J Ornithol (2015) 156:955–962
DOI 10.1007/s10336-015-1210-9

ORIGINAL ARTICLE

Wanderer of the deepest seas: migratory behaviour and distribution of the highly pelagic Bulwer's petrel

Maria P. Dias[1,2] · Maria Alho[3] · José P. Granadeiro[4] · Paulo Catry[1]

Received: 13 September 2014 / Revised: 19 January 2015 / Accepted: 16 March 2015 / Published online: 29 March 2015

Abstract Small-sized nocturnal Procellariiformes are abundant predators in oceanic areas worldwide and are thought to play an important role in many marine food webs as consumers of superabundant mesopelagic prey. However, the spatial ecology and foraging behaviour of the great majority of these species remain largely unknown. We studied the non-breeding distribution and at-sea activity of a migratory small-sized Procellariiform, the Bulwer's petrels *Bulweria bulwerii*, from the Selvagem Island colony (subtropical Northeast Atlantic). We found that soon after breeding Bulwer's petrels migrate towards deep (mean depth of 4416 m), open oceanic waters of the tropical Atlantic, spending the winter far from shelf and shelf-break areas, on regions avoided by most other avian migrants in the Atlantic. When at sea, Bulwer's petrels spent more time flying during the night (>90 %, all year round) than any other seabird studied so far. This nighttime activity was not influenced by the lunar cycle, suggesting that this highly specialised nocturnal seabird is probably very well adapted to locating and capturing prey even in very dark conditions. The results from the present study may have important implications for the identification of important bird areas in the marine realm, whose boundaries have been delineated so far mostly on the basis of the distribution and behaviour of better studied medium- to large-sized seabirds.

Keywords At-sea activity · Bulwer's petrels · Migration · Procellariiformes · Seabirds

Zusammenfassung

Wanderer über der Tiefsee: Zugverhalten und Verbreitung des hochgradig pelagischen Bulwersturmvogels

Kleine nachtaktive Röhrennasenarten (Procellariiformes) sind häufige Prädatoren ozeanischer Lebensräume weltweit und spielen als Konsumenten der reichlichst vorhandenen mesopelagischen Beutetiere vermutlich eine wichtige Rolle in vielen marinen Nahrungsnetzen. Allerdings sind die Raumnutzungsökologie und das Nahrungssuchverhalten der allermeisten dieser Arten noch weitestgehend unbekannt. Wir untersuchten die Verbreitung außerhalb der Brutzeit sowie die Aktivität auf See bei einer ziehenden kleinen Röhrennasenart, dem Bulwersturmvogel *Bulweria bulwerii*, anhand der Kolonie auf der Insel Selvagem (Portugal) im subtropischen Nordostatlantik. Wir stellten fest, dass die Bulwersturmvögel kurz nach dem Ende der Brutzeit zu tiefen (mittlere Tiefe 4.416 m), offenen ozeanischen Gewässern des tropischen Atlantiks aufbrechen und den Winter fern von Schelf- und Schelfrandbereichen verbringen, in Gebieten, die von den meisten anderen Zugvögeln des Atlantiks gemieden werden. Waren sie über dem Meer, verbrachten die Bulwersturmvögel

---

Communicated by N. Chernetsov.

✉ Maria P. Dias
mariapdias@fc.ul.pt

[1] MARE-Marine and Environmental Sciences Centre, ISPA-Instituto Universitário, Rua Jardim do Tabaco 34, 1149-041 Lisbon, Portugal

[2] Present Address: BirdLife International, Wellbrook Court, Girton Road, Cambridge CB3 0NA, UK

[3] Departmento de Biologia Animal, Faculdade de Ciências da Universidade de Lisboa, Lisbon, Portugal

[4] Departamento de Biologia Animal, Centro de Estudos do Ambiente e do Mar, Faculdade de Ciências da Universidade de Lisboa, Lisbon, Portugal

mehr Zeit mit nächtlichen Flügen (ganzjährig >90 %) als alle anderen bislang untersuchten Seevögel. Diese nächtliche Aktivität wurde nicht von der Mondphase beeinflusst, was nahelegt, dass dieser hochspezialisierte nachtaktive Seevogel vermutlich sehr gut daran angepasst ist, seine Beute selbst unter sehr dunklen Bedingungen zu entdecken und zu fangen. Die Ergebnisse der vorliegenden Studie könnten weitreichende Konsequenzen für die Ausweisung von Vogelschutzgebieten (Important Bird Areas, IBAs) im marinen Bereich haben, deren Grenzen bisher hauptsächlich auf der Grundlage von Verbreitung und Verhalten der besser untersuchten mittelgroßen bis großen Seevögel festgelegt wurden.

Introduction

The study of the migratory behaviour of pelagic seabirds, such as the Procellariiformes, has been remarkably expanded in recent decades as a consequence of the development of tracking technologies (Burger and Shaffer 2008). The large quantity of data collected by tracking individual birds has allowed furthering the knowledge about the behavioural ecology of these species in several new fronts (e.g., Block et al. 2011; Dias et al. 2012a; Weimerskirch et al. 2014). Furthermore, this information has also been used as a critical tool for seabird and broad scale ecosystem conservation through the identification of the most intensively used areas, thus supporting the delimitation of important bird and biodiversity areas in the marine environment (Lascelles et al. 2012; Corre et al. 2012).

Nevertheless, the vast majority of these studies have focused on large- to medium-sized species, such as albatrosses and shearwaters (Wakefield et al. 2009). The huge bias in the knowledge gathered so far for these species, compared with what little is known for small-sized Procellariiformes, is mainly due the technological limitations involved in manufacturing small and light tracking devices (Burger and Shaffer 2008). This constraint has been gradually alleviated (Pollet et al. 2014a, b) but still to date very few small-sized seabird species (200 g or less) have been studied in relation to their migratory and at-sea distribution patterns (but see, e.g., Rayner et al. 2011, 2012; Quillfeldt et al. 2012; Zino and Biscoito 2013; Navarro et al. 2013; Pollet et al. 2014a, b). This is despite the fact small Procellariiformes represent about 40 % of all species in their order (Harrison 1983).

Although sharing many of the life-history traits of their larger relatives (such as a K-type life strategy—high longevity, delayed age at first breeding, clutch size of 1, and extensive parental care), small-sized Procellariiformes are thought to differ in many other ecological characteristics, mainly related to their diet and foraging habits. While most albatrosses and shearwaters prey upon epipelagic species, away from Polar regions most small-sized Procellariiformes are specialised predators of mesopelagic fishes and squids (Spear et al. 2007). Small petrels (except diving petrels) are usually shallow divers; therefore, their feeding opportunities are strongly constrained by the surface availability of these species, which is known to be highly variable throughout the diurnal cycle. Mesopelagic fishes and squids typically display diel vertical migrations (DVM) that make them more available at the sea surface during darkness (Roper and Young 1975; Gjøsaeter and Kawaguchi 1980; Harrison et al. 1983), but the behavioural adaptations of seabirds to this temporal variability of their prey items remains mostly unknown. On the other hand, mesopelagic species are much more abundant in open, oceanic waters than in the continental shelf (Kozlov 1995; Nybakken 2001; Catul et al. 2011), which likely shapes the at-sea distribution of their avian predators, in particular during the non-breeding season, when they are free from spatial constraints linked to colony attendance and reproduction (Mackley et al. 2010).

In this study we analysed the at-sea behaviour and distribution of a small-sized Procellariiform species, the Bulwer's petrel, during its non-breeding season. Bulwer's petrels are amongst the smallest members of the Procellariidae family (length: 26 cm; approximately weight: 100 g). They are shallow divers (Mougin and Mougin 2000) whose diet is mostly based on mesopelagic fishes (Zonfrillo 1986; Neves et al. 2011; Carvalho 2012). Therefore, and for the reasons stated above, we could expect this species to present a migratory strategy and an at-sea distribution and behaviour considerably different from other much better studied Procellariidae. In particular, we hypothesise that its non-breeding range would be, at a broad scale, centred in open and deep oceanic waters, away from the main continental shelves. In such areas, Bulwer's petrels can take advantage of the (presumably) high abundance of mesopelagic prey by adapting their daily foraging schedules to the dynamic surface availability of DVM fish and squid.

Materials and methods

We deployed 22 geolocators (Mk 5093 model, manufactured by BioTrack and weighing, 1.2 g) on adult breeding Bulwer's petrels from the Selvagem Grande colony (30°09′N, 15°52′W) during their chick-rearing period of 2012 (early August) and recovered 20 in the beginning of the incubation period (late June) of 2013. From these, 13 collected data for the most part of the wintering period (i.e., until the end of January), 5 collected data for the entire deployment period and 1 failed during the first few weeks after deployment [mean duration of the devices 210 days (range 75–372 days)]. As a consequence, the sample sizes for different migratory timings calculated afterwards varied.

Devices were attached to a plastic flag ring specifically designed for this purpose with a cable tie and provided information on light intensity and duration of saltwater immersion. Light intensity data were analysed in order to estimate the latitude and longitude, following the standard procedures based on the duration of daylight time and local midday time, described in Phillips et al. (2004) (sun elevation angle was set between -3° and -4.5°, based on positions collected during the breeding period). Days in active migration were considered as those with a clear directionality (latitudinal and/or longitudinal) in consecutive positions, recorded immediately after colony departure (i.e., when no locations where detected within a 200-km radius from the colony after the breeding season) or before colony arrival in the beginning of the following breeding season. These were detected by the visual analysis of the daily positions of each bird in a GIS software and by inspection of longitude variation (during equinox periods, when latitude estimate based on daylight duration is not possible). The location of the main wintering areas was derived for each individual using kernel density contours estimation (50 %).

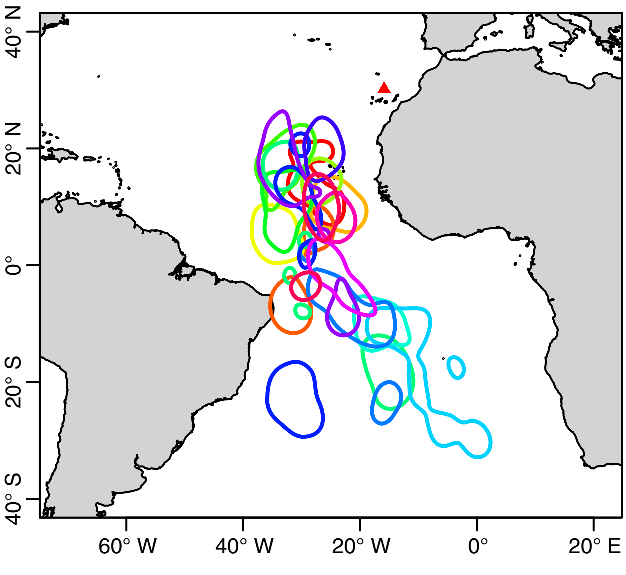


Fig. 1 Non-breeding distribution of Bulwer's petrels from Selvagens. Individual kernel density contours (50 %) are shown in *different colours*. Each kernel contour is based on 70 random positions, chosen from those recorded between November and January (only birds with at least 70 locations within this period are shown; $n = 17$; see "Methods"). *Triangle* indicates colony location

Some individuals made large-scale movements during the wintering period (Fig. 1); in these cases, arrival/departure dates to/from the wintering areas were considered as the dates of arrival to the first main wintering area and the date of departure from the last one. These intra-winter movements could cause a bias towards location estimates closer to the colony in birds carrying devices that failed prematurely (see above). We analysed this potential bias by comparing the maximum distances from the colony achieved by birds with both complete (until colony arrival; $n = 7$) and incomplete journeys ($n = 10$). We found no difference between the maximum distances achieved by both groups (mean ± SE of the 30 highest values per bird with: complete journeys—3687 ± 500 km; incomplete journeys—4484 ± 483 km; $t = 1.2$, $p = 0.270$, $df = 14.187$).

The mean sea depth values of the areas used by the Bulwer's petrels during the winter were estimated by calculating, for each bird location, the closest value of bathymetry (obtained from http://www.ngdc.noaa.gov/mgg/global/global.html, with a resolution of 1 arc-minute).

Breeding success of studied birds was obtained by a concurrent study carried out at the same time in this colony (Pinto 2013). As some of the tracked birds were members of a pair, nest identity was included as a random factor in the analysis of the influence of the breeding success on migratory schedules.

We characterised the activity patterns using the saltwater immersion data provided by the devices, which record the number of immersion events (registered every 3 s) in 10-min blocks (thus varying between 0 events, when the bird is flying for the entire 10 min period, and 200 events when immersed permanently). We estimated, for each bird and in each day, the percentage of time that each individual spent flying during daylight and darkness (sunrise and sunset times for each day derived from light data—see above). Different stages of the breeding cycle were considered separately (late breeding, outward migration, winter and return migration). Breeding data only included those recorded during the after-brooding phase (mid-August and September; Nunes and Vicente 1998; Pinto 2013); nights with records of more than 4.3 h with continuous dry events, which might indicate colony attendance, were excluded (this threshold was set based on the 99 % percentile of continuous time flight during the wintering period).

Two-way ANOVA tests, using bird identity as a random factor, were used to (1) compare nocturnal and diurnal activity patterns (% of time spent flying) in the several stages of the breeding cycle (breeding, outward migration, winter and return migration) and (2) analyse the influence of the lunar cycle on the nocturnal activity during the several stages of the breeding cycle. The fraction of the moon illuminated at midnight was obtained for each day from http://aa.usno.navy.mil/data/docs/MoonFraction.php and grouped in three phases: new moon (less than 30 % of moon illuminated), quarters (30–70 % of illuminated moon) and full moon (more than 70 % of illuminated moon).

Light data from geolocators were analysed with Transedit and Birdtracker software (British Antarctic Survey, Cambridge, UK), and all the remaining analyses were carried out using the software R (R Core Team 2012).

Results

Migratory schedules

Bulwer's petrels left the colony area between mid-August and late September, and took 10 days on average to arrive in the main wintering areas (Table 1).

Unsuccessful breeders left the colony and arrived at the main wintering areas more than 3 weeks earlier than those that successfully raised a chick ($F_{1,13} = 29.03$, $p < 0.001$ and $F_{1,13} = 28.36$, $p < 0.001$, respectively; Table 1).

Main wintering areas

The study birds spent the winter in open and deep oceanic areas on the tropical Atlantic, between 20°N and 30°S. However, most individuals remained north of 15°S, and only four moved further south (Fig. 1). The mean sea depth in the wintering areas of the Bulwer's petrels successfully tracked was 4416 ± 1035 m (± SD) (individual means ranging between 3798 ± 605 and 4792 ± 574 m; Fig. 2).

Activity patterns during the non-breeding period

The study birds spent significantly more time flying during the night (92.6 %) than during daylight (36.8 %) ($F_{1,119} = 1401.5$; $p < 0.001$). The difference between the nocturnal and diurnal percentages of time flying varied throughout the annual cycle (Fig. 3) and was particularly high during the winter (significant interaction between stage and daylight/night factors: $F_{3,119} = 133.4$; $p < 0.001$).

The moon phase had no significant effect on the percentage of time spent flying during the night ($F_{1,7960} = 0.037$; $p = 0.848$), which did not vary more than 6 % between new and full moons within each stage of the annual cycle.

Discussion

Results show that during the non-breeding period Bulwer's petrels avoid shelf and shelf-break areas, living exclusively over deep-sea areas in the open ocean, and that these birds are mainly active during darkness, especially when freed from travel constraints. Interestingly, night-time activity at sea is not influenced by moonlight levels in this species as found in other species (Phalan et al. 2007; Yamamoto et al. 2008; Dias et al. 2012a).

The deployment of geolocators did not seem to have any major negative impact on studied individuals, considering their relatively high returning rate (20/22, or 91 %, which is similar to the typical survival rate of small-medium sized Procellariiformes; e.g., Ramos et al. 2012) and breeding success (85 %, similar to values recorded in previous studies conducted in this and in a nearby colony, both below 80 %; Nunes and Vicente 1998; Pinto 2013).

Bulwer's petrels started their southbound migration soon after the breeding season and returned to the colony approximately 6 weeks before the laying date (which occurs in early June; Nunes and Vicente 1998; Pinto 2013). This resulted in a considerably long period away from the waters surrounding the breeding colony (216 days, on average), especially when compared to other Procellariiform species from this and adjacent colonies, such as the Cory's

Table 1 Migratory schedules of Bulwer's petrels

	Mean ± SD (days)	Range (min–max)	*n*
Departure from the colony (all birds)	10 Sep ± 10	12 Aug–24 Sep	20
Successful breeders	14 Sep ± 5	4 Sep–24 Sep	17
Failed breeders	21 Aug ± 10	12 Aug–1 Sep	3
Arrival at wintering area (all birds)	20 Sep ± 12	17 Aug–05 Oct	19
Successful breeders	24 Sep ± 7	12 Sep–05 Oct	16
Failed breeders	29 Aug ± 11	17 Aug–08 Sep	3
Departure from the wintering area	16 Apr ± 5	11 Apr–23 Apr	7
Return to the colony	23 Apr ± 4	18 Apr–30 Apr	7
Duration of outward migration	9.65 d ± 4.77	5–23	19
Duration of wintering period	209.29 d ± 10.89	197–227	7
Duration of return migration	6.43 d ± 2.51	4–10	7

Fig. 2 Depths (in m) of the areas used by Bulwer's petrels during the wintering period. Data from all individuals ($n = 19$) pooled. *Dashed vertical line* represents overall mean. *Horizontal lines* represent mean ± SD depth values for birds shown in Fig. 1

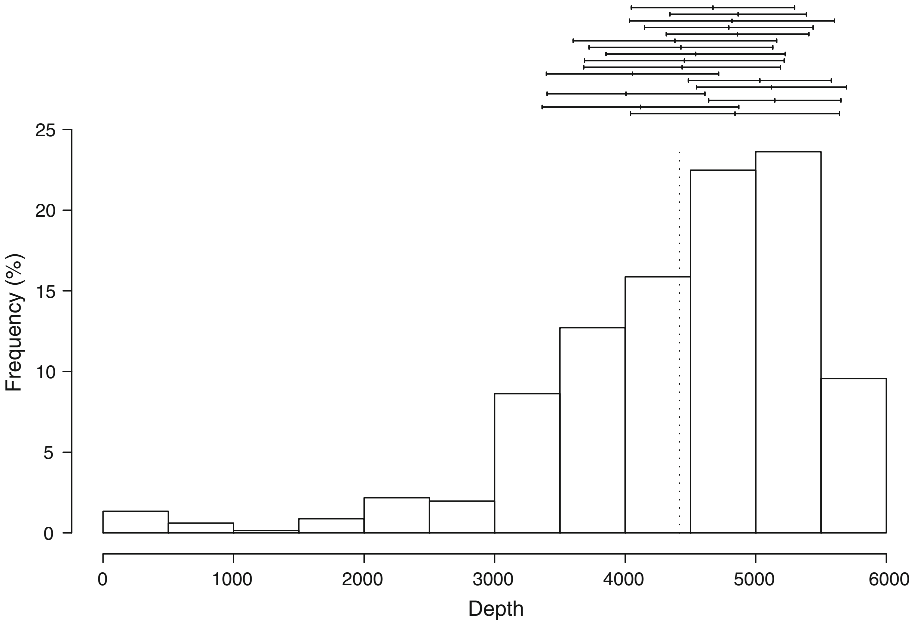
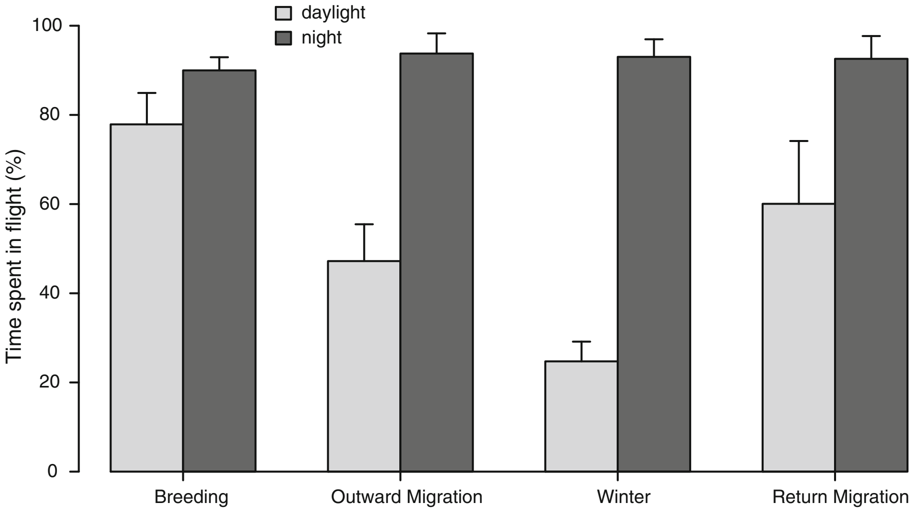


Fig. 3 Percentage of time spent in flight by Bulwer's petrels during day light and during the night (mean ± SD)



Shearwater *Calonectris diomedea*, the Zino's petrel *Pterodroma madeira* and the Desertas petrel *Pterodroma deserta* (Dias et al. 2011; Zino and Biscoito 2011; Ramírez et al. 2013). Failed breeders left the colony (and arrived at the wintering areas) significantly earlier than successful birds, again in contrast with the pattern revealed for Cory's Shearwater, in which breeding success do not influence the time of arrival at the wintering areas (Catry et al. 2013). The migratory timings of this latter species are believed to be strongly influenced by the wind conditions in the Intertropical Convergence Zone, where the calms, near surface westerlies (10°–20° N) during the summer months (June–October), delay the southbound migration to late October and early November (Felicísimo et al. 2008; Dias et al. 2011, 2013). In contrast, Bulwer's petrels crossed the area as soon as their breeding season ceased, suggesting that the seasonal variation in westerlies may not have a strong influence on smaller species.

As hypothesised, all the studied individuals spent the major part of their non-breeding season on deep waters of the Tropical Atlantic, rarely in areas shallower than 3000 m deep and located at more than 1000 km from the nearest continental coast (Fig. 1). Several mid-to-long distance migratory seabirds have been tracked throughout their annual cycle in the Atlantic, and a considerable number amongst them migrate through the offshore tropical Atlantic, but with the exception of Zino's petrel (Zino and Biscoito 2011), none select the areas used by Bulwer's petrels during winter (Ronconi 2007; Guilford et al. 2009; Dias et al. 2011; Kopp et al. 2011; Sittler et al. 2011; Hedd et al. 2012; Stenhouse et al. 2012). These tropical mid-Atlantic areas are mostly known to be of low productivity (Ramírez et al. 2013) and have even been suggested to act as an ecological barrier for long distance seabird migrants (Dias et al. 2012a). The fact that Bulwer's petrels can survive in these environments is possibly linked to their very low wing-loading (being able to benefit from the light tropical winds), plus their ability to efficiently locate and capture mesopelagic prey, which may be largely unavailable to many other of the larger, diurnal migratory seabird species studied so far, but are abundant in open oceanic areas (Kozlov 1995; Nybakken 2001; Catul et al. 2011).

Bulwer's petrels revealed a remarkable flight activity during darkness, spending more than 90 % of their at-sea time flying, all year round. Some other Procellariiformes are also known to be more active during the night period (Rayner et al. 2012; Ramírez et al. 2013), but to the best of our knowledge none spend so much time flying during darkness, especially in the wintering areas (70 % in Chatham petrels *Pterodroma magentae*, 60 % in Desertas petrels; Rayner et al. 2012; Ramírez et al. 2013). Given that the nighttime flight budget could hardly be expanded, during migration Bulwer's petrels increased their travelling time by spending more time flying during the day (Fig. 3), in contrast with what is observed in diurnal seabirds, which tend to increase nocturnal flight when migrating (Dias et al. 2012a). Nevertheless, it is during the chick rearing that Bulwer's petrels spend more time flying during the day, possibly because of the need to commute frequently between the nest site and foraging grounds. This result is in line with what was observed for other nocturnal Procellariiformes, such as the White-chinned petrels *Procellaria aequinoctialis*, Chatham petrels and Desertas petrels (Péron et al. 2010; Mackley et al. 2011; Rayner et al. 2012; Ramírez et al. 2013).

We did not detect any visible effect of the moon on the nocturnal activity of Bulwer's petrels: the percentage of time flying during darkness varied by less than 6 % throughout the lunar cycle. Moonlight has a clear effect on the nocturnal at-sea activity of other Procellariiform species (Phalan et al. 2007; Yamamoto et al. 2008; Pinet et al. 2011; Dias et al. 2012a), although the main reasons for this are not yet fully understood. Some likely causes are the increased visibility provided by the moonlight and the influence of the lunar cycle on the surface availability of mesopelagic prey species performing DVM, upon which many Procellariiform birds prey (Phalan et al. 2007; Pinet et al. 2011; Dias et al. 2012b). The absence of an obvious influence of the moon on Bulwer's petrel behaviour suggests that this species is a highly specialised nocturnal seabird, probably very well adapted to locating and capturing prey during the night, even in very dark conditions.

Small-sized nocturnal seabirds are abundant in many pelagic areas worldwide and so potentially are an important component of marine trophic webs (Guinet et al. 1996). Their at-sea behaviour and distribution clearly contrasts with that of the larger, best studied Procellariiform species such albatrosses and shearwaters (e.g., Phalan et al. 2007; Mackley et al. 2010), but so far most studies aiming to identify important bird and biodiversity areas for seabirds during their non-breeding season were mainly focused on these medium- to large-sized species (BirdLife International 2010). Many of the small nocturnal Procellariiform species, such as gadfly petrels *Pterodroma* spp., are also among the most threatened species worldwide (Croxall et al. 2012), which reinforces the need to improve the knowledge about their foraging ecology (Croxall et al. 2012; Rayner et al. 2012; Ramírez et al. 2013) and the importance of results such as those presented here.

Acknowledgments This study was funded by Fundação para a Ciência e a Tecnologia (FCT, Portugal) and the European Regional Development Fund through the PTDC/MAR/121071/2010 and PEst-OE/MAR/UI0331/2011 projects and a postdoctoral fellowship (MD; FCT-BPD/46827/08). Serviço do Parque Natural da Madeira (Paulo Oliveira, Dília Menezes, Carolina Santos, Jaques da Mata and Clemente Abreu) provided permission and logistic support to work on Selvagem Grande. Teresa Catry, Silke Waap, Hany Alonso, Letízia Campioni, Pedro Lourenço, Maria Pinto, Cristobal Pérez and Rui Rebelo helped with fieldwork.

All work was approved by the relevant authorities (Instituto da Conservação da Natureza e da Biodiversidade and Serviço do Parque Natural da Madeira; research permits 107/2006, 116/2007 and 107/2010/CAPT) and carried out in compliance with current Portuguese laws.

References

BirdLife International (2010) Marine important bird areas toolkit: standardised techniques for identifying priority sites for the conservation of seabirds at sea. BirdLife International, Cambridge

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison AL, Ganong JE, Swithenbank A, Castleton M, Dewar H, Mate BR, Shillinger GL, Schaefer KM, Benson SR, Weise MJ, Henry RW, Costa DP (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90. doi:10.1038/nature10082

Burger AE, Shaffer SA (2008) Application of tracking and data-logging technology in research and conservation of seabirds. Auk 125:253–264. doi:10.1525/auk.2008.1408

Carvalho AT (2012) Ecologia alimentar de duas aves pelágicas das Ilhas Selvagens. Dissertation, University of Lisbon

Catry P, Dias MP, Phillips RA, Granadeiro JP (2013) Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. Ecology 94:1230–1235. doi:10.1890/12-2177.1

Catul V, Gauns M, Karuppasamy PK (2011) A review on mesopelagic fishes belonging to family Myctophidae. Rev Fish Biol Fish 21:339–354. doi:10.1007/s11160-010-9176-4

Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessment. Bird Cons Int 22:1–34. doi:10.1017/S0959270912000020

Dias MP, Granadeiro JP, Phillips RA, Alonso H, Catry P (2011) Breaking the routine: individual Cory's shearwaters shift winter destinations between hemispheres and across ocean basins. Proc R Soc B 278:1786–1793. doi:10.1098/rspb.2010.2114

Dias MP, Granadeiro JP, Catry P (2012a) Do seabirds differ from other migrants in their travel arrangements? On route strategies of Cory's shearwater during its trans-equatorial journey. PLoS One 7:e49376. doi:10.1371/journal.pone.0049376

Dias MP, Granadeiro JP, Catry P (2012b) Working the day or the night shift? Foraging schedules of Cory's shearwaters vary according to marine habitat. Mar Ecol Prog Ser 467:245–252. doi:10.3354/meps09966

Dias MP, Granadeiro JP, Catry P (2013) Individual variability in the migratory path and stopovers of a long-distance pelagic migrant. Anim Behav 86:359–364. doi:10.1016/j.anbehav.2013.05.026

Felicísimo AM, Munõz J, González-Solís J (2008) Ocean surface winds drive dynamics of transoceanic aerial movements. PLoS One 3:e2928. doi:10.1371/journal.pone.0002928

Gjøsaeter J, Kawaguchi K (1980) A review of the world resources of mesopelagic fish. FAO Fish Tech Pap 193:1–51

Guilford T, Meade J, Willis J, Phillips RA, Boyle D, Roberts S, Collett M, Freeman R, Perrins CM (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. Proc R Soc B276:1215–1223. doi:10.1098/rspb.2008.1577

Guinet C, Cherel Y, Ridoux V, Jouventin P (1996) Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters—changes in relation to consumer biomass 1962–65. Antarc Sci 8:23–30. doi:10.1017/S0954102096000053

Harrison P (1983) Seabirds, an identification guide. Houghton Mifflin, Boston

Harrison CS, Hida TS, Seki MP (1983) Hawaiian seabird feeding ecology. Wildl Monogr 85:1–71

Hedd A, Montevecchi WA, Otley H, Phillips RA, Fifield D (2012) Trans-equatorial migration and habitat use by sooty shearwaters *Puffinus griseus* from the South Atlantic during the nonbreeding season. Mar Ecol Prog Ser 449:277–290. doi:10.3354/meps09538

Kopp M, Peter H-U, Mustafa O, Lisovski S, Ritz MS, Phillips RA, Hahn S (2011) South polar skuas from a single breeding population overwinter in different oceans though show similar migration patterns. Mar Ecol Prog Ser 435:263–267. doi:10.3354/meps09229

Kozlov AN (1995) A review of the trophic role of mesopelagic fish of the family Myctophidae in the Southern Ocean ecosystem. CCAMLR Sci 2:71–77

Lascelles BG, Langham GM, Ronconi RA, Reid JB (2012) From hotspots to site protection: identifying marine protected areas for seabirds around the globe. Biol Conserv 156:5–14. doi:10.1016/j.biocon.2011.12.008

Le Corre M, Jaeger A, Pinet P, Kappes M, Weimerskirch H, Catry T, Ramos J, Russell J, Shah N, Jaquemet S (2012) Tracking seabirds to identify potential marine protected areas in the tropical western Indian Ocean. Biol Conserv 156:83–93. doi:10.1016/j.biocon.2011.11.015

Mackley EK, Phillips RA, Silk JRD, Wakefield ED, Afanasyev V, Fox JW, Furness RW (2010) Free as a bird? Activity patterns of albatrosses during the nonbreeding period. Mar Ecol Prog Ser 406:291–303. doi:10.3354/meps08532

Mackley EK, Phillips RA, Silk JRD, Wakefield ED, Afanasyev V, Furness RW (2011) At-sea activity patterns of breeding and nonbreeding white-chinned petrels *Procellaria aequinoctialis* from South Georgia. Mar Biol 158:429–438. doi:10.1007/s00227-010-1570-x

Mougin J-L, Mougin MC (2000) Maximum diving depths for feeding attained by Bulwer's petrels (*Bulweria bulwerii*) during the incubation period. J Zool 250:75–77

Navarro J, Votier SC, Aguzzi J, Chiesa JJ, Forero MG, Phillips RA (2013) Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. PLoS One 8:e62897. doi:10.1371/journal.pone.0062897

Neves VC, Nolf D, Clarke MR (2011) Diet of Bulwer's petrel (*Bulweria bulwerii*) in the Azores, NE Atlantic. Waterbirds 34:357–362. doi:10.1675/063.034.0310

Nunes M, Vicente L (1998) Breeding cycle and nestling growth of Bulwer's petrel on the Desertas Islands, Portugal. Colon Waterbirds 21:198–204

Nybakken JW (2001) Marine biology, an ecological approach. Benjamin Cummings, San Francisco

Péron C, Delord K, Phillips RA, Charbonnier Y, Marteau C, Louzao M, Weimerskirch H (2010) Seasonal variation in oceanographic habitat and behaviour of white-chinned petrels *Procellaria aequinoctialis* from Kerguelen Island. Mar Ecol Prog Ser 416:267–284. doi:10.3354/meps08785

Phalan B, Phillips RA, Silk JRD, Afanasyev V, Fukuda A, Fox J, Catry P, Higuchi H, Croxall JP (2007) Foraging behaviour of four albatross species by night and day. Mar Ecol Prog Ser 340:271–286. doi:10.3354/meps340271

Phillips R, Silk J, Croxall J, Afanasyev V, Briggs D (2004) Accuracy of geolocation estimates for flying seabirds. Mar Ecol Progr Ser 266:265–272. doi:10.3354/meps266265

Pinet P, Jaeger A, Cordier E, Potin G, Le Corre M (2011) Celestial moderation of tropical seabird behavior. PLoS One 6:e27663. doi:10.1371/journal.pone.0027663

Pinto M (2013) Brooding behaviour and influence of moon cycle on chick provisioning in a pelagic seabird, the Bulwer's petrel (*Bulweria bulwerii*). Dissertation, University of Lisbon

Pollet IL, Hedd A, Taylor PD, Montevecchi WA, Shutler D (2014a) Migratory movements and wintering areas of Leach's storm-petrels tracked using geolocators. J Field Ornithol 85:321–328. doi:10.1111/jofo.12071

Pollet IL, Ronconi RA, Jonsen ID, Leonard ML, Taylor PD, Shutler D (2014b) Foraging movements of Leach's storm-petrels *Oceanodroma leucorhoa* during incubation. J Avian Biol 45:305–314. doi:10.1111/jav.00361

Quillfeldt P, McGil RAR, Furness RW, Möstlm E, Ludynia K, Masello JF (2012) Impact of miniature geolocation loggers on a small petrel, the thin-billed prion *Pachyptila belcheri*. Mar Biol 159:1809–1816

R Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramírez I, Paiva VH, Menezes D, Silva I, Phillips RA, Ramos JA, Garthe S (2013) Year-round distribution and habitat preferences of the Bugio petrel. Mar Ecol Prog Ser 476:269–284. doi:10.3354/meps10083

Ramos R, Granadeiro JP, Nevoux M, Mougin J-L, Dias MP, Catry P (2012) Combined spatio-temporal impacts of climate and longline fisheries on the survival of a trans-equatorial marine migrant. PLoS One 7:e40822. doi:10.1371/journal.pone.0040822

Rayner MJ, Hauber ME, Steeves TE, Lawrence HA, Thompson DR, Sagar PM, Bury SJ, Landers TJ, Phillips RA, Ranjard L, Shaffer SA (2011) Contemporary and historical separation of transequatorial migration between genetically distinct seabird populations. Nat Commun 2:332. doi:10.1038/ncomms1330

Rayner MJ, Taylor GA, Gummer HD, Phillips RA, Sagar PM, Shaffer SA, Thompson DR (2012) The breeding cycle, year-round distribution and activity patterns of the endangered chatham petrel (*Pterodroma axillaris*). Emu 112:107–116. doi:10.1071/MU11066

Ronconi RA (2007) The spectacular migration of greater shearwaters. Birdwatch Can 39:4–7

Roper CFE, Young RE (1975) Vertical distribution of pelagic cephalopods. Smithson Contrib Zool 209:1–51

Sittler B, Aebischer A, Gilg O (2011) Post-breeding migration of four long-tailed skuas (*Stercorarius longicaudus*) from North and East Greenland to West Africa. J Ornithol 152:375–381. doi:10.1007/s10336-010-0597-6

Spear LB, Ainley DG, Walker WA (2007) Foraging dynamics of seabirds in the eastern tropical pacific ocean. Stud Avian Biol 35:1–99

Stenhouse IJ, Egevang C, Phillips RA (2012) Trans-equatorial migration, staging sites and wintering area of Sabine's Gulls *Larussabini* in the Atlantic Ocean. Ibis 154:42–51. doi:10.1111/j.1474-919X.2011.01180.x

Wakefield ED, Phillips RA, Matthiopoulos J (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. Mar Ecol Prog Ser 391:165–182. doi:10.3354/meps08203

Weimerskirch H, Cherel Y, Delord K, Jaeger A, Patrick SC, Riotte-Lambert L (2014) Lifetime foraging patterns of the wandering albatross: life on the move! J Exp Mar Biol Ecol 450:68–78. doi:10.1016/j.jembe.2013.10.021

Yamamoto T, Takahashi A, Yoda K, Katsumata N, Watanabe S, Sato K, Trathan PN (2008) The lunar cycle affects at-sea behaviour in a pelagic seabird, the streaked shearwater, *Calonectris leucomelas*. Anim Behav 76:1647–1652. doi:10.1016/j.anbehav.2008.07.019

Zino F, Phillips RA, Biscoito M (2011) Zino's petrel movements at sea—a preliminary analysis of datalogger results. Bird World 24:216–219

Zino F, Phillips RA, Biscoito M (2013) Bulwer's petrel movements at sea—a preliminary analysis of data logger results from Selvagem Grande (30°09′N, 15°52′W). Bird World 26:79–81

Zonfrillo B (1986) Diet of Bulwer's petrel *Bulweria bulwerii* in the Madeiran Archipelago. Ibis 128:570–572