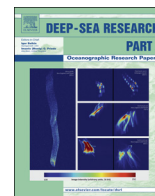




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Distribution and at-sea activity of a nocturnal seabird, the Bulwer's petrel *Bulweria bulwerii*, during the incubation period



Maria P. Dias^{a,b,*}, Joana Romero^b, José Pedro Granadeiro^c, Teresa Catry^c, Ingrid L. Pollet^d, Paulo Catry^b

^a BirdLife International, The David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK

^b MARE – Marine and Environmental Sciences Centre, ISPA - Instituto Universitário, Rua Jardim do Tabaco 34, 1149-041 Lisboa, Portugal

^c Centro de Estudos do Ambiente e do Mar (CESAM), Departamento de Biologia Animal, Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisboa, Portugal

^d Dalhousie University, Halifax, NS, Canada

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ABSTRACT

Bulwer's petrels are nocturnal seabirds that mostly prey on mesopelagic fauna. As aerial foragers and shallow divers, their feeding opportunities are limited by near-surface availability of their prey, which is highly variable both temporally (reflecting diurnal and lunar cycles) and spatially. Here we studied how Bulwer's petrels cope with these constraints by analysing their at-sea distribution and activity during the incubation period. We tracked the movements of 20 birds from Selvagem Grande (NE Atlantic) during a complete lunar cycle, and recorded 30 foraging trips that lasted 11 days on average. Birds were both distributed around the colony and in waters close to the Azorean archipelago (mid-Atlantic) located 1700 km away, and were significantly more active at night (especially just after sunset and before sunrise), when mesopelagic fauna is also closer to the sea surface due to their diel vertical migrations. Bulwer's petrels spent significantly more time flying during moonlight, although the effect of the moon was relatively weak (ca. 10–15% difference between moonlit and dark periods of the night), and not obvious when birds were foraging in mid-Atlantic waters, which were also targeted more often during full-moon. These results reveal key adaptations of the Bulwer's petrel to the highly dynamic ecology of its mesopelagic prey.

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1. Introduction

Many marine animals are specialized predators of abundant mesopelagic fauna, which is a major source of biomass in the oceans (Gjøsaeter and Kawaguchi, 1980). The vertical distribution of mesopelagic fishes and invertebrates is highly variable throughout the daily cycle – these animals move closer to the sea surface during the night (performing a diel vertical migration, or DVM; reviewed by Hays, 2003), when they become much more accessible to air-breathing predators such as seals, penguins, petrels and shearwaters (Harrison et al., 1983; Croxall et al., 1985; Spear et al., 2007; Scheffer et al., 2010; Regular et al., 2010). Mesopelagic fauna also show a marked spatial variability closely linked to bathymetry, and are the dominant component of food webs in deep, open oceanic water (Nybakken, 2001; Pusch et al., 2004).

The foraging activity and distribution of predators that specialise on mesopelagic species is therefore highly constrained by

the diel cycles of their vertically migrating prey (Hays, 2003). This is particularly true for shallow divers, such as many small Procellariiformes (storm-petrels, gadfly and other petrels). These species are markedly nocturnal and more abundant in oceanic waters than the larger members of the Procellariiformes order; the latter are diurnal foragers on epipelagic prey, and tend to occur in comparatively shallow and more productive areas, often associated with upwelling regions (Spear et al., 2007; Wakefield et al., 2011). Small, nocturnal Procellariiformes (< 200 g) represent about 40% of all species in their order (Harrison, 1983). Until the recent development of small data loggers, their small size hampered the study of their at-sea distribution (Rayner et al., 2011, 2012; Navarro et al., 2013; Pollet et al., 2014a, 2014b).

Here we present the results of a tracking study of a small procellariiform seabird, the Bulwer's petrel *Bulweria bulwerii*. This species breeds on tropical and sub-tropical islands of the Atlantic and Pacific oceans, in colonies located in mid-ocean archipelagos (e.g. Azores and Hawaii) or islands near the continental shelf (e.g. Cape Verde, Madeira and Canary islands; Hoyo et al., 1992). The Bulwer's petrel is one of the most nocturnal of all seabirds (Spear et al., 2007), actively foraging for 90% on average of the night,

* Corresponding author at: BirdLife International, The David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK.

E-mail address: maria.dias@birdlife.org (M.P. Dias).

which is more than any other seabird species studied so far (Dias et al., 2015). It is also a shallow diver (< 3 m; Mougin and Mougin, 2000) and a predator of mesopelagic fishes and cephalopods (Zonfrillo, 1986; Neves et al., 2011). It is therefore an excellent model for investigating the foraging adaptations of air-breathing predators to the high spatial and temporal variability in abundance of mesopelagic fauna near the sea surface. Although one of the most abundant seabird species in Atlantic tropical and sub-tropical waters (del Hoyo et al.), the at-sea distribution and foraging strategies of Bulwer's petrels during the breeding season remains very little known. Previous studies have shown that after breeding they migrate to deep oceanic waters of the tropical Atlantic to spend the winter in areas not used by other abundant seabirds of sub-tropical Atlantic, such as Cory's shearwaters *Calonectris borealis* (Dias et al., 2015; Ramos et al., 2015).

We investigated how Bulwer's petrels cope with several constraints related to prey availability during the breeding period, in particular the influence of the diel cycle and bathymetry on abundance of their mesopelagic prey. During this time of year, seabirds are limited spatially by colony location, acting as central place foragers (i.e., they forage at sea, but must return regularly to the colony due to breeding duties). We carried out our study in Selvagem Grande, an oceanic island located in the sub-tropical north-eastern Atlantic, about 300 km off the African continental shelf. We characterised the at-sea diurnal and nocturnal activity of Bulwer's petrels, and examined the influence of the lunar cycle on their flying behaviour during foraging trips. A previous study carried out during the non-breeding season revealed that the lunar cycle has no effect on the flying activity of the Bulwer's petrel (Dias et al., 2015). This clearly contrasts with results for other seabird species, which typically spend more time flying when foraging during nights with a full-moon (Yamamoto et al., 2008; Mackley et al., 2011; Pinet et al., 2011). Here we addressed this question by analysing the effect of moonlight during the breeding period, when Bulwer's petrels are considerably more spatially and temporarily constrained, and so may respond differently to some of the major factors affecting prey availability. We analysed changes in their activity during the lunar cycle and, at a more detailed scale, compared their behaviour before and after the setting and rising of the moon during the first and third quarter of the moon cycle. We also mapped the at-sea distribution of the Bulwer's petrel during the new and full-moon, and hypothesized that the distribution of these highly mobile birds may change according to moon phase. For example, since moonlight depresses the surface abundance of mesopelagic prey in deep oceanic waters (Horning and Trillmich, 1999; Hernández-Leon et al., 2001), we might predict that birds will shift their distribution towards the African shelf or shelf-break during the full-moon, when they might complement their diet with epipelagic prey, which are also known to be consumed by Bulwer's petrels (Spear et al., 2007). The African shelf and shelf-break is amongst the most productive areas in the NE Atlantic (due to the influence of the Canary Current) and is used by Bulwer's petrels from a local colony in the Canary Islands (Rodríguez et al., 2013) and also by many other seabird species (e.g. Camphuysen and van der Meer, 2005; Ramos et al., 2013).

2. Methods

2.1. Deployment of the tracking devices

We deployed 20 geolocators (GLS; Mk5093 model, manufactured by Biotrack and weighing 1.2 g) on incubating Bulwer's Petrels (unknown sex) from the Selvagem Grande colony (30°09'N, 15°52'W) on 7–13 June 2012, which were all recovered

approximately one month later (4–14 July 2012), during the late incubation or brood-guarding period (therefore covering a complete lunar cycle). Devices were attached to a plastic flag ring with a cable-tie, and provided information on light intensity and salt-water immersion.

We did not detect any detrimental effect of the device deployment on birds, either in terms of the survival rate of the tracked individuals while carrying the device (100%) or their subsequent breeding success (45%, similar to the value recorded in this same colony and year in a parallel study with $n=88$; Pinto, 2013).

2.2. Analysis of the foraging movements

Light intensity data were analysed in order to provide two estimates of latitude and longitude per day based on the duration of daylight time (estimated from sunset and sunrise events) and timing of local midday, as described in Phillips et al. (2004). Light threshold was set as 10 and sun elevation angle was set between -1° and -2° .

Locations derived from light-based geolocation methods have an average accuracy of 186 ± 114 km and can be affected by weather conditions, feather shading of the light sensor, or high daily travel speeds (Phillips et al., 2004; Gutowsky et al., 2014; Pollet et al., 2014a). We used hierarchical state-space models, fitted to data from foraging trips performed by studied individuals, to filter and correct observed locations for logger error (Jonsen et al., 2005, 2013). A foraging trip started from the first location after deployment with a record of saltwater immersion (followed by consecutive periods of any saltwater immersion activity), whereas the last location was that preceding a period of several days of complete darkness associated with lack of saltwater immersion records (when individuals were in their burrows). Before and after each foraging trip, we knew the position of individuals as being that of the colony. The state-space models were fitted using Markov Chain Monte Carlo (MCMC) sampling using JAGS software accessed through the R interface with the *rjags* package. We used a fixed geolocation error (SD of latitudinal and longitudinal error: 1.66° and 1.82° , respectively; Phillips et al., 2004) as an estimate of the uncertainty in positions, a parameter required in these models (Winship et al., 2012). Two chains of 100000 samples from the joint posterior probability distribution were generated after discarding the initial burn-in period of 100000 iterations. To reduce sample autocorrelation, one out of 100 of the remaining samples were retained, yielding a total of 2000 samples from the joint posterior probability distribution. MCMC convergence was assessed visually by checking trace, density and autocorrelation plots (Pollet et al., 2014a). The final state-space model processed locations were obtained from the mean of the appropriately converged posterior distributions.

For each trip ($n=30$, two trips were recorded for 10 birds; see Appendix A) we calculated (1) the maximum distance from the colony (in km; hereafter foraging range) and (2) the trip duration (in days). We also associated each location with the closest value for bathymetry and with the phase of the moon on that day (new, first-quarter, full-moon and third-quarter moon days ± 3 days each). The fraction of the moon illuminated and the moonset and moonrise times were obtained for each day (for the colony location) from http://aa.usno.navy.mil/data/docs/RS_OneYear.php; bathymetric values in grid cells of 1 arc-minute were obtained from the NOAA National Geophysical Data Center using the R package *marmap* (Pante and Simon-Bouhet, 2013).

The at-sea distribution during new and full-moon periods were mapped using kernel density estimation (smoothing factor estimated by Least Square Cross Validation; Calenge, 2006), by pooling all the locations recorded in each phase (excluding first and

last two days of each trip, likely corresponding to commuting days). We also compared the influence of the moon on flight activity of birds when located in western and eastern of the centroid of their distribution (22° West).

2.3. Activity data processing

We characterised the activity patterns of Bulwer's petrels using the saltwater immersion data provided by the devices, which record the number of immersion events (registered every 3 sec) in 10 min blocks (thus varying between values of 0, when the bird is flying for the entire 10 min period, and 200, when immersed permanently). We estimated, for each bird and day, the percentage of time spent flying during daylight and darkness (sunrise and sunset times for each day derived from GLS light data - see previous sub-chapter), and also in hourly intervals during the 24 h cycle.

We investigated the influence of the lunar cycle on the activity of Bulwer's petrels by comparing the percentage of diurnal, nocturnal and overall time flying in different moon-phases. We also analysed in more detail the at-sea behaviour on quarter-moon nights (20–80% of illuminated moon), by comparing the flight activity before and after the moon rise (waning moon nights) or set (waxing moon nights).

Light data from the geolocators were analysed with TransEdit2 and Locator software (British Antarctic Survey, Cambridge, UK), and all the remaining analyses were carried out using the software R (R Core Team, 2014). Bird identity was included as a random factor in all linear-mixed effects models (function *lmer* under the R package *lme4*; Bates et al., 2015). Proportion values were analysed after arcsine transformation (square root arcsine). Analysis of variance tables were computed for each fitted model to test whether the terms were significant (function *anova*).

3. Results

3.1. Foraging trips

The foraging trips of Bulwer's petrels during the incubation period lasted, on average, 10.8 ± 3.3 days (range 5–19 days, $n=30$; Appendix B). Birds were frequently distributed around the colony (18 out of 30 trips), but they also moved to areas as distant as 1700 km to the W-NW, around the Azores (Fig. 1 and Appendixes A and B). No relationship was found between the foraging range and trip duration (mixed model, estimate: 4.73×10^{-4} [1.13×10^{-3} s.e.], $F_{1,23}=0.174$, $p=0.681$). We did not find any influence of the progression of the breeding season (departure

date) on trip duration (mixed model, estimate: 0.02 [0.05 s.e.], $F_{1,12}=0.130$, $p=0.725$) or on foraging range (mixed model, estimate: 9.20 [8.67 s.e.], $F_{1,14}=0.126$, $p=0.306$). The mean depth of the waters overlapping with the Bulwer's petrels distribution ranged from 2056 m to 4480 m (mean \pm SD = 3594 ± 672 m, $n=30$ trips; Fig. 1). The sites located further away from the colony were, on average, less deep than the waters found on the way there (Fig. 2).

3.2. Activity patterns

Bulwer's petrels spent, on average, almost 90% of the night in flight, significantly more than during the day (approx. 73%; Table 1). Birds targeting areas further away from the colony spent a significantly higher proportion of their time flying during the day (Fig. 3; significant effect of maximum foraging range on percentage of diurnal time flying; mixed model, estimate: 8.79×10^{-5} [2.85×10^{-5} s.e.], $F_{1,28}=9.53$, $p=0.005$; no significant effect on percentage of nocturnal time flying: mixed model, estimate: 4.80×10^{-5} [4.30×10^{-5} s.e.], $F_{1,28}=1.242$, $p=0.275$).

A detailed analysis of the flight behaviour during the daily cycle revealed an

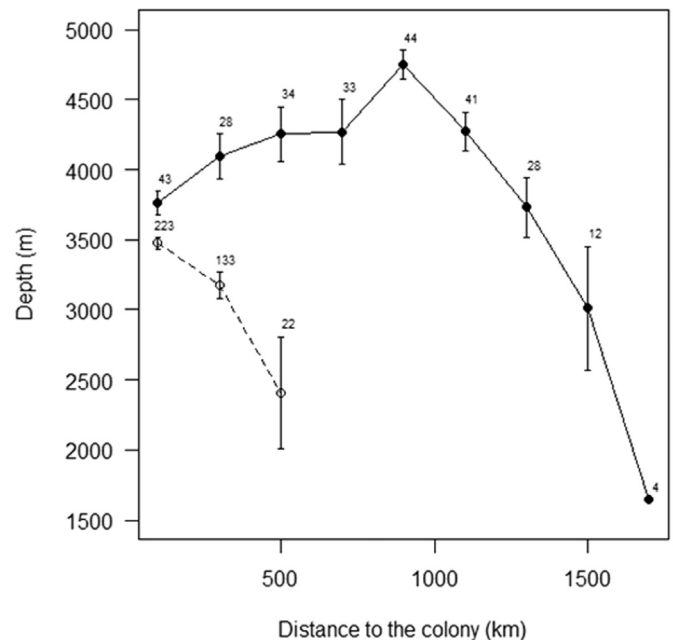


Fig. 2. Relationship between the distance to the colony (grouped in 200 km intervals) and bathymetry (average \pm SE) at the locations of trips by Bulwer's petrels to distant areas (i.e., > 800 km from the colony; solid line) and trips around the colony (dashed line). Values on top of the bars correspond to sample sizes (number of locations).

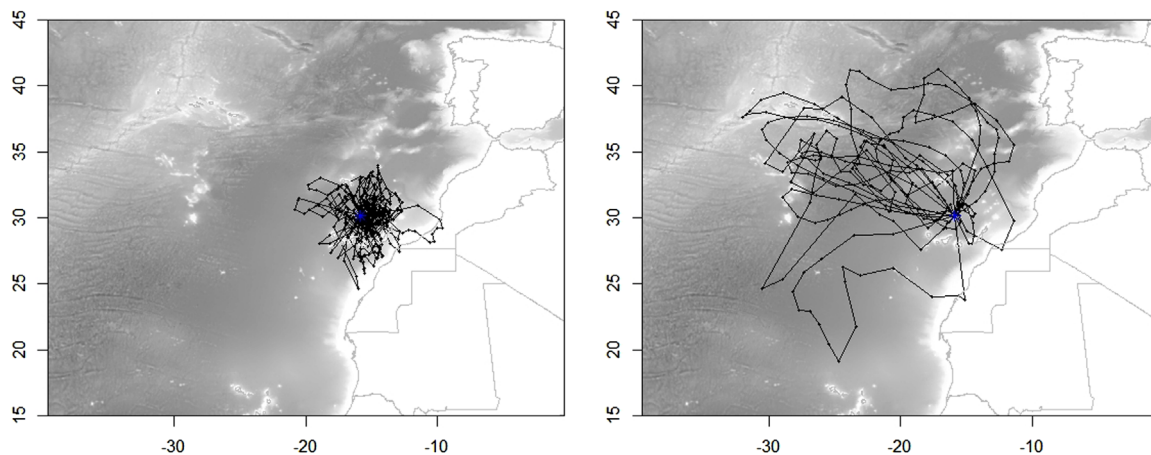


Fig. 1. Foraging trips of 20 Bulwer's petrels from Selvagem Grande colony (indicated by a blue star) during incubation. Panels show trips targeting areas located < 800 km (short range trips; left panel) and > 800 km (long range trips; right panel) from the colony (mean trip duration 10.61 and 11.08 days; $n=18$ and $n=12$, respectively). Individual trips are presented in Appendix A and characteristics of the foraging trips are summarized in Appendix B. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Flight activity of Bulwer's petrels in foraging trips during incubation (% of time flying: mean of each birds \pm SD). Sample sizes correspond to the number of individual trips. Both the daily light cycle (daylight vs night) and the moon phase had a significant effect on the percentage of time flying (mixed model: day/night effect: $F_{1,614}=240.39$, $p < 0.0001$; moon effect: $F_{3,629}=11.37$, $p < 0.0001$; interaction moon-day/night: $F_{3,614}=1.80$, $p=0.145$).

	Daylight	Night
Overall (n=30)	72.95 \pm 7.62	88.21 \pm 8.10
New moon days (n=19)	71.52 \pm 9.92	84.77 \pm 10.14
Waxing moon days (n=13)	75.11 \pm 6.28	88.96 \pm 7.31
Full-moon days (n=11)	78.36 \pm 6.38	95.27 \pm 3.08
Waning moon days (n=17)	69.57 \pm 13.28	87.37 \pm 8.48

increase in the activity of the tracked birds just before sunrise and soon after sunset (Fig. 4).

3.3. Effect of the moon

Moon phase had a significant effect on the at-sea behaviour of Bulwer's petrels, with birds spending 10% more time flying during full-moon, particularly during the night (Table 1). A comparison of the flight behaviour during quarter-moons also revealed higher activity during the moonlit part of the night (Fig. 5).

The at-sea distribution during full and new-moon periods largely overlap, although birds tended to distribute more westwards during full-moon (Fig. 5; significant effect of moon phase [full vs new moon] on longitude; mixed model, estimate: -3.35 [0.71 s.e.], $F_{1,101}=22.51$, $p < 0.0001$). The night flight activity of birds foraging further west (i.e., longitude < -22) were not affected by the moon (mixed model, estimates: full-moon=0.03 [0.05 s.e.], waxing moon= -0.001 [0.04 s.e.], $F_{2,47}=0.376$, $p=0.688$), while the moon phase had a significant effect on birds foraging at eastern longitudes (which spent significantly more time flying in full-moon nights; Fig. 5; mixed model, estimates: waning moon=0.04 [0.03], full-moon=0.16 [0.04 s.e.], waxing moon=0.04 [0.03 s.e.], $F_{3,205}=7.040$, $p < 0.001$).

4. Discussion

4.1. At-sea movements and distribution

Our results revealed considerable inter-individual variability in the at-sea distribution of Bulwer's petrels during the incubation period, with birds targeting waters located at a wide range of

distances from the colony (Figs. 1 and 3, Appendixes A and B). Part of this variation might be due to the error inherent in light-based geolocation (Phillips et al., 2004); however, the positive correlation between the diurnal flight activity (typically associated with travelling time in this species; Dias et al., 2015) and the maximum foraging range supports the location estimates, which were also considerably improved using a state-space modelling approach (Jonsen et al., 2005).

One third of the incubation trips were to the waters NW of Selvagem Grande, towards the region of the Azorean Archipelago (38 °N, 27 °W) or waters to the N-NW (latitudes around 35–40 °N), located > 1000 km from the colony (up to 1700 km), resulting in some cases of a total trip of more than 5000 km (Appendix B). Some authors had previously hypothesized that Bulwer's petrel could cover large distances during the incubation phase (Mougin and Mougin, 2000), and others report long foraging trips, but during late chick-rearing (probably coinciding with post-breeding dispersal; Rodríguez et al., 2013). That such a small petrel is able to travel so far during the breeding season (in the same order of magnitude as some shearwaters and albatrosses; Phalan et al., 2007; Kappes et al., 2010) is remarkable, but in line with recent results for other small Procellariiformes, including the Leach's storm-petrel *Oceanodroma leucorhoa*, a 45 g bird able to forage at 1000 km from the colony during incubation trips (Pollet et al., 2014a). Indeed, the recent effort in tracking small, nocturnal seabirds (Rayner et al., 2012; Pinet et al., 2012; Pollet et al., 2014a, 2014b) shows that these species tend to travel much farther than initially thought (reviewed by Pollet et al., 2014a). This highlights the need to increase knowledge of their foraging grounds, particularly given widespread interest in identifying key marine areas for these species (Thaxter et al., 2012), several of which are highly threatened (Croxall et al., 2012).

The decision to travel farther away from the colony was not influenced by the advancement of the breeding season, although it is a common behaviour among seabirds to perform longer and more distant trips earlier in the incubation period (e.g. González-Solís, 2004). Interestingly, trips to Azorean waters lasted as long as the trips around the colony (11 days, on average, in both cases), and we did not find any correlation between foraging range and

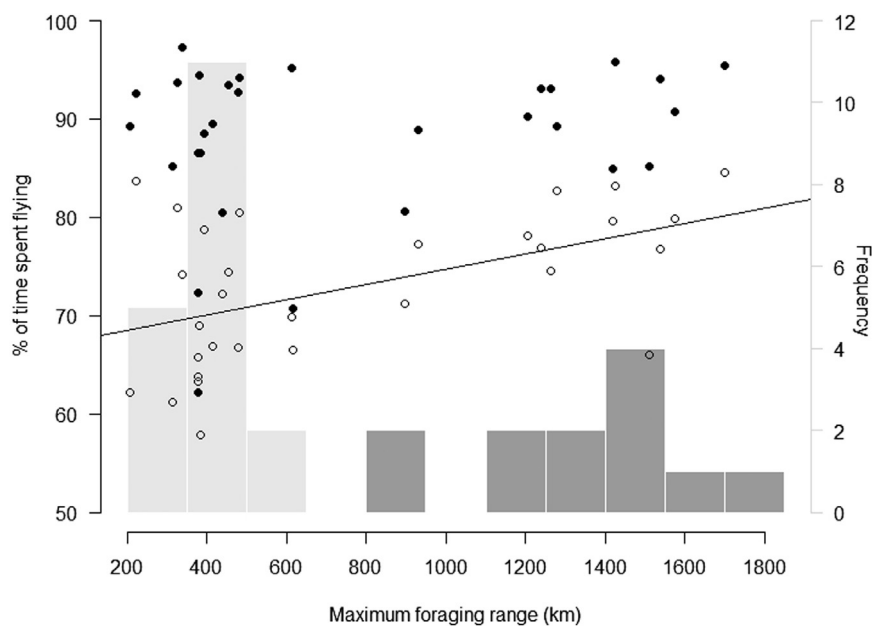


Fig. 3. Percentage of time spent flying during the day (open symbols) and night (closed symbols) in trips of Bulwer's petrels to various distances from the colony. The fitted line represents the significant relationship between diurnal flight and maximum foraging distance (left axis). The histogram represents the number of trips in each class of foraging range (right axis); different shadings represent trips classified as "short range" or "long range" in Fig. 1 (see also Appendix B).

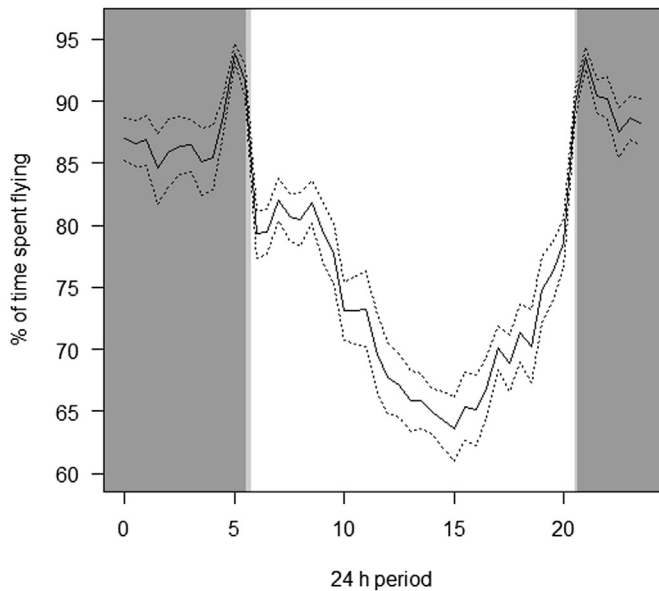


Fig. 4. Flight activity (average \pm SE percentage of time flying, represented by the solid and dashed lines respectively) of Bulwer's petrels throughout a 24 h period (GMT time) during foraging trips in the incubation period. Dark grey areas represent the periods of darkness, and light grey areas represent the sunrise and sunset moments (intervals experienced by all the birds taking into consideration the variation in sunset and sunrise times due to their distribution).

trip duration. This suggests that birds travelling to distant, open oceanic waters were relying on more predictable food sources compared to those staying closer to the colony, which necessarily spent less time commuting. This is somehow surprising considering that the overall abundance of mesopelagic fishes is very high towards the east of the central Atlantic Ocean, where the Selvagem Grande colony is located (Gjøsaeter and Kawaguchi, 1980). A possible explanation can be a local effect of enhanced surface availability of DVM prey due to the seafloor topography of these distant waters, dominated by seamounts that trap the downwardly migrating organisms and induce mid-oceanic

upwelling phenomena (e.g. Rogers 1994; Boehlert, 1998; Fock et al., 2002). The Azorean seamounts, in particular, are important foraging hotspots for many seabirds and other marine predators such as tunas and dolphins (Morato et al., 2008; Amorim et al., 2009). The lack of accuracy in geolocation estimates hampers any detailed analysis of bathymetry and other habitat characteristics that could confirm that Bulwer's petrels are, in fact, targeting these seamounts. However, an analysis of the (broad-scale) bathymetry in waters overlapping with the distribution of the birds shows that these distant areas are less deep than the waters over which they transited (Fig. 2).

4.2. At-sea activity

Bulwer's petrels spent almost all the night time flying, as shown here and in previous studies during the non-breeding season (Dias et al., 2015; Ramos et al., 2015). Given that this species preys mostly upon species only available at sea-surface during the night (Zonfrillo, 1986; Neves et al., 2011), an increased flight activity during darkness is likely to represent an intensified foraging effort. Further evidence for this link between nocturnal time flying and foraging effort comes from the detailed analysis of flight activity throughout the 24 period, with pronounced increases just before sunrise and after sunset (Fig. 4). This pattern mirrors the typical increase in foraging activity at these times found in several predators of mesopelagic prey (Croxall et al., 1985; Falk et al., 2002; Regular et al., 2010; Scheffer et al., 2010; Dias et al., 2012), most likely linked to improved visibility during the period when DVM species are still abundant near the surface (Piersma et al., 1988; Regular et al., 2010; Scheffer et al., 2010).

4.3. Influence of moon phase

The foraging effort of the Bulwer's petrel was highest during full-moon nights, or in the moonlit parts of quarter moon nights (Table 1 and Fig. 5). A similar pattern has been described for other visual predators (Phalan et al., 2007; Yamamoto et al., 2008; Mackley et al., 2011; Pinet et al., 2011) and attributed to the improved visibility of prey in moonlight, assuming that an increase in

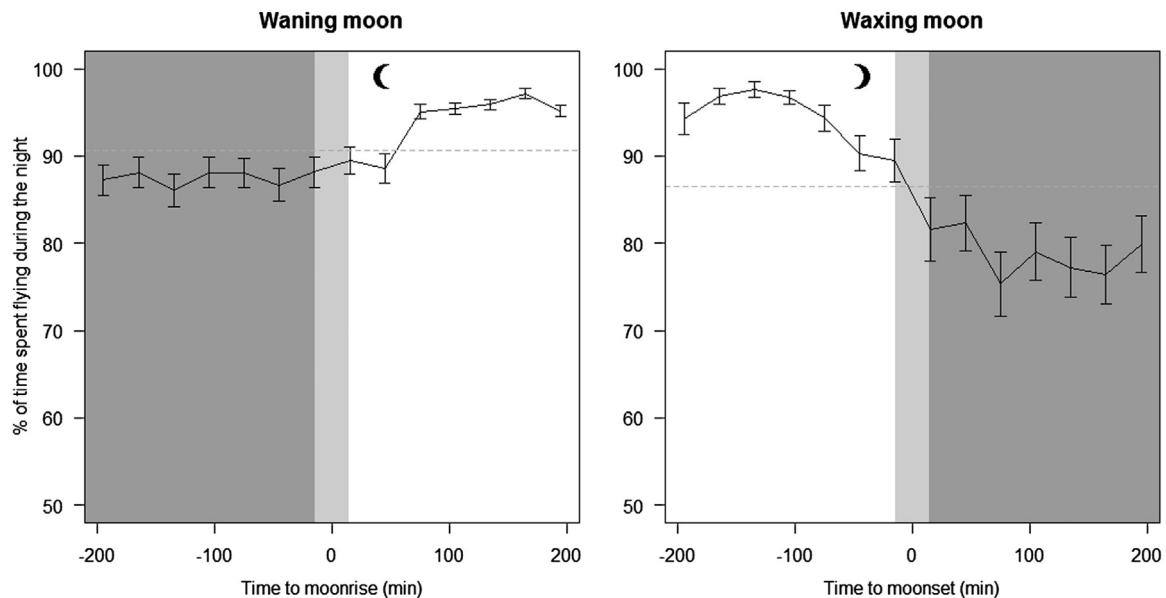


Fig. 5. Percentage of the time spent flying (mean \pm SE) before and after the rising and setting of the moon on nights with a waning and a waxing moon, respectively, in foraging trips by Bulwer's petrels during incubation. Dark grey area represents the part of the night without moonlight, and the light grey area represent the interval of moonset and moonrise times experienced by the birds depending on their location. The dashed line represents the overall average. We found a significant difference between the flight behaviour before and after the moon rise/set (comparison between moonlit and dark periods of the night: paired *t*-test [by bird] $t=3.25$, $p=0.004$, $d.f.=17$, $n=18$ birds).

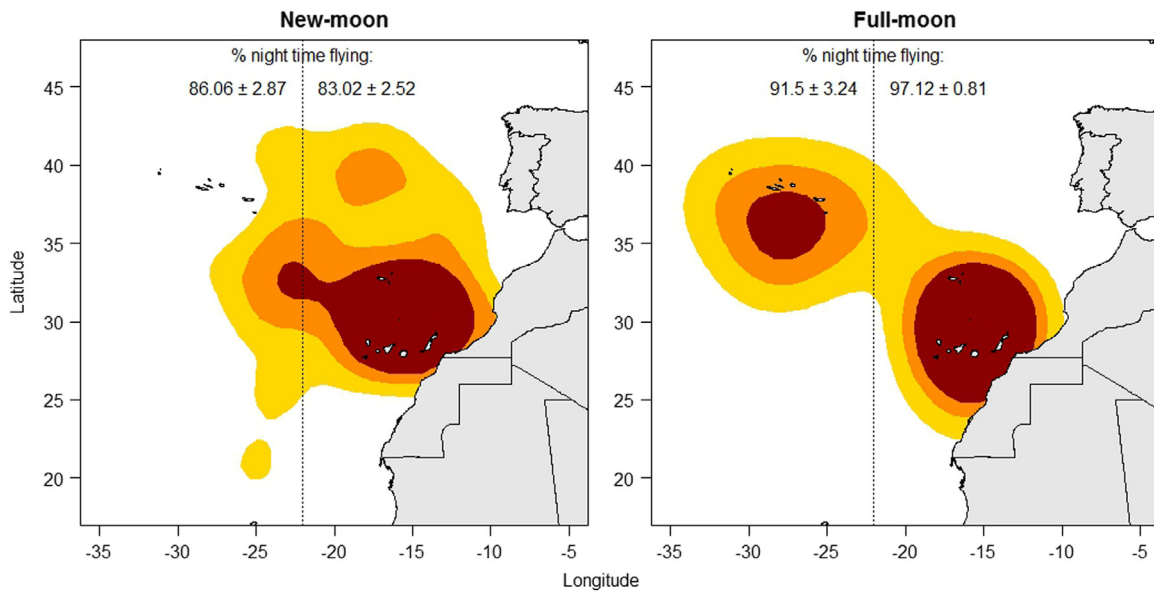


Fig. 6. At-sea distribution (50%, 70% and 90% kernel density areas represented in yellow, orange and red, respectively) of Bulwer's petrels around the new-moon ± 3 days (138 positions from 18 birds pooled together) and the full-moon ± 3 days (84 locations from 9 birds pooled together). Values indicate the % of night time flying when birds are located west or east of meridian 22° West (dashed line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

searching effort reflects higher foraging success (Phalan et al., 2007; Rubolini et al., 2014). Nevertheless, the surface availability of DVM prey is several times lower during nights with a full-moon (Horning and Trillmich, 1999; Hernández-Leon et al., 2001; Regular et al., 2011) and for predators of DVM prey, such as the Bulwer's petrel, an increase in foraging effort in the presence of moonlight might instead be a response that compensates for the reduced accessibility of prey (Klomp and Furness, 1992).

It is important to highlight that the effect of the lunar cycle was obvious and significant, but not particularly relevant in absolute terms – 10% difference in flight time between new and full-moons (or parts of the night with and without moonlight), and absent during the non-breeding season (Dias et al., 2015). Indeed, during the new moon, when prey availability is presumably much higher, the percentage of time flying was already close to the 100% ceiling (noting that birds need to spend some time in the water when capturing and handling prey; nevertheless, Bulwer's petrels feed on relatively large prey items that are swallowed whole, and therefore this time should be generally short). The small scope for an increased effort during moonlight might imply that intake rates are reduced significantly during full moon, should foraging efficiency decline substantially. However, we would then expect that when the moon is visible during part of the night, the birds would exploit the period of greater darkness and forage for as long as possible, which was not the case (the difference in flight activity between dark and moonlit parts of the quarter-moon nights – Fig. 5 – was in the same order of magnitude as variation throughout the lunar cycle – Table 1). Therefore, the likely cause for the increase in flying activity in moonlight in Bulwer's petrels is a small decrease in their foraging efficiency (Klomp and Furness, 1992), or an increase in aerial activity for other purposes (e.g. commuting). Nevertheless, we cannot exclude the possibility that the birds increased the flight activity to exploit the greater visibility of prey under moonlight (i.e., the improved visibility would compensate the decrease in prey availability). In any case, such a small change in foraging activity is surprising, considering the reported large difference in sub-surface abundance of their prey during moonlight (Horning and Trillmich, 1999; Hernández-Leon et al., 2001).

On the other hand, we detected an influence of the moon on

the large-scale distribution of Bulwer's petrels (Fig. 6). However, and in contrast to what we could expect, the Bulwer's petrels did not rely more on the African shelf or shelf-break during full-moon in response to a presumed reduction of prey abundance in open oceanic water. Our broad-scale analysis revealed the opposite trend – a slight shift towards Azorean waters during this phase. Moreover, we found that the lunar cycle did not affect the night flight activity in these western locations. This result gives further support to the hypothesis that birds foraging at distant waters are taking advantage of the trapping effect on downwardly migrating organisms caused by the seamounts (see above). This trapping effect might assume a greater relevance for the Bulwer's petrels during full-moon periods, due to the presumable reduced accessibility to their prey on this stage. In line with these results, the moon did not affect also the foraging strategies of Bulwer's petrels during the non-breeding period, when birds are freed from the spatial and temporal constraints related to the need for regular nest attendance (Dias et al., 2015). This contrast with the pattern found for other highly nocturnal seabirds (Mackley et al., 2011; Cruz et al., 2013). Future research should aim at quantifying foraging efficiency and intake rates of nocturnally active seabirds in relation to moonlight, and to identify possible fine-scale adjustments in foraging distribution (e.g. in relation to the presence of seamounts). Nevertheless, the results from our study suggest that Bulwer's petrels are very well adapted to exploit the highly dynamic nature of their DVM prey throughout the lunar cycle.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2016.03.006>.

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