

1 Original Article

2 **Leapfrog migration and habitat preferences of a small oceanic seabird, Bulwer's petrel**
3 **(*Bulweria bulwerii*)**

4 Running title: At-sea distribution of Bulwer's petrel

5

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26 ABSTRACT

27 **Aim** Our current understanding of migratory strategies and the reasons for their high
28 variability along the phylogenetic tree remains relatively poor. Most of the hypotheses
29 relating to migration have been formulated for terrestrial taxa; classically, oceanic migrations
30 were considered as merely dispersive due to the scarcity of observations in the open ocean.
31 We describe for the first time, the migration strategy of a small seabird, the Bulwer's petrel
32 (*Bulweria bulwerii*), and provide new insights into the ecology and evolution of long-distance
33 marine migrations.

34 **Location** Subtropical and tropical Atlantic Ocean.

35 **Methods** Using cutting-edge geolocators, we examined the year-round distribution and at-sea
36 activity patterns of adult Bulwer's petrels sampled at 5 localities throughout its breeding
37 range in the Atlantic: the Azores, Salvages, Canary and Cape Verde archipelagos. We
38 assessed the migratory connectivity of the species and its habitat use at population and meta-
39 population scales.

40 **Results** Our results provide the first evidence of an oriented leapfrog migration in oceanic
41 seabirds. Ecological niche models based on breeding-season data effectively predicted that
42 subtropical waters of the South Atlantic would be the preferred habitat for the northern
43 populations of Bulwer's petrels during the non-breeding season. Habitat modelling also
44 highlighted similarities in distributions between the breeding and non-breeding periods for the
45 southern populations. Data on at-sea activity patterns suggested that birds from the northern
46 and southern populations behave differently during the breeding season, as well as in the
47 northern and southern non-breeding ranges during the non-breeding period.

48 **Main conclusions** These results indicate that specific habitat preferences, presumably related
49 to differences in prey availability, explain the observed distributions and hence the pattern of
50 leapfrog migration described for Bulwer's petrel. Our study demonstrates the utility of

51 integrating diverse tracking data from multiple populations across international boundaries,
52 and habitat modelling, for identifying important areas common to many marine species in the
53 vast oceanic environments.

54

55 *Keywords:* Activity patterns, *Bulweria bulwerii*, Bulwer's petrel, capture-mark-recapture,
56 geolocator data, habitat modelling, Macaronesian seabirds, meta-population studies, oceanic
57 migrations.

58 INTRODUCTION

59 Migration is an integral part of the annual life-cycle and life-history of many animal species.
60 Migration strategies differ greatly not only among species, but between populations, age and
61 sex classes (Ketterson & Nolan, 1983; Alerstam & Hedenström, 1998). However, our current
62 understanding of migratory connectivity among different breeding populations of the same
63 species, as well as of the mechanisms underlying intra-specific variation in migratory
64 strategies, is much less extensive (e.g. Zink, 2002; Bairlein, 2003). This is despite the
65 profound implications for conservation biology and management of these populations, many
66 of which are threatened by ongoing climatic and other deleterious environmental changes
67 (Esler, 2000).

68

69 Migratory species show various patterns of partial and differential migration (at intra-
70 population level; Cristol *et al.*, 1999; Holberton & Able, 2000), as well as different degrees of
71 segregation among breeding populations (Bell, 2005; Newton, 2008). For instance, at the
72 meta-population level, chain migration occurs when a northerly breeding population winters
73 within the breeding range of another population that migrates further south. In such cases,
74 migration distances are broadly similar among populations breeding along a latitudinal
75 gradient (Lundberg & Alerstam, 1986; Fort *et al.*, 2012). In other species, northerly breeding
76 populations migrate longer distances to spend the non-breeding season further south than
77 individuals from the southerly breeding populations. Such systems have generally been
78 termed leapfrog migrations (Salomonsen, 1955; Alerstam & Högstedt, 1980). The latter is an
79 unusual migration pattern at the species level, first described in a North American passerine,
80 the Fox sparrow (*Passerella iliaca*; Swarth, 1920) and later reported in other passerine (Bell,
81 1996, 1997; Fraser *et al.*, 2012; Stanley *et al.*, 2014) and non-passerine species, particularly
82 waders (Charadriiformes; Salomonsen, 1955; Pienkowski *et al.*, 1985; Boland, 1990; Alves *et*

83 *al.*, 2012; Duijns *et al.*, 2012). Among seabirds however, leapfrog migration has never been
84 reported, suggesting it is uncommon in this group of birds (but see Wernham *et al.*, 2002;
85 Hallgrimsson *et al.*, 2012).

86

87 Classically, three explanations or hypotheses have been suggested by different authors that
88 would favour the evolution of a leapfrog migration pattern (reviewed in Lundberg &
89 Alerstam, 1986): conspecific competition (Salomonsen, 1955; Pienkowski *et al.*, 1985),
90 environmental predictability at the onset of the breeding season (Alerstam & Högstedt, 1980),
91 and time allocation (Greenberg, 1980). The first hypothesis -competition among conspecifics
92 for limited food resources on the non-breeding grounds- is also considered to explain chain
93 migrations; however, competition and food availability may not fully explain why the
94 northernmost populations of a leapfrog migrant bear the additional energetic cost of the extra
95 flight distance. Similarly, the environmental predictability hypothesis suggests that birds
96 wintering closer to the breeding grounds might more easily predict the occurrence of optimal
97 environmental conditions for breeding; these individuals might better time their return to the
98 nest site and achieve higher breeding success as a consequence (e.g. Bregnballe *et al.*, 2006;
99 Garthe *et al.*, 2012). However, again, this fails to explain why the northern populations of a
100 given species should leapfrog those that breed to the south. Finally, the hypothesis relating to
101 optimal time allocation in migratory birds predicts that the benefits of wintering at a more
102 distant site with better survival prospects (through high food availability, for instance) may be
103 higher if the leapfrog migrants can arrive sooner and so spend more time at the favourable
104 site. In this regard, northerly populations that breed later may winter further south to take
105 advantage of late spring food availability (e.g. Bell, 1997). However, results from other
106 species tend not to support this hypothesis (reviewed in Sandercock & Jaramillo, 2002).

107

108 In addition to the three hypotheses outlined above, a further hypothesis, here termed
109 *differential habitat preference*, could explain spatial segregation among populations, in some
110 cases leading to leapfrog migration, during the non-breeding season. For instance, migrants
111 from the north of the breeding distribution may be adapted to specific climatic conditions or
112 to feeding on particular resources that only occur in the southernmost areas of the non-
113 breeding range, which would compensate for the extra flight time and energetic cost of the
114 longer-distance movement. Surprisingly, to our knowledge, habitat selection has never been
115 considered as a driver of the evolution of leapfrog migration. At present, there is no consensus
116 on how leapfrog migration originated or why it occurs, although this is crucial for answering
117 fundamental questions about the evolution of migration patterns in general.

118

119 Here, using miniaturized geolocator-immersion loggers, we examined the at-sea distribution
120 and activity patterns of a small oceanic seabird, Bulwer's petrel (*Bulweria bulwerii*, Jardine &
121 Selby, 1828) from the major colonies across its breeding range in the North Atlantic (the
122 Azores, Salvages, Canary and Cape Verde archipelagos). This species is relatively abundant
123 in offshore waters of the northeast and central east Atlantic, during the summer, but, like
124 many subtropical and tropical seabirds, little is known about individual movements and
125 foraging ecology, particularly during the non-breeding season. Based on at-sea observations
126 from the last century, the Macaronesian populations of Bulwer's petrel were thought to winter
127 in a huge area in the central Atlantic between 20°N and 20°S (van Oordt & Kruijt, 1953;
128 Cramp, 1977; Bourne, 1995). However, at-sea observation does not allow determination of
129 the origin of birds, is subject to major sampling biases, and provides no information on the
130 timing of movements, segregation among populations, or variation within populations. A
131 recent study showed the first preliminary tracks of Bulwer's petrels for a few days after
132 breeding (Rodríguez *et al.*, 2013). Although valuable, the study only included three birds

133 tracked for 11-15 days after colony departure and devices were heavy in relation to body
134 mass, which may have affected the documented behaviour of the birds (>5% of body mass;
135 Phillips et al., 2003), therefore precluding any fruitful comparison with our data. Our aims
136 here were to: (1) identify for the first time the foraging areas used during the breeding and
137 non-breeding seasons by the main populations of Bulwer's petrel in Macaronesia, (2) define
138 the migration strategy of this small predator in the subtropical and tropical Atlantic Ocean,
139 and most importantly, (3) provide new insights into the ecology and evolution of long-
140 distance seabird migrations. To do so, we quantified the relative importance of different
141 foraging areas for each breeding population; assessed the degree of spatial overlap among
142 populations as well as the annual variability in at-sea distributions; characterized at-sea
143 activity patterns, and finally; defined the key oceanographic factors determining habitat use
144 by Bulwer's petrels at population and meta-population scales.

145

146 METHODS

147 *Species ecology*

148 Bulwer's petrel is a small (80-120g) procellariiform seabird (Fig. 1), which shows a highly
149 pelagic, pan-tropical and subtropical distribution, including the Atlantic, Pacific and Indian
150 oceans (Brooke, 2004). Within the Atlantic, it breeds on a few islets and islands throughout
151 much of Macaronesia (from the Azores to the Cape Verde archipelagos, including Madeira,
152 Salvages and Canary Islands), with an estimated total population of *ca.* 11,000 breeding pairs
153 (Mougin, 1989; Hernández *et al.*, 1990; Hazevoet, 1995; Monteiro *et al.*, 1996; Nunes &
154 Vicente, 1998; Luzardo *et al.*, 2008). Most adults arrive at the colony in late April, females
155 lay a single egg in late May/early June, chicks hatch at the end of July and fledge in mid to
156 late September (Nunes & Vicente, 1998). During the breeding season, Bulwer's petrels are
157 thought to be nocturnal feeders, specialized in exploiting mesopelagic prey that perform daily

158 vertical migrations (from 200 to 1000 m depth), including fish, especially lanternfish
159 *Myctophidae* (Zonfrillo, 1986; Mougín & Mougín, 2000; Neves *et al.*, 2011).

160

161 *Bird tracking data*

162 The present study was conducted at five breeding colonies at four Macaronesian archipelagos
163 (Fig. 2), over seven years (2007-2013; Table 1). At each colony, breeding adults incubating
164 an egg or rearing a chick were fitted with a small, leg-mounted, combined geolocator-
165 immersion logger (Mk13, Mk14, Mk18 [British Antarctic Survey, Cambridge, UK] and W65
166 [Migrate Technology Ltd, Cambridge, UK] models, weighing 1.8, 1.4, 1.9, and 0.65g,
167 respectively, corresponding to 0.7-2.0% of body mass). We deployed a total of 172
168 geolocators of which 115 (55.2-74.2%, depending on the colony) were recovered. To check
169 for short term effects of the logger deployment on adult survival, we constructed capture-
170 mark-recapture models (M-Surge version 1.8; Choquet *et al.*, 2006; we analysed 311 capture-
171 recapture histories over the period 2007-2014; see Table S1 in Appendix S1 for details).

172

173 Geolocators provide two positions per day based on light levels (one at local midday and
174 other at local midnight), with an average accuracy of ~200 km (or ~ 2°; Phillips *et al.*, 2004).
175 Positions were calculated using TransEdit and BirdTracker software (British Antarctic
176 Survey, 2008) by inspecting the integrity of the light curve day-by-day, and estimating dawn
177 and dusk times. We excluded long periods spent in burrows during incubation, based on light
178 data recorded by the logger. To filter unrealistic positions, we removed those that were (1)
179 obtained from light curves showing interference at dawn or dusk; (2) within the 20 closest
180 days to the equinoxes; and (3) that resulted in unrealistic flight speeds (>40 km h⁻¹ sustained
181 over 48 h) using bespoke software routines written in R (R Development Core Team, 2010).
182 Validated data were smoothed twice by interpolating intermediate fixes between successive

183 locations with fixed start and end points around any periods of missing data (Phillips *et al.*,
184 2004).

185

186 The loggers also registered saltwater immersion (wet/dry) at 3-s intervals using 2 electrodes
187 and stored the number of positive tests from 0 (continuously dry) to 200 (continuously wet) at
188 the end of each 10-min period. Light and immersion data were used simultaneously to (1)
189 distinguish time spent at sea from time at the colony (darkness in the burrows) and (2)
190 estimate the percentage of time spent on the sea surface as a proxy of foraging effort (Shaffer
191 *et al.*, 2001), separately for daylight and night periods. Following Dias *et al.* (2012), we
192 calculated a ‘night flight index’ (NFI) as the difference between the proportion of time spent
193 flying during night and during daylight, divided by the highest of these two values; this index
194 varies between -1 (flight activity restricted to daylight) and 1 (flight restricted to night).

195

196 *Spatial analyses and migratory connectivity*

197 We estimated six phenological and spatial parameters for every complete migration cycle (i.e.
198 non-breeding event): (1) departure date, (2) arrival date, (3) duration of the non-breeding
199 period (in days), (4) area exploited throughout the non-breeding period (as indicated by the
200 50% Utilization Distribution from kernel analysis, hereafter referred to as UD; in 10^6 km²),
201 (5) non-breeding range (orthometric distance between the breeding colony and the average
202 position of locations within the 5% UD; in km), and (6) latitude of the centroid of the non-
203 breeding period (i.e. mean latitude of all positions within the 5% UD; in degrees). After
204 normality checks (using Q-Q plots) and using model information criteria, we evaluated the
205 effect of colony of origin on migration parameters by fitting a set of candidate generalised
206 linear mixed models (GLMMs), where each of the six parameters described above was the
207 response variable and breeding colony was the main (fixed) explanatory variable (Table S2 in

208 Appendix S1). To account for annual and potential individual heterogeneity in migration
209 parameters, year of sampling and bird identity were included in all the GLMMs as random
210 terms. Gaussian distribution of error terms and the identity link function were used in the
211 modelling. The best-supported models were selected using the Akaike Information Criteria
212 corrected for small sample sizes (AICc) and the corresponding AICc weights (Johnson &
213 Omland, 2004). GLMMs were conducted in R with additional functions provided by the R
214 packages ‘lme4’ (lmer; Bates *et al.*, 2008) and ‘MuMIn’ (dredge; Bartoń, 2009).

215

216 To quantify spatial overlap among colonies during the non-breeding period, and also to assess
217 the effect of year within each colony, we also calculated the overlap in distribution between
218 the 14 non-breeding events (Table 2). Overlap indices between every pair of non-breeding
219 distributions were calculated using the 95% UDs and the ‘kerneloverlap’ function in the
220 ‘adehabitat’ package (VI method; Fieberg & Kochanny, 2005). Following Ambrosini *et al.*
221 (2009), we assessed the migratory connectivity among the five sampled colonies (using
222 breeding and non-breeding matrices of orthometric distances and Mantel correlation
223 coefficients), and the number of potential clusters in case of migratory structuring and sub-
224 structuring (using the ‘pamk’ function in the R package cluster). Importantly, this approach
225 did not force us to define *a priori* the number of breeding and non-breeding sub-ranges (or
226 clusters), which may be difficult when the species of interest shows continuous distributions
227 both in the breeding and non-breeding ranges. Statistical significance of the Mantel
228 correlation coefficient was determined by 9,999 random permutations. The number of clusters
229 was identified as the number that maximized the overall average silhouette width (oasw), a
230 measure of the goodness of fit of the overall classification of points in a given number of
231 clusters (Rousseeuw, 1987).

232

233 *Environmental data and habitat modelling*

234 To determine the oceanographic characteristics of areas used by the tracked birds, we
235 considered the seafloor depth (BAT, m), surface chlorophyll *a* concentration (CHLa, mg m⁻³),
236 salinity (SAL, g of salt per kg of water), sea surface temperature (SST, °C), and wind speed
237 (WIND, m s⁻¹). All remote sensing products were extracted from NOAA CoastWatch
238 (<http://coastwatch.pfeg.noaa.gov/>) for a grid including the whole Atlantic Ocean. The static
239 BAT variable and monthly composites of CHLa, SST and WIND (dynamic variables
240 downloaded for the period 2007-2013) were rescaled to a common spatial resolution of 2.0°,
241 which matches the accuracy of geolocation data. In addition to these five oceanographic
242 variables, gradients for BAT, CHLa and SST were also considered (BATG, CHLG and
243 SSTG, respectively). Dynamic variables were averaged by: a) breeding period, from April to
244 August, b) non-breeding period, from October to February, and c) year-round, from January
245 to December, for every year. To exclude redundant variables, pairwise correlations among the
246 eight environmental variables were evaluated separately for each period (i.e. breeding, non-
247 breeding, and year-round) using Spearman methodology with Holm adjustments (Table S3 in
248 Appendix S1).

249

250 Bulwer's petrel habitat probability models were developed using the MaxEnt v.3.3.3e
251 software (Phillips *et al.*, 2006), a program for modelling ecological niches from presence-only
252 records. In a first modelling approach, habitat probability models were run with six non-
253 redundant variables (i.e. BAT, BATG, CHLa, SST, SSTG and WIND) for each of the ten data
254 subsets, including the five colonies (separately and jointly) during the breeding period (6
255 models), the two main wintering regions (i.e., the two main clusters derived from the
256 migratory connectivity assessment; separately and jointly) during the non-breeding period (3
257 models), and year-round (1 model). All habitat use models were developed on the basis of a

258 logistic output format and with 100 bootstrapped replicates, each of them built on randomly
259 sampled subsets of 10% of the bird positions as training points. This conservative approach
260 (i.e. 90% of seabird records were used for model testing) avoids model over-fitting and
261 minimizes effects of spatial autocorrelation in both seabird presence and environmental
262 covariates. The data were jack-knifed to evaluate each variable's importance in explaining the
263 observed distribution. The percentage of contribution of each variable was calculated on the
264 basis of how much the variable contributed to an increase in the regularized model gain as
265 averaged over each model run. To determine the permutation importance of each variable, the
266 values in the training presence and background data were randomly varied and the resulting
267 change in the area under the curve (AUC) statistic was examined, normalized to percentages
268 (Phillips *et al.*, 2006). The results were summarized as the average of the 100 models, and
269 model evaluation was performed using the AUC statistic, which measures the ability of model
270 predictions to discriminate seabird presence from background points (Table 3). In a second
271 modelling approach, the five predictive models developed for the breeding period (and for
272 each colony) were used to build probability maps for each of the populations during the non-
273 breeding season using the relevant environmental variables averaged for the non-breeding
274 period (Fig. 3).

275

276 RESULTS

277 First of all, capture-mark-recapture models revealed no effect of logger deployment on the
278 survival probability of Bulwer's petrel (estimated annual survival rate= 0.76 ± 0.19), although
279 recapture probability was higher in equipped birds due to the incentive of the researchers to
280 recover devices ($p=0.66 \pm 0.14$ and 0.77 ± 0.15 for non-equipped and equipped birds,
281 respectively). Likewise, studies using geolocators on another small seabird species (thin-
282 billed prions *Pachyptila belcheri* weighing ca.130 g; Quillfeldt *et al.*, 2012) found no obvious

283 effect of logger deployment on foraging ability, although a significant ecophysiological effect
284 is expected on those birds carrying devices due to the higher load.

285

286 We obtained 104 complete tracks from 98 individual Bulwer's petrels from five different
287 colonies during the breeding and non-breeding seasons (Table 1). After filtering and
288 interpolation, we obtained a total of 50,543 positions, of which 38.4% and 61.6% were from
289 the breeding and non-breeding periods, respectively.

290

291 *Non-breeding distribution and migratory characteristics*

292 During the non-breeding period, Bulwer's petrels were concentrated around a core area in
293 equatorial waters in the central Atlantic (Fig. 2). Overall, 60.4% of the birds (range among
294 colonies 40.0-85.0%) spent the entire non-breeding period in this area. However, a substantial
295 proportion of birds from Vila (45.5%), Selvagem Grande (53.3%) and Montaña Clara (50.0%)
296 migrated further south to an area in the southern Atlantic Ocean situated between 10° and 30°
297 S. Most of these birds staged in the equatorial region for several days during their outward
298 and return migrations.

299

300 Substantial variation in migratory phenology and in the spatial components of migration
301 occurred among populations but also among individuals (Table 1). Overall, the duration of the
302 non-breeding period, the non-breeding range, the area visited and the latitude of the core area
303 exploited during the non-breeding period tended to be greater in the birds from subtropical
304 colonies (i.e. Vila, Selvagem Grande and Montaña Clara), than those from Cape Verde (Table
305 S2 in Appendix S1). In particular, the distance between the breeding colony and the average
306 position of the non-breeding area (i.e. the non-breeding range) was colony-dependent (Fig. 1),
307 with subtropical colonies ranging 1,646.5-7,342.5 km (on average $4,631.7 \pm 1,629.3$), and Cape

308 Verde colonies ranging 256.2-3,540.2 km (on average 1,691.4±911.3) from their respective
309 wintering areas.

310

311 *Migratory connectivity and overlap of non-breeding grounds*

312 Bulwer's petrels showed significant migratory connectivity (n = 104, Mantel correlation
313 coefficient $r_M = 0.042$, P = 0.047), and could be grouped into two distinct clusters (overall
314 average silhouette width value, $oasw = 0.529$; Fig. S1 in Appendix S2). The northern cluster
315 (A) included petrels from all five breeding colonies that wintered north and south of the
316 Equator in the central Atlantic, whereas the southern cluster (B) was mainly constituted by
317 individuals from northern colonies that wintered further south of the Equator (Fig. 2). While
318 the southern cluster showed non-significant connectivity (n = 42, $r_M = 0.065$, P = 0.128), the
319 northern cluster was structured as two significant sub-clusters (n = 62, $r_M = 0.071$, P = 0.019,
320 $oasw = 0.547$): sub-cluster A1 only included individuals breeding in the northern colonies,
321 whereas sub-cluster A2 consisted exclusively of birds from the two Cape Verde colonies.

322

323 In agreement with the results shown above, overlap analyses identified two distinctive groups
324 of non-breeding birds: (i) Cape Verde colonies (Raso and Cima Islets) which showed a
325 relatively high overlap (68.6% on average; Table 2), and (ii) Vila, Selvagem Grande and
326 Montaña Clara, which also showed considerable overlap (52.6%). In contrast, there was
327 considerably less overlap between these two groups (33.9%; Table 2). In addition, the areas
328 exploited by birds from the same colony in different years showed a relatively high overlap
329 (mean of 57.1, 51.9, 70.6, 73.1 and 72.6% for Vila, Selvagem Grande, Montaña Clara, Raso
330 and Cima Islets, respectively; Table 2).

331

332 *Habitat modelling*

333 The MaxEnt variable importance and the percentage of variable contribution rankings differed
334 both between seasons, and among groups of birds (i.e., colonies and clusters; Table 3). Jack-
335 knife tests identified SST as the most important variable, which also accounted for the highest
336 percentage contribution to both breeding and non-breeding model sets. During the breeding
337 season, the highest-ranked variable was either SST or WIND, whereas for the non-breeding
338 season, SST and SSTG (for cluster A), and SST and CHLa (for cluster B) were the most
339 important variables. In general during the breeding season, there was a consistent preference
340 by birds from all colonies for areas with warm waters (range: 15-25 °C for subtropical
341 colonies and 24-28 °C for Cape Verde colonies) and low wind intensity (5-8 m s⁻¹ for all
342 colonies). Similarly, modelling of the habitat used during the non-breeding period also
343 indicated that birds tended to select areas of warm waters (Table 3).

344

345 Habitat modelling for the birds from the Azores, Salvages and Canary Islands suggested that
346 the calm and warm waters around the Azores archipelago were the most suitable habitat for
347 these populations (Figs 3a, 3c & 3e), whereas for the birds from Cape Verde, it was the
348 warmer areas south of this archipelago in the Central Atlantic (Figs 3g & 3i). Additionally,
349 suitable non-breeding habitats were also estimated for the different populations using
350 prediction models developed for birds during the breeding season. The predicted wintering
351 distributions of the birds from the Azores, Salvages and Canary Islands were similar, and
352 indicated that oceanic areas in the South Atlantic should be the most preferred (Figs 3b, 3d &
353 3f). The most suitable areas predicted for the two Cape Verde colonies expanded over the
354 central equatorial area of the Atlantic Ocean (Figs 3h & 3j), therefore differing from those
355 predicted for the subtropical populations.

356

357 *At-sea activity patterns*

358 Analysis of at-sea activity patterns revealed substantial heterogeneity between seasons,
359 among breeding colonies, among non-breeding latitudes, and between daylight and darkness
360 periods (Table 4). Overall, birds tended to spend more time flying at night than during the day
361 throughout the year (Fig. 4), and this was particularly noticeable during the non-breeding
362 period (i.e. there was a significant interaction between period and day/night factors; Table 4).
363 Night flight index showed a latitudinal gradient during both the breeding and non-breeding
364 periods. During the breeding period, birds foraging at northern latitudes spent more time
365 flying at night than during the day, whereas those foraging at southern latitudes spent similar
366 amounts of time in flight during the day and at night. Conversely, birds that spent the non-
367 breeding period at northern latitudes displayed more diurnal activity than those at southern
368 latitudes (Figs 4a & 4c). During the breeding period, the best-supported models for the time
369 spent flying included an interaction between colony and day/night (Table 4), i.e., the time
370 spent flying differed between daylight and darkness, but only for the birds from the
371 northernmost colonies (Fig. 4b). These differences among colonies were observed during
372 daylight, but not during darkness, when the time spent flying was always substantial,
373 representing around 80% of time. During the non-breeding period, the best supported model
374 also revealed a significant interaction in time spent flying between latitude and day/night,
375 highlighting that the variation in flying activity duration followed a latitudinal trend which
376 differed between daylight and darkness (Table 4). That is, the proportion of time spent flying
377 during the night was constantly high irrespective of latitude, whereas during daylight, it was
378 lower in those birds that wintered further south (Fig. 4d).

379

380 DISCUSSION

381 *Non-breeding distribution of Bulwer's petrel in the Atlantic Ocean*

382 During the non-breeding season, the tracked Bulwer's petrels congregated in large numbers
383 within a relatively restricted area in the mid-equatorial Atlantic Ocean, north of the Saint
384 Peter and Saint Paul archipelago (0°55'N, 29°20'W; hereafter Saint Paul's Rocks). Previous
385 results from at-sea surveys had suggested that this might be an important wintering area for
386 Bulwer's petrels (van Oordt & Kruijt, 1953; Bourne, 1995). Our results confirm this for a
387 large proportion of birds from different breeding populations. Among these birds, those from
388 Cape Verde highlighted by their strategy of partial migration (Chapman *et al.*, 2011), where
389 many birds remained during the non-breeding period in broadly the same area that they used
390 during the breeding season while others dispersed south, around the Equator (Fig. 2).

391
392 In addition, a substantial proportion of birds from the northernmost populations (Azores,
393 Salvages and Canary Islands) leapfrog the birds from more southerly colonies, which winter
394 north of Saint Paul's Rocks, to spend the non-breeding period further south. There have been
395 few reports of Bulwer's petrels in these subtropical waters (van Oordt & Kruijt, 1953;
396 Bourne, 1995), probably because of the extensive areas and the apparent absence of high
397 concentrations of wintering birds (Fig. 2). Thus, at a meta-population scale, all the
398 Macaronesian populations of Bulwer's petrels largely overlap during the non-breeding season
399 in tropical waters north of Saint Paul's Rocks, and only birds from the northern populations
400 exploit the subtropical Atlantic Ocean further south than 20°.

401
402 *Leapfrog migration: avoidance of competition or differential habitat preference hypothesis?*

403 The decision of an individual to spend time in a given area is dictated by the suitability of the
404 habitat (Guisan & Zimmermann, 2000). The latter depends largely on two non-exclusive
405 factors: the number of conspecifics and competitors, and the inherent productivity and quality
406 of the habitat itself. In addition, for long-distance migrants, the distance between the foraging

407 habitat and the breeding grounds might also play a role in habitat selection (e.g., Duijns *et al.*,
408 2012). Therefore, oceanic migrants must take complex decisions when selecting their habitat,
409 at least twice a year: during the breeding period, when they behave as central place foragers
410 and are tied to the waters surrounding their colonies, and also in the non-breeding season,
411 when, unconstrained, they can virtually access any area where conditions are suitable.

412

413 In oceanic areas, the trophic resources of pelagic predators are patchy and very often
414 dispersed over immense oligotrophic waters. Spatial predictability and general availability of
415 prey in these vast pelagic environments are thus expected to be lower than in productive but
416 spatially restricted upwelling regions. Under these conditions, direct competition among
417 individuals for specific prey in pelagic areas could be considered very low indeed. Therefore,
418 individual movements and specific migratory strategies in a long-distance migrant such as
419 Bulwer's petrel could be linked more to the habitat characteristics of both the breeding and
420 non-breeding areas than to intra-specific competition for food.

421

422 The habitat modelling of the geolocation data from Bulwer's petrels accurately predicted the
423 foraging range of five populations during the breeding season. According to the ecological
424 niche models for this period, the key habitat variables were sea surface temperature and wind
425 intensity (Table 3). These environmental characteristics differed substantially between
426 seasons in the subtropical areas of both hemispheres, but remained relatively constant year-
427 round in the equatorial waters. Based on the ecological niche models for the breeding season,
428 the spatial distribution of each population was predicted well during the non-breeding season
429 (Fig. 3). The breeding-season models for the subtropical populations of Bulwer's petrels
430 extrapolated to the non-breeding period tended to assign more importance to the subtropical
431 waters of the southern Atlantic than to tropical waters. For the tropical populations, the

432 MaxEnt models predicted similar distributions during the breeding and non-breeding periods
433 (within tropical waters). These models performed relatively well when predicting non-
434 breeding distributions, especially for tropical populations. For the subtropical populations, the
435 most preferred habitat was predicted to be the subtropical waters of the southern hemisphere
436 (Fig. 3), which was exploited by around half of the tracked birds, whereas the others remained
437 in equatorial waters, sharing this habitat with conspecifics from Cape Verde.

438

439 In addition to habitat modelling, we provide critical clues to the variety of foraging tactics
440 used by Bulwer's petrel. Indeed, the exploitation of different areas throughout the year
441 indicates a degree of habitat specialization by some individuals or populations, as well as
442 differences in habitat quality. Activity patterns clearly differed among breeding populations,
443 but also among wintering areas (Fig. 4). On the one hand, individuals from subtropical
444 populations tended to forage more intensively at night than during the day during breeding, as
445 did the birds that wintered in the southern subtropical Atlantic. On the other hand, birds from
446 tropical populations tended to forage during the day as much as at night while breeding, as did
447 those individuals that spent the non-breeding season around the equator. This suggests that
448 prey behaviour and availability in the area exploited by tropical populations during the
449 breeding season are similar to those in tropical waters during the non-breeding season, which
450 would allow petrels to forage day and night. Such habitat or prey specialization might reflect
451 local adaptation by the Bulwer's petrels breeding in the Cape Verde archipelago. In contrast,
452 prey availability would be mainly restricted to darkness in the areas exploited by subtropical
453 populations during the breeding period, and in the subtropical waters of the south Atlantic
454 during the non-breeding season. Thus, prey availability and specific habitat preferences
455 (rather than the need to avoid competitors) could be the main factors explaining the observed
456 distribution and the leapfrog migration described for Bulwer's petrel.

457

458 However, another factor should be taken into account that might explain the non-breeding
459 distribution of Bulwer's petrels in the Atlantic. Otherwise, why did half of the individuals
460 from the subtropical populations migrate to the subtropical (and preferred) non-breeding sub-
461 range, while the other half stayed closer in the tropical (and less suitable) sub-range? A trade-
462 off might exist between the benefit of exploiting a more suitable, familiar habitat and
463 energetic constraints. The higher costs of longer migrations might be compensated by a more
464 efficient exploitation of more distant wintering grounds, so that neither a short- nor a long-
465 distance migratory strategy is consistently more successful (e.g. Hestbeck *et al.*, 1992). In this
466 regard, the longer period spent in subtropical wintering areas by individuals from subtropical
467 colonies (see Table 1), compared with the relatively shorter non-breeding season of tropical
468 birds (by *ca.* 50 days on average), would further support the *differential habitat preference*
469 hypothesis for leapfrog migrations in this species. This would explain why southerly birds
470 migrated relatively short distances and remained within the tropics in winter, while part of the
471 northern populations engaged in longer migrations, and spent the winter south of the Tropic
472 of Capricorn. The cost of transit to this more distant area would encourage other individuals
473 from the northern populations to stay within the tropical, less-preferred region during the non-
474 breeding season, where they overlap with the southern populations.

475

476 *Conclusions*

477 Understanding the spatiotemporal importance of habitats and areas used by marine fauna,
478 defined at local, regional and international scales, should be a first priority to try and ensure
479 their conservation (Game *et al.*, 2009). In this regard, our study not only provides evidence
480 and tools to researchers for designing appropriate studies aiming to disentangle migratory
481 patterns of marine species at sea, but also provides a good example for those investigations

482 focussing on understanding the ecological basis for inter- and intra-specific variation in
483 strategies of long-distance migrants. Using tracking technology and habitat modelling, we
484 determined the spatiotemporal distribution and migration pattern of a given species; assessed
485 migratory connectivity and habitat use; and explored alternative explanations for the
486 strategies observed. Our study demonstrates the utility of integrating diverse tracking data
487 from multiple populations/species across international boundaries, and habitat modelling, for
488 identifying important areas common to many marine species in the vast oceanic
489 environments. This will ultimately allow improving and optimizing the targeting of broad-
490 scale marine conservation efforts.

491
492 To our knowledge, this is the first time that an oceanic seabird has been identified as a
493 leapfrog migrant. As discussed above and as reported for several leapfrog migratory species
494 occurring in terrestrial habitats (e.g., Duijns *et al.*, 2012; Fraser *et al.*, 2012; Stanley *et al.*,
495 2014), competition *per se* and food availability may not fully explain why some individuals
496 from the northernmost populations of Bulwer's petrel undertake a leapfrog migration during
497 which they bear the additional energetic cost of the extra flight distance. Instead, these
498 individuals may prefer specific environmental conditions or be adapted to feed on particular
499 resources that only occur in the southernmost part of the non-breeding range, which would
500 partially compensate for the extra flight time and cost (Boland, 1990; Bell, 1997; Garthe *et*
501 *al.*, 2012). Comparative studies conducted on individuals tracked over several years under
502 contrasting conditions and at several localities would add valuable information on individual
503 plasticity. Furthermore, complementary studies of trophic ecology based on, for example,
504 stable isotope analyses of feathers moulted at different periods of the annual cycle would shed
505 light on habitat and diet preferences in the different breeding and non-breeding quarters, and

506 potentially provide more insights into the reasons underlying leapfrog migration (Ramos &
507 González-Solís, 2012).

508

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522

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- 682

683

684 SUPPORTING INFORMATION

685 Additional Supporting Information may be found in the online version of this article:

686 Appendix S1. Additional Supporting Tables showing modelling of capture-mark-recapture
687 data (Table S1), generalised linear mixed models of migratory characteristics (Table S2), and
688 correlation among oceanographic variables used in habitat modelling of Bulwer's petrel
689 (*Bulweria bulwerii*; Table S3).

690 Appendix S2. Silhouette plot showing the classification of Bulwer's petrel (*Bulweria*
691 *bulwerii*) individuals in two first-level clusters (Fig. S1).

692

693 BIOSKETCH

694 Raül Ramos is currently interested in the spatial and temporal responses of seabirds to the
695 marine environment. He has combined several interdisciplinary approaches such as intrinsic
696 biogeochemical markers (trace elements and stable isotope analysis), tracking devices and
697 capture-mark-recapture data to ascertain the distribution, abundance and demography of
698 seabirds in the marine environment. His previous work focussed on the trophic ecology of
699 seabirds and their long-distance migratory strategies. More recently, his interests have
700 expanded into several fields involving the epidemiology and the immune system acquisition
701 of long-lived seabirds.

702

703 Author contributions: R.R. and J.G-S. designed the study; R.R., V.S., T.M., J.B., V.C.N.,
704 M.B., R.A.P., F.Z. and J.G-S. conducted the fieldwork; R.R., V.S., T.M., analysed the data;
705 R.R. and J.G-S. wrote the first complete version of the manuscript; J.B., R.A.P., F.Z. read and
706 commented on the manuscript.

707

708 Editor: Michael Patten

709 **Table 1.** Migration characteristics (mean±SD) of Bulwer's petrels (*Bulweria bulwerii*) tracked from five colonies in the Macaronesian

710 archipelagos of the Azores, Salvages, Canaries, and Cape Verde. For each population, "Total" refers to total number of migrations tracked.

| Breeding colony (archipelago) | Year | n | Colony departure date | Colony arrival date | Duration of the non-breeding period (days) | Area during the non-breeding period (10 ⁶ km ²) | Distance to non-breeding range (km) | Centroid latitude of the non-breeding period (°) |
|------------------------------------|--------------|-----------|-----------------------|----------------------|--|--|-------------------------------------|--|
| Vila Islet (Azores Islands) | 2007 | 8 | 03 Sep ± 4.1 | 05 May ± 3.6 | 244.6 ± 5.7 | 3.5 ± 1.4 | 5605.7 ± 1528.9 | -12.7 ± 13.9 |
| | 2008 | 1 | 21 Sep | 14 May | 235 | 5.6 | 5705.6 | -12.8 |
| | 2010 | 5 | 01 Sep ± 6.1 | 06 May ± 0.9 | 247.2 ± 5.5 | 2.2 ± 0.9 | 4786.2 ± 1372.4 | -4.9 ± 12.8 |
| | 2012 | 1 | 12 Oct | 24 Apr | 194 | 1.8 | 3306.9 | 8.6 |
| | Total | 15 | 06 Sep ± 12.1 | 05 May ± 4.7 | 241.5 ± 14.4 | 3.1 ± 1.5 | 5185.9 ± 1461.5 | -8.7 ± 13.4 |
| Selvagem Grande (Salvages Islands) | 2009 | 4 | 26 Aug ± 14.0 | 13 Apr ± 3.3 | 230.2 ± 14.2 | 1.7 ± 1.2 | 3885.3 ± 1883.3 | -1.6 ± 18.1 |
| | 2012 | 7 | 01 Sep ± 0.8 | 30 Mar ± 0.8 | 209.6 ± 1.0 | 1.9 ± 1.2 | 5135.5 ± 1159.1 | -14.2 ± 11.9 |
| | Total | 11 | 30 Aug ± 8.6 | 04 Apr ± 7.3 | 217.1 ± 13.0 | 1.8 ± 1.1 | 4680.9 ± 1506.0 | -9.6 ± 14.9 |
| Montaña Clara (Canary Islands) | 2010 | 14 | 27 Aug ± 19.9 | 28 Apr ± 7.9 | 244.4 ± 20.7 | 4.1 ± 2.2 | 4555.3 ± 1736.6 | -8.4 ± 18.1 |
| | 2011 | 6 | 05 Sep ± 30.8 | 29 Apr ± 3.0 | 237.0 ± 28.4 | 4.6 ± 1.6 | 5387.2 ± 1311.0 | -16.0 ± 13.8 |
| | 2012 | 21 | 09 Sep ± 29.0 | 21 Apr ± 6.1 | 223.6 ± 28.1 | 2.7 ± 1.8 | 4045.1 ± 1724.1 | -4.0 ± 16.9 |
| | Total | 41 | 04 Sep ± 26.7 | 25 Apr ± 7.4 | 232.7 ± 27.0 | 3.5 ± 2.0 | 4415.7 ± 1703.5 | -7.3 ± 17.1 |
| Raso Islet (Cape Verde) | 2007 | 8 | 24 Oct ± 15.5 | 22 Apr ± 6.8 | 181.0 ± 13.5 | 0.8 ± 0.4 | 2097.5 ± 1047.1 | 0.1 ± 9.2 |
| | 2008 | 5 | 09 Sep ± 26.7 | 24 Apr ± 8.6 | 227.6 ± 24.9 | 1.4 ± 1.4 | 2212.0 ± 1220.3 | -1.9 ± 9.9 |
| | 2009 | 4 | 25 Sep ± 18.9 | 19 Apr ± 3.5 | 205.5 ± 15.9 | 1.1 ± 0.4 | 1343.4 ± 810.8 | 8.5 ± 10.5 |
| | Total | 17 | 04 Oct ± 27.4 | 22 Apr ± 6.8 | 200.5 ± 26.6 | 1.1 ± 0.8 | 1953.7 ± 1048.6 | 1.5 ± 9.9 |
| Cima Islet (Cape Verde) | 2010 | 6 | 09 Aug ± 11.5 | 03 Feb ± 14.7 | 177.5 ± 19.4 | 1.3 ± 0.4 | 1210.1 ± 751.6 | 6.5 ± 6.3 |
| | 2011 | 14 | 03 Aug ± 17.5 | 14 Jan ± 29.5 | 164.1 ± 28.7 | 1.8 ± 0.7 | 1579.2 ± 720.4 | 3.7 ± 6.7 |
| | Total | 20 | 05 Aug ± 15.9 | 22 Jan ± 27.2 | 168.1 ± 26.5 | 1.6 ± 0.7 | 1468.4 ± 730.6 | 4.5 ± 6.6 |

711

712 **Table 2.** Overlap in the 95% kernel UD of Bulwer's petrels (*Bulweria bulwerii*) tracked during the non-breeding period. Pairwise comparisons are
 713 of the fourteen non-breeding events considered in this study.

714

| Non-breeding event | Vila 2007-08 | Vila 2008-09 | Vila 2010-11 | Vila 2012-13 | Selvagem 2009-10 | Selvagem 2012-13 | M. Clara 2010-11 | M. Clara 2011-12 | M. Clara 2012-13 | Raso 2007-08 | Raso 2008-09 | Raso 2009-10 | Cima 2010-11 |
|--------------------|--------------|--------------|--------------|--------------|------------------|------------------|------------------|------------------|------------------|--------------|--------------|--------------|--------------|
| Vila 2008-09 | 65.8 | | | | | | | | | | | | |
| Vila 2010-11 | 73.6 | 52.0 | | | | | | | | | | | |
| Vila 2012-13 | 51.3 | 34.7 | 65.1 | | | | | | | | | | |
| Selvagem 2009-10 | 45.0 | 27.4 | 53.9 | 48.7 | | | | | | | | | |
| Selvagem 2012-13 | 58.6 | 44.7 | 51.8 | 34.3 | 51.9 | | | | | | | | |
| M. Clara 2010-11 | 57.6 | 51.5 | 54.7 | 43.1 | 60.2 | 49.3 | | | | | | | |
| M. Clara 2011-12 | 56.2 | 52.4 | 54.1 | 35.3 | 59.5 | 57.9 | 76.1 | | | | | | |
| M. Clara 2012-13 | 49.5 | 44.4 | 49.2 | 41.1 | 59.2 | 47.5 | 75.5 | 66.2 | | | | | |
| Raso 2007-08 | 35.5 | 30.6 | 39.1 | 33.2 | 38.1 | 21.8 | 38.0 | 25.9 | 40.7 | | | | |
| Raso 2008-09 | 30.8 | 31.1 | 31.1 | 26.6 | 32.0 | 20.2 | 33.7 | 23.6 | 38.6 | 76.1 | | | |
| Raso 2009-10 | 34.0 | 30.9 | 37.2 | 35.6 | 35.5 | 22.0 | 37.5 | 27.5 | 45.0 | 73.4 | 68.3 | | |
| Cima 2010-11 | 33.2 | 22.7 | 39.6 | 40.1 | 45.7 | 21.2 | 35.2 | 24.8 | 36.0 | 69.3 | 62.0 | 57.9 | |
| Cima 2011-12 | 41.0 | 31.7 | 46.8 | 44.8 | 48.0 | 25.7 | 40.9 | 29.4 | 44.4 | 73.3 | 68.1 | 65.4 | 72.6 |

715

716

717

718 **Table 3.** Estimates of model fit (AUC) and relative importance (contribution percentage and permutation importance, both normalized to percentages) of the
719 environmental variables to the modelled Bulwer's petrel (*Bulweria bulwerii*) presence probability (relevant values > 20% in bold). The percentage contribution
720 of each variable was calculated on the basis of how much the variable contributed to an increase in the regularized model gain as averaged over each model run.
721 Permutation importance of a given variable derived from the resulting change in training AUC when values of this variable on training presence and background
722 data were randomly varied. Analyses were carried out separately for the breeding and non-breeding periods, and year-round. Colony of origin and main non-
723 breeding areas (i.e. connectivity cluster) were included as fixed factors for the breeding and non-breeding datasets, respectively. Values shown are averages over
724 100 model replicates. AUC: area under the receiver operating characteristic curve; BAT: bathymetry; BATG: gradient of BAT; CHLa: chlorophyll *a*
725 concentration; SST: sea surface temperature, SSTG: gradient of SST, and WIND: wind speed.

| | AUC | Percentage of contribution | | | | | | Permutation importance | | | | | |
|---------------------------|-------------|----------------------------|------|-------------|-------------|------|-------------|------------------------|------|------|-------------|-------------|-------------|
| | | BAT | BATG | CHLa | SST | SSTG | WIND | BAT | BATG | CHLa | SST | SSTG | WIND |
| Breeding period | | | | | | | | | | | | | |
| Vila | 0.966±0.004 | 4.1 | 1.9 | 4.5 | 37.4 | 12.1 | 40.0 | 3.4 | 1.1 | 1.5 | 26.6 | 8.7 | 58.7 |
| Selvagem | 0.902±0.008 | 4.5 | 6.0 | 4.4 | 38.6 | 7.5 | 38.9 | 8.8 | 4.8 | 7.2 | 31.2 | 11.2 | 36.7 |
| Montaña Clara | 0.915±0.007 | 3.7 | 3.9 | 5.1 | 48.8 | 8.3 | 30.2 | 6.0 | 4.0 | 6.3 | 40.2 | 15.0 | 28.5 |
| Raso | 0.920±0.008 | 9.4 | 2.4 | 13.9 | 60.5 | 3.5 | 10.3 | 10.5 | 4.5 | 14.7 | 56.3 | 5.5 | 8.6 |
| Cima | 0.943±0.005 | 12.1 | 2.6 | 15.1 | 55.4 | 2.3 | 12.5 | 15.4 | 3.3 | 14.3 | 43.1 | 3.2 | 20.8 |
| <i>Total breeding</i> | 0.864±0.008 | 7.3 | 4.8 | 7.9 | 30.3 | 6.7 | 43.0 | 12.3 | 7.2 | 10.7 | 25.6 | 12.0 | 32.1 |
| Non-breeding period | | | | | | | | | | | | | |
| <i>cluster A</i> | 0.851±0.006 | 3.8 | 3.4 | 13.3 | 58.1 | 19.2 | 2.3 | 7.4 | 3.7 | 7.0 | 57.1 | 21.7 | 3.2 |
| <i>cluster B</i> | 0.838±0.006 | 4.4 | 3.2 | 32.0 | 49.4 | 4.7 | 6.4 | 11.1 | 5.4 | 15.5 | 46.7 | 9.6 | 11.7 |
| <i>Total non-breeding</i> | 0.829±0.006 | 4.7 | 3.2 | 27.9 | 54.2 | 8.1 | 1.9 | 9.8 | 5.8 | 12.5 | 53.6 | 15.6 | 2.7 |
| Year round | 0.812±0.006 | 6.4 | 5.1 | 18.3 | 54.6 | 9.1 | 6.6 | 12.8 | 6.8 | 9.8 | 45.4 | 16.3 | 8.9 |

726

727 **Table 4.** Parameter estimates (\pm SE) from generalised linear mixed models fitted to at-sea activity (estimated as number of hours spent flying) of
728 Bulwer's petrels (*Bulweria bulwerii*) throughout the year. Time spent flying was modelled considering breeding colony and day/night as fixed
729 factors for the breeding period, ranges of 15 degrees of latitude and day/night as fixed factors for the non-breeding period, and season (i.e. breeding
730 and non-breeding periods) and day/night as fixed factors for the entire annual period. In all cases, the interaction between the two fixed effects was
731 included (i.e. colony*daynight, latitude*daynight, and season*daynight, respectively). All evaluated models included individual and year of
732 sampling as random factors. AICc refers to the corrected (c) Akaike's Information Criterion (AIC).

| | Time spent flying _{breeding} | | | | Time spent flying _{non-breeding} | | | | Time spent flying _{year} | | | | | |
|-----------------------------------|---------------------------------------|-----------------|----------------|-----------------------------------|---|-----------|-----------------|-----------------------------------|-----------------------------------|--------------------------|---------------|-----------------|----------------|------------|
| | k | AICc | Δ AICc | AICc Wgt | k | AICc | Δ AICc | AICc Wgt | k | AICc | Δ AICc | AICc Wgt | | |
| colony * daynight | 13 | 127565.8 | 0.0 | 1.0 | latitude * daynight | 13 | 188023.9 | 0.0 | 1.0 | season * daynight | 7 | 323853.8 | 0.0 | 1.0 |
| colony + daynight | 9 | 129460.1 | 1894.4 | 0.0 | latitude + daynight | 9 | 189433.6 | 1409.8 | 0.0 | season + daynight | 6 | 326824.3 | 2970.5 | 0.0 |
| colony | 8 | 131867.1 | 4301.4 | 0.0 | latitude | 8 | 210197.2 | 22173.3 | 0.0 | season | 5 | 345114.3 | 21260.6 | 0.0 |
| daynight | 5 | 129590.2 | 2024.5 | 0.0 | daynight | 5 | 190820.8 | 2796.9 | 0.0 | daynight | 5 | 334415.7 | 10561.9 | 0.0 |
| null | 4 | 132009.7 | 4443.9 | 0.0 | null | 4 | 210828.2 | 22804.3 | 0.0 | null | 4 | 350022.5 | 26168.8 | 0.0 |
| Fixed effects (estimate \pm SE) | | | | Fixed effects (estimate \pm SE) | | | | Fixed effects (estimate \pm SE) | | | | | | |
| | | | 10.5 \pm 0.8 | | | | 6.7 \pm 0.2 | | | | | 7.1 \pm 0.3 | | |
| | | | -5.9 \pm 0.4 | | | | -0.6 \pm 0.1 | | | | | -2.0 \pm 0.0 | | |
| | | | -1.1 \pm 0.4 | | | | -1.8 \pm 0.1 | | | | | | | |
| | | | -4.0 \pm 0.4 | | | | -3.0 \pm 0.1 | | | | | | | |
| | | | -2.1 \pm 0.4 | | | | -3.9 \pm 0.1 | | | | | | | |
| | | | 0.3 \pm 0.1 | | | | 2.3 \pm 0.2 | | | night | | | 3.0 \pm 0.0 | |
| | | | 3.5 \pm 0.1 | | | | -0.4 \pm 0.2 | | | Non-breeding & night | | | -0.2 \pm 0.0 | |
| | | | 1.5 \pm 0.2 | | | | 0.6 \pm 0.2 | | | | | | | |
| | | | 2.2 \pm 0.1 | | | | 2.0 \pm 0.2 | | | | | | | |
| | | | 2.9 \pm 0.1 | | | | 1.9 \pm 0.2 | | | | | | | |
| Random effect (variance \pm SE) | | | | Random effect (variance \pm SE) | | | | Random effect (variance \pm SE) | | | | | | |
| | | | 0.9 \pm 0.9 | | | | 1.6 \pm 1.2 | | | | | | 0.8 \pm 0.9 | |
| | | | 3.7 \pm 1.9 | | | | 0.1 \pm 0.4 | | | | | | 0.6 \pm 0.8 | |
| | | | 2.8 \pm 1.7 | | | | 2.8 \pm 1.7 | | | | | | 3.3 \pm 1.8 | |

733 **Figure 1.** Estimated distance (in kilometres) between the breeding and non-breeding areas of
734 every tracked petrel from each of the five study colonies. Latitude of each colony (in degrees)
735 is used in the x-axis. Picture courtesy of Olli Tenouvo.

736

737 **Figure 2.** Kernel density distributions (25, 50, 75, and 95%, from darker to lighter tone
738 contours, respectively) of Bulwer's petrels (*Bulweria bulwerii*) tracked during the non-
739 breeding periods from different colonies: (a) Vila Islet in the Azores, (b) Selvagem Grande in
740 Salvages Islands, (c) Montaña Clara in the Canaries, and (d) Raso Islet and Cima Islet both in
741 Cape Verde. Black circles show the location of the respective breeding colony and white/grey
742 symbols represented individual averaged non-breeding positions (computed as averaged
743 coordinates of every individual 5% UD) in the appropriate plot. In addition to that, migratory
744 connectivity at meta-population scale is also indicated in the figures; two differentiated and
745 significant clusters are depicted in white and grey (for A and B, respectively) and relevant
746 sub-clusters of the first cluster are shown in white squares and white circles (for A.1 and A.2,
747 respectively, see Results for details).

748

749 **Figure 3.** Habitat suitability of Bulwer's petrels (*Bulweria bulwerii*) from five different
750 colonies assessed from MaxEnt models. Five right habitat modellings were performed with
751 the breeding positions of the individuals from each colony and the environmental conditions
752 while breeding (in a, c, e, g, and i). Complementarily, five probability maps (on the left) for
753 each of the populations were built for the non-breeding season using the respective and
754 aforementioned breeding habitat models and the non-breeding environmental conditions (in b,
755 d, f, h, and j). Kernel density distributions (25, 50, 75 and 95%, from thicker to lighter line
756 contours, respectively) of each petrel colony during the breeding and non-breeding seasons
757 are also depicted in the respective map. White stars indicate the position of the colony.

758

759 **Figure 4.** Spatial variation in activity patterns during daylight and night by Bulwer's petrels
760 (*Bulweria bulwerii*) tracked during the breeding and non-breeding seasons. Night flight index
761 (in a and c, breeding and non-breeding, respectively) reflects the relative amount of flight
762 during night, ranging from -1 (i.e., flying exclusively during the daytime) to +1 (i.e. flying
763 exclusively at night). Meta-population kernel density distributions (25, 50, 75 and 95%, from
764 thicker to lighter line contours) during the breeding and non-breeding periods are also
765 depicted. Box-plots represent number of hours spent flying during daylight and night by
766 petrels tracked during the breeding (by colony in b) and non-breeding (by each 15 degrees of
767 latitude in d) seasons. White and grey boxes represent diurnal and nocturnal activity,
768 respectively.

Figure 1.

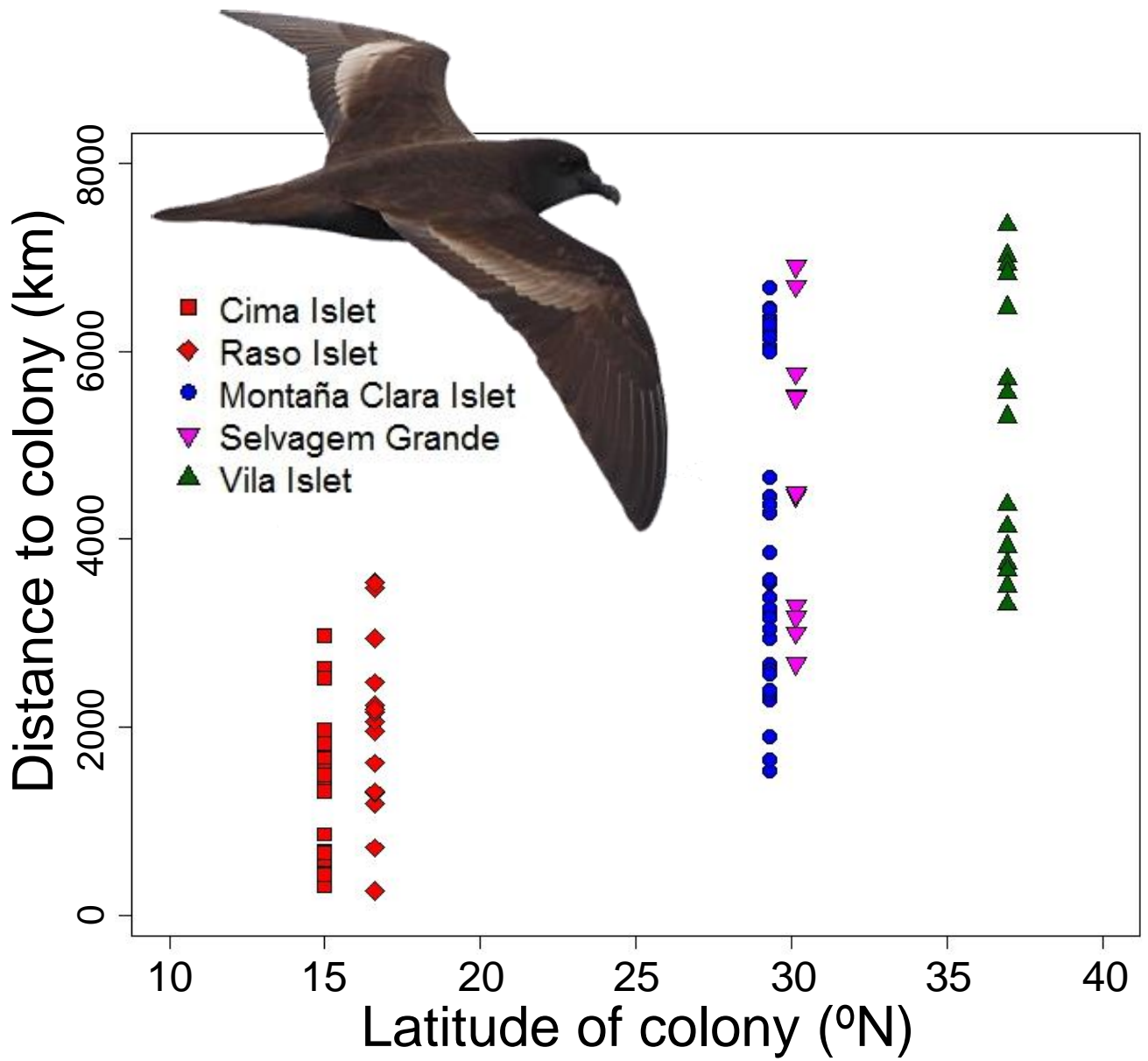


Figure 2.

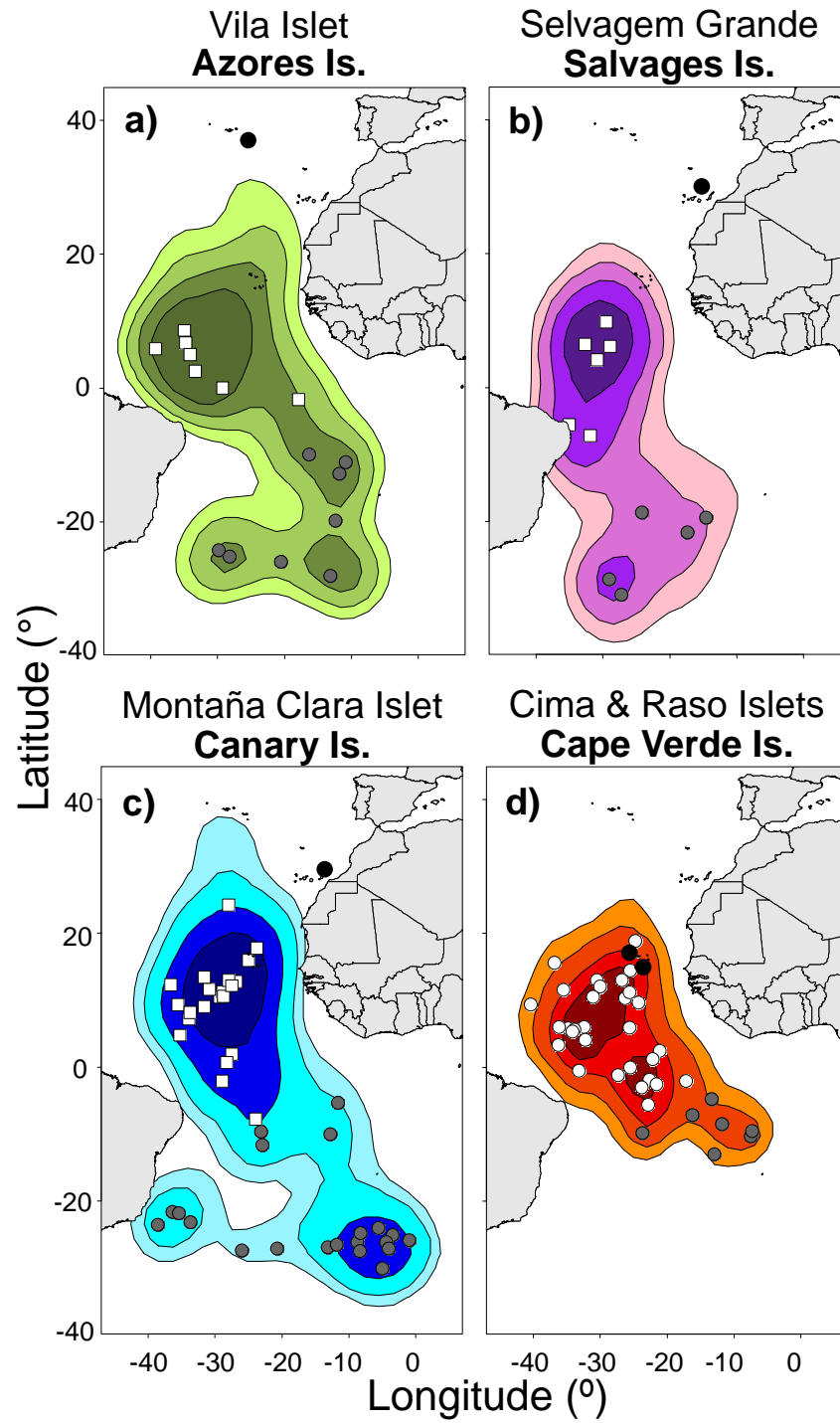


Figure 3.

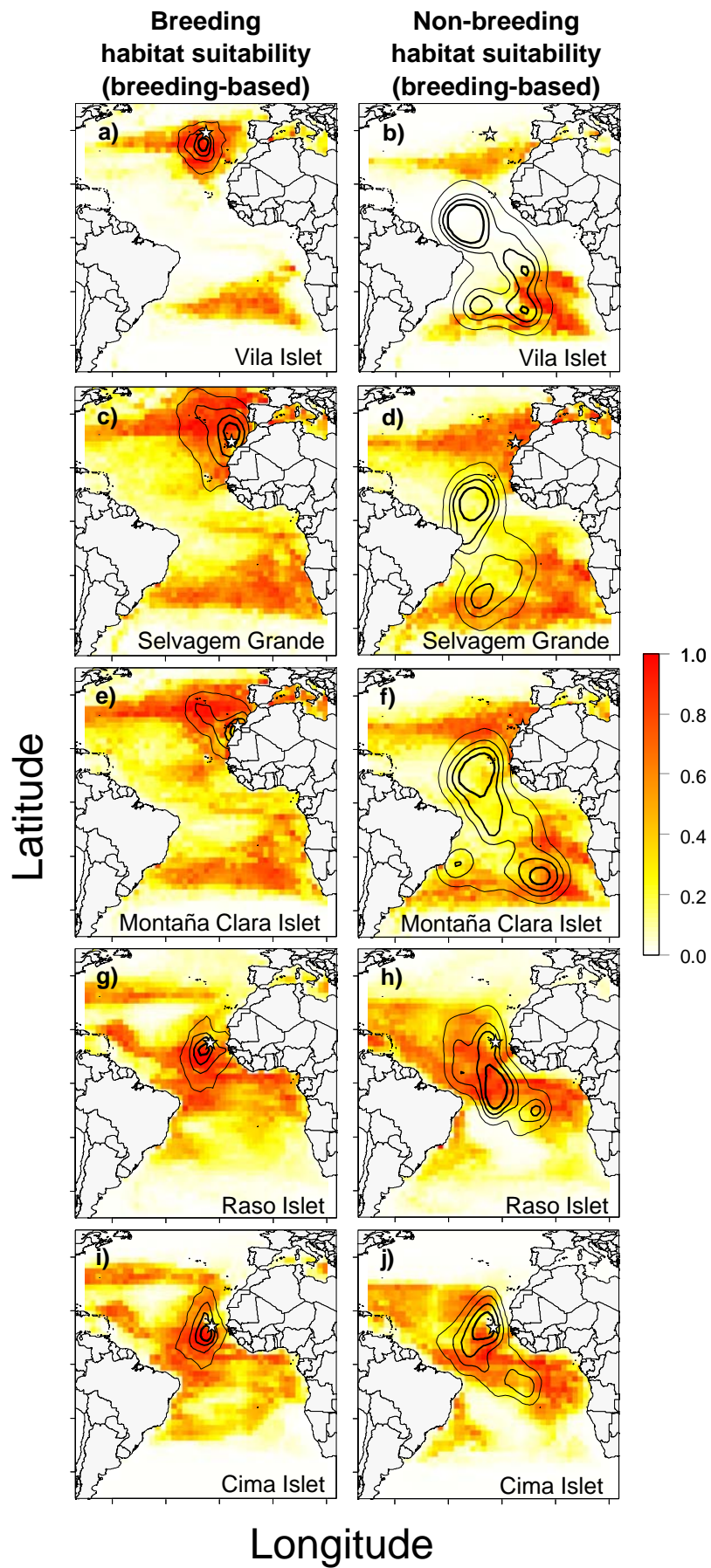
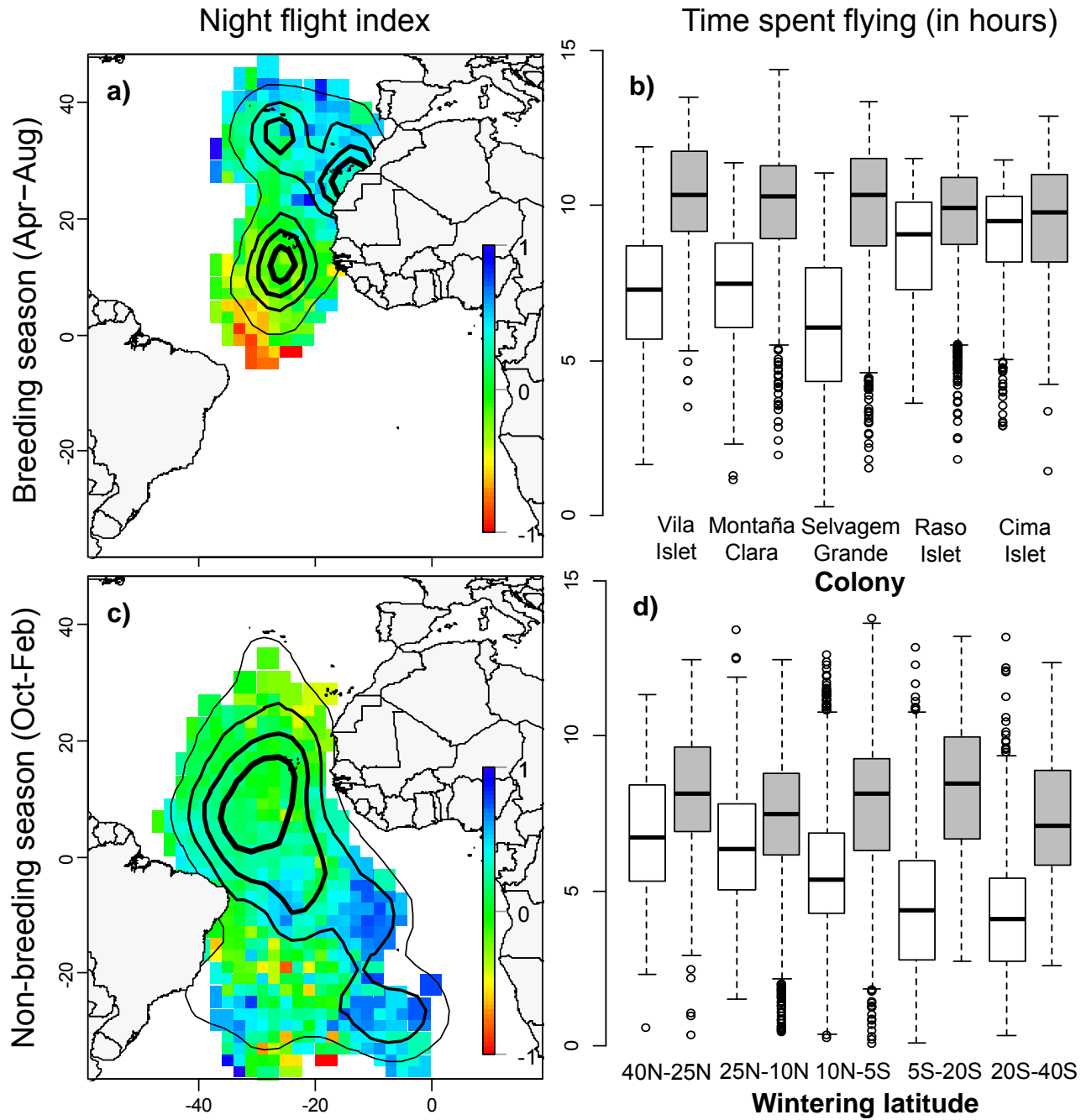


Figure 4.



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SUPPORTING INFORMATION

Leapfrog migration and habitat preferences of a small oceanic seabird, Bulwer's petrel (*Bulweria bulwerii*)

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Table S1. Modelling capture (p) and survival (Φ) probabilities of the adult Bulwer's petrels (*Bulweria bulwerii*) which were included in the study. Demographic parameters were estimated with capture-mark-recapture (CMR; Lebreton et al. 1992) models, using M-Surge version 1.8 (Choquet et al. 2006) and a total of 311 adult capture-recapture histories (172 equipped birds and 139 non-equipped controls, i.e., the breeding partners of those equipped birds), over the 2007-2014 period. We started with the Cormarck-Jolly-Seber (CJS) model where survival (Φ , probability that a petrel alive at year t survives at year $t+1$) and capture (p , probability that a petrel alive and present at the breeding colony at year t is captured during the year t) were time (t) and group (GLS deployment) dependent. The fit of the general model to the data was investigated with goodness-of-fit (GOF) tests for each group using program U-Care version 2.2 (Choquet et al. 2005). Model selection was done using the Akaike Information Criterion corrected for small sample sizes and overdispersion (QAICc; Burnham and Anderson 1998). When

16 comparing two models, if $\Delta\text{QAICc} > 2$, the preferred model is the one with the smallest QAICc value (i.e. the most parsimonious model in terms
 17 of the number of parameters and model deviance; Lebreton et al. 1992). First, models with various capture probability structures were compared,
 18 and then we considered models with various survival probability structures. The most parsimonious model obtained was $\Phi_{(t)} p_{(gls^*t)}$, where
 19 survival only depended on the year of sampling, and capture probability both on year and whether the bird was fitted with a GLS logger. This
 20 suggests there was no effect of logger deployment on subsequent survival.

| n° | Model | np | DEV | QAICc | ΔQAICc |
|---|---|-----------|--------------|--------------|----------------------|
| Modelling capture probability (p) | | | | | |
| 1 | $\Phi (gls^*t) p (gls^*t)$ | 78 | 841.4 | 997.4 | 19.7 |
| 2 | $\Phi (gls^*t) p (t)$ | 62 | 883.7 | 1007.7 | 30.0 |
| 3 | $\Phi (gls^*t) p (\cdot)$ | 49 | 914.5 | 1012.5 | 34.8 |
| Modelling survival probability (Φ) | | | | | |
| 4 | $\Phi (t) p (gls^*t)$ | 62 | 853.7 | 977.7 | 0.0 |
| 5 | $\Phi (\cdot) p (gls^*t)$ | 49 | 885.4 | 983.4 | 5.7 |

np number of parameters estimated; DEV deviance; QAICc quasi-likelihood Akaike's information criterion values; ΔQAIC difference between the current and the lowest QAICc model.

28 **Table S2.** Parameter estimates (\pm standard error) from generalised linear mixed models fitted to six migratory characteristics of Bulwer's petrels
 29 (*Bulweria bulwerii*) from five Macaronesian colonies. The best supported model (in bold) included breeding colony as a fixed effect in all cases.
 30 All evaluated models included individual identity and year of sampling as random effects. AICc refers to the corrected (c) Akaike's Information
 31 Criterion (AIC).

32

| | Colony departure date* | Colony arrival date* | Duration of the non- breeding period (days) | Area of the non- breeding period (10^6 km 2) | Distance to non- breeding range (km) | Centroid latitude of the non- breeding period ($^{\circ}$) |
|---|------------------------------|----------------------------|---|---|--|--|
| <i>AICc values</i> | | | | | | |
| Breeding colony | 901.6 | 806.3 | 917.1 | 372.0 | 1729.4 | 813.4 |
| Null | 958.8 | 1216.2 | 1022.7 | 409.4 | 1857.0 | 846.8 |
| <i>Fixed effects (estimate\pmSE)</i> | | | | | | |
| Cima (Intercept) | 219.9 \pm 7.0 | 386.0 \pm 3.9 | 168.7 \pm 8.6 | 1.5 \pm 0.5 | 1291.7 \pm 394.4 | 5.8 \pm 3.7 |
| Raso | 58.1 \pm 9.4 | -274.5 \pm 5.4 | 28.5 \pm 10.9 | -0.5 \pm 0.6 | 551.7 \pm 559.2 | -3.4 \pm 5.3 |
| Montaña Clara | 23.6 \pm 6.8 | -269.4 \pm 4.1 | 71.2 \pm 7.4 | 2.3 \pm 0.5 | 3186.3 \pm 432.0 | -13.4 \pm 4.2 |
| Selvagem Grande | 18.5 \pm 9.6 | -289.1 \pm 5.7 | 56.6 \pm 10.6 | 0.8 \pm 0.7 | 3625.9 \pm 595.5 | -17.2 \pm 5.7 |
| Vila | 26.3 \pm 8.8 | -261.4 \pm 5.2 | 74.4 \pm 9.8 | 1.6 \pm 0.6 | 3831.0 \pm 545.1 | -13.9 \pm 5.3 |
| <i>Random effect (variance\pmSE)</i> | | | | | | |
| Individual | 183.5 \pm 13.6 | 0.0 \pm 0.0 | 131.4 \pm 11.5 | 1.2 \pm 1.1 | 1033518.0 \pm 1016.6 | 107.8 \pm 10.4 |
| Year | 71.9 \pm 8.5 | 16.9 \pm 4.1 | 155.3 \pm 12.5 | 0.2 \pm 0.5 | 123521.0 \pm 351.5 | 8.8 \pm 3.0 |
| Residual | 254.9 \pm 16.0 | 167.6 \pm 13.0 | 366.9 \pm 19.2 | 0.9 \pm 1.0 | 904191.0 \pm 950.9 | 79.7 \pm 8.9 |

33 * expressed as ordinal date (numerical within the Julian year)

34

35

36 **Table S3.** Analysis of collinearity between the eight oceanographic variables used in the habitat models (breeding: April to August, non-
 37 breeding: October to February of consecutive years, and year-round: January to December). For each combination, the matrices show the sign
 38 and magnitude of the Spearman correlation coefficient (above diagonal) and the significance level (P-values; below diagonal). Highly correlated
 39 (-rs- > 0.5) predictors depicted in bold. BAT: bathymetry, BATG: bathymetry gradient, CHLa: chlorophyll *a* concentration, CHLG: CHLa
 40 gradient, SAL: salinity, SST: sea surface temperature, SSTG: SST gradient, WIND: wind speed.

| Breeding period | BAT | BATG | CHLa | CHLG | SAL | SST | SSTG | WIND |
|---------------------|------------|-------------|-------------|--------------|---------------|------------|-------------|-------------|
| BAT | **** | 0.254 | 0.482 | 0.425 | -0.183 | -0.198 | 0.422 | 0.087 |
| BATG | <0.001 | **** | 0.244 | 0.209 | -0.112 | -0.140 | 0.164 | 0.031 |
| CHLa | <0.001 | <0.001 | **** | 0.915 | -0.728 | -0.058 | 0.487 | -0.087 |
| CHLG | <0.001 | <0.001 | <0.001 | **** | -0.663 | 0.122 | 0.411 | -0.131 |
| SAL | <0.001 | 0.026 | <0.001 | <0.001 | **** | -0.154 | -0.343 | 0.140 |
| SST | <0.001 | 0.003 | 0.402 | 0.011 | 0.001 | **** | -0.375 | -0.418 |
| SSTG | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | **** | 0.038 |
| WIND | 0.126 | 0.659 | 0.126 | 0.006 | 0.003 | <0.001 | 0.659 | **** |
| Non-breeding period | BAT | BATG | CHLa | CHLG | SAL | SST | SSTG | WIND |
| BAT | **** | 0.254 | 0.336 | 0.357 | -0.144 | -0.197 | 0.393 | 0.014 |
| BATG | <0.001 | **** | 0.227 | 0.193 | -0.124 | -0.157 | 0.195 | 0.084 |
| CHLa | <0.001 | <0.001 | **** | 0.909 | -0.438 | -0.206 | 0.430 | 0.465 |
| CHLG | <0.001 | <0.001 | <0.001 | **** | -0.613 | 0.036 | 0.366 | 0.264 |
| SAL | 0.001 | 0.008 | <0.001 | <0.001 | **** | -0.222 | -0.174 | 0.040 |
| SST | <0.001 | <0.001 | <0.001 | 0.922 | <0.001 | **** | -0.489 | -0.426 |
| SSTG | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | **** | 0.195 |
| WIND | 0.922 | 0.115 | <0.001 | <0.001 | 0.922 | <0.001 | <0.001 | **** |

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Solís

Figure S1. Silhouette plot showing the classification of Bulwer's petrel (*Bulweria bulwerii*) individuals in two first-level clusters. Each bar represents the silhouette values s_i for a single petrel (see also Methods: Spatial analyses and migratory connectivity) and is displayed according to the breeding colony of origin (yellow for Cima-Cape Verde, orange for Raso-Cape Verde, green for Montaña Clara-Canaries, sky blue for Salvages and dark blue for Vila-Azores). Within each cluster, bars are drawn in decreasing length order. Large values indicate good classification.

