Short Communication

Early-life development of contrasting outbound and return migration routes in a long-lived seabird

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Although mechanisms of genetic and social inheritance have been implicated in determining the migratory routes of birds, it is unclear what their relative contributions are in species where outbound and return migration routes differ (‘loop migrants’). Here, we used biologging devices to follow Manx Shearwaters Puffinus puffinus, a long-lived seabird with a trans-Atlantic loop migration, from before their first migration until their 3rd calendar year. We found that Shearwaters undertake first migration without their parents, setting off almost immediately upon fledging and moving along a more direct trajectory than adults, before wintering in the same part of the South Atlantic as adult conspecifics and subsequently iteratively developing their return migration route over the next 3 years, each time returning – unlike adults – via a Western Atlantic route. We propose that the first outbound migration in Manx Shearwaters is broadly consistent with a genetically inherited vector, that both the outbound and the return migration trajectories are unlikely to be learnt from experienced conspecifics, and that return migration in Manx Shearwaters (and perhaps loop migrants more generally) may be informed by genetically inherited information and/or local environmental conditions.

Keywords: development of navigation, genetics, inheritance of migratory route, learning, loop migration, navigation, seabird.

It is essential that naïve migratory animals inherit (by whatever mechanism) information that will allow them to reach their wintering grounds. It is equally important they are also equipped with information that allows them to return to a suitable breeding site. Among birds, the outbound migratory trajectory is thought to be underpinned by (epi)genetically inherited information (Helbig 1991, Merlin & Liedvogel 2019), typically thought to comprise ‘clock and compass’ vector navigation; a compass to give a direction and a clock to encode distance (Perdeck 1958, Mouritsen & Larsen 1998, Mouritsen 1998, Thorup et al. 2007, Yoda et al. 2017). In addition, there is evidence that the cultural inheritance of migratory routes can occur through social learning among both related and unrelated conspecifics, with the precise migratory route taken at least in part informed by the routes of experienced adults migrating simultaneously (Chernetsov et al. 2004, Harrison et al. 2010, Palacin et al. 2011, Mueller et al. 2013, Rotics et al. 2016). There is also a growing body of evidence for asocial learning in determining migratory route (‘exploration refinement’), phenology, destination and efficiency, with individuals of long-lived species honing migratory behaviours over successive attempts (Thorup et al. 2003, Guilford et al. 2011, Campioni et al. 2020, Fayet 2020, Wynn et al. 2020a).

In contrast to outbound migration, comparatively little is known about the navigational mechanisms underpinning first return migration. The majority of migratory birds exhibit an ability to return precisely to the natal site (Newton & Brodie 2008), a process known as ‘natal philopatry’, which is thought to involve learnt cues associated with the natal site (Baker 1978). Experienced navigators of multiple taxa may use wide-ranging gradient cues during long-distance navigation, with empirical evidence supporting the use of both olfactory (Gagliardo 2013, Gagliardo et al. 2013, Pollonara et al. 2015, Padget et al. 2017) and geomagnetic cues (Bulte et al. 2017, Chernetsov et al. 2017, Wynn et al. 2020b). Such cues could act as a bi-coordinate ‘map’ during long-distance navigation (e.g. Padget et al. 2019), and it has also been suggested that similar cues could be used to target the natal site over very long distances (Baker 1978, Lohmann et al. 2008). Alternatively, a vector navigation

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system may be used (as is the case in outbound migration; Perdeck 1958, Mouritsen 2003, Holland 2014).

Not all birds follow the same route on both outbound and return migration, with so-called ‘loop migrants’ taking contrasting outbound and return trajectories (e.g. Mellone et al. 2013, Willemoes et al. 2014, Katzner et al. 2016). One such loop-migrant, the burrow-nesting, pelagic Manx Shearwater *Puffinus puffinus*, migrates from Western Europe to the Patagonian Shelf in the South Atlantic, with adults known to migrate south via the East Atlantic and return north via the West Atlantic (Guilford et al. 2009). Scant ringing recoveries in the South Atlantic imply that juvenile Shearwaters migrate south almost immediately upon fledging (Brooke 1990), with colony-based ringing recoveries suggesting that the majority of Shearwaters return to the natal colony around their 3rd year post-fledging (Harris 1966, Perrins et al. 1973).

How juvenile Manx Shearwaters undertake their first trans-equatorial migration, and how they then return with almost perfect accuracy to their natal colony (Wynn et al. 2020b), remains unknown. Here, using radio frequency identification (RFID) detectors, archival geolocators (GLS) and remote-download Platform Terminal Transmitter GPS devices (PTT-GPS), we explored the information underpinning the outbound migratory trajectory in immature Shearwaters and how Shearwaters construct their return migratory route.

**METHODS**

Geolocators devices (BAS Mk19, weight \(\sim 2\) g) were deployed on 54 fledgling Manx Shearwaters on Lighthouse Island, Copeland Archipelago, Northern Ireland (54.69°N, -5.530°W) in late August 2011 (following methods in Guilford et al. 2009), with three devices subsequently retrieved successfully with data (for 127, 559 and 1041 days, respectively). Additionally, 38 adult Manx Shearwaters were tracked from Copeland in 2010, 2011 and 2012. Twice-daily positions were calculated for all birds using the ‘Geolight’ package in R (see Supporting Information Appendix S1–S3 for details; Lisovski & Hahn 2012), and saltwater immersion data were logged in 10-min bins, which could be assigned as resting, foraging or flight behaviour using a threshold model (Shoji et al. 2015).

Platform Terminal Transmitter GPS (PTT-GPS) devices were deployed on Skomer Island, Pembrokeshire (51.73°N, -5.28°W) in 2019. Ten devices (Lotek Wireless PinPoint, weight \(\sim 3.5\) g) were deployed dorsally using Tesa® marine tape (Guilford et al. 2008) on fledgling Shearwaters, with data obtained from all 10 birds for periods of 2–21 days. Additionally, seven of the tagged chicks had at least one parent tracked using GLS and three chicks had both parents tracked (see above). Although PTT-GPS deployment could potentially affect at-sea foraging ecology of Shearwaters (Gillies et al. 2020), we reasoned this would not impact the analyses undertaken here given their navigational focus. Additionally, Gillies et al. (2020) did not find any detectable effects of GLS deployments.

In 2018 \((n = 70)\) and 2019 \((n = 10)\), the movement of fledglings and their parents into and out of their burrows was monitored on Skomer Island using RFID detectors positioned in burrow entrances. Chicks and both their parents were fitted with passive integrated transponder (PTT) tags, programmed with a unique serial number so that individuals could be identified (Tyson et al. 2017). Analyses pertaining to the pre-fledging behaviour of chicks can be found in the Supporting Information Appendix S2, and analyses from adult birds are presented in the main text.

All analyses and statistics were computed in R (R Core Team 2017). Our formal statistical analysis broke down into three broad themes: pre-fledging behaviour (which is presented in Supporting Information Appendix S2), first outbound migration and return migration. Owing to the necessarily smaller sample sizes gathered on return migration, we conducted no quantitative statistical analysis. Detailed information on how the spatial and statistical analyses of the outbound migration were conducted is available in Appendix S1.

All devices were deployed with landowner permission under a special methods licence granted by the BTO (permit number C/5311), with all empirical protocols passed by the University of Oxford Animal Welfare Ethical Review Board.

**RESULTS**

**Outbound migration**

We found that the parents of our tracked chicks stopped visiting the colony on average 9.74 \((\pm 2.42 (95\% \text{ CI}))\) days prior to fledging, with the chick encountering its final parental visit 8.1 \((\pm 2.36)\) days prior to fledging. No parents were detected at the colony the night that chicks fledged, and no parental visits were recorded post-fledging, suggesting that juvenile Shearwaters fledged independently of their parents.

All three GLS-tracked fledglings migrated towards the Patagonian Shelf, completing the journey in around 2 months (see Fig. 1). Immersion data implied that the onset of migration following fledging was near instantaneous, with all three fledglings completing a minimum of 10 h of continuous flight in the first week post-fledging, with one bird completing \(> 50\) h (Fig. 1a). This is consistent with data from the PTT-GPS-tracked fledglings, with the three birds for which we have a position on the seventh day post-fledging having
moved 890, 1837 and 2036 km from the colony, respectively (Fig. 1c). By comparing the positions of the PTT-GPS-tracked fledglings to the GLS-estimated positions of their parents, we found that fledglings were likely to have migrated independently of their parents, with fledglings on average 545 km away from their parents on any given day over the tracking period. Further, fledglings were not significantly closer to their parents than to randomly selected adults, both when considering the straight-line distance between birds (randomization, see Appendix S1; $P = 0.38$) and when considering the longitudinal distance (which is less susceptible to GLS positional error; randomization; $P = 0.22$). Additionally, GLS-tracked fledglings were significantly closer than adults to both the beeline (Great Circle) linking the breeding and wintering site (linear mixed model [LMM]; LR test; $\chi^2_1 = 5.74$, $P = 0.002$) and the shortest across-water route to the wintering site (LMM; LR test; $\chi^2_1 = 12.8$, $P = 0.0003$; see Appendix S1).

**Return migration**

In December, immatures had a median latitude of $-39.97^\circ$ ($\pm 4.62^\circ$) and a median longitude of $-59.04^\circ$ ($\pm 6.48^\circ$), with the positions of adults over the same position very similar, $-41.53^\circ$ ($\pm 1.37^\circ$) latitude and $-61.94^\circ$ ($\pm 1.98^\circ$) longitude, implying that the wintering distribution of immature and adult Shearwaters overlapped.

For two of the three GLS-tracked immatures, the GLS device continued to record into the second calendar year following deployment. Unlike the adult Shearwaters tracked over the same period which, consistent with previous studies, had all returned to the North Atlantic by April, both immatures remained on the Patagonian Shelf until 16 July 2012, at which point they started moving slowly north (Fig. 2). This was asynchronous with all recorded adult movements. Both immatures reached around $-25^\circ$ latitude (level with central Brazil) with one bird moving further north on 6 August to reach $-2^\circ$ latitude. Both immatures returned to the wintering site in early September, with the majority of the adult population joining them by late November (see Appendix S3).

One GLS device continued recording into the third calendar year post-deployment, meaning that any movement after this date was recorded in just one bird. This bird, now in its 2nd year post-fledging, started northwards migration on 23 May 2013 (around a month earlier than in the previous year), moving north faster than in the first year ($2.81^\circ$ latitude per day in 2013 versus $0.695^\circ$ per day in 2012), reaching a maximum latitude of around $52^\circ$, approximately the latitude of the breeding colony, on 10 July. Although the timing of the immature’s northward migration was much later than adult birds tracked over the same season, the routes of the immature and adults were similar, following the eastern seaboard of North America northwards before crossing the Atlantic at around $40^\circ$N. However, the
immature did not completely cross the Atlantic but, instead, stopped at around \(-16^\circ\) longitude (approximately south of Iceland; Fig. 2), only around 500 km from the natal site. Unlike any recorded adult Shearwater from eastern Atlantic colonies (Guilford et al. 2009), the fledgling then returned to the wintering site via the West Atlantic, arriving back at the wintering grounds in late September (almost exactly the same time as in the previous year; see Fig. 2).

In 2014, now in its 3rd calendar year, the immature started northward migration earlier than in the two previous years, with migration estimated to begin on 11 May (again, much later than any adult birds tracked in the same year). Migration speed was comparable with the previous year (3.19° latitude per day) and proceeded along a similar route, with the immature reaching \(-30^\circ\) longitude in late June 2014 (Fig. 2) at which point the logger stopped recording. The bird was not encountered again until 2015, when it was found dead near the natal site, and consequently it was not possible to deduce whether it made landfall at the natal colony in 2014.

**DISCUSSION**

Using a combination of loggers, we tracked the behaviour and movements of fledgling Manx Shearwaters from before fledging until, in one case, 3 years post-fledging. Based on these data, we below propose that social learning and cultural inheritance are of limited importance when considering both the outbound and the return migration trajectories of Manx Shearwaters; instead, genetic inheritance and asocially learnt information inform their migration routes. We suggest, more generally, that this may be consistent across animals undertaking loop migrations independently of their parents.

Radio frequency identification records showed that parents visited their offspring for the last time around a week prior to fledging, with no parents recorded on the colony on the night of fledging of their chick or afterwards. This, combined with our finding that tracked fledglings were several hundred kilometres away from their parents, indicates that there is little if any sensory contact between fledglings and related adults. Although it is possible that first years follow non-related adults, this might seem unlikely, given that fledglings seemingly follow a more direct route than all observed adults. Further, at-sea sightings data from the Joint Nature Conservation Committee seabirds-at-sea survey (‘JNCC SAS’) suggest that the majority of Manx Shearwaters, presumably including non-breeding individuals, have left Europe by the time fledging occurs (with only 5% of JNCC

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**Figure 2.** The development of migration in Manx Shearwaters. (a) GLS positions for the two fledglings for which > 1 year’s data were collected, coloured by year. (b) The latitudinal position over time for these two birds, with dotted lines showing estimated latitudinal position over the equinox periods.

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SAS sightings recorded after 7 September; Camphuysen et al. 2004). This necessarily reduces the likelihood that cultural transmission from breeding adults influences migration route, consistent with other studies of procellariform migration (Yoda et al. 2017, 2021). If the information used on first migration is unlikely to be learnt socially, it is therefore possible that it is inherited genetically or epigenetically, possibly as a vector. Indeed, the straight-line trajectory taken by fledglings, which is more direct than that seen in adults, is consistent with an inherited vector (as has been noted in procellariforms and avian taxa more generally; Hake et al. 2003, Yoda et al. 2017, 2021).

Despite wintering in a similar area to their adult conspecifics, immature Shearwaters exhibited very different return migratory behaviour. Although only two GLS loggers lasted into their 2nd year, the phenology and trajectory taken by the tracked individuals were entirely separate from that of any adults tracked over the same period. As such, in spite of the small sample size, we believe that our observations of return migration are of some qualitative interest when considering the development of return migration. A key difference was the timing of northwards movement, with both immatures for which we have complete 2nd calendar year tracks starting northwards movement 3–4 months later than breeding adults. The differing phenomenology of adult and immature Shearwaters implies that the route followed by immatures cannot be learned by following breeding adults, and hence that social learning is unlikely to underlie the westerly trajectory into the Caribbean characteristic of the returning Manx Shearwater’s loop migration. Social learning of the northbound migration route involving non-breeding adults is possible, though this might seem unlikely given that such birds are present on the colony from mid-June (Harris 1966, Perrins et al. 1973, Fayet et al. 2015). In turn, this implies that the loop migration structure is unlikely to be the result of cultural transmission. We might, therefore, suggest that the decision to take a different return migration route could be encoded genetically (Mouritsen 2003). Alternatively, or additionally, the observed route taken may instead result from conditions in the West Atlantic rendering this route more efficient, with the favourable winds around the North Atlantic gyre reducing the likelihood of headwinds on return migration (Guilford et al. 2009, Fayet et al. 2020). This latter suggestion would be consistent with other loop migrants, where differences in trajectory have been attributed to differing environmental conditions (and different ecological requirements) on the return migration leg (e.g. Mellone et al. 2013, Lisovski et al. 2021).

Unlike southwards migration, the return migration route in Manx Shearwaters appears to be built up iteratively over a series of years, with birds reaching greater latitudes in later years. We believe this is the first reported example of such age-related route extension. It is unclear whether this reflects younger birds limiting their migration because they do not need to return to the colony, or implies a process whereby birds use information gathered on the previous leg of the iteration to inform navigation on the current leg. Such a process of iteratively refining the migration route over successive years would be consistent with the ‘exploration-refinement’ of migratory routes seen in other long-lived seabirds (Guilford et al. 2011, Campioni et al. 2020). Between legs of this iterative process, the tracked immatures returned to the wintering site via the West Atlantic, with the immature bird tracked into its 3rd year returning to the wintering site via a route unseen in European adult Shearwaters (see Fig. 2). Differing southbound migration routes between adults and immatures implies that Shearwaters do not simply store innate outbound and return migration trajectories and execute the relevant trajectory at the correct time of year. If this were the case, we would not expect such marked differences in birds of different ages. However, given the small sample size, it is unclear why the fledgling returned to the wintering site via the West Atlantic, especially given that the route selected would probably involve flying into a headwind (Guilford et al. 2009, Fayet et al. 2020) and is approximately 2745 km longer than if the immature had extended its northbound migration to the natal site and then returned via the same trajectory it took in their first calendar year.

Our results imply that Manx Shearwaters rely primarily on genetic inheritance to inform their outbound migration route. We further propose that, given the lack of opportunity for cultural inheritance, it is possible that a similar mechanism underlies return migration also and that the iterative construction of a return migration route may reflect ‘exploration-refinement’ in route selection. Conclusions based on such small sample sizes must be necessarily made with caution, and further study is essential, but we suggest that our results inform on loop migration more generally and highlight the utility of a biologging approach when studying the early-life ontogeny of migratory behaviour.

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**ETHICAL NOTE**

None.

**AUTHOR CONTRIBUTIONS**

Fieldwork was carried out by J.W., O.P., N.M., N.G., C.T., B.D., H.K. and A.L.F. Analysis was carried out by J.W. with input from A.L.F., O.P., C.P. and T.G. A draft was written by J.W. and A.L.F. upon which all authors commented prior to submission.

**DATA AVAILABILITY STATEMENT**

Raw data is available online in the Dryad repository https://doi.org/10.5061/dryad.ht76hdrfr

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Extended methods.

Appendix S2. Supplementary results and discussion.

Appendix S3. Supplementary figures and references.