



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

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### ABSTRACT

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

**Location** Subtropical and tropical Atlantic Ocean.

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

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

**Main conclusions** These results indicate that specific habitat preferences, presumably related to differences in prey availability, explain the observed distributions and hence the pattern of leapfrog migration described for Bulwer's petrel. Our study demonstrates the utility of integrating diverse tracking data from multiple populations across international boundaries, and habitat modelling, for identifying important areas common to many marine species in the vast oceanic environments.

### Keywords

Activity patterns, *Bulweria bulwerii*, Bulwer's petrel, capture–mark–recapture, geolocator data, habitat modelling, Macaronesian seabirds, metapopulation studies, oceanic migrations.

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## INTRODUCTION

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

Migratory species show various patterns of partial and differential migration (at intra-population level; Cristol *et al.*, 1999; Holberton & Able, 2000), as well as different degrees of segregation among breeding populations (Bell, 2005; Newton, 2008). For instance, at the metapopulation level, chain migration occurs when a northerly breeding population winters within the breeding range of another population that migrates further south. In such cases, migration distances are broadly similar among populations breeding along a latitudinal gradient (Lundberg & Alerstam, 1986; Fort *et al.*, 2012). In other species, northerly breeding populations migrate longer distances to spend the non-breeding season further south than individuals from the southerly breeding populations. Such systems have generally been termed leapfrog migrations (Salomonsen, 1955; Alerstam & Höglstedt, 1980). The latter is an unusual migration pattern at the species level, first described in a North American passerine, the fox sparrow (*Passerella iliaca*; Swarth, 1920) and later reported in other passerine (Bell, 1996, 1997; Fraser *et al.*, 2012; Stanley *et al.*, 2015) and non-passserine species, particularly waders (Charadriiformes; Salomonsen, 1955; Pienkowski *et al.*, 1985; Boland, 1990; Alves *et al.*, 2012; Duijns *et al.*, 2012). Among seabirds, however, leapfrog migration has never been reported, suggesting that it is uncommon in this group of birds (but see Wernham *et al.*, 2002; Hallgrímsson *et al.*, 2012).

Classically, three explanations or hypotheses have been suggested by different authors that would favour the evolution of a leapfrog migration pattern (reviewed in Lundberg & Alerstam, 1986): conspecific competition (Salomonsen, 1955; Pienkowski *et al.*, 1985), environmental predictability at the onset of the breeding season (Alerstam & Höglstedt, 1980), and time allocation (Greenberg, 1980). The first hypothesis – competition among conspecifics for limited food resources on the non-breeding grounds – is also considered to explain chain migrations; however, competition and food availability may not fully explain why the northernmost populations of a leapfrog migrant bear the additional energetic cost of the extra flight distance. Similarly, the environmental predictability hypothesis suggests that birds wintering closer to the breeding grounds might more easily predict the occurrence of optimal environmental conditions for breeding; these individuals

might better time their return to the nest site and achieve higher breeding success as a consequence (e.g. Bregnballe *et al.*, 2006; Garthe *et al.*, 2012). However, again, this fails to explain why the northern populations of a given species should leapfrog those that breed to the south. Finally, the hypothesis relating to optimal time allocation in migratory birds predicts that the benefits of wintering at a more distant site with better survival prospects (through high food availability, for instance) may be higher if the leapfrog migrants can arrive sooner and so spend more time at the favourable site. In this regard, northerly populations that breed later may winter further south to take advantage of late spring food availability (e.g. Bell, 1997). However, results from other species tend not to support this hypothesis (reviewed in Sandercock & Jaramillo, 2002).

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

Here, using miniaturized geolocator-immersion loggers, we examined the at-sea distribution and activity patterns of a small oceanic seabird, Bulwer's petrel [*Bulweria bulwerii* (Jardine & Selby, 1828)], from the major colonies across its breeding range in the North Atlantic (the Azores, Salvages, Canary and Cape Verde archipelagos). This species is relatively abundant in offshore waters of the north-east and central east Atlantic, during the summer, but, like many subtropical and tropical seabirds, little is known about individual movements and foraging ecology, particularly during the non-breeding season. Based on at-sea observations from the last century, the Macaronesian populations of Bulwer's petrel were thought to winter in a huge area in the central Atlantic between 20° N and 20° S (Van Oordt & Kruijt, 1953; Cramp, 1977; Bourne, 1995). However, at-sea observation does not allow determination of the origin of birds, is subject to major sampling biases, and provides no information on the timing of movements, segregation among populations, or variation within populations. A recent study showed the first preliminary tracks of Bulwer's petrels for a few days after breeding (Rodríguez *et al.*, 2013). Although valuable, the study only included three birds tracked for 11–15 days after colony departure and devices were heavy in relation to body mass, which may have affected the documented behaviour of the birds (> 5% of body mass; Phillips *et al.*, 2003), therefore precluding any fruitful comparison with our data. Our aims

here were: (1) to identify for the first time the foraging areas used during the breeding and non-breeding seasons by the main populations of Bulwer's petrel in Macaronesia, (2) to define the migration strategy of this small predator in the sub-tropical and tropical Atlantic Ocean, and most importantly, (3) to provide new insights into the ecology and evolution of long-distance seabird migrations. To do so, we quantified the relative importance of different foraging areas for each breeding population; assessed the degree of spatial overlap among populations as well as the annual variability in at-sea distributions; characterized at-sea activity patterns; and finally, defined the key oceanographic factors determining habitat use by Bulwer's petrels at population and metapopulation scales.

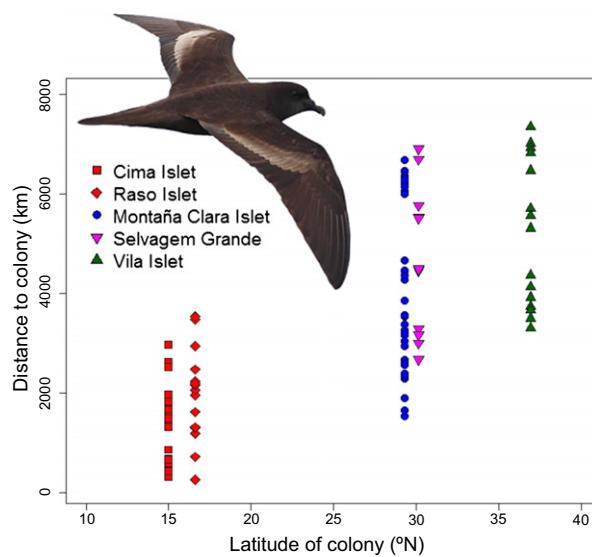
## MATERIALS AND METHODS

### Species ecology

Bulwer's petrel is a small (80–120 g) procellariiform seabird (Fig. 1), which shows a highly pelagic, pan-tropical and sub-tropical distribution, including the Atlantic, Pacific and Indian oceans (Brooke, 2004). Within the Atlantic, it breeds on a few islets and islands throughout much of Macaronesia (from the Azores to the Cape Verde archipelagos, including Madeira, Salvages and Canary Islands), with an estimated total population of c. 11,000 breeding pairs (Mougin, 1989; Hernández *et al.*, 1990; Hazzevoet, 1995; Monteiro *et al.*, 1996; Nunes & Vicente, 1998; Luzardo *et al.*, 2008). Most adults arrive at the colony in late April, females lay a single egg in late May/early June, chicks hatch at the end of July and fledge in mid- to late September (Nunes & Vicente, 1998). During the breeding season, Bulwer's petrels are thought to be nocturnal feeders, specialized in exploiting mesopelagic prey that perform daily vertical migrations (from 200 to 1000 m depth), including fish, especially lanternfish, Myctophidae (Zonfrillo, 1986; Mougin & Mougin, 2000; Neves *et al.*, 2011).

### Bird tracking data

The present study was conducted at five breeding colonies within four Macaronesian archipelagos (Fig. 2), over 7 years (2007–2013; Table 1). At each colony, breeding adults incubating an egg or rearing a chick were fitted with a small, leg-mounted, combined geolocator-immersion logger [Mk13, Mk14, Mk18 (British Antarctic Survey, Cambridge, UK) and W65 (Migrate Technology Ltd, Cambridge, UK) models, weighing 1.8, 1.4, 1.9 and 0.65 g, respectively, corresponding to 0.7–2.0% of body mass]. We deployed a total of 172 geolocators of which 115 (55.2–74.2%, depending on the colony) were recovered. To check for short-term effects of the logger deployment on adult survival, we constructed capture–mark–recapture models (M-SURGE version 1.8; Chouquet *et al.*, 2006; we analysed 311 capture–recapture histories over the period 2007–2014; see Table S1 in Appendix S1 in Supporting Information).



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

Geolocators provide two positions per day based on light levels (one at local midday and other at local midnight), with an average accuracy of c. 200 km (or c. 2°; Phillips *et al.*, 2004). Positions were calculated using TRANSEDIT and BIRDTRACKER software (British Antarctic Survey, 2008) by inspecting the integrity of the light curve day-by-day, and estimating dawn and dusk times. We excluded long periods spent in burrows during incubation, based on light data recorded by the logger. To filter unrealistic positions, we removed those that were (1) obtained from light curves showing interference at dawn or dusk, (2) within the 20 closest days to the equinoxes, and (3) that resulted in unrealistic flight speeds (> 40 km h<sup>-1</sup> sustained over 48 h) using bespoke software routines written in R 3.1.1 (R Core Team, 2014). Validated data were smoothed twice by interpolating intermediate fixes between successive locations with fixed start and end points around any periods of missing data (Phillips *et al.*, 2004).

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

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

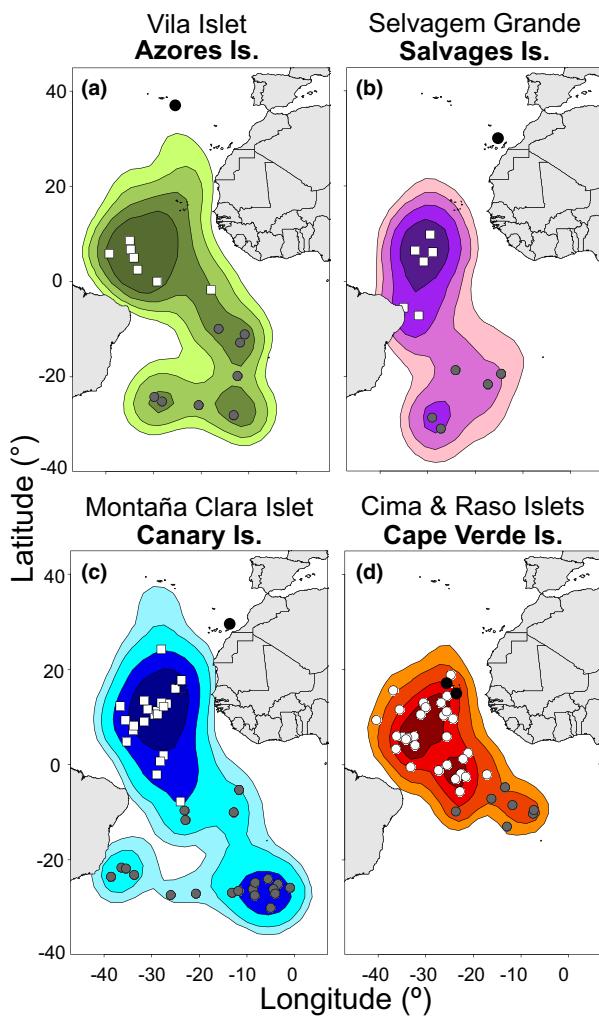
### Spatial analyses and migratory connectivity

We estimated six phenological and spatial parameters for every complete migration cycle (i.e. non-breeding event): (1) departure date, (2) arrival date, (3) duration of the non-breeding period (in days), (4) area exploited throughout the non-breeding period (as indicated by the 50% utilization distribution from kernel analysis, hereafter referred to as UD; in  $10^6 \text{ km}^2$ ), (5) non-breeding range (orthometric distance between the breeding colony and the average position of locations within the 5% UD; in km), and (6) latitude of the centroid of the non-breeding period (i.e. mean latitude of all positions within the 5% UD; in degrees). After normality checks (using Q–Q plots) and using model information criteria, we evaluated the effect of colony of origin on migration parameters by fitting a set of candidate generalized linear mixed models (GLMMs), where each of the six parameters described above was the response variable and breeding colony was the main (fixed) explanatory variable (see Table S2 in Appendix S1). To account for annual and potential individual heterogeneity in migration parameters, year of sampling and bird identity were included in all the GLMMs as random terms. Gaussian distribution of error terms and the identity link function were used in the modelling. The best-supported models were selected using the Akaike information criterion corrected for small sample sizes ( $AIC_c$ ) and the corresponding  $AIC_c$  weights (Johnson & Omland, 2004). GLMMs were conducted in R with additional functions provided by the R packages **LME4** ('lmer'; Bates *et al.*, 2008) and **MUMIN** ('dredge'; Bartoń, 2009).

To quantify spatial overlap among colonies during the non-breeding period, and also to assess the effect of year within each colony, we also calculated the overlap in distribution between the 14 non-breeding events (Table 2). Overlap indices between every pair of non-breeding distributions were calculated using the 95% UDs and the 'kerneloverlap' function in the **ADEHABITAT** package (VI method; Fieberg & Kochanny, 2005). Following Ambrosini *et al.* (2009), we assessed the migratory connectivity among the five sampled colonies (using breeding and non-breeding matrices of orthometric distances and Mantel correlation coefficients), and the number of potential clusters in case of migratory structuring and substructuring (using the 'pamk' function in the R package **CLUSTER**; Maechler *et al.*, 2015). Importantly, this approach did not force us to define a priori the number of breeding and non-breeding subranges (or clusters), which may be difficult when the species of interest shows continuous distributions both in the breeding and non-breeding ranges. Statistical significance of the Mantel correlation coefficient was determined by 9999 random permutations. The number of clusters was identified as the number that maximized the overall average silhouette width (oasw), a measure of the goodness-of-fit of the overall classification of points in a given number of clusters (Rousseeuw, 1987).

### Environmental data and habitat modelling

To determine the oceanographic characteristics of areas used by the tracked birds, we considered the seafloor depth (BAT, m), surface chlorophyll *a* concentration (CHL<sub>a</sub>,  $\text{mg m}^{-3}$ ), salinity (SAL, g of salt per kg of water), sea sur-



**Figure 2** Kernel density distributions (25, 50, 75 and 95%, from darker to lighter tone contours, respectively) of Bulwer's petrels (*Bulweria bulwerii*) tracked during the non-breeding periods from different colonies: (a) Vila Islet in the Azores, (b) Selvagem Grande in Salvages Islands, (c) Montaña Clara in the Canaries, and (d) Raso Islet and Cima Islet both in Cape Verde. Black circles show the location of the respective breeding colony and white/grey symbols represented individual averaged non-breeding positions (computed as averaged coordinates of every individual 5% utilization distribution) in the appropriate plot. In addition to that, migratory connectivity at metapopulation scale is also indicated in the figures; two differentiated and significant clusters are depicted in white and grey (clusters A and B, respectively) and relevant subclusters of the first cluster are shown in white squares and white circles (subclusters A1 and A2, respectively; see Results for details).

face temperature (SST, °C), and wind speed (WIND,  $\text{m s}^{-1}$ ). All remote sensing products were extracted from NOAA CoastWatch (<http://coastwatch.pfeg.noaa.gov/>) for a grid including the whole Atlantic Ocean. The static BAT variable and monthly composites of CHLa, SST and WIND (dynamic variables downloaded for the period 2007–2013) were rescaled to a common spatial resolution of 2.0°, which matches the accuracy of geolocation data. In addition to

these five oceanographic variables, gradients for BAT, CHLa and SST were also considered (BATG, CHLG and SSTG, respectively). Dynamic variables were averaged by: (1) breeding period, from April to August, (2) non-breeding period, from October to February, and (3) year-round, from January to December, for every year. To exclude redundant variables, pairwise correlations among the eight environmental variables were evaluated separately for each period (i.e. breeding, non-breeding and year round) using Spearman methodology with Holm adjustments (see Table S3 in Appendix S1).

Bulwer's petrel habitat probability models were developed using the MAXENT 3.3.3e software (Phillips *et al.*, 2006), a program for modelling ecological niches from presence-only records. In a first modelling approach, habitat probability models were run with six non-redundant variables (i.e. BAT, BATG, CHLa, SST, SSTG and WIND) for each of the 10 data subsets, including the five colonies (separately and jointly) during the breeding period (six models), the two main wintering regions (i.e. the two main clusters derived from the migratory connectivity assessment; separately and jointly) during the non-breeding period (three models), and year round (one model). All habitat use models were developed on the basis of a logistic output format and with 100 bootstrapped replicates, each of them built on randomly sampled subsets of 10% of the bird positions as training points. This conservative approach (i.e. 90% of seabird records were used for model testing) avoids model over-fitting and minimizes effects of spatial autocorrelation in both seabird presence and environmental covariates. The data were jackknifed to evaluate each variable's importance in explaining the observed distribution. The percentage of contribution 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. To determine the permutation importance of each variable, the values in the training presence and background data were randomly varied and the resulting change in the area under the receiver operating characteristic curve (AUC) statistic was examined, normalized to percentages (Phillips *et al.*, 2006). The results were summarized as the average of the 100 models, and model evaluation was performed using the AUC statistic, which measures the ability of model predictions to discriminate seabird presence from background points (Table 3). In a second modelling approach, the five predictive models developed for the breeding period (and for each colony) were used to build probability maps for each of the populations during the non-breeding season using the relevant environmental variables averaged for the non-breeding period (Fig. 3).

## RESULTS

First of all, capture–mark–recapture models revealed no effect of logger deployment on the survival probability of Bulwer's petrels (estimated annual survival rate =  $0.76 \pm 0.19$ ),

**Table 2** Overlap in the 95% kernel utilization distribution (UD) of Bulwer's petrels (*Bulweria bulwerii*) tracked during the non-breeding period. Pairwise comparisons are of the 14 non-breeding events considered in this study.

| 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         |

although recapture probability was higher in equipped birds because of the incentive of the researchers to recover devices ( $P = 0.66 \pm 0.14$  and  $0.77 \pm 0.15$  for non-equipped and equipped birds, respectively). Likewise, studies using geolocators on another small seabird species (thin-billed prions, *Pachyptila belcheri*, weighing c. 130 g; Quillfeldt *et al.*, 2012) found no obvious effect of logger deployment on foraging ability, although a significant ecophysiological effect is expected on those birds carrying devices because of the higher load.

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

### Non-breeding distribution and migratory characteristics

During the non-breeding period, Bulwer's petrels were concentrated around a core area in equatorial waters in the central Atlantic (Fig. 2). Overall, 60.4% of the birds (range among colonies 40.0–85.0%) spent the entire non-breeding period in this area. However, a substantial proportion of birds from Vila (45.5%), Selvagem Grande (53.3%) and Montaña Clara (50.0%) migrated further south to an area in

the southern Atlantic Ocean situated between  $10^{\circ}$  and  $30^{\circ}$  S. Most of these birds staged in the equatorial region for several days during their outward and return migrations.

Substantial variation in migratory phenology and in the spatial components of migration occurred among populations but also among individuals (Table 1). Overall, the duration of the non-breeding period, the non-breeding range, the area visited and the latitude of the core area exploited during the non-breeding period tended to be greater in the birds from subtropical colonies (i.e. Vila, Selvagem Grande and Montaña Clara) than those from Cape Verde (Table S2 in Appendix S1). In particular, the distance between the breeding colony and the average position of the non-breeding area (i.e. the non-breeding range) was colony-dependent (Fig. 1), with subtropical colonies ranging 1646.5–7342.5 km (on average  $4631.7 \pm 1629.3$ ), and Cape Verde colonies ranging 256.2–3540.2 km (on average  $1691.4 \pm 911.3$ ) from their respective wintering areas.

### Migratory connectivity and overlap of non-breeding grounds

Bulwer's petrels showed significant migratory connectivity ( $n = 104$ , Mantel correlation coefficient  $r_M = 0.042$ ,  $P = 0.047$ ), and could be grouped into two distinct clusters (overall average silhouette width value, oasw = 0.529; see

Appendix S2). The northern cluster (A) included petrels from all five breeding colonies that wintered north and south of the equator in the central Atlantic, whereas the southern cluster (B) was mainly constituted by individuals from northern colonies that wintered further south of the equator (Fig. 2). Whereas the southern cluster showed non-significant connectivity ( $n = 42$ ,  $r_M = 0.065$ ,  $P = 0.128$ ), the northern cluster was structured as two significant subclusters ( $n = 62$ ,  $r_M = 0.071$ ,  $P = 0.019$ , oasw = 0.547): subcluster A1 only included individuals breeding in the northern colonies, whereas subcluster A2 consisted exclusively of birds from the two Cape Verde colonies.

In agreement with the results shown above, overlap analyses identified two distinctive groups of non-breeding birds: (1) Cape Verde colonies (Raso and Cima Islets) which showed a relatively high overlap (68.6% on average; Table 2), and (2) Vila, Selvagem Grande and Montaña Clara, which also showed considerable overlap (52.6%). In contrast, there was considerably less overlap between these two groups (33.9%; Table 2). In addition, the areas exploited by birds from the same colony in different years showed a relatively high overlap (mean of 57.1, 51.9, 70.6, 73.1 and 72.6% for Vila, Selvagem Grande, Montaña Clara, Raso and Cima Islets, respectively; Table 2).

### Habitat modelling

The MAXENT variable importance and the percentage of variable contribution rankings differed both between seasons, and among groups of birds (i.e. colonies and clusters;

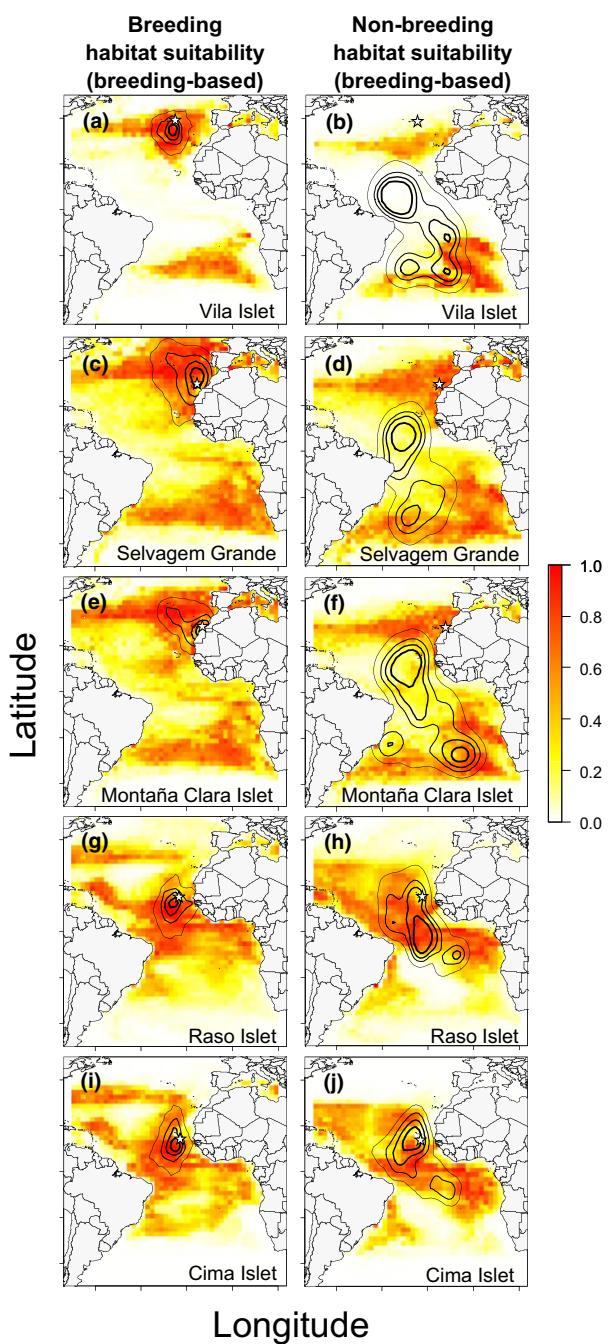
Table 3). Jackknife tests identified SST as the most important variable, which also accounted for the highest percentage contribution to both breeding and non-breeding model sets. During the breeding season, the highest-ranked variable was either SST or WIND, whereas for the non-breeding season, SST and SSTG (for cluster A), and SST and CHLa (for cluster B) were the most important variables. In general during the breeding season, there was a consistent preference by birds from all colonies for areas with warm waters (range: 15–25 °C for subtropical colonies and 24–28 °C for Cape Verde colonies) and low wind intensity (5–8 m s<sup>-1</sup> for all colonies). Similarly, modelling of the habitat used during the non-breeding period also indicated that birds tended to select areas of warm waters (Table 3).

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

**Table 3** Estimates of model fit (AUC) and relative importance (contribution percentage and permutation importance, both normalized to percentages) of the environmental variables to the modelled Bulwer's petrel (*Bulweria bulwerii*) presence probability (relevant values > 20% in bold). The percentage contribution 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. Permutation importance of a given variable derived from the resulting change in training AUC when values of this variable on training presence and background 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-breeding areas (i.e. connectivity cluster) were included as fixed factors for the breeding and non-breeding datasets, respectively.

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

Values shown are averages over 100 model replicates. AUC, area under the receiver operating characteristic curve; BAT, bathymetry; BATG, gradient of BAT; CHLa, chlorophyll *a* concentration; SST, sea surface temperature; SSTG, gradient of SST; WIND, wind speed.



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

## At-sea activity patterns

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

## DISCUSSION

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

During the non-breeding season, the tracked Bulwer's petrels congregated in large numbers within a relatively restricted area in the mid-equatorial Atlantic Ocean, north of the Saint Peter and Saint Paul archipelago ( $0^{\circ}55' N$ ,  $29^{\circ}20' W$ ; hereafter Saint Paul's Rocks). Previous results from at-sea surveys had suggested that this might be an important wintering area for Bulwer's petrels (Van Oordt & Kruijt, 1953; Bourne, 1995). Our results confirm this for a large proportion of birds from different breeding populations. Among these birds, those from Cape Verde are notable for their strategy of partial migration (Chapman *et al.*, 2011), where many birds remained during the non-breeding period in broadly the same area that they used during the breeding season whereas others dispersed south, around the equator (Fig. 2).

In addition, a substantial proportion of birds from the northernmost populations (Azores, Salvages and Canary

Islands) leapfrog the birds from more southerly colonies, which winter north of Saint Paul's Rocks, to spend the non-breeding period further south. There have been few reports of Bulwer's petrels in these subtropical waters (Van Oordt & Kruijt, 1953; Bourne, 1995), probably because of the extensive areas and the apparent absence of high concentrations of wintering birds (Fig. 2). Thus, at a metapopulation scale, all the Macaronesian populations of Bulwer's petrels largely overlap during the non-breeding season in tropical waters north of Saint Paul's Rocks, and only birds from the northern populations exploit the subtropical Atlantic Ocean further south than 20°.

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

The decision of an individual to spend time in a given area is dictated by the suitability of the habitat (Guisan & Zimmermann, 2000). The latter depends largely on two non-exclusive factors: the number of conspecifics and competitors, and the inherent productivity and quality of the habitat itself. In addition, for long-distance migrants, the distance between the foraging habitat and the breeding grounds might also play a role in habitat selection (e.g. Duijns *et al.*, 2012). Therefore, oceanic migrants must take complex decisions when selecting their habitat, at least twice a year: during the breeding period, when they behave as central place foragers and are tied to the waters surrounding their colonies, and also in the non-breeding season, when, unconstrained, they can virtually access any area where conditions are suitable.

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

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

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

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

However, another factor should be taken into account that might explain the non-breeding distribution of Bulwer's petrels in the Atlantic. Otherwise, why did half of the individuals from the subtropical populations migrate to the subtropical (and preferred) non-breeding subrange, while the other half stayed closer to the tropical (and less suitable) subrange? A trade-off might exist between the benefit of exploiting a more suitable, familiar habitat and energetic constraints. The higher costs of longer migrations might be compensated by a more efficient exploitation of more distant wintering grounds, so that neither a short- nor a long-distance migratory strategy is consistently more successful (e.g. Hestbeck *et al.*, 1992). In this regard, the longer period spent in subtropical wintering areas by individuals from subtropical colonies (see Table 1), compared with the relatively shorter non-breeding season of tropical birds (by c. 50 days

**Table 4** Parameter estimates ( $\pm$ SE) from generalized linear mixed models fitted to at-sea activity (estimated as number of hours spent flying) of Bulwer's petrels (*Bulweria bulwerii*) throughout the year. Time spent flying was modelled considering breeding colony and day/night as fixed factors for the breeding period, ranges of  $15^\circ$  of latitude and day/night as fixed factors for the non-breeding period and season (i.e. breeding 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 included (i.e. colony \* daynight, latitude \* daynight and season \* daynight, respectively). All evaluated models included individual and year of sampling as random factors. AIC<sub>c</sub> refers to the corrected Akaike's information criterion. *k* represents the number of parameters estimated.

|                                   | Time spent flying <sub>breeding</sub> |                  |                           |     | Time spent flying <sub>non-breeding</sub> |          |                  |                           | Time spent flying <sub>year</sub> |                            |          |                  |           |
|-----------------------------------|---------------------------------------|------------------|---------------------------|-----|---|----------|------------------|---------------------------|-----------------------------------|----------------------------|----------|------------------|-----------|
|                                   | <i>k</i>                              | AIC <sub>c</sub> |                           | Wgt | AIC <sub>c</sub>                          | <i>k</i> | AIC <sub>c</sub> |                           | Wgt                               | AIC <sub>c</sub>           | <i>k</i> | AIC <sub>c</sub> |           |
|                                   |                                       | AIC <sub>c</sub> | $\Delta$ AIC <sub>c</sub> |     |   |          | AIC <sub>c</sub> | $\Delta$ AIC <sub>c</sub> |                                   |                            |          | AIC <sub>c</sub> |           |
| 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       |
| 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    |
| Colony                            | 8                                     | 131867.1         | 4301.4                    | 0.0 | Latitude                                  | 8        | 210197.2         | 22173.3                   | 0.0                               | Season                     | 5        | 345114.3         | 21260.6   |
| Daynight                          | 5                                     | 129590.2         | 2024.5                    | 0.0 | Daynight                                  | 5        | 190820.8         | 2796.9                    | 0.0                               | Daynight                   | 5        | 334415.7         | 10561.9   |
| Null                              | 4                                     | 132009.7         | 4443.9                    | 0.0 | Null                                      | 4        | 210828.2         | 22804.3                   | 0.0                               | Null                       | 4        | 350022.5         | 26168.8   |
| Fixed effects (estimate $\pm$ SE) |                                       |                  |                           |     |   |          |                  |                           |                                   |                            |          |                  |           |
| Cima & day (Intercept)            |                                       | 10.5             | $\pm$ 0.8                 |     | Lat 40N–25N & day (Intercept)             |          | 6.7              | $\pm$ 0.2                 |                                   | Breeding & day (Intercept) |          | 7.1              | $\pm$ 0.3 |
| Raso                              |                                       | -5.9             | $\pm$ 0.4                 |     | Lat 25N–10N                               |          | -0.6             | $\pm$ 0.1                 |                                   | Non-breeding               |          | -2.0             | $\pm$ 0.0 |
| Montaña Clara                     |                                       | -1.1             | $\pm$ 0.4                 |     | Lat 10N–5S                                |          | -1.8             | $\pm$ 0.1                 |                                   |                            |          |                  |           |
| Selvagem                          |                                       | -4.0             | $\pm$ 0.4                 |     | Lat 5S–20S                                |          | -3.0             | $\pm$ 0.1                 |                                   |                            |          |                  |           |
| Vila                              |                                       | -2.1             | $\pm$ 0.4                 |     | Lat 20S–40S                               |          | -3.9             | $\pm$ 0.1                 |                                   |                            |          |                  |           |
| Night                             |                                       | 0.3              | $\pm$ 0.1                 |     | Night                                     |          | 2.3              | $\pm$ 0.2                 |                                   | Night                      |          | 3.0              | $\pm$ 0.0 |
| Raso & night                      |                                       | 3.5              | $\pm$ 0.1                 |     | Lat 25N–10N & night                       |          | -0.4             | $\pm$ 0.2                 |                                   | Non-breeding & night       |          | -0.2             | $\pm$ 0.0 |
| Montaña Clara & night             |                                       | 1.5              | $\pm$ 0.2                 |     | Lat 10N–5S & night                        |          | 0.6              | $\pm$ 0.2                 |                                   |                            |          |                  |           |
| Selvagem & night                  |                                       | 2.2              | $\pm$ 0.1                 |     | Lat 5S–20S & night                        |          | 2.0              | $\pm$ 0.2                 |                                   |                            |          |                  |           |
| Vila & night                      |                                       | 2.9              | $\pm$ 0.1                 |     | Lat 20S–40S & night                       |          | 1.9              | $\pm$ 0.2                 |                                   |                            |          |                  |           |
| Random effect (variance $\pm$ SE) |                                       |                  |                           |     |   |          |                  |                           |                                   |                            |          |                  |           |
| Individual                        |                                       | 0.9              | $\pm$ 0.9                 |     | Individual                                |          | 1.6              | $\pm$ 1.2                 |                                   | Individual                 |          | 0.8              | $\pm$ 0.9 |
| Year                              |                                       | 3.7              | $\pm$ 1.9                 |     | Year                                      |          | 0.1              | $\pm$ 0.4                 |                                   | Year                       |          | 0.6              | $\pm$ 0.8 |
| Residual                          |                                       | 2.8              | $\pm$ 1.7                 |     | Residual                                  |          | 2.8              | $\pm$ 1.7                 |                                   | Residual                   |          | 3.3              | $\pm$ 1.8 |

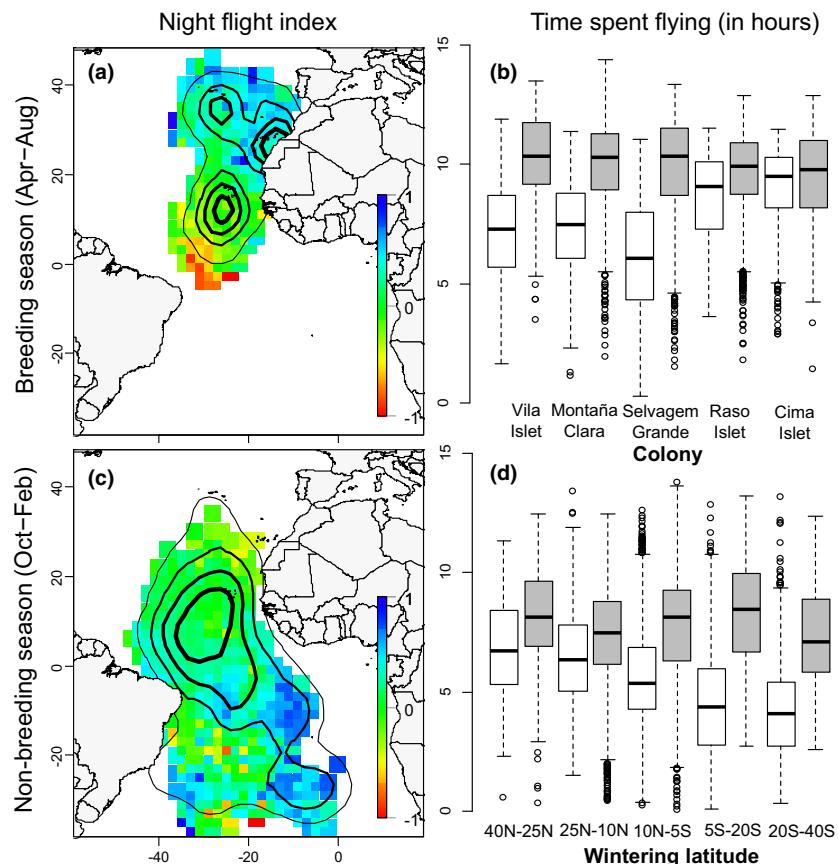
on average), would further support the *differential habitat preference* hypothesis for leapfrog migrations in this species. This would explain why southerly birds migrated relatively short distances and remained within the tropics in winter, whereas part of the northern populations engaged in longer migrations and spent the winter south of the Tropic of Capricorn. The cost of transit to this more distant area would encourage other individuals from the northern populations to stay within the tropical, less-preferred region during the non-breeding season, where they overlap with the southern populations.

## CONCLUSIONS

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

standing the ecological basis for inter- and intra-specific variation in strategies of long-distance migrants. Using tracking technology and habitat modelling, we determined the spatio-temporal distribution and migration pattern of a given species; assessed migratory connectivity and habitat use; and explored alternative explanations for the strategies observed. Our study demonstrates the utility of integrating diverse tracking data from multiple populations/species across international boundaries, and habitat modelling, for identifying important areas common to many marine species in the vast oceanic environments. This will ultimately enable improvement and optimization of the targeting of broad-scale marine conservation efforts.

To our knowledge, this is the first time that an oceanic seabird has been identified as a leapfrog migrant. As discussed above and as reported for several leapfrog migratory species occurring in terrestrial habitats (e.g. Duijns *et al.*, 2012; Fraser *et al.*, 2012; Stanley *et al.*, 2015), competition *per se* and food availability may not fully explain why some individuals from the northernmost populations of Bulwer's petrel undertake a leapfrog migration during which they bear the additional energetic cost of the extra flight distance.



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

Instead, these individuals may prefer specific environmental conditions or be adapted to feed on particular resources that only occur in the southernmost part of the non-breeding range, which would partially compensate for the extra flight time and cost (Boland, 1990; Bell, 1997; Garthe *et al.*, 2012). Comparative studies conducted on individuals tracked over several years under contrasting conditions and at several localities would add valuable information on individual plasticity. Furthermore, complementary studies of trophic ecology based on, for example, stable isotope analyses of feathers moulted at different periods of the annual cycle, would shed light on habitat and diet preferences in the different breeding and non-breeding quarters, and potentially provide more insights into the reasons underlying leapfrog migration (Ramos & González-Solís, 2012).

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## SUPPORTING INFORMATION

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

**Appendix S1** Additional supporting tables, showing modelling of capture–mark–recapture data (Table S1), generalized linear mixed models of migratory characteristics (Table S2), and correlation among oceanographic variables used in habitat modelling of Bulwer's petrel (*Bulweria bulwerii*; Table S3).

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

## BIOSKETCH

**Raül Ramos** is currently interested in the spatial and temporal responses of seabirds to the marine environment. He has combined several interdisciplinary approaches such as intrinsic biogeochemical markers (trace elements and stable isotope analysis), tracking devices and capture–mark–recapture data to ascertain the distribution, abundance and demography of seabirds in the marine environment. His previous work focused on the trophic ecology of seabirds and

their long-distance migratory strategies. More recently, his interests have expanded into several fields involving the epidemiology and the immune system acquisition of long-lived seabirds.

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

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