MANX SHEARWATERS *PUFFINUS PUFFINUS* BREEDING IN THE WESTERN ATLANTIC FOLLOW A DIFFERENT MIGRATION ROUTE FROM THEIR EASTERN-ATLANTIC CONSPECIFICS

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ABSTRACT

FAYET, A.L., SHANNON, P., LYONS, D.E. & KRESS, S.W. 2020. Manx shearwaters *Puffinus puffinus* breeding in the western Atlantic follow a different migration route from their eastern-Atlantic conspecifics. *Marine Ornithology*

Manx Shearwaters are transequatorial migrants, and most of the world's population breeds in Britain and winters off the Patagonian Shelf in the western South Atlantic. The migration route of British birds follows a well-known clockwise movement moving between North and South Atlantic, taking advantage of the winds. Whether this main Manx Shearwater migration corridor is used by the smaller populations breeding in the western North Atlantic is unknown. Here we report results of tracking two adults from a newly-established colony of Manx Shearwaters in Maine (USA) using miniature geolocators. Results show that they followed a post-breeding migration route southward along the US East Coast, through the Caribbean Sea and along the coast of eastern South America. Such a route greatly differs from the western North Atlantic birds' southbound migration route, being instead the reverse of the British birds' spring migration route. We also used the tracking data to provide insight into the phenology of the birds' annual cycle. Although our sample size is very small, our findings reveal a previously unknown migration route of Manx Shearwaters. Questions

arise about the origin of birds on western North Atlantic colonies and the mechanisms controlling migratory direction in the species.

Key words: migration, Manx Shearwater, *Puffinus puffinus*, geolocation, annual cycle, phenology

INTRODUCTION

Many seabirds are long-distance migrants, and understanding their migration patterns provides new insights into their ecology, especially by identifying marine areas or migration corridors important to each species. Manx Shearwaters *Puffinus puffinus* are a prevalent procellariiform seabird in the North Atlantic. Most of the world's population breeds on islands in the eastern Atlantic, mainly coastal islands of Britain and Ireland, with some smaller colonies further north in the Faroes and Iceland and further south in France and the Azores (Brooke 1990). The migration patterns of those birds are well known: after breeding, they head south along the coast of Spain and west Africa, cross the Atlantic ocean until they arrive north of Brazil. There they follow the South American coast south until reaching the Patagonian Shelf (González-Solís *et al.* 2009, Guilford *et al.* 2009, Kirk 2016). In spring, they do not retrace that route but instead while progressing north take a large detour towards the Caribbean Sea and the North American coast before heading east across the North Atlantic. However, while the migration ecology of eastern-Atlantic Manx Shearwaters has been studied in depth (Shoji *et al.* 2015; Fayet *et al.* 2016), little is known about the small populations breeding on the western side of the Atlantic. A key question in particular is whether they follow or not the same migration corridors as eastern Atlantic populations.

Here we investigate the migration movements of Manx Shearwaters breeding in the western North Atlantic on Matinicus Rock, a small island off the coast of Maine (US). Non-breeding birds have visited the island since 1998, and the first breeding pair was recorded in 2005. Five pairs were found breeding in 2018. We deployed miniature geolocators to follow the movements of two breeding adults between 2018 and 2019. We use the saltwater activity data recorded by the logger to examine aspects of the behaviour of the birds throughout the migration and wintering periods, and during the early breeding season.

METHODS

The study was conducted on Matinicus Rock (Maine, USA, 43.784°N, 68.855°W). Research permits were obtained from the U.S. Geological Survey Bird Banding Lab, U.S. Fish and Wildlife Service, and Maine Department of Inland Fisheries and Wildlife. These allowed us to tag up to 20% of the breeding population, i.e., two breeding birds, which explains our small sample size. In August 2018, towards the end of the breeding season, breeding adults from two different nests and of unknown sex were caught at their burrow during a nocturnal chick-provisioning visit. They were fitted with a miniature geolocator (Migrate Technology Ltd, C65, 1g) on a plastic leg ring, using two lightweight cable ties, a method commonly used on this species (Shoji *et al.* 2015, Fayet *et al.* 2016). The devices, representing <1% of the birds' body mass, were programmed to record the maximum light level per 5 min window, measure saltwater immersion every 30 s and record the proportion of time spent dry per 10 min window. In June 2019, the two birds were recaptured at their nests during incubation and the devices were removed.

Data were processed with IntiProc (Migrate Technology Ltd) to decompress and convert the light data into positions (light threshold: 2, sunset angle parameter: -6.7). Positions (lat/lon), light and immersion data were then further processed and analysed in R (version 3.6.0, R Core Team 2019). First, bi-daily locations obtained from light curves were filtered to remove locations having an improbably high latitude (> 60 or < -70) or speed (> 1000 km/d), and within seven days on the summer side and 15 d on the winter side of each equinox; in total excluding 16% of locations. We also removed locations during breeding (May-August). Two-day medians were calculated on the remaining data. Despite this filtering, a few locations appeared on land due to the inherent inaccuracy in geolocation data (~ 185 km; Phillips *et al.* 2004). They do not represent the birds actually flying over land, but we did not remove them manually so as not to bias the error in the data (Guilford *et al.* 2009). Wind conditions at the time and location of each position were obtained from the NOAA EUMETSAT's Metop-A Satellite (three-day composite, resolution = 0.25 decimal degrees). These data were used to calculate the mean wind direction the birds were exposed to during the southbound migration, before they reached the corner of Brazil (during which their route differed from Manx shearwaters breeding in the eastern North Atlantic), and after they departed that area (when they followed a similar route to eastern Atlantic birds).

To estimate the birds' behaviour, we used a combination of saltwater immersion and light data. We analysed separately the data from the breeding season (May-August) and from the non-breeding season (September – April). The data were classified into behavioural classes based on a combination of light and immersion thresholds, following the method in Fayet *et al.* (2016). During non-breeding, data were classified into sitting on the water: < 3% dry, flight: > 97% dry, foraging-related activities: ≥ 3% and ≤ 97% dry. The total time spent in each behaviour each day was then calculated. For each bird, the daily night flight level combined with location data were used to identify the beginning and end of southbound and northbound migration journeys. The advantage of using light and immersion data to define phenology is that they are available throughout the annual cycle, unlike spatial data, which can be inaccurate and becomes unusable close to the equinoxes. We defined the start and end date of each migration as the start and end of the autumn and spring peaks in nocturnal flight behaviour. Sustained nocturnal flight only occurs during migration (Kirk 2016) so is a better metric than total flight. The latter includes foraging flight occurring throughout the year. Stopovers were identified as periods during migration lasting at least two days, when the daily amount of time in flight was < 10 h (in contrast, on average on other days birds flew for ~ 15 h/d and up to 21 h/d). We validated this threshold with stopovers visible in the spatial data as very close consecutive locations. Additionally, the light and immersion data during breeding were analysed to identify dry and dark periods occurring during daylight. These would correspond to incubation stints (the birds nest in burrows).

RESULTS

The two Manx Shearwaters followed the same migration route (Fig 1). From the breeding colony, they headed southeast towards South America, possibly as far east as the mid-Atlantic ridge, and then appeared to stick closely to the South American coast along Brazil and Argentina. They wintered on the Patagonian Shelf, between Bahía Blanca and the San Jorge Gulf. After the winter, they took the same route in reverse, staying possibly closer to the Antilles than on the southbound migration. The birds made several stopovers during the southbound migration, mostly around the northeast corner of Brazil (see below for details). The birds flew into easterly winds (86.6 ± 0.4^{o}) during the first part of the southbound migration (until they passed the corner of Brazil) and north-easterly winds during the second part (77.1 ± 0.4^{o}).

Analysis of the light and immersion data gave insight into the phenology of the birds' annual cycle. The migrations were clearly visible as peak in nocturnal flight behaviour (Fig. 2A&B). Post-breeding migration took place from 19 September to 27 October (38 d, bird 1), and from 14 September to 30 October (46 d, bird 2). Northbound migration was much shorter and took place from 18 March to 3 April (16 d, bird 1) and from 2 April to 20 April (18 d, bird 2). Both birds made stopovers during the southbound migration (bird 1: four stopovers of 2.3 ± 0.3 d between 26 September and 27 October; bird 2: three stopovers of 3.3 ± 0.9 d between 4 and 27 October). Of these seven stopovers, four occurred near the northeast corner of Brazil, two occurred farther south on the way towards the wintering area, and one was too close to the equinox to produce reliable spatial data. The birds did not make any stopover during the northbound migration.

The immersion and light data also allowed us to identify daylight nest visits and incubation stints after returning to Matinicus Rock in April. Bird 1, which returned from migration in early April, started spending multiple days at the nest—perhaps reuniting with its mate—shortly after returning, with three visits of two, four, and three days during April. After a 21-d gap, the bird then started longer visits (usually a sign of incubation) on 19 May, completing five-day and four-day incubation stints before we removed the geolocator. Bird 2, which returned from migration later, made a short two-day visit to the nest soon after returning, then, after a 25-d gap, likely started incubation on 22 May, completing four-day and five-day stints before we retrieved its geolocator.

DISCUSSION

Both adult Manx Shearwaters breeding in Maine followed similar movement patterns during the non-breeding season. The routes they followed on southbound and northbound migration were similar, they wintered in the same area, and the timing of their migrations were also comparable. This apparent similarity between individuals, although here limited to two birds, reflects the low inter-individual variation in non-breeding patterns of Manx Shearwaters at other colonies (Guilford *et al.* 2009). While the birds used the same wintering grounds as eastern-Atlantic conspecifics, they followed a different post-breeding migration route to get there. Instead of following a clockwise migration pattern, they used the reverse of their spring migration route. The British Manx Shearwaters are thought to use a clockwise pattern to take advantage of trade winds in the North Atlantic Gyre (Guilford *et al.* 2009). By following their southbound routes, the Maine Manx Shearwaters do not have this advantage; indeed on the first part of their southbound migration until the corner of Brazil they flew mainly into headwinds. However, this may be balanced by the fact that it is substantially shorter than the alternative of crossing the Atlantic eastwards to join the other Manx Shearwaters' route, which would add ~ 4 000 km to their trip. As such, the Maine Manx Shearwaters' southbound migration covers ~ 12 000 km, similar to the British birds' route. This lack of beneficial winds may, however, explain the slower progress made by Maine shearwaters, which took 38-46 d to complete their southbound migration, vs 25-35 d for British birds (Guilford *et al.* 2009). The birds may have been slowed down by headwinds, or alternatively, to reduce energy expenditure and fly into crosswinds—their preferred wind direction (Spear & Ainley 1997), they may have tacked one way, then the other, hereby increasing the duration of the trip. Unfortunately, the resolution of our data during this period (close to the Autumn equinox) precluded us from investigating this in detail. The immersion data revealed that birds made regular stopovers on their way south, particularly near the northern corner of Brazil. Conversely, spring migration was much quicker (16-18 d) and without stopovers. This differs from the British birds' northbound migration, which follows a similar route (although the detour towards the western Atlantic coast is not always as pronounced) before crossing the Atlantic eastwards to their breeding colonies. That journey lasts ~ 40 d and contains ~30% of stopovers (Kirk 2016).

The timings of migration of Maine shearwaters on the southbound migration (from ~ mid-September to late October) were similar to those of British birds but differed for the northbound migration, with Maine birds leaving the wintering ground later (Kirk 2016), likely because of the shorter duration of their migration. The timing of breeding also seemed similar to British colonies, with the birds starting to visit their nests shortly after their return from migration and incubation starting just after mid-May. That is also the peak laying period for Manx Shearwaters on eastern North Atlantic colonies such as Skomer Island, Wales (Brooke 1990).

Although our sample size is very small, the unusual southbound migration of these Maine shearwaters raises interesting questions about the origin of those birds. There are very few breeding Manx Shearwaters in the western North Atlantic, and colonies appear to be recent. The largest colony, on Middle Lawn Island (Newfoundland, Canada), initiated breeding in the 1970s. Several hundred birds now visit the colony but there are very few breeding attempts (Fraser *et al.* 2013). As such, it seems unlikely that Middle Lawn Island produces enough birds to account for the recent colonisation of Matinicus Rock. Instead, the high number of Manx Shearwaters visiting the colony but not breeding, combined with the high number of sightings of Manx Shearwaters in the Bay of Fundy during summer, indicates that many of these visitors are immature birds, presumably from the much larger eastern North Atlantic populations. Although the movements of immature Manx Shearwater prior to breeding remain mostly unknown, there have been several ringing recoveries of one- to five-year-old birds hatched in Britain near Newfoundland in summer (Brooke 1990), which supports this hypothesis. Investigating genetic population differences between breeders established on western and eastern North Atlantic colonies would possibly give insight into the origin of immigration patterns.

Another interesting question raised by the newly revealed Manx Shearwater southbound migration route relates to the mechanisms controlling migratory direction and the development of migration routes. As adults from tracked eastern populations follow a similar southbound migration (Kirk 2016), and ringing recoveries seem to indicate that fledglings from those populations are no exception (Brooke 1990), this indicates that migratory direction in Manx Shearwaters may be genetically inherited. However, if birds in the western North Atlantic are indeed immigrating from eastern North Atlantic colonies, their southbound migration route indicates that this may not be the case. Instead, birds may adapt their migratory route depending on which side of the Atlantic they breed. Alternatively, it is also possible that fledglings following an inherited southwards orientation from Maine would 'bounce' off the North American coast repeatedly until reaching the corner of northern Brazil and then joining the usual migratory route. Tracking the post-fledging movements of birds from western North Atlantic colonies, as well as the movements of eastern North Atlantic juvenile and immature birds, would help to address this question. Further research into the ecology of Manx Shearwaters at this new colony on Matinicus Rock may also provide interesting insights into the mechanisms of colony establishment in long-lived seabirds.

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AUTHOR CONTRIBUTIONS

ALF and SWK designed the study, PSS and DEL collected the data, ALF analysed the data, all authors wrote the manuscript.

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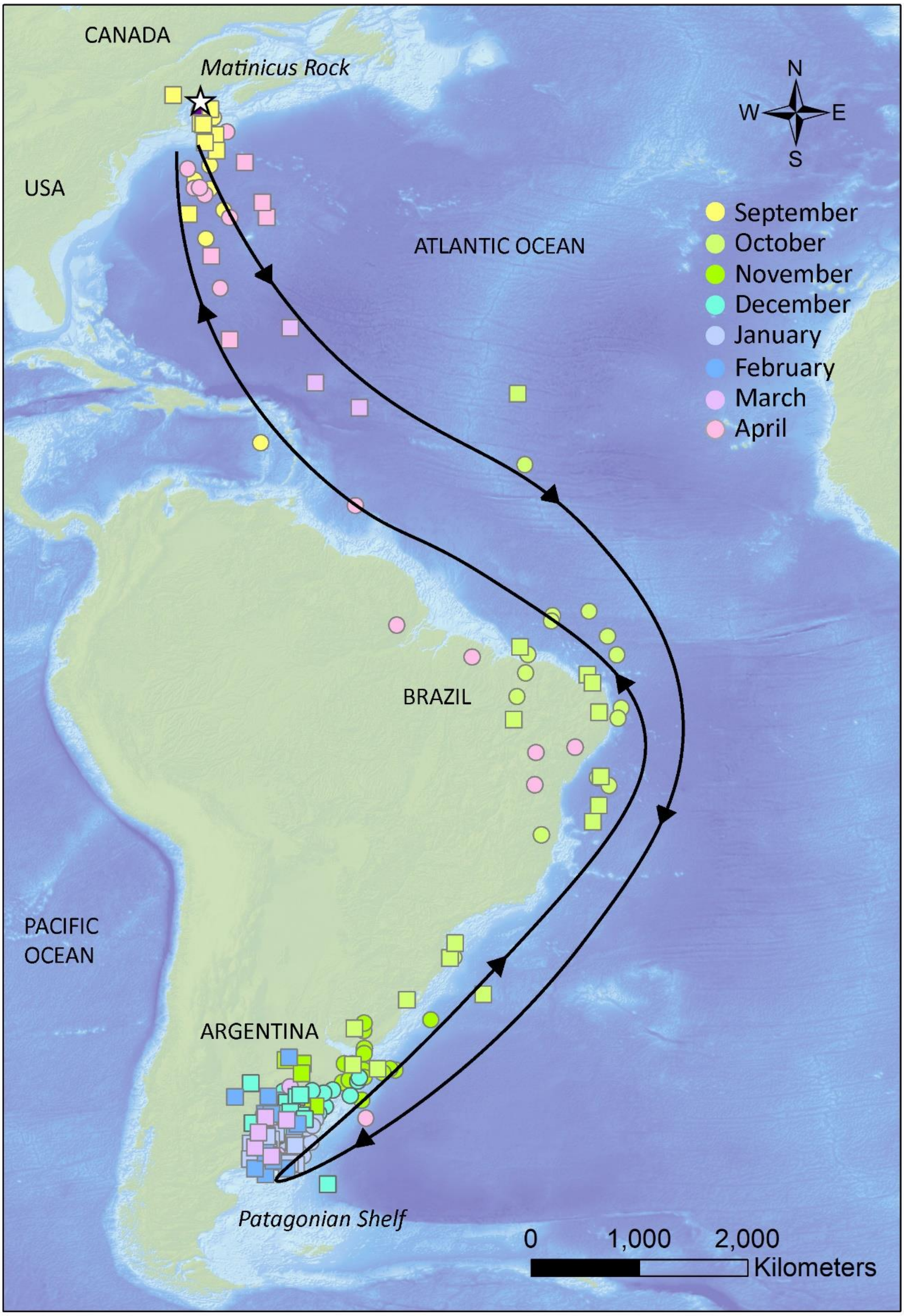
235 **Figures**



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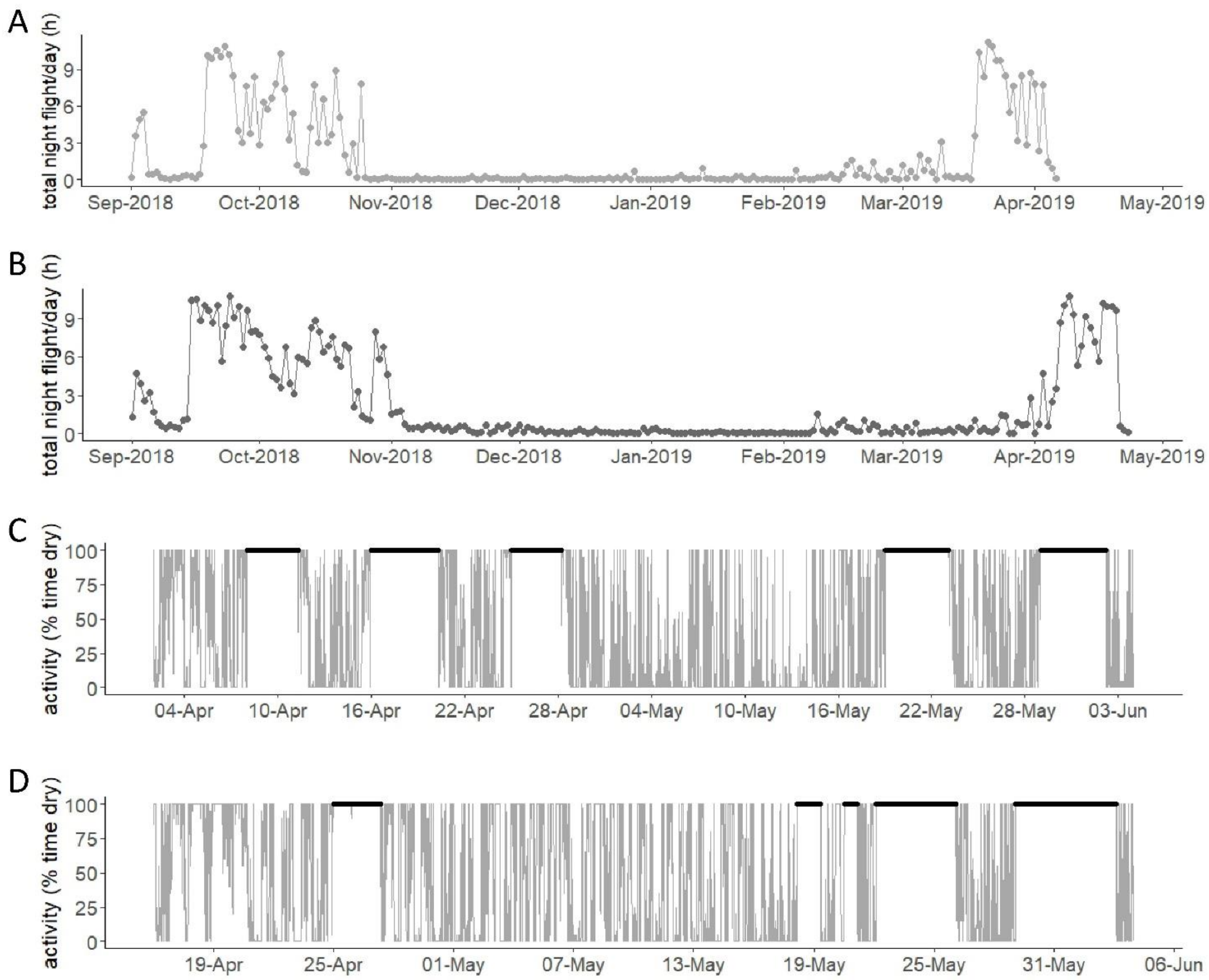
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25-May
31-May
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Captions

Fig. 1. Migratory movements of two Manx Shearwaters breeding on Matinicus Rock (white star) between August 2018 and April 2019. Each point represents a two-day median position, and different shapes (circles and squares) represent the different birds. Different colours represent different months (see legend). The black line illustrates the direction of movement but does not represent an exact trajectory. Note that the points on land are due to the inherent inaccuracy in geolocation data and do not represent the birds actually flying over land.

Fig. 2. Behaviour of Manx Shearwaters from Matinicus Rock during the annual cycle. (A-B) Cumulative nocturnal flight time per day throughout the non-breeding season for two individuals (A = bird 1, B = bird 2). The large peaks indicate the southbound and northbound migrations. (C-D) Activity data (proportion of each 10-min window spent dry) for the two birds (C = bird 1, D = bird 2) after return to the colony in April. The nest visits (in black) are indicated by long periods of full dryness (and darkness, although light levels are not visible on the graph). Note the first long visit in (D) indicates that the bird spent a few days in the burrow immediately upon return to the colony, but is too soon after migration to represent breeding.