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Article

An assay to investigate factors influencing initial orientation in nocturnally fledging seabirds

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The first solitary migration of juvenile birds is difficult to study because of a low juvenile survival rates and sometimes long delays in return to the breeding grounds. Consequently, little is known about this crucial life event for many bird species, in particular the sensory guidance mechanisms facilitating the first migratory journey. Initial orientation during the first migration is a key measure to investigate these mechanisms. Here, we developed an assay to measure initial orientation as flight direction upon first take-off in nocturnally fledging juvenile seabirds. We dorsally deployed a coloured LED on juvenile birds to allow researchers to observe the vanishing bearings of individuals as they flew out to sea. Additionally, we co-deployed either a small Neodymium magnet or glass bead (control) on top of the bird's head to investigate the use of magnetoreception, previously unexplored in this early life stage.

We used this assay to observe the first flight of Manx shearwaters *Puffinus puffinus* and found that they did not orient towards their wintering ground straight after taking off. Further, we did not find an effect of the magnetic treatment on juveniles' flight direction, though whether this is due to the birds not using magnetoreception, other salient cues being available or a lack of motivation to orient to the migratory beeline is unclear. We were, however, able to identify wind direction and topography as drivers of first flight direction in Manx shearwaters, which fledged with wind component between a crosswind and a tailwind and directed their maiden flight towards the sea and away from the land.

This novel assay will facilitate the study of the maiden flight of nocturnally fledging birds and will help advance the study of sensory guidance mechanisms underpinning migratory orientation in a wide range of taxa, including species which are traditionally challenging to study.

Keywords: magnetoreception, navigation, permutation test, *Puffinus puffinus*, seabirds, vanishing bearing



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Introduction

Annual autumn migration is undertaken by many species in a range of taxa (Brower 1996, Perryman and Lynn 2002, Itoh et al. 2003, Guilford et al. 2009, Egevang et al. 2010). This movement towards more productive areas is a crucial behaviour to ensure fitness and survival (Newton 2008, Harrison et al. 2011). While in some species juveniles simply follow adult conspecifics on their first journeys (Valenzuela et al. 2009, Harrison et al. 2010, Mueller et al. 2013), the mechanisms underpinning the first migration of juvenile animals which migrate separately from adults remains puzzling (Bingman and Cheng 2005). All of the information for the first lone migration must be inherited or learnt prior to fledging (Liedvogel et al. 2011). Studies investigating the behaviour of wild birds have revealed evidence for inheritance of migratory direction in small passerines (Perdeck 1958, Berthold et al. 1992, Helbig 1994, Berthold 1999), but the extent to which this may also be true for long-lived species such as seabirds, which may take several years before returning to breed, remains unresolved (Guilford et al. 2011a, Yoda et al. 2017a).

Miniature biotelemetry systems may one day be the best tool to answer questions about the guidance of first-time migration. Indeed, recent improvements in the accuracy, data quality and miniaturisation of biologging technology have permitted the collection of much more detailed information about the flight behaviour of birds (Lord et al. 1962, Wikelski et al. 2007, Robinson et al. 2010, Guilford et al. 2011b). For example, tracking studies in juvenile raptors (Sergio et al. 2014, Harel et al. 2016) and seabirds (Riotte-Lambert and Weimerskirch 2013, de Grissac et al. 2016, 2017, Collet et al. 2020) reveal that young birds tend to be more affected by wind conditions in their initial flights than adults, suggesting a mechanism of learning and improvement of flight mechanics (Fayet 2020). There is, however, an inevitable trade-off when tracking all but the largest birds between the weight, size and cost of devices, the quality and amount of the resulting data (Wilson et al. 2004, Shillinger et al. 2012, Venabele et al. 2015, Bodey et al. 2018). Furthermore, while transmitting devices might in future allow more flexible tracking of animals without the need to be recovered, currently the majority of affordable devices must be retrieved from the animal to download the data, and consequently cannot be used on individuals which are unlikely to be captured again. This is particularly the case for fledgling birds with high degrees of dispersal, low survival or a long breeding deferral period.

Until these devices become available, alternative means to collect relevant orientation data from animals without the need for tracking technology are needed to answer some of the outstanding questions in animal migration. One option is to infer aspects of animals' orientation behaviour through behavioural assays. One such example is the Emlen funnel and its modern, automatic modifications that allow for identifying orientation of night-migrating passerine species by recording the directional activity of birds in a cage

with a circular bottom (Emlen 1975, Bianco et al. 2016). Unfortunately, while these methods can be used to achieve a large sample size at a relatively low cost, they are not suitable for larger avian species. Prior to the development of GPS tracking devices, an assay was developed to identify the vanishing bearings, a proxy for initial orientation, of larger birds (Kramer and von Saint Paul 1950a, b, Matthews 1951, Kramer 1953). Under this method, observers use binoculars to visually track a bird's flight trajectory following its release. Sandberg et al. (2000) modified this assay to observe nocturnally migrating passerines by dorsally attaching lightsticks and observing the light via binoculars. The initial orientation of red-eyed vireo *Vireo olivaceus* and northern waterthrush *Seiurus noveboracensis* measured using such vanishing bearings was correlated with the bearing from orientation cages (Sandberg et al. 2000). This method, however, was developed for small adult passerines and has never been applied to any other avian species.

These behavioural assays have helped to determine the navigational mechanisms which facilitate the migration of birds. In particular, they have helped shed light on the role of magnetoreception in providing a compass bearing during migration for some species (Wiltschko and Gwinner 1974, Sandberg et al. 2000, Muheim et al. 2002, Wiltschko and Wiltschko 2006), but how widespread the magnetic compass is across taxa remains unknown. Whilst night-migrating songbirds are hypothesised to make use of a light-mediated magnetic inclination compass (ostensibly located in the retina of the eye, Hein et al. 2010) in combination with celestial cues to control orientation during migration (Muheim et al. 2002, Wiltschko and Wiltschko 2002), evidence for a role of a magnetic compass is much more equivocal across other avian taxa. In seabirds, for example, numerous attempts to disrupt any putative magnetoreceptor – using a jostling rare earth magnet inside a box attached to the bird's head – found no evidence for a role of a magnetoreception during large-scale movements (Massa et al. 1991, Benhamou et al. 2003a, b, Bonadonna et al. 2003, 2005, Mouritsen 2003, Pollonara et al. 2015, Padget et al. 2017). These studies however were all conducted in adult birds, so a magnetic compass remains a potential candidate at least for movement on first migration (Liedvogel et al. 2011).

Here, we aimed to 1) adapt an assay (Sandberg et al. 2000) for the study of initial orientation, defined as flight direction upon take-off, in large numbers of nocturnal fledging young seabirds, and 2) use this to test which environmental variables fledglings are attending to when embarking on their maiden flight. Specifically, we were interested in whether access to the undisturbed geomagnetic field is crucial to initial orientation in a nocturnal migratory seabird, the Manx shearwater *Puffinus puffinus*, during fledging. In many species of bird, young, inexperienced individuals are known to be particularly affected by environmental variables during fledging, especially wind (Riotte-Lambert and Weimerskirch 2013, de Grissac et al. 2016, 2017, Collet et al. 2020). Thus, we additionally investigated the role of wind and topography on initial flight direction.

Material and methods

Species and site

Manx shearwaters *Puffinus puffinus* are burrow-nesting seabirds from the Procellariiformes order. They are mainly active during the day and rest during the night (Shoji et al. 2016). However, during the breeding season, they visit their nests exclusively at night, possibly to avoid predation (Watanuki 1986, Keitt et al. 2004, Silva et al. 2011). Similarly, young Procellariiformes leave their burrows only during the nights to exercise their wings and build their flight muscles (Yoda et al.

2017b). Ringing data suggest that young Manx shearwaters spend winters in the South Atlantic in waters along the Patagonian shelf (Fig. 1a, Brooke 1990).

The study was undertaken on Skomer Island, Wales (51°44'N, 5°17'W, Fig. 1b), the biggest colony of Manx shearwaters in the world, with around 317 000 breeding pairs (Perrins et al. 2012). The island is located in St Brides Bay within a kilometre of the Pembrokeshire coast. To reduce geographical biases, two locations on Skomer Island were chosen for this study, Skomer Head and Pigstone Bay. Both locations are near to a high concentration of Manx shearwater burrows and are coastal and west-facing, with a view

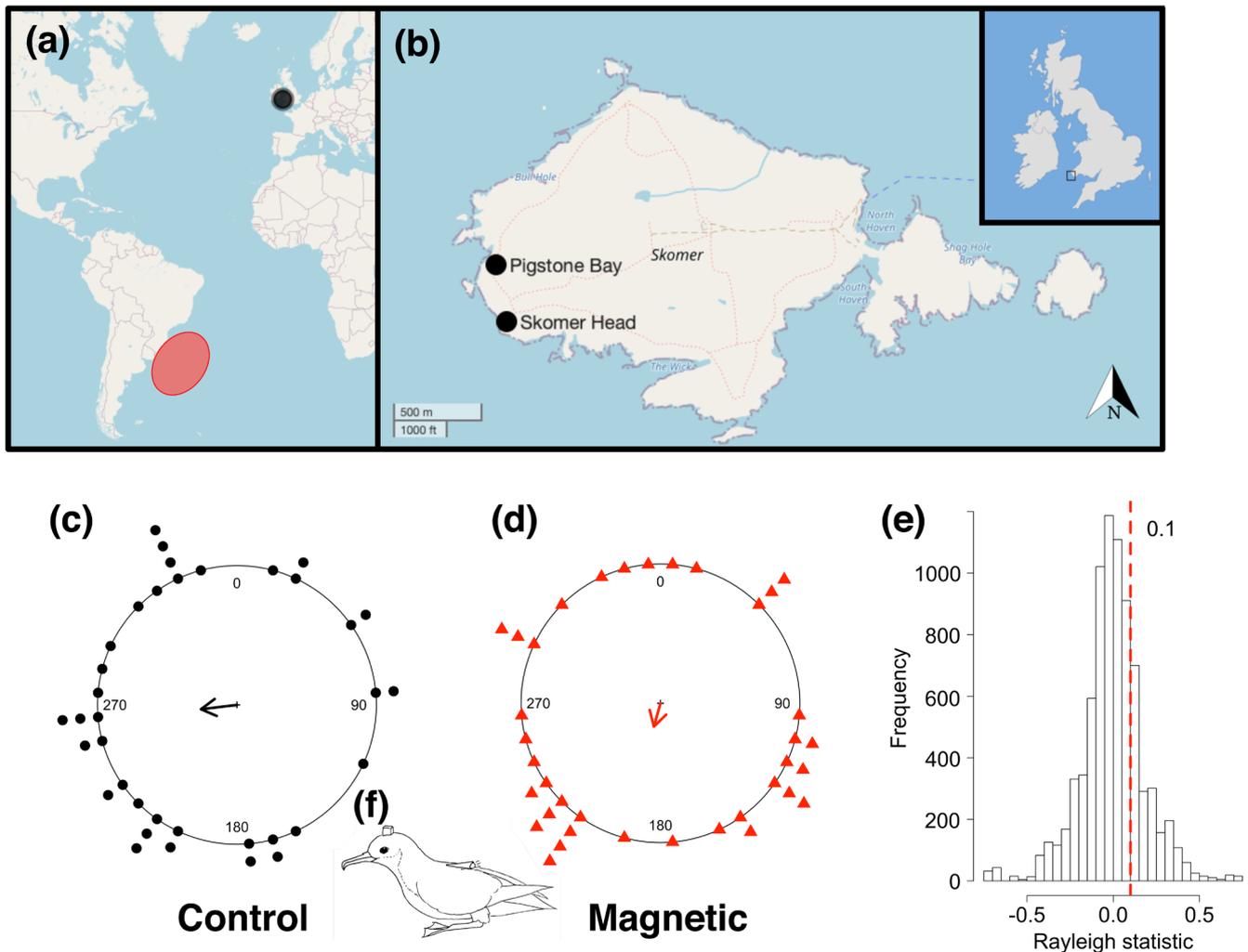


Figure 1. (a) Map with the location of Skomer Island (black dot) and the wintering grounds (red circle) of Manx shearwaters (OpenStreetMap® 2020a). (b) Map of Skomer Island. The two black dots mark our study sites, Skomer Head and Pigstone Bay, where the experiment were undertaken (OpenStreetMap® 2020b). (c) Flight direction of control Manx shearwaters. Each black dot indicates the direction of fledging of an individual bird. The arrow indicates the mean direction of the group ($\alpha=263^\circ$) and its vector length ($r=0.26$). (d) Flight direction of experimental birds. Each red triangle indicates the direction of fledging of an individual bird. The arrow indicates the mean direction of the group ($\alpha=195^\circ$) and its vector length ($r=0.17$). (e) We used a permutation test to examine if the variation in orientation of magnetic and control birds differed. First, we calculated observed global mean of all differences, for each day, between Rayleigh statistics of magnetic and control bearings (mean = 0.1, red dashed line). Then, to compute a null expectation (the histogram shown), we calculated global means of all differences for each day between Rayleigh statistics of bearing of 1000 times randomised magnetic and control identities. The calculated p value = 0.272. (f) Schematic drawing of a Manx shearwater with a box on its head and an LED light on its back.

of the sea along a large arc of the horizon. Locations where coastal developments and ships could be seen prominently were avoided owing to the known effect of light pollution on shearwaters soon after fledging (Syposz et al. 2018). The area around Skomer Island, however, is surrounded by light pollution from the coast of Wales, and thus it was inevitable that part of the horizon was lit. The attraction of fledging shearwaters to light is known to be lower on moonlit nights (Miles et al. 2010, Syposz et al. 2018), so we collected additional data on seabirds' flight direction on both moonlit and moonless nights (Supporting information). The local geomagnetic characteristics of Skomer Island during the study were as follows: intensity = 48789 nT (secular variation = 31), inclination = +66.488° (SV = -0.3), declination = -2.15° (SV = 11.7, IGRF 2020).

Behavioural assay

The study was undertaken during the peak fledging period in September 2017 and 2018. Additional data were gathered in 2019 specifically with the aim of assessing the role of moonlight levels on vanishing bearing of seabirds, and these are provided in the Supporting information. Fledgling Manx shearwaters were captured after emergence from their burrows within 500 m of the two chosen release sites. All birds were weighed and were selected to have a low down score (0–1 corresponding to little or no down – the down score is 0 when there is no down visible and 3 if the whole bird has down on all of its body, Perrins 2014). To record vanishing bearings at night, we deployed a small coloured LED on the back of each bird (ca 4 g, Fig. 1f, Sandberg et al. 2000, Lorne and Salmon 2007). The LED was attached with a thin strip of TESA marine tape laid underneath very small bunches of contour feathers loosely enough that the light would fall off soon after fledgling (this attachment method is a modification of a commonly used protocol for GPS attachments on this species; Guilford et al. 2008). The LED was additionally wrapped in TESA tape to avoid the spill of light towards the bird's head and which could potentially disturb its flight. To test the role of the magnetic field on initial orientation, we fitted a 1 × 1 cm cardboard box on top of each bird's head using a drop of glue applied to the feathers. Each box contained either a strong cylindrical Neodymium magnet (5 mm in diameter × 8.47 mm thick, mass 1.2 g, vertical pull 0.91 kg; magnetic treatment) or a glass bead of similar dimensions (control treatment). The magnet was free to tumble inside the box to produce a rapidly varying artificial magnetic field stronger than ambient, hence disrupting the birds' ability to read the earth's magnetic field (as in Pollonara et al. 2015). Each treatment group was assigned a different LED colour each night (green and red in 2017 and green and blue in 2018) and observers were blind to the treatments.

After fitting the light and magnet, birds were placed apart from each other on the ground and left to walk around (within observers' view) and eventually fledge of their own accord. Once a bird took off, a standing observer followed it with binoculars (Nikon Prostaff 8 × 30) until it vanished

from sight. Another observer with a compass recorded the bearing of the bird using a red head torch to illuminate a notebook. The compass was placed directly below the binoculars and the first observer made sure that it rotated their body in direction of the flying bird. In 2017 only the vanishing bearing (to the nearest 1°) was recorded and in 2018, bearings were taken every 10 s. Birds sometimes disappeared from the observer's view which led to a gap between recordings, in which case the time was noted.

Environmental factors

Meteorological data, including cloud cover, wind direction and wind speed, were collected at least every 32 min. An observer measured the cloud cover on a nine-point scale (0 oktas being clear sky and 8 being completely opaque). Wind direction and speed were measured by a handheld Vaavud anemometer (Vaavud ApS, Copenhagen S, Denmark). For safety, releases were not carried out on nights with strong wind (maximum wind speed 16 m s⁻¹, mean = 6 m s⁻¹, median = 8 m s⁻¹). Releases were also not carried out during rainy weather due to the sensitivity of the deployed equipment to water damage. Additionally, we calculated moon illuminance to test for a potential effect of light pollution on fledgling direction (Methods in Supporting information for details).

Data analysis

We investigated how the magnetic treatment, wind and topography influenced Manx shearwater initial fledging direction. We used direction to the final observation as a proxy for initial orientation, analogous to the vanishing bearing commonly used in the avian literature (Matthews 1951, Sandberg et al. 2000). Analyses were conducted in R (ver. 1.1.456, <www.r-project.org>) using the package 'circular' (Lund et al. 2017).

First, we conducted a permutation test to determine whether there was a difference in the circular variance (measured as a Rayleigh value) in final vanishing bearings between the magnetic and control treatments, since we expect that disrupted orientation (from the magnetic treatment) would result in initial orientations closer to a random distribution. To account for changes in the environmental variables between days, only days with at least three releases per treatment were kept. We calculated each day's deflection by comparing Rayleigh statistics of all magnetic and control bearings and then calculating the global mean across dates. We then randomised the treatment identity of each bird 1000 times and calculated the global difference between the Rayleigh statistics of magnetic and control treatments for each run. Finally, we used a Rayleigh test, using only the final vanishing bearings of control birds, to examine if the control group of Manx shearwaters are oriented towards the wintering grounds during their maiden flight.

To analyse the effect of wind direction and topography on the flight direction, we used the vanishing bearing from all the days that the experiment was undertaken. We generated a

null distribution by randomising the vanishing bearings with respect to wind direction 1 000 000 times and calculated the global mean for each run. We then calculated the actual mean of the angles (0–180°) between the vanishing bearings and wind direction and compared it to the null distribution. We also investigated whether the angle between wind direction and birds' flight direction was affected by wind speed (Methods in Supporting information for details). To investigate the influence of topography, we divided data into two locations and, further, by four main wind directions (northerly, westerly, southerly, easterly). We tested if birds in each group were significantly oriented using a Rayleigh test. We also conducted Watson–Wheeler tests to examine whether there was a difference in flight direction between the two locations, controlling for the effect of the wind direction.

Results

Observation performance

Out of 169 LEDs deployed (36 in 2017 and 133 in 2018), we successfully collected data on the direction of fledging of 95 juvenile seabirds (19 in 2017, 76 in 2018). Some of the birds did not take off and their devices were subsequently removed (7 – 2017, 35 – 2018), while others wandered away, were lost or we failed to collect the data (10 – 2017; 22 – 2018). For analysis, we used data from 93 birds out of 95 observed birds, because two birds landed on the water, so their fledging was marked as unsuccessful. The average weight of a bird used in the study was 416 g (median = 420 g, SD = 27 g, Table 1). Observation durations varied from 30 s to 405 s (median = 133 s, SD = 80 s).

Influence of the magnetic treatment on Manx shearwater bearing

There were seven days on which the sample size in each treatment was three or more, giving an overall sample size of

73 birds (36 magnetic and 37 control) for this test. A permutation test showed that there was no significant difference in variance between the magnetic and control treatments (permutation test, iteration = 1000, p value = 0.272, Fig. 1c–e), indicating that variance in orientation of birds fitted with magnets was similar to that of control birds. Furthermore, we investigated if control birds were appropriately oriented towards their wintering ground (SW). A Rayleigh test revealed that control birds were not significantly oriented in any direction (Rayleigh test, $t = 0.26$, p value = 0.088, mean orientation = 263°, Fig. 1c).

Influence of environmental variables on flight direction

To test the effect of wind direction and topography on fledging direction, we collected all vanishing bearings, because we found no evidence for a difference between control and magnetic birds. The permutation test revealed that birds were more likely to fly in a consistent direction relative to the wind than expected by chance (iterations = 1 000 000, $n = 93$, p value < 0.001, Fig. 2a). The average angle between flight direction of birds and wind direction was 116° (SD = 44°, Fig. 2b–c).

When taking into account the wind direction and the location of the release site, we found a significant difference between flight direction in westerly (Watson–Wheeler test, $W = 26.812$, $df = 2$, p -value < 0.001) and southerly winds ($W = 13.252$, $df = 2$, p -value = 0.0013), whereas in northerly winds, we found no significant difference (Watson–Wheeler test, $W = 2.2283$, $df = 2$, p -value = 0.3282; Fig. 3). The results suggest that, when taking wind direction into account, the flight direction of Manx shearwaters depends on the location of fledging. Each group of birds was significantly directed (Table 2). These directions, when looking at the topography of Skomer Island, resulted in birds flying away from land and towards the sea. We found no effect of moonlight levels or wind speed on flight direction (Results in Supporting information).

Table 1. Summary of the schedule of the experiment with dates, average wind direction, wind speed ($m s^{-1}$), number of marked birds fledged split into control and magnetic treatment and average weight of birds (g).

Year	Date	Location	Wind direction	Avg wind speed ($m s^{-1}$)	No. of fledged birds		Weight (average in g)
					Control	Magnetic	
2017	18/09/2017	Skomer Head	WNW	–	7	3	408
	19/09/2017	Skomer Head	SE	–	4	5	396
2018	09/09/2018	Pigstone Bay	W	9.05	2	0	450
	12/09/2018	Pigstone Bay	W	5.83	2	2	442
	13/09/2018	Pigstone Bay	WSW	7.37	2	1	438
	14/09/2018	Pigstone Bay	SW	6.76	4	5	413
	15/09/2018	Pigstone Bay	S	7.92	3	3	408
	16/09/2018	Pigstone Bay	WSW	3.00	2	4	423
	18/09/2018	Skomer Head	SSW	7.85	3	4	421
	21/09/2018	Skomer Head	WNW	7.31	2	3	405
	22/09/2018	Skomer Head	NE	5.10	5	7	404
	23/09/2018	Pigstone Bay	NNW	4.84	5	6	408
	24/09/2018	Pigstone Bay	E	1.87	5	4	404
Total					46	47	

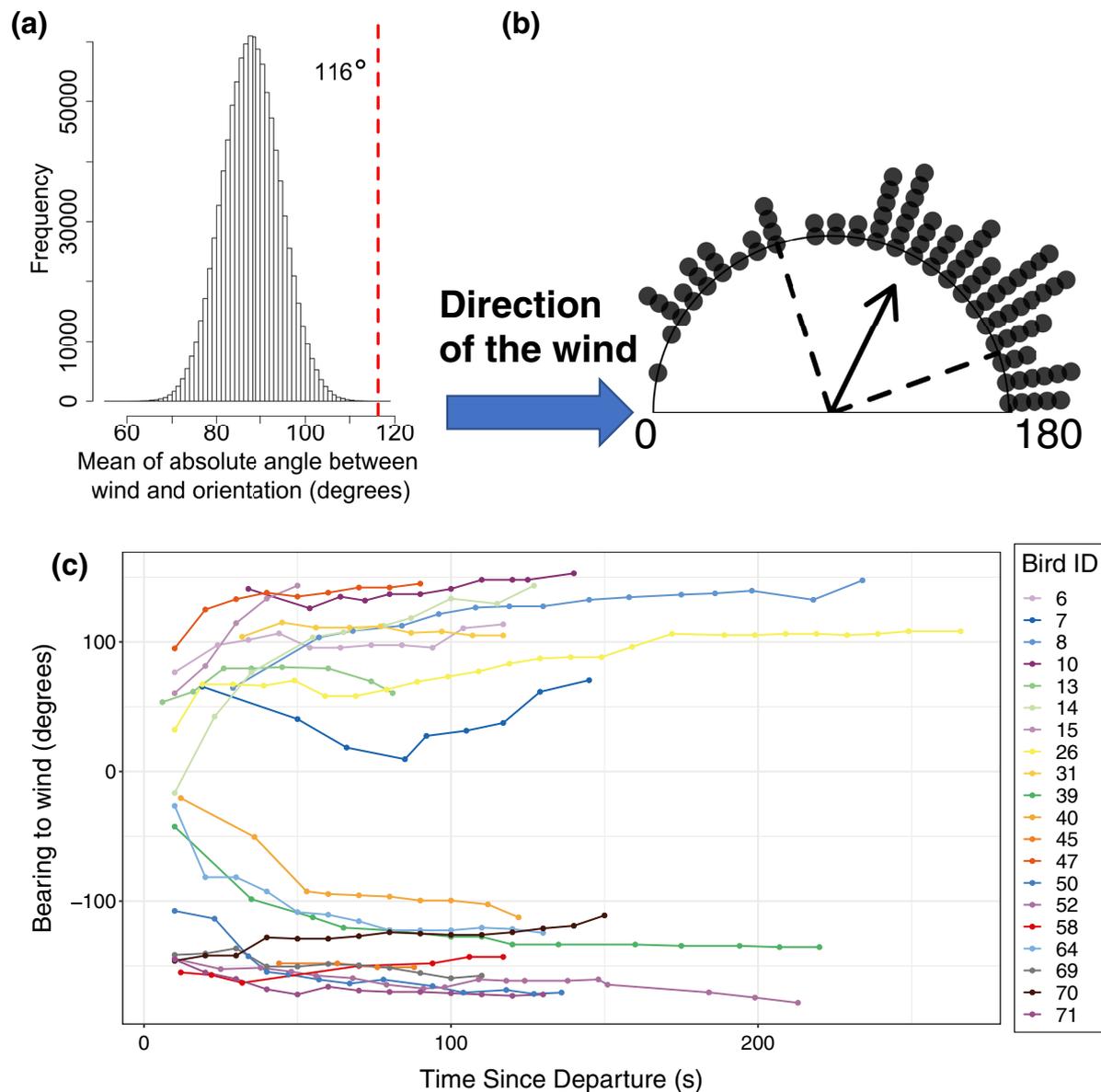


Figure 2. (a) Null distribution of vanishing bearings randomised with respect to wind and observed mean of the angles between the bearing of birds and wind direction (116° , red, dashed line). (b) Flight direction of birds (0 – 180°) with respect to wind direction (blue arrow). Each dot represents the angle between an individual bird's flight direction and the wind. The black arrow indicates the birds' mean direction (116°) and the dashed lines represent standard deviation ($\pm 44^\circ$). (c) Change over time (s) of the angle between wind and flight direction after take-off (from -180° to $+180^\circ$). Each line (and colour) represents a bird. For clarity, only a subset of 20 birds are shown.

Discussion

We developed a novel assay to observe orientation during the first flight of juvenile migratory shearwaters and investigated whether they may use the magnetic field to determine their orientation. Using this minimally-invasive assay, we successfully observed a large number of Manx shearwater fledglings (95 birds) departing from their natal colony at night and investigated the drivers of their initial flight direction. The attachment of LED lights to the backs of birds allowed us to observe them for a long time after their take off (up to 6 min 45 s) and record their precise bearings. Pairing this

with a small, light cardboard box with a rare earth magnet enabled us further to test the magnetic sense of the birds. This method, affordable and weighing very little, could be widely applicable for even smaller species from a range of taxa and thus is a useful addition to the growing toolkit for tracking birds, which mostly comprises expensive, larger devices limited to large species. Further studies, however, could consider validation of vanishing bearings as a proxy for initial orientation by comparing bearings recorded by an observer and those recorded by a GPS device or include calculation of the distance between observer and a bird to improve the detail of an observation (Richards et al. 2019). While our assay

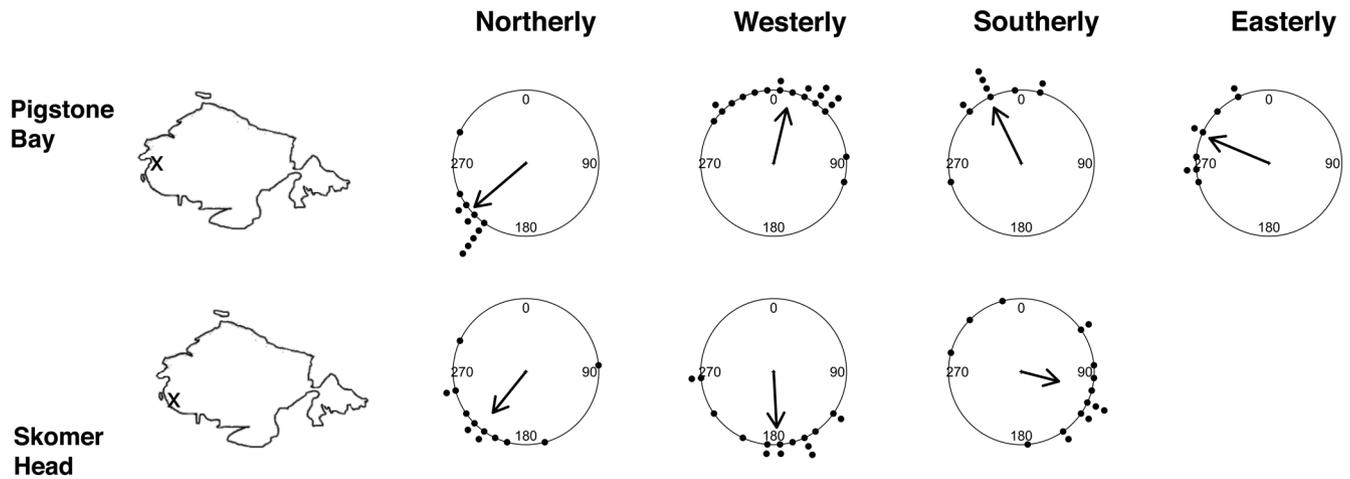


Figure 3. Vanishing bearing of Manx shearwaters at different locations, split by wind direction. Each circular graph represents a group of Manx shearwaters in one of the four winds (northerly, westerly, southerly and easterly) and one of the two locations (top – Pigstone Bay, bottom – Skomer Head). Each dot represents the vanishing bearing of an individual bird. The arrow indicates each group’s mean direction and vector length. Two outlines of a map represent Skomer Island, and the black crosses indicate the location of respective experimental sites on the island (Pigstone Bay and Skomer Head). All graphs are presented in relation to geographic north.

permits asking only a limited number of questions compared to a wider array of hypotheses available when using tracking devices, it could still be useful when researching fledgling birds, which are unlikely to be captured again, and thus could improve our understanding of early migratory navigation.

Our assay revealed that juvenile shearwaters do not orient towards their wintering ground during the very start of their initial flight. Whilst our result is consistent with previous experiments in that we found no difference between magnetically treated and control groups (Massa et al. 1991, Benhamou et al. 2003a, b, Bonadonna et al. 2003, 2005, Mouritsen 2003, Pollonara et al. 2015, Padget et al. 2017), we noted no overall orientation in the control group and as such it is unclear whether juvenile shearwaters do or do not utilise magnetic cues (but see Wynn et al. 2020). We cannot determine whether the signal was overridden by environmental variables (such as wind), Manx shearwaters utilised other cues available or lacked the motivation to orient to the migratory beeline on first flight. Whilst the overall migratory direction is a reasonable expectation for a young bird’s first flight, it is also possible that birds are instead motivated to explore the natal area or seek foraging grounds as they leave their birth place (Zwarts et al. 1990, Catty et al. 2011). The migratory

orientation of passerines is mostly tested on the migratory route and not at its start (Sandberg et al. 2000, Muheim et al. 2002, Bianco et al. 2016). Thus, further research investigating migration in young seabirds should consider undertaking experiments at later stages of migration.

Despite not finding evidence for Manx shearwaters orienting in the migratory direction at the start of their maiden flight, our assay was successful in identifying wind direction and topography as important drivers of initial flight direction. Flight direction was affected by the location from which birds began their flight. We found a difference in initial flight direction depending on the location with southerly and westerly wind, but not in northerly winds. The topography of land in both release locations allowed only for one crosswind direction (westerly) with northerly winds which would result in birds flying away from land and towards the sea. These results further support the conclusion that initial flight direction in juveniles is driven by an interaction between topography and wind.

Our results revealed that birds tended to fly with a bearing to the wind somewhere between a crosswind and a tailwind, averaging 116 degrees. It has been suggested that some juvenile seabirds might be constrained to fly with tailwinds.

Table 2. Group’s sample size, circular mean flight direction and the results of Rayleigh tests (Rayleigh value and p value) when testing whether birds were significantly directed, accounting for fledgling location and wind direction. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Location	Wind direction	Group sample size	Group’s mean direction (degrees)	Rayleigh statistic (0–1)	p-value
Pigstone bay	Northerly	11	230	0.926	< 0.001***
	Westerly	20	13	0.77	< 0.001***
	Southerly	10	334	0.845	< 0.001***
	Easterly	9	293	0.884	< 0.001***
Skomer head	Northerly	12	219	0.722	0.001**
	Westerly	15	177	0.765	< 0.001***
	Southerly	16	104	0.532	0.009**

Riotte-Lambert and Weimerskirch (2013) and Collet et al. (2020) found that young seabirds depart mostly with tail-wind directions in their first weeks of exploring, and only after a few weeks do the wind conditions progressively lose influence on their foraging directions, suggesting that juvenile birds require a learning phase of flight and/or navigational skills to overcome wind constraints on flight direction (Riotte-Lambert and Weimerskirch 2013, de Grissac et al. 2016, 2017, Harel et al. 2016). Wind has been shown to affect flight stability and energetics (Yamamoto et al. 2017) as well as efficiency (Harel et al. 2016) in juvenile birds. Muscle reinforcement and optimal flight practice has to be developed over the first weeks of their life (de Grissac et al. 2017). Thus, fledgling Manx shearwaters from our study might have been buffeted by winds on their maiden flight due to their lack of flight experience. This hypothesis is supported by reports on grounding events in Procellariiform juveniles in areas with high levels of light pollution, which show an increased number of collected seabirds when the wind was blowing onshore, from the colony towards the light polluted area (Rodríguez et al. 2014, Syposz et al. 2018). It has been proposed that this may be a result of the interaction between wind direction and the effect of light pollution, with inexperienced juveniles blown in the direction of the lights and therefore increasing their chance of being affected by them.

Light pollution alone may also affect the flight of young seabirds and so their orientation may be biased towards light-polluted areas (Rodríguez et al. 2015). Testing this hypothesis was beyond the scope of this study and would have required an experimental set up where we could manipulate the level of light pollution, which was not possible at our study colony. However there have been reports of decrease in fallout during the full moon (Telfer et al. 1987, Rodríguez and Rodríguez 2009, Miles et al. 2010, Syposz et al. 2018) perhaps due to a lower contrast between light polluted and dark parts of the horizon (Miles et al. 2010). We conducted a simple comparison of the orientation of fledglings on a moonlit and a moonless night (Supporting information), but found no difference. This suggests that light pollution may not have affected the orientation of Manx shearwater fledglings in our study. The light pollution levels were very low at our study sites, therefore further orientation experiments, including in more light-polluted areas, would be required to investigate the effect of light pollution on the seabirds' maiden flight.

Conclusion

We developed a behavioural assay to measure initial orientation in nocturnal juvenile migratory birds. We did not find any evidence that Manx shearwaters orient towards the wintering grounds nor that they use magnetoreception on their first flight, but found that wind direction and topography seem to play an important role. This minimally-invasive, simple and affordable assay will facilitate the study of the maiden flight of a large number of nocturnally migrating birds and is applicable to a wide range of taxa. It could be a useful

tool to improve our understanding of the sensory guidance mechanisms underpinning birds' maiden flights, especially of species which are typically difficult to research due their low chance of recovery or their unsuitability for large tracking devices.

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Conflicts of interest – The authors declare that they have no conflicts of interest.

Permits – All work adheres to the ASAB/ABS guidelines for the Use of Animals in Research and was conducted after ethical approval by Natural Resources Wales, Islands Conservation Advisory Committee for Skomer and Skoholm Islands and the University of Oxford's Local Ethical Review Process. LED and magnets deployments were approved by the British Trust for Ornithology Unconventional Methods Technical Panel (permit C/6128).

Author contributions

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Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.k0p2ngf6t>> (Syposz et al. 2020).

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