearwaters.
743 *Anim Behav.* 2008;76(5):1743-8.
744
~~745~~ Teets DA. Predicting Sunrise and Sunset Times. *The College*
746 *Mathematics Journal.* 2003;34(4):317.
747
~~748~~ Padget O. *Navigation in Procellariiform Seabirds.* University of Oxford;
749 2017.
750
~~751~~ Gillies N. *The mechanisms and consequences of parental coordination in*
752 *Procellariiform seabirds.* University of Oxfordth; 2021.
753
~~754~~ Benaglia T, Chauveau D, Hunter DR, Young DS. *mixtools : An R Package*
755 *for Analyzing Finite.* *J Stat Softw.* 2009;32(6).
756

457. Machado I, Barreiro M, Calliari D. Variability of chlorophyll-a in the
758 Southwestern Atlantic from satellite images: Seasonal cycle and ENSO
759 influences. *Cont Shelf Res.* 2013;53:102–9.
760
- ~~461~~ Stenseth NC, Ottersen G, Hurrell JW, Mysterud A, Lima M, Chan KS, et
762 al. Studying climate effects on ecology through the use of climate indices:
763 The North Atlantic Oscillation, El Niño Southern Oscillation and beyond.
764 *Proceedings of the Royal Society B: Biological Sciences.*
765 2003;270(1529):2087–96.
766
- ~~467~~ Barnagaud JY, Crochet PA, Magnani Y, Laurent AB, Menoni E, Novoa C,
768 et al. Short-term response to the North Atlantic Oscillation but no long-
769 term effects of climate change on the reproductive success of an alpine
770 bird. *J Ornithol.* 2011;152(3):631–41.
771
- ~~482~~ NASA. Moderate-resolution Imaging Spectroradiometer (MODIS) Aqua
773 [Internet]. 2023. Available from:
774 <https://oceancolor.gsfc.nasa.gov/data/aqua/>
775
- ~~486~~ Lleras C. Path Analysis. Vol. 3, *Encyclopedia of Social Measurement.*
777 2005. p. 25–30.
778
- ~~509~~ Roseel Y. lavaan: An R Package for Structural Equation Modeling. *J Stat*
780 *Softw.* 2012;48(2):1–36.
781
- ~~512~~ Smith CE, Cribbie RA. Multiplicity Control in Structural Equation
783 Modeling: Incorporating Parameter Dependencies. *Structural Equation*
784 *Modeling.* 2013;20(1):79–85.
785
- ~~526~~ Hooper D, Coughlan J, Mullen MR. Structural equation modelling:
787 Guidelines for determining model fit. *Electronic Journal of Business*
788 *Research Methods.* 2008;6(1):53–60.
789
- ~~529~~ Hu L, Bentler PM. Cutoff criteria for fit indexes in covariance structure
791 analysis: Conventional criteria versus new alternatives. *Structural*
792 *Equation Modeling: A Multidisciplinary Journal.* 2009;6:1–55.
793
- ~~544~~ Bates D, Mächler M, Bolker BM, Walker SC. Fitting linear mixed-effects
795 models using lme4. *J Stat Softw.* 2015;67(1).
796
- ~~557~~ Gelman A, Hill J. *Data Analysis Using Regression and*
798 *Multilevel/Hierarchical Models (Analytical Methods for Social Research).*
799 Cambridge: Cambridge University Pres; 2006.
800
- ~~561~~ Grémillet D, Boulinier T. Spatial ecology and conservation of seabirds
802 facing global climate change: A review. *Mar Ecol Prog Ser.*
803 2009;391(2):121–37.
804

~~805~~ Weimerskirch H, Prudor A. Cyclone avoidance behaviour by foraging
806 seabirds. *Sci Rep.* 2019;9(1):1-9.
807
~~808~~ Risaro DB, Chidichimo MP, Piola AR. Interannual Variability and Trends
809 of Sea Surface Temperature Around Southern South America. *Front Mar*
810 *Sci.* 2022;9(March):1-20.
811
~~812~~ Szostek KL, Becker PH. Survival and local recruitment are driven by
813 environmental carry-over effects from the wintering area in a migratory
814 seabird. *Oecologia.* 2015;178(3):643-57.
815
~~816~~ Lyngsgaard MM, Markager S, Richardson K, Møller EF, Jakobsen HH.
817 How Well Does Chlorophyll Explain the Seasonal Variation in
818 Phytoplankton Activity? *Estuaries and Coasts.* 2017;40(5):1263-75.
819
~~820~~ Cai W, Santoso A, Collins M, Dewitte B, Karamperidou C, Kug JS, et al.
821 Changing El Niño-Southern Oscillation in a warming climate. *Nat Rev*
822 *Earth Environ.* 2021;2(9):628-44.
823
~~824~~ Gordo O. Why are bird migration dates shifting? A review of weather and
825 climate effects on avian migratory phenology. *Clim Res.* 2007;35(1-2):37-
826 58.
827
~~828~~ Perrins CM, Harris MP, Britton CK. Survival of manx shearwaters. *Ibis.*
829 1973;115:535-48.
830
~~831~~ Schaper S V., Dawson A, Sharp PJ, Caro SP, Visser ME. Individual
832 variation in avian reproductive physiology does not reliably predict
833 variation in laying date. *Gen Comp Endocrinol.* 2012;179(1):53-62.
834
~~835~~ Winkler DW, Hallinger KK, Pegan TM, Taff CC, Verhoeven MA, Chang
836 van Oordt D, et al. Full lifetime perspectives on the costs and benefits of
837 lay-date variation in tree swallows. *Ecology.* 2020;101(9):1-19.
838
~~839~~ Lambrechts MM, Blondel J, Maistre M, Perret P. A single response
840 mechanism is responsible for evolutionary adaptive variation in a bird's
841 laying date. *Proc Natl Acad Sci U S A.* 1997;94(10):5153-5.
842
~~843~~ Fayet AL, Freeman R, Anker-Nilssen T, Diamond A, Erikstad KE, Fifield
844 D, et al. Ocean-wide Drivers of Migration Strategies and Their Influence
845 on Population Breeding Performance in a Declining Seabird. *Current*
846 *Biology.* 2017;27(24):3871-3878.e3.
847
~~848~~ Finch T, Pearce-Higgins JW, Leech DI, Evans KL. Carry-over effects from
849 passage regions are more important than breeding climate in
850 determining the breeding phenology and performance of three avian
851 migrants of conservation concern. *Biodivers Conserv.* 2014;23(10):2427-
852 44.
853

854 Calvert AM, Walde SJ, Taylor PD. Nonbreeding-Season Drivers of
855 Population Dynamics in Seasonal Migrants: Conservation Parallels Across
856 Taxa. *Avian Conservation and Ecology*. 2009;4(2).
857

858 Remisiewicz M, Underhill LG. Large-Scale Climatic Patterns Have
859 Stronger Carry-Over Effects than Local Temperatures on Spring
860 Phenology of Long-Distance Passerine Migrants between Europe and
861 Africa. *Animals*. 2022;12(13).
862

863 Horn LC, Rimmel TK, Stutchbury BJM. Weak evidence of carry-over
864 effects of overwinter climate and habitat productivity on spring passage
865 of migratory songbirds at a northern stopover site in Ontario.
866 *Ornithological Applications*. 2021;123(1):1-16.
867

868 Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC.
869 Ecological effects of the North Atlantic Oscillation. *Oecologia*.
870 2001;128(1):1-14.
871

872 Mokhov II, Smirnov DA. El Niño-Southern Oscillation drives North
873 Atlantic Oscillation as revealed with nonlinear techniques from climatic
874 indices. *Geophys Res Lett*. 2006;33(3):2-5.
875

876

877

878