



Research

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Pelagic seabird flight patterns are consistent with a reliance on olfactory maps for oceanic navigation

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Homing studies have provided tantalizing evidence that the remarkable ability of shearwaters (*Procellariiformes*) to pinpoint their breeding colony after crossing vast expanses of featureless open ocean can be attributed to their assembling cognitive maps of wind-borne odours but crucially, it has not been tested whether olfactory cues are actually used as a system for navigation. Obtaining statistically important samples of wild birds for use in experimental approaches is, however, impossible because of invasive sensory manipulation. Using an innovative non-invasive approach, we provide strong evidence that shearwaters rely on olfactory cues for oceanic navigation. We tested for compliance with olfactory-cued navigation in the flight patterns of 210 shearwaters of three species (Cory's shearwaters, *Calonectris borealis*, North Atlantic Ocean, Scopoli's shearwaters, *C. diomedea* Mediterranean Sea, and Cape Verde shearwaters, *C. edwardsii*, Central Atlantic Ocean) tagged with high-resolution GPS loggers during both incubation and chick rearing. We found that most (69%) birds displayed exponentially truncated scale-free (Lévy-flight like) displacements, which we show are consistent with olfactory-cued navigation in the presence of atmospheric turbulence. Our analysis provides the strongest evidence yet for cognitive odour map navigation in wild birds. Thus, we may reconcile two highly disputed questions in movement ecology, by mechanistically connecting Lévy displacements and olfactory navigation. Our approach can be applied to any species which can be tracked at sufficient spatial resolution, using a GPS logger.

1. Introduction

After foraging in the open ocean, *Procellariiformes* (albatrosses, petrels and shearwaters) are able to pinpoint their breeding colonies, often located on small remote islands in apparently featureless seascapes. It has been hypothesized that this remarkable ability to navigate over vast distances can be attributed to the birds being able to learn an olfactory map or landscape on the basis of local wind-borne odours rather than their relying on geomagnetic cues [1–4]. Dimethyl sulfide and other biogenic odours whose concentration varies predictably in space may contribute to form an olfactory landscape used in navigation [5]. In long-lived birds like *Procellariiformes*, these odours may be learnt (dimethyl sulfide originates in high quantity from phytoplankton and is persistent in marine seascapes) but airborne odour concentrations are highly intermittent due to the presence of atmospheric turbulence, and, as a result, olfactory cues for navigation will not always be present [6].

Recently, the odour-map hypothesis gained considerable credence from a study of the homing flights of displaced Cory's shearwaters that had been subject

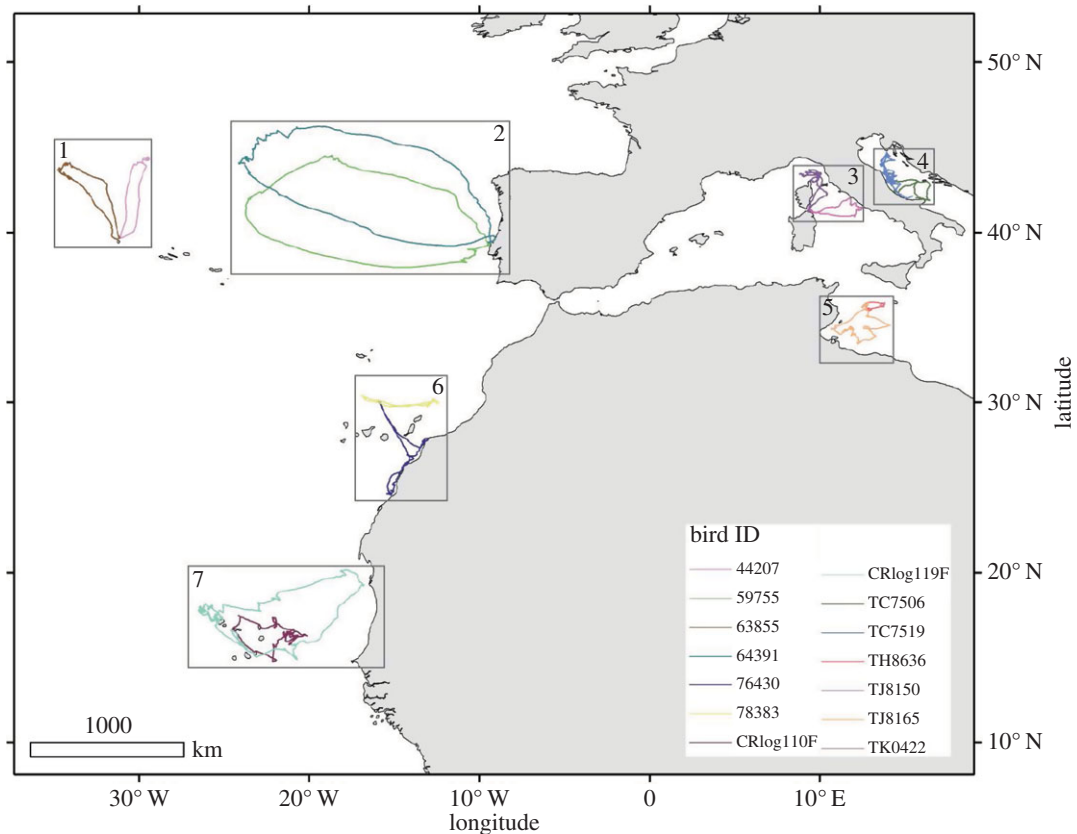


Figure 1. Illustrative trips from Cory's shearwaters breeding at (1) Corvo, (2) Berlenga and (6) Selvagem Grande islands; Scopoli's shearwaters from (3) La Madalena, (4) Tremiti and (5) Linosa islands and; Cape Verde shearwaters from (7) Raso islet. Different colours represent different individuals (Bird_ID) and the black star their breeding colonies location. Most flights are made over open seas rather than close to the coastline where birds might use known landmarks for orientations towards the colony. Numbered subplots are reported at higher resolution in electronic supplementary material, figure S1.

to sensory manipulation [7]. Gagliardo *et al.* [7] reported that Cory's shearwaters deprived of their sense of smell showed dramatically impaired homing ability, whereas magnetically disturbed shearwaters showed unaltered navigational performance similar to that of unmanipulated control birds. Eight birds were yielded anosmic by washing their olfactory mucosa with a zinc sulfate solution [8]. However, this experiment [7], as well as the few attempts to demonstrate olfactory maps in wild birds [9–11], only suggests that olfaction plays a role in homing, without demonstrating the use of olfactory navigation. It also leaves open the question of whether olfactory cues are of crucial importance to pelagic seabirds in oceanic navigation when, for example, heading to favoured and profitable foraging areas [12] as shown in figure 1. Nonetheless, it is known that at small spatial scales (tens to hundreds of square kilometres), procellariiform seabirds use odours and also visual cues to pinpoint and capture prey directly [13].

Neuroanatomical comparisons [14] suggest that olfactory navigation is common in vertebrates, and genetic studies show that the olfactory gene repertoire is well developed in birds [15]. However, it is impossible to obtain a satisfactory sample size using intrusive experimental approaches on pelagic birds, such as shearwaters and albatrosses, especially when there are concerns for their conservation. This fact casts away the possibilities to use classical experimental/control groups of treatments [16] and one has to rely on spontaneous birds displacements.

Here, using an innovative non-invasive approach, we provide evidence that shearwaters rely on olfactory cues for

oceanic navigation. It is based upon a mathematically rigorous and general description of olfactory-cued navigation in the presence of atmospheric turbulence. This theory accounts for how odours disperse in the atmosphere and for how birds can use these odours to orient their flights. The approach used to model the process of olfactory navigation is displayed in figure 2. When the odours are continually present above the threshold of detection, then the 'odour map' is present and the birds will maintain nearly unidirectional flight. But when the odour concentration falls below this level, the birds are without their map and so effectively lost. They may change course either because they become disoriented or because they are attempting to re-establish contact with the odour map. The lengths of the unidirectional flights are predicted to be distributed according to exponentially truncated power-laws that are characterized by a universal exponent whose value, $3/2$, is independent of ecological context (electronic supplementary material, Level-crossing statistics of concentration fluctuations in odour plumes dispersing in turbulent flows). The $3/2$ scaling is not model-specific as all physically realistic models of odour dispersal in turbulent flows will produce it by virtue of the Sparre Andersen theorem [17,18]. We assessed whether the flight-segment lengths empirically determined in tracking experiments displayed the expected distribution. This was done using standard techniques in the literature on Lévy flights [19]. The presence of these distributions indicates that the flight patterns are consistent with a reliance on olfactory maps for oceanic navigation. This provides a new diagnostic test for olfactory-cued navigation; a test which can be made without interfering with the animal's sensory mechanisms.

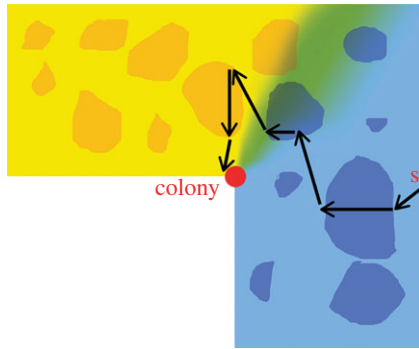


Figure 2. A sketch of the proposed mechanism of olfactory navigation in pelagic birds. Birds associate odours to wind directions, so that a bird knows that when on the colony odours ‘blue’ and ‘yellow’ are emanating from East and North, respectively (the green colour indicates that there are areas where odours may mix). Thus, if a bird at S aims to come back to the colony, it will head westward (black arrows represents displacements, smaller changes of direction are overlooked). However, because of atmospheric turbulence, the ‘blue’ odour is not present at detectable concentrations and the bird changes orientation to try to relocate the cue (dark and light colours indicate areas where the animal is able to orientate or not towards the colony). When it does relocate the odour, it resumes flying westward. If it arrives in a zone when ‘yellow’ odour is dominating, it will head southward. In this way, the bird is led to the neighbourhood of the colony. When pelagic birds get close enough to their target, they may rely on other sources of information (landmarks, flights of other birds and ‘colony odours’). Our model is also consistent with the ‘odour maps’ proposed by Gagliardo *et al.* [7] and Jacobs [14].

2. Material and methods

(a) Bird species and colonies

The location of the studied colonies is reported in figure 1 and electronic supplementary material, figure S1. The ecology of the study species is described in detail in electronic supplementary material, Species ecology and study sites. Our samples are reported in electronic supplementary material, table S1.

(b) GPS-logger deployment

Birds were tracked using five models of GPS loggers: one by Earth & Ocean Technologies (Kiel, Germany) (mini-GPS, 19.4 g, battery 500 mA), two different models by Technosmart (Guidonia, Italy) (GiPSy-2, 11.9 g, battery 500 mA, and GiPSy-2, 9.8 g, battery 250 mA), and two different models by Perthold Engineering LLC (CatTraQ GT-120, 16 g, battery 500 mA, and CatTraQ GT-120, 11 g, battery 250 mA). All GPS loggers were configured to record the position of the bird every 10 min which was empirically selected as a good compromise between battery consumption and resolution. Shorter times would make impossible to record the longer trips to which we are especially interested. Devices were attached to the back feathers using three to four strips of Tesa® marine cloth tape (Tesa SE, Hamburg, Germany). During incubation, birds were captured, ringed and equipped with GPS loggers during the day. Afterwards, burrows were checked every day to record departure of the tagged bird, and, subsequently, the return of the equipped individuals. Loggers were removed immediately after a bird returned from a foraging trip. During chick rearing, birds were handled during the night after chick feeding. As adults normally spent little time in their burrow, it was not always possible to recapture the equipped bird after the first foraging trip, and hence more than one trip might have been recorded for a given bird. Nevertheless, only the first trip of each bird was included in the analyses. Electronic supplementary material, table S1, reports metadata used in this study.

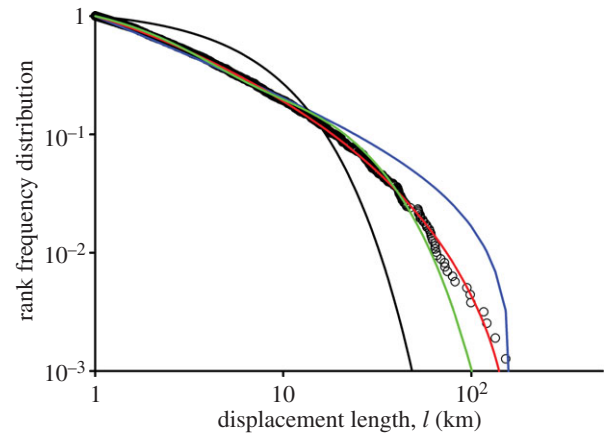


Figure 3. Rank frequency plot of the 32 flights recorded from Maddalena island in the Mediterranean showing evidence of scale-free behaviour consistent with olfactory-map navigation. Circles show number of flight-segments (bouts of unidirectional flight) with flight-segment length more than or equal to l (calculated by ranking flight-segment lengths by size). The red curve is the fit to an exponentially truncated power-law with a maximum-likelihood estimate of $\mu = 1.61$ (95% CI 1.56–1.66), obtained by maximizing the log-likelihood function. Shown for comparison are fits to a truncated power (blue), an exponential (black) and a bi-exponential (green). The Akaike weight 1.00 overwhelmingly favours the exponentially truncated power-law as being the best model distribution.

As recommended by several authors [20,21], the weight of GPS loggers was kept below 3% of the birds’ body mass (range = 1.9–2.9%; median = 2.6%). External devices of this size are considered not to have any detectable influence on the foraging behaviour of Scopoli’s shearwater [22,23], though they may possibly reduce nestling feeding rate and hamper nestling growth [23]. Deployment of data-loggers took less than 10 min and birds were returned to their nest immediately afterwards. Handling and GPS deployment during incubation did not affect hatching success at the Linosa colony in 2008 [24] nor the fledging success at Berlenga colony during 2006 [25].

(c) Model flight-segment-length frequency distributions

Birds belonging to seven colonies of three species were tagged with high-resolution GPS loggers during both incubation and chick rearing (electronic supplementary material, Species ecology and study sites). To test for the hallmark of olfactory navigation, we used robust and accurate statistical methods [19,26,27]. Displacement length frequency distributions were fitted to exponentially truncated power-laws (the theoretical expectation for olfactory-cued navigation), power-laws (indicative of random Lévy flight searching and the absence of knowledge about prey locations [28,29], bi-exponentials (indicative of two-mode searching, occasionally seen in seabirds [12]; tri-modal searching has never been observed in seabirds) and exponentials (a null model of the flight pattern data).

These model distributions are prescribed by

$$p_1(l) = N_1 l^{-\mu} \exp(-\lambda_1 l) \exp\left(\frac{-\lambda_2}{l}\right), \quad (2.1a)$$

$$p_2(l) = N_2 l^{-\mu} \quad (2.1b)$$

and

$$p_3(l) = AN_3 \exp(-\lambda_3 l) + (1 - A)N_4 \exp(-\lambda_4 l), \quad (2.1c)$$

where N_1 , N_2 , N_3 and N_4 are normalization factors which ensure that the frequency distributions sum correctly to unity when integrated over all lengths between the lower and upper cut-offs; μ is the power-law (known as the Lévy exponent in the literature on Lévy flight foraging); λ_1 and λ_2 are related to atmospheric

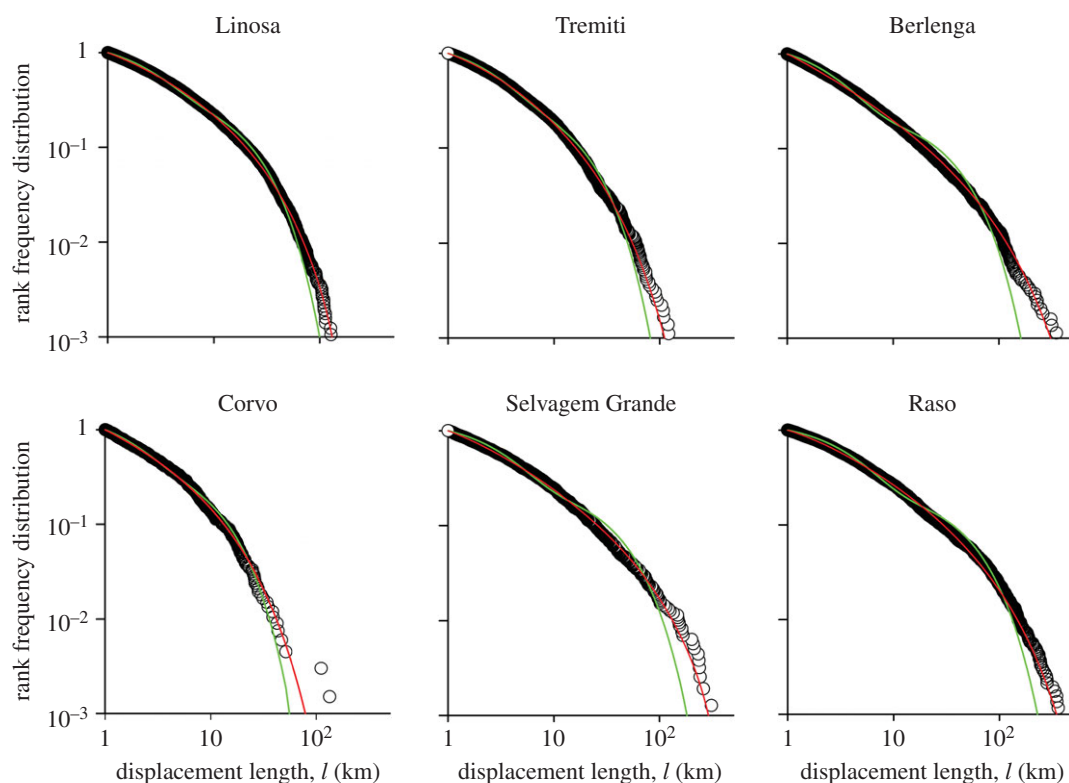


Figure 4. Rank frequency plots of flights recorded from Linosa island in the Mediterranean, Tremiti island in the Adriatic and four North Atlantic islands, Berlenga, Corvo, Selvagem Grande and Raso, showing evidence of scale-free behaviour consistent with olfactory-map navigation. Circles show number of flight-segments (bouts of unidirectional flight) with length more than or equal to l (calculated by ranking flight-segment lengths by size). The red curves are the fits to an exponentially truncated power-law (equation 2.1a) with maximum-likelihood estimates and 95% CIs of $\mu = 1.39 \pm 0.03$, 1.59 ± 0.04 , 1.64 ± 0.03 , 1.38 ± 0.05 , 1.61 ± 0.02 and 1.59 ± 0.03 , respectively, obtained by maximizing the log-likelihood functions. Shown for comparison are fits to bi-exponentials (green). For clarity, we have omitted poorer fits to powers and to exponentials. The Akaike weight for the exponentially truncated power-law is 1.00 for every colony.

conditions (see equation S4 in electronic supplementary material, Level-crossing statistics of concentration fluctuations in odour plumes dispersing in turbulent flows); and λ_3^{-1} and λ_4^{-1} are the characteristic flight lengths in the intensive and extensive phases of a bi-modal search, respectively. A simple exponential is obtained from equation (2.1c) by setting $A = 1$.

Until recently, the identification of turns (and so bouts of unidirectional flight) within two-dimensional flight patterns relied on ad hoc parameter choices for critical turning angles [26]. We overcome this limitation by projecting the flight patterns onto the x - and y -axes to create two one-dimensional movement patterns for each individual. Turns in these projected movement patterns can be identified in an unambiguous way as occurring where the direction of travel along the x - and y -axes changes [26]. It can be shown that the projection preserves any power-law scaling characteristics in the original data [26]. We checked for consistent scaling in the x - and y -directions and consequently we merged the two datasets. Model distribution functions were truncated below 1 km and above the length of the longest recorded displacement. Analysis outcomes did not change in a meaningful way when a shorter lower truncation scale was used. The lower truncation excludes from the analysis more convoluted parts of the flight patterns that are presumably associated with feeding or resting rather than with navigation.

3. Results

Here, we analysed the flight patterns of 210 shearwaters belonging to three species (figure 1; electronic supplementary material, Species ecology and study sites).

We found clear and persistent evidence of exponentially truncated power-laws that are consistent with the theoretical

expectations for olfactory-cued navigation. This was evident in 69% of the birds analysed (electronic supplementary material, table S2). Relative maximum-likelihood estimates for model fits to the displacement-length distributions for all three species and seascapes strongly support exponentially truncated power-law distributions, typically over 2 or more orders of magnitude, with characteristic power-law exponents close to the theoretical expectation of $3/2$ (figures 3 and 4).

This is evident in birds which may rely more (Maddalena, Tremiti, Mediterranean Sea) or rely less (Corvo, Cape Verde, North Atlantic Ocean) on previous coastal landscape knowledge (figure 1). At the individual level, we computed the best-fitting distribution and estimates of μ , λ_1 and λ_2 (electronic supplementary material, table S2). More specifically, our estimates of μ (figure 5) are biased high with respect to the reference value (Student's $t = 5.37$, $p < 0.0001$), but this difference vanishes (Student's $t = 0.31$, $p = 0.75$) after taking into account the effect of the number of displacements (reported in electronic supplementary material, table S2) used to compute μ .

Our indicator of olfactory-cued navigation was evident in nearly all of the flights lasting 4 or more days but was only present in about 50% of the shorter flights lasting less than 2 days. The other flights were better represented as bi-exponentials. This is not at variance with the predominance of olfactory hallmarks at the population level as long records are required to reliably distinguish between exponentially truncated power-laws and bi-exponentials. Indeed, we found that the proportion of synthetic olfactory-cued flights (produced in numerical simulations) that were misidentified by our statistical diagnostics decreases as the flight length increases. This decrease mirrors that seen in our empirical data (electronic

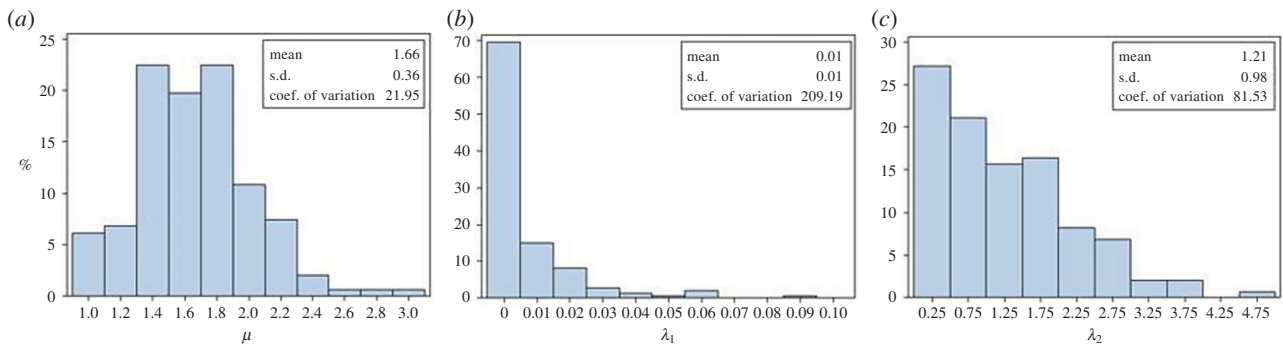


Figure 5. Distribution of the maximum-likelihood estimates for the power-law exponents, μ (a), and exponential decay rates, λ_1 (b) and λ_2 (c), for birds using olfactory-cued navigation.

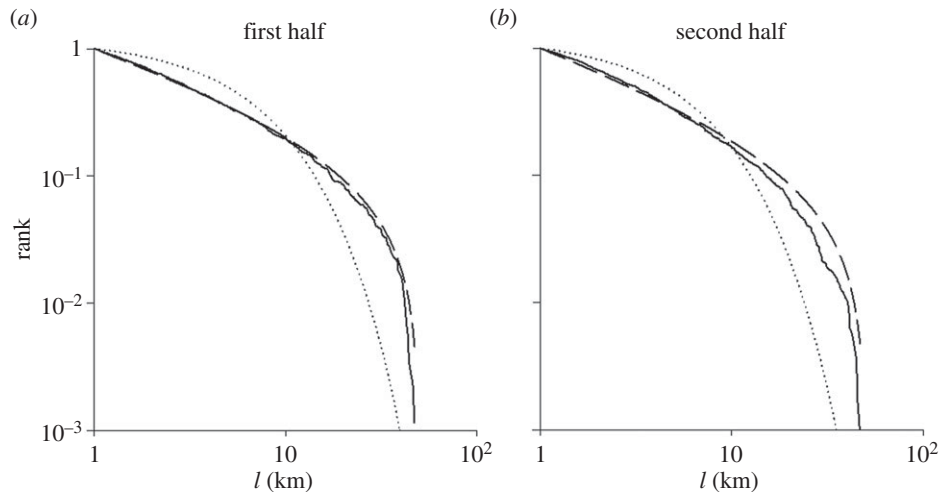


Figure 6. (a,b) Rank frequency plot showing evidence of truncated scale-free behaviour consistent with olfactory-map navigation during the first and second halves of foraging trips for the shearwaters breeding at Maddalena. The observations (continuous lines) are shown together with the best-fit for exponentially truncated power-laws (dashed lines) and bi-exponentials (dotted lines). The two halves of each flight pattern have the same length.

supplementary material, figure S3). This artefact was not present at the population level when data for many synthetic flights was pooled for data analysis purposes (electronic supplementary material, Synthetic flights).

In contrast with the maximum-likelihood estimates for the power-law exponent which, in accordance with theoretical expectation, show only modest variation, there is about a 10-fold variation in individual estimates for the exponential decay rates, λ_1 and λ_2 (figure 5). This variation is not surprising and is indicative of a wide variety of weather conditions.

We claim that shearwaters use olfactory maps for navigation and hence during both the forward and return branches of their foraging trips. We therefore expect to find the hallmark statistical signatures of olfactory-cued navigation in both of these branches. This expectation is supported by our data. This is illustrated in figure 6, which shows that the first and second halves of the flight patterns of the shearwaters breeding at Maddalena share common statistical properties that are consistent with olfactory-cued navigation.

4. Discussion

Antecedents of our findings on shearwaters can be found in previous studies [26,30,31]. Reynolds *et al.* [30] reported that male *Agrotis segetum* moths flying in the presence of dispersing sex pheromone have scale-free dynamics, and Focardi & Cecere [31] reported that 36 out of a set of 77

foraging flight patterns made by Scopoli's shearwaters from two Mediterranean colonies had scale-free characteristics with power-law exponents around 1.6. Humphries *et al.* [26] reported on strong evidence for 20 out of 27 wandering albatross *Diomedea exulans* foraging patterns having truncated scale-free characteristics and these were attributed to the execution of advantageous random searching strategies; patterns of movement that are expected in probabilistic foragers with little or no knowledge of their environment. This interpretation is based upon model expectations for random searching but these authors did not consider olfactory models and so we do not know which interpretation is more appropriate for *D. exulans*. We showed that the hallmark of olfactory-cued navigation is a universal exponentially truncated power-law. We therefore suggest that these birds together with shearwaters rely on cognitive olfactory maps rather than on Lévy flight random searching to find preferred foraging locations and breeding colonies. Taken together the theoretical deduction and the analysis of the empirical data are seemingly compelling because as noted by Stumpff & Porter [32, p. 666] 'a statistically sound power-law is no evidence of universality without a concrete underlying theory'.

Shearwaters may, however, use some form of random searching strategy at smaller scales to locate prey within their preferred feeding locations or they may exploit the presence of odour plumes emanating from the target [33]. Our analysis thus provides novel insights into scale-free patterns and indicate that Lévy flight research still has much to learn from the

touchstone flight patterns of the wandering albatross [34]. They reconcile Lévy flight characteristics with the presence of directed flights (map-like behaviour) which are quite unlike the freely roaming patterns seen in probabilistic foragers. This study thereby introduces a novel conceptual connection between two highly disputed questions of movement ecology, namely Lévy displacements [28] and olfactory navigation [10] showing that the occurrence of the former can mechanistically be caused by the latter.

As previously noted, flight patterns may also be influenced by factors other than olfactory navigation, such as the presence of landmarks, fishing boats [35] and conspecifics or competitors leading to a movement pattern based on multi-modal cuing. However, the availability of such additional information is quite different among the studied populations. For instance, shearwaters nesting at Maddalena might navigate only using landmarks, as the northern Tyrrhenian Sea is full of islands, with a very high density of boats, a situation quite different from that experienced by the shearwaters nesting at Raso or Berlenga patrolling vast extensions of open ocean. Despite these important differences in seascape, we demonstrated that all these animals share the same basic pattern, strongly suggesting the presence of an underlying common mechanism of orientation which we have identified as olfactory-cued navigation. Our interpretation accounts naturally for the ability of seabirds to pinpoint their feeding colony and their preferring foraging locations after crossing vast expanses of featureless open ocean.

The ‘biologging revolution’, a discipline taking advantage of technological advancements and miniaturization [36] makes it possible, by the methods underlined here, to test the hypothesis of olfactory navigation in a large number of different organisms, living in most of Earth’s ecosystems. Indeed, it would be interesting to test for scale-free

characteristics in the movement patterns of other animals, such as turtles and seals that can detect airborne odours when they surface to breathe, and under natural conditions, this sensory ability might function in navigation [36–38]. Furthermore, it is possible to speculate on the use of olfactory navigation for bird migration [10].

Ethics. All the fieldwork was undertaken (capture, handling and ringing) under national and European laws, which regulates studies on wild bird species.

Data accessibility. Data have been uploaded to The Seabird Tracking Database managed by BirdLife International (<http://www.seabird-tracking.org/>).

Authors’ contributions. A.M.R. and S.F. wrote the paper with inputs from J.G.C., V.P. and J.R. J.G.C., V.P. and J.R. collected the data. A.M.R. analysed the data with inputs from S.F.

Competing interests. We declare we have no competing interests.

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