Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird

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Foraging animals are expected to adapt their movement patterns to their environment in a way that maximizes efficiency. The search strategies they rely on to achieve this is an enduring question in ecology. Scale-free Lévy and Brownian search strategies have received particular attention as both strategies are considered effective when prey are abundant and Lévy search is thought to optimize success when prey are patchy. Environmental context has been shown to explain Lévy and Brownian movement patterns for various marine predators, but potential effects of habitat structure and cognitive skills are often overlooked. We used bird-borne global positioning sensors (GPS) and temperature depth recorders (TDR) to assess flight paths and dive profiles of foraging parental common murres, *Uria aalge*. Movement patterns while flying and diving were best approximated by Brownian motion even though their primary prey, capelin, *Mallotus villosus*, are patchily distributed. Contrary to expectations, there was virtually no support for Lévy flights. Further analyses revealed that murre foraging activities are not random, but are rather more deterministic. Murres repeatedly returned to previously visited sites (within ~2 km), indicating a role of memory, and they focused foraging activities using small-scale area restricted search (ARS; <2 km radius). Such behaviour appears to induce movement patterns that reflect the distribution of capelin. These findings highlight the efficacy of assessing deterministic search behaviour when interpreting the movement patterns of animals that may be informed about their environment.

Successful and efficient foraging by predators depends largely on the spatial and temporal distribution of prey and the search strategies used to find them (Bell 1991). Because finding food is crucial to survival, strategies that maximize net energy gain are expected to emerge through natural selection (MacArthur & Pianka 1966). The strategies predators should use to maximize encounter rates with prey are a central, but largely unresolved, issue in ecology (Stephens & Krebs 1986). To help resolve the issue, recent work in optimal foraging theory has drawn extensively from concepts and methods used in statistical physics to quantify diffusion processes, such as Lévy and Brownian flights (Viswanathan 2011). The concept of Lévy flights has received particular attention because it describes scale-free fractal movement patterns that theoretically optimize encounters with unpredictable prey that are patchily or uniformly distributed (Viswanathan et al. 1999). Brownian motion describes more localized searching behaviour, which may be equally efficient when prey are uniformly distributed (Bartumeus

et al. 2002). Lévy and Brownian search patterns have been demonstrated in a wide range of taxa, from bacteria to great white sharks (Korobkova et al. 2004; Humphries et al. 2010, 2012; Sims et al. 2011; Hays et al. 2012). The general assumption under the Lévy flight foraging (LFF) hypothesis is that movement patterns represent innate random searching behaviour that maximizes foraging efficiency under specific prey landscapes (Viswanathan 2011). Recent research supports the possibility that such a search strategy could have evolved in response to unpredictable resources (Humphries et al. 2012). In some cases, however, Lévy and Brownian search patterns may be outperformed and can emerge from processes such as composite Brownian walks (Benhamou 2007), olfactory search behaviour (Reynolds 2012b) or memory-based foraging (Boyer et al. 2006). Nevertheless, most studies accept observed patterns as optimal and scale-free without ruling out other processes.

In nature, resources are rarely uniformly distributed; rather, prey are typically clustered hierarchically with fine-scale high-density patches nested within broad-scale low-density patches. Most predators therefore have to respond to complex heterogeneity at multiple scales in order to maximize overlap with prey (Russell et al. 1992). As such, widespread observations of scale-dependant shifts

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in movement patterns, commonly termed area restricted search (ARS), have often been interpreted as adaptive behavioural responses to local prey abundance (Tinbergen et al. 1967; Fauchald & Tveraa 2003; Thums et al. 2011). Under this strategy, the forager is expected to travel rapidly across large-scale, low-density prey patches and increase searching effort when it enters finer-scale, higher-density patches (Fauchald 1999). ARS shares similarities with Lévy or composite Brownian random walk models since clustered movements are typically separated by longer steps (Grünbaum 1998). A Lévy distribution may therefore emerge from ARS behaviour, or vice versa (Avgar et al. 2011). The question then remains whether the organism acts autonomously by adjusting foraging decisions based on recent experience or whether behaviour can be explained by statistically optimal movement patterns.

Beyond random or ARS, it is well known that some animals rely on cognitive maps to navigate their environment (Gould 1986; Garber 1989; Laughlin & Mendl 2000). These maps contain information, outside the individual's perceptual range, on the location and perhaps quality of various targets and their geometric relationships (Burt de Perera 2004). Cognitive maps allow predators to make optimal foraging decisions that minimize search time while maximizing overlap with prey. Such deterministic foraging behaviour generates individual space use features like site fidelity (Gautestad & Mysterud 2010; Gautestad 2011) and has obvious benefits for foraging success (Boyer & Walsh 2010). Individuals under the statistical diffusion paradigm are assumed to lack the capacity for spatial memory. The danger with this assumption is that scale-free movement patterns may emerge from spatially aware foraging animals that are interacting with a particular distribution of resources (Boyer et al. 2006). A memory-based strategy, however, is contingent upon the cognitive capacity of individuals and the predictability of their prey (Kamil & Roitblat 1985). In the real world, information is rarely perfect. Resources are often ephemeral and quasi-predictable, and as such a forager capable of applying such cognitive skills may have to rely on a combination of strategies to efficiently acquire prey (Boyer & Walsh 2010).

Efficient search strategies are particularly important to central place foragers raising offspring in a location that is physically separated from their foraging environment (Orians & Pearson 1979). In contrast to free-ranging predators, central place foragers must balance self and offspring provisioning while travelling to and from prey patches. Time spent travelling and searching for prey are critical constraints to reproductive performance since both factors limit provisioning rates (Clode 1993). Central place foragers are therefore expected to employ tactics that minimize time spent searching for prey. Here we attempt to reveal the foraging strategies employed by parental common murres, *Uria aalge*, using global positioning sensors (GPS) and temperature depth recorders (TDR). During the breeding season in Newfoundland, murres feed themselves and their chicks primarily on capelin, *Mallotus villosus* (Piatt 1987; Davoren & Montevecchi 2003; Wilhelm et al. 2003). Capelin is a small, schooling, pelagic fish that aggregates in large staging and spawning sites along the Newfoundland coast during summer (Templeman 1948). Capelin are distributed in hierarchical patches, which can be ephemeral but can also be persistent (Rose & Leggett 1989; Davoren et al. 2006). Such a system allows for testing scale-free, scale-dependent and memory-based foraging strategies. Since capelin patches are sparse and often unpredictable, our null hypothesis is that murre foraging patterns are governed by innate scaling laws approximated by Lévy flight. Alternatively, murres may utilize deterministic foraging strategies to maximize overlap with prey. Given the hierarchical and quasi-predictable nature of capelin patches, previous research suggests that murre foraging efficiency could be improved by applying ARS (Fauchald et al. 2000) or cognitive maps (Davoren et al. 2003). These strategies, however,

require higher-order sensory abilities not required for Lévy search; it is unclear whether murres have such capabilities. Scale-free search is therefore an important limiting model to test. We realize that these strategies may not be mutually exclusive; depending on navigational and learning abilities, it is plausible that murres rely on a combination of strategies to efficiently acquire capelin. By considering a variety of possibilities, we hope to elucidate the most parsimonious explanation.

METHODS

Study Sites and Field Methods

Research was conducted at two Seabird Ecological Reserves in Newfoundland, Canada: Gull Island (47.26°N, 52.78°W), Witless Bay (~100 000 breeding pairs in the reserve) and Funk Island (49.75°N, 53.19°W; 500 000+ pairs; Canadian Wildlife Service, unpublished data). Archival temperature depth recorders (TDR; <5 g, Lotek LTD 1110, LAT 1500 or 2500) were deployed on murres from both colonies between 2007 and 2010, and global positioning systems (GPS; ~17 g, earth & OCEANS mGPS, Kiel, Germany) were deployed on Gull Island murres in 2010 and 2011. Chick-rearing adults were captured between July and August using a telescopic noose pole and were equipped with an archival tag. TDRs were set to record temperature (accuracy $<0.2\,°C$) and depth (accuracy $<1\,m$) every 2 s for each dive. TDRs were secured to plastic leg bands (Pro-Touch Engraving, Saskatoon, SK, Canada) and attached to the left legs of study birds. GPS devices recorded locations (accuracy $<20\,m$) at 2 min intervals and were attached to the back feathers of study birds using Tesa® tape. All loggered birds were banded with a Canadian Wildlife Service metal band on the right leg. A total of 79 TDR (39 on Gull Island: $N_{2007} = 6$, $N_{2008} = 11$, $N_{2009} = 14$, $N_{2010} = 8$; 40 on Funk Island: $N_{2007} = 15$, $N_{2008} = 15$, $N_{2009} = 10$) and 17 GPS deployments were made (all on Gull Island: $N_{2010} = 10$, $N_{2011} = 7$). Birds were typically recaptured after 3 days (range 2–7 days). TDR birds were handled for about 5 min and GPS birds for about 10 min during logger deployment and recapture. Forty-seven of 53 recovered TDRs and 11 of 13 recovered GPS devices were successfully downloaded; 45 TDR and 10 GPS records, respectively, were used in the analysis following the exclusion of records that did not capture chick-rearing foraging activity. TDRs captured 36–130 h of data (memory limited) and GPS devices captured 28–48 h of data (battery limited). These data were processed and analysed using the statistical software R (R Development Core Team 2011).

Data Analysis

Lévy and Brownian models were fitted to both flying and diving movement patterns. Flights and dives were identified using temperature and pressure data from TDRs (for methods, see Tremblay et al. 2003). For presentation purposes, the distance (m) of each flight was estimated by multiplying flight duration by 19.1 m/s (estimate of mean flight speed of common murres; Pennycuick 1987) and dive depth (m) was characterized by the maximum depth reached during each dive. GPS data confirmed that flight distance is an appropriate measure of horizontal steps since there were few significant turns within flights (see Results). This measure is analogous to the step values used in Humphries et al. (2012) as it represents the distance between landed sites. Nevertheless, for comparison against the TDR-derived distributions, we fitted Lévy and Brownian models to step distances derived from flights from GPS-equipped murres (course alterations >90° were considered significant turns; Reynolds et al. 2007). Similarly, maximum dive depths were used to represent the vertical step length as 99% of

dives were U- or V-shaped and unlike W-shaped dives, U- and V-shaped dives lack significant within-dive turns (i.e. analogous to step values used in Humphries et al. 2010). Unless murres are capable of limiting their foraging efforts to areas where prey encounters are high, neither measure should be confounded by resource detection patterns (sensu Miramontes et al. 2012) because water turbidity likely limits large-scale patch-to-patch visibility of capelin. There were no apparent spatiotemporal shifts in flying behaviour, but clear diurnal patterns in diving behaviour were apparent (Hedd et al. 2009; Regular et al. 2010). Split-moving window analysis (30 min window size; for methods, see Humphries et al. 2010) corroborated these results; thus, diurnal, crepuscular (twilight) and nocturnal dives were analysed separately. Since GPS-tracked murres showed commuting behaviour (see Results; Weimerskirch 2007), TDR-derived flight distances were analysed with and without inclusion of inbound and outbound flights. Using methods outlined in Edwards et al. (2007) and Edwards (2011), maximum likelihood estimation (MLE; numerical optimization of likelihood functions performed using R function 'nlm') was used to fit exponential (Exp), bounded exponential (ExpB), power law (Lévy; PL) and bounded power law (Pareto-Lévy; PLB) models to step distributions for all birds combined on an individual basis (sensu Petrovskii et al. 2011). Values of parameter a were set to 100 m and 5 m for flights and dives, respectively, and b values were set as the maximum observed step length. Exponential (λ) and power law (μ) parameter and log likelihood estimates were calculated for each model and Akaike Information Criteria (AIC) values computed. Models were ranked by Akaike weights and evidence ratios were computed; best-fit models were considered those with evidence ratios <2.7 (Burnham & Anderson 2002). Lévy or Brownian type walks were further teased apart by applying the power spectra and first significant digit methods outlined in (Reynolds 2012a). These methods ensure that composite Brownian random walks (mixture of two Brownian walks) are not misidentified as Lévy walks (Reynolds 2012a). The start and end of each flight and dive characterized the time series of significant steps for the spectral analysis (pauses on the surface and at the colony were excluded). Spectral density was calculated using function 'spec.pgram'. Flight distances ≥100 m and dive depths ≥10 m were used in first significant digit analyses.

To identify zones of ARS, we applied first-passage time (FPT) analysis to GPS data, following Fauchald & Tveraa (2003), using the R function 'fpt' ('adehabitat' package). Locations along the whole track were interpolated at a uniform distance interval of 100 m, ensuring that all points along foraging tracks are equally represented (Pinaud 2008). FPT was then calculated every 100 m for a radius r from 1 m to 100 km. Plots representing variance in log(FPT) as a function of r allows the identification of ARS scales by peaks in the variance. ARS could not be tested for murre dives since the devices used in this study could not record underwater horizontal movements.

To assess the potential use of memory, we examined indicators of homing behaviour and site fidelity in murre foraging behaviour. Using GPS data, straightness index (straight line distance/path length; a value of 1 represents the most efficient flight: Benhamou 2004) was calculated for each flight to assess the degree of active orientation between locations. As a course indicator of site fidelity, departure bearings were compared to the return bearing from the previous trip (Weimerskirch et al. 2010). Finer-scale site fidelity was assessed by calculating the distance of each presumed foraging location (sites where birds were sitting on the water) from all locations visited in the previous 48 h; if individuals are site faithful, they are expected utilize known locations and forage near those sites. Persistent use of areas at-depth were assessed by comparing

maximum diving depths of TDR-loggered individuals that performed more than 40 diurnal, crepuscular or nocturnal dives at separate locations (i.e. areas separated by flights). Period and location subsets accounted for spatial and temporal shifts in depth utilization. Pearson correlation was used to test for fidelity in locations (longitude and latitude) and circular correlation tested for fidelity in bearings (package 'circular' in R). Autocorrelation values were calculated for dive depths by location and period. Unless stated otherwise, means are presented with standard errors.

RESULTS

Scale-free Search

Through TDR tagging efforts, 1073 flights (23.8 ± 1.8 flights/individual, range 2–57) and 9446 dives (209.9 ± 43.0 dives/individual, range 5–1873) were recorded from murres foraging from Gull and Funk Islands. Distributions of flight durations and daytime dive depths showed rapid decay and were approximated by Brownian (Exp or ExpB) models (flights: $\lambda \approx 0.0001/m$, dives: $\lambda \approx 0.02/m$; Fig. 1a). PL and PLB models were not competitive. Ensemble-averaged power spectra (Fig. 1b) provided further support for Brownian type walks ($\beta \approx 0$) over Lévy walks ($\beta \approx 0.7$). Finally, first digit distributions (Fig. 1c) significantly deviated from values expected from Lévy walks (flights: $\chi_8^2 = 643$, $P < 0.001$; dives: $\chi_8^2 = 6341$, $P < 0.001$). Results were similar across individuals (see Supplementary Figs S1–S5), for twilight and nocturnal dives, and for flight distances with inbound and outbound flights excluded. The same analyses were performed on flight distance distributions derived from GPS tracks and they yielded similar results.

Area Restricted Search

From GPS data, we obtained 26 tracks (2.6 ± 0.6 tracks/individual, range 1–4; for a map displaying all tracks, see Supplementary Fig. S6) from murres foraging from Gull Island. While visual inspection suggested little evidence of ARS behaviour, FPT analyses revealed fine-scale peaks in the variance of log(FPT); ARS zones were primarily centred on presumed foraging locations (sites where birds were sitting on the water or diving; Fig. 2a). Peaks in FPT occurred at a median scale of 1.3 km (range 0.2–6.9 km); 32% of zones were less than 500 m and 68% were less than 2 km (Fig. 3a). Overall, these results show that murres rarely perform coarse-scale area restricted searches while flying; rather they primarily perform finer-scale searches while they are sitting on the water.

Memory-based Search

Taking a sequential look at GPS tracks, the directed nature of murre foraging paths becomes apparent. Foraging tracks of murres from Gull Island revealed several generalities; flights were straight, path headings matched those of return headings from previous trips and locations visited were close to previously visited sites (Fig. 2b, c). Analyses confirmed that flights were primarily straight; 88% of flights showed a straightness index >0.8 (Fig. 3b). This finding supports our contention that flights are directed and involve little active search. Murres also showed a tendency to depart from the colony on the same heading that they used to return to the colony during the previous foraging trip (50% of departure headings were within 20° of return headings of previous trip; Fig. 3c), although headings were not significantly correlated (circular correlation: $r_{14} = 0.36$, $P = 0.18$). Finally, murres visited sites within close range of sites with which they had previous experience (30% of locations were with 2 km of a previous location;
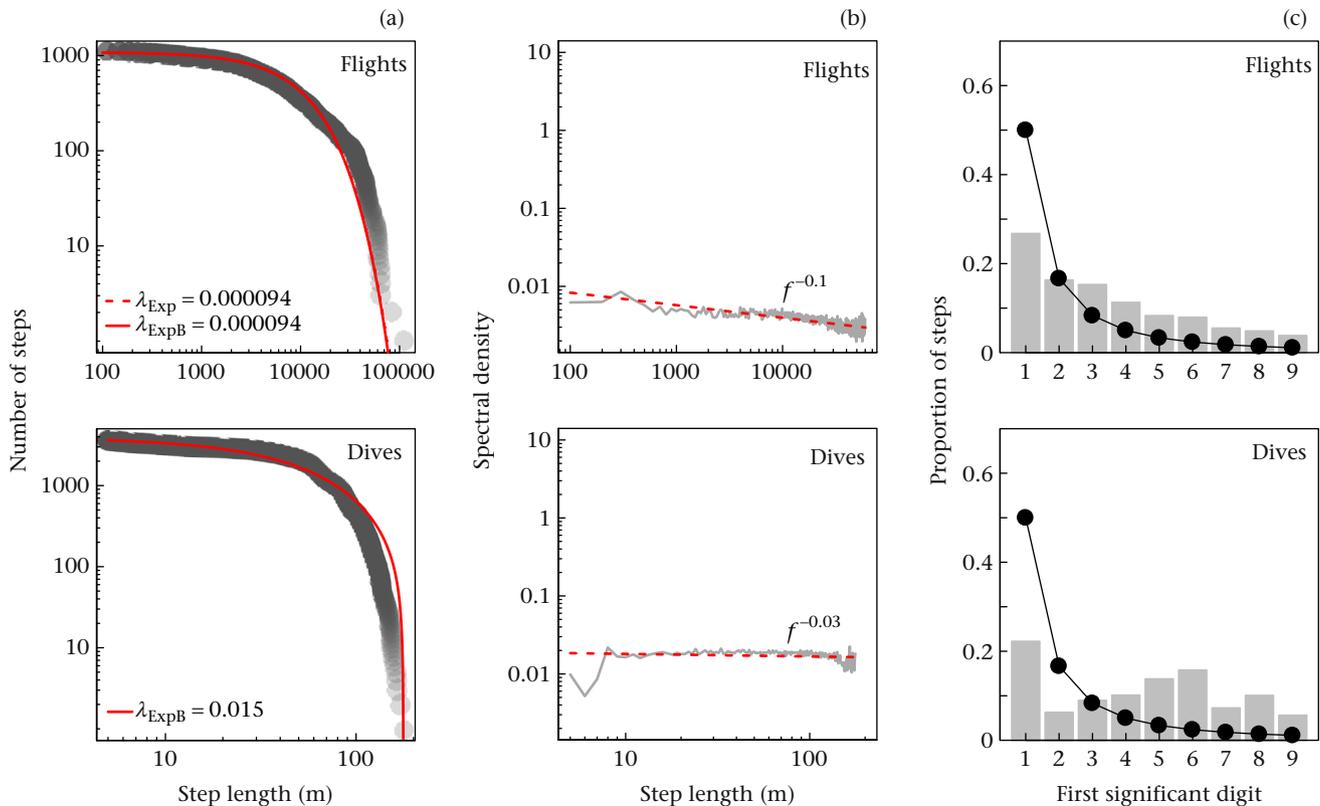
Figure 1. (a) Rank−frequency distribution showing model fits and parameter estimates of μ and/or λ for best-fit exponential (Exp), bounded exponential (ExpB), power law (Lévy; PL) and bounded power law (Pareto-Lévy; PLB) models. (b) Ensemble-averaged power spectrum of the time series of 'turning points' ($f^{-\beta}$ presented). (c) First significant digit distribution (bars); analytic prediction of a Lévy walk with μ = 2.0 is shown for comparison (line) of flight distances and daytime dive depths of all murres fitted with temperature depth recorders.

Fig. 3d); the latitude and longitude of these nearest neighbours were correlated (Pearson correlation: latitude: $r_{41} = 0.80$, $P < 0.001$; longitude: $r_{41} = 0.35$, $P = 0.02$). Autocorrelation values also showed that murres' dive depths were positively correlated, repeatedly taking them to the same general depth (∼4 dives; Fig. 3e). Such behaviour is not expected for a randomly foraging predator. These results suggest that horizontal and vertical site fidelity are driven by memory.

DISCUSSION

Despite increasing support for scale-free Lévy search behaviour across a range of species (reviewed in Viswanathan 2011), our analysis provided little support for Lévy flights in murre movement patterns (see also Elliott et al. 2009; Miramontes et al. 2012). Instead, movement patterns were best approximated by Brownian motion. Under the LFF hypothesis, predators displaying Brownian movement patterns are thought to be searching for abundant and uniformly distributed prey (Humphries et al. 2010). Capelin, however, are distributed in discrete horizontal and vertical patches (Davoren et al. 2006); thus, Brownian motion would be an inefficient strategy to use to maximize overlap with prey (Bartumeus et al. 2002). It therefore seems likely that murres are employing more deterministic strategies to find capelin.

Given the hierarchical distribution of capelin patches, murres are expected to display ARS behaviour (Fauchald et al. 2000). Here we confirm the presence of ARS in murres and show that murres primarily exhibit this behaviour at small scales (<2 km) when sitting on the water. At this scale, Fauchald et al. (2000) found no overlap between the at-sea distribution of capelin and murres because capelin patches are much more unpredictable at this scale.

The murres studied here may have used ARS to find small-scale stochastic prey patches. There was little indication of larger-scale (>2 km) ARS behaviour because of the directed nature of murre flights. Straight flights suggest that murres navigate to and from known locations. This supposition is supported by the finding that murres tended to visit the same general area (∼2 km) they visited previously. In a landscape where their degree of freedom is hundreds of kilometres, it is impressive that foraging murres return to the same general area with such consistency. In all, murre search patterns were characterized by relatively long travel times interspersed with small-scale ARS. This strategy is likely reinforced by the spatiotemporal dynamics of capelin patches. As in the Barents Sea, medium-scale capelin patches likely persist for days, and hence are more predictable, than smaller-scale patches (Fauchald et al. 2000). Overall, this indicates that murres may rely on memory to relocate medium-scale patches and use ARS to hone in on the best small-scale patches. This foraging strategy is expected to minimize costly search activity.

Using memory to return repeatedly to previously visited sites might be an efficient foraging strategy given the temporal persistence (both inter- and intra-annually) of some capelin hotspots (Davoren et al. 2003). In Newfoundland, capelin shoals are often predictable in both horizontal and vertical dimensions. As diel vertical migrants, capelin aggregate near the bottom during the day and migrate to shallower depths at night (Davoren et al. 2006). Previous studies have shown that murres adjust the depth at which they focus foraging activity according to the diel, and perhaps lunar, vertical migration of capelin (Regular et al. 2010, 2011). Although vertical movement patterns within diurnal, crepuscular and nocturnal periods were approximated by Brownian motion, positive autocorrelation of diving depths across multiple dives showed
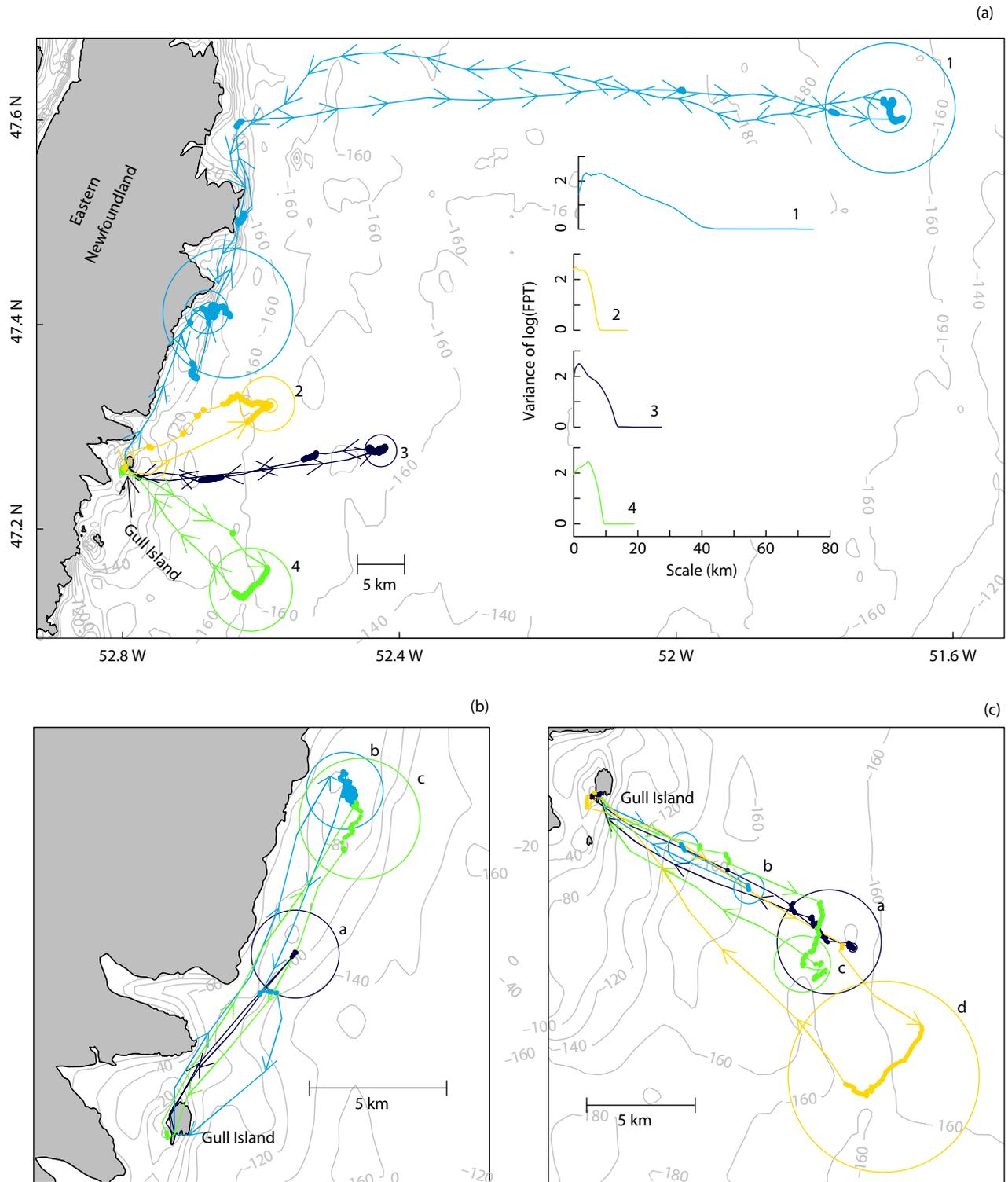
Figure 2. Individual GPS tracks from four loggered murres with (a) corresponding plots of variance in log(first-passage time, FPT) and (b, c) sequential foraging tracks from two loggered murres. Lines with arrows represent flights, dots indicate fixes where birds were sitting on the water or diving and circles are area restricted search (ARS) zones.

that murre diving activity is directed. This suggests that murres are often aware of the vertical location of capelin and they repeatedly visit the same patch at-depth.

These findings draw attention to the efficacy of assessing both random and deterministic search behaviour when interpreting movement patterns. Sole reliance on the LFF hypothesis could have led us to assume that murres were foraging for uniformly distributed capelin using a Brownian search strategy. Careful consideration of prey landscape characteristics and navigational abilities, however, suggest that murres utilize information gained on capelin distribution in the short term to guide foraging decisions. Species that utilize cognitive maps can show diffuse properties (e.g. Lévy), but these patterns can simply emerge from the distribution of prey patches (e.g. Boyer et al. 2006). Such
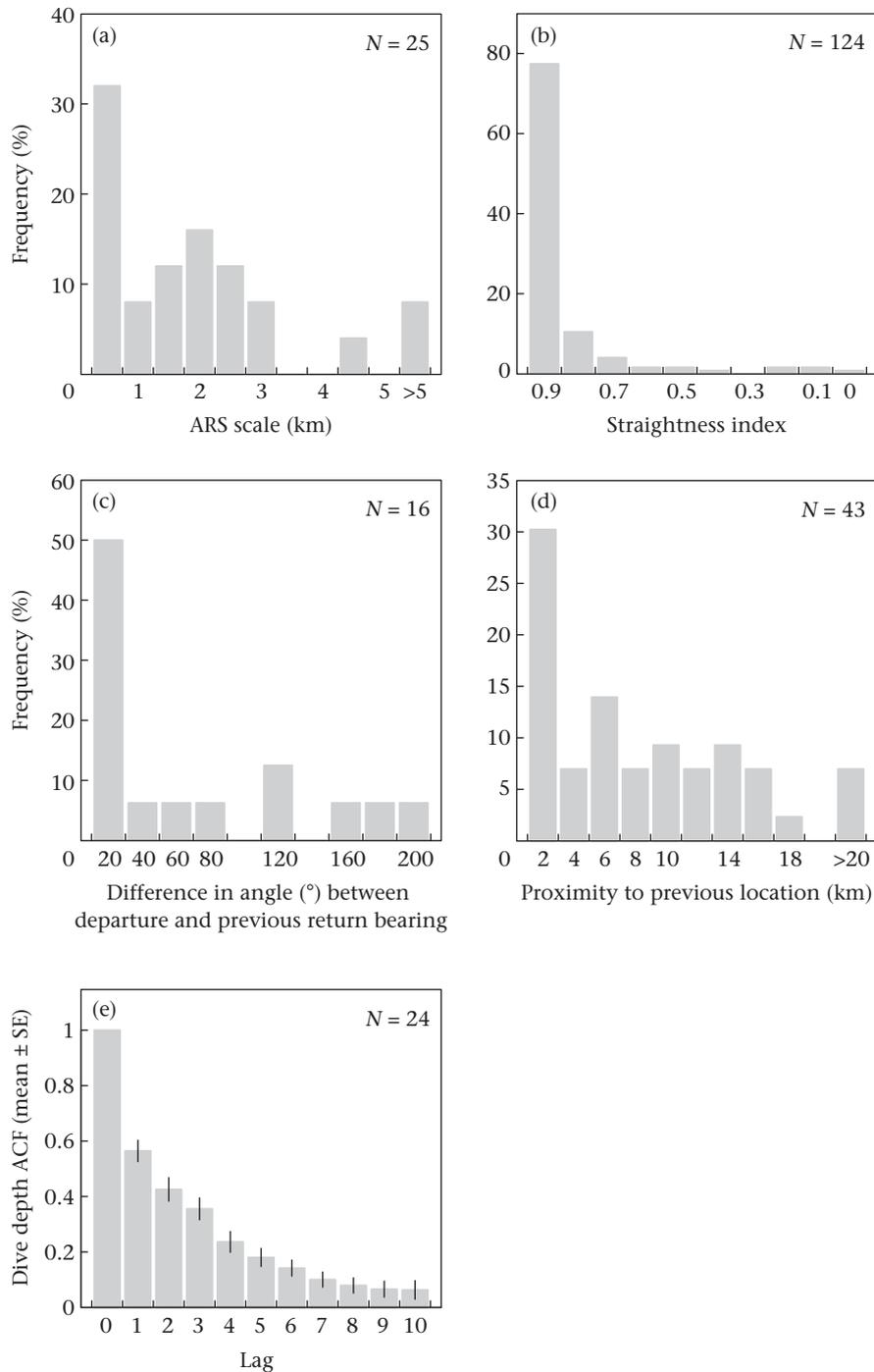
Figure 3. Distributions of the (a) scale of area restricted search (ARS) zones, (b) straightness index of flights (straight line distance/path length), (c) difference in angle between return and departure bearing during the next foraging trip, (d) proximity of locations to previously visited locations for murres tracked using GPS devices and (e) autocorrelation of murre dive depths from murres fitted with temperature depth recorders.

appears to be the case for murres; when we plotted the horizontal and vertical distribution of capelin shoals (Fig. 4; digitized data from Figure 3a in Davoren et al. 2006), patterns and model exponents roughly matched those observed in the flying and diving movements of murres (cf. Fig. 1a and Fig. 4).

Repeated returns to known capelin patches would be reinforced through repeated success but would extinguish after a few visits of limited success (win–stay/lose–switch rule; Kamil 1983). The searching component of this strategy occurs when predators have to switch locations. The presence of small-scale ARS behaviour suggests that murres would utilize this strategy when searching at

larger scales. Although longer-term tracking efforts may reveal periods when birds utilize Lévy search, it seems likely that murres would use short-term information in combination with that gained through lifetime foraging efforts. Learning how and where to forage is considered a protracted process for seabirds (Lack 1968). Young and naïve seabirds are less proficient foragers than more experienced adults (Daunt et al. 2007). Murres show delayed maturity and spend several years visiting the colony before recruiting into the population (∼6 years; Halley et al. 1995). This period may be an important life-history stage to gather information on the local environment before attempting to breed, ultimately improving
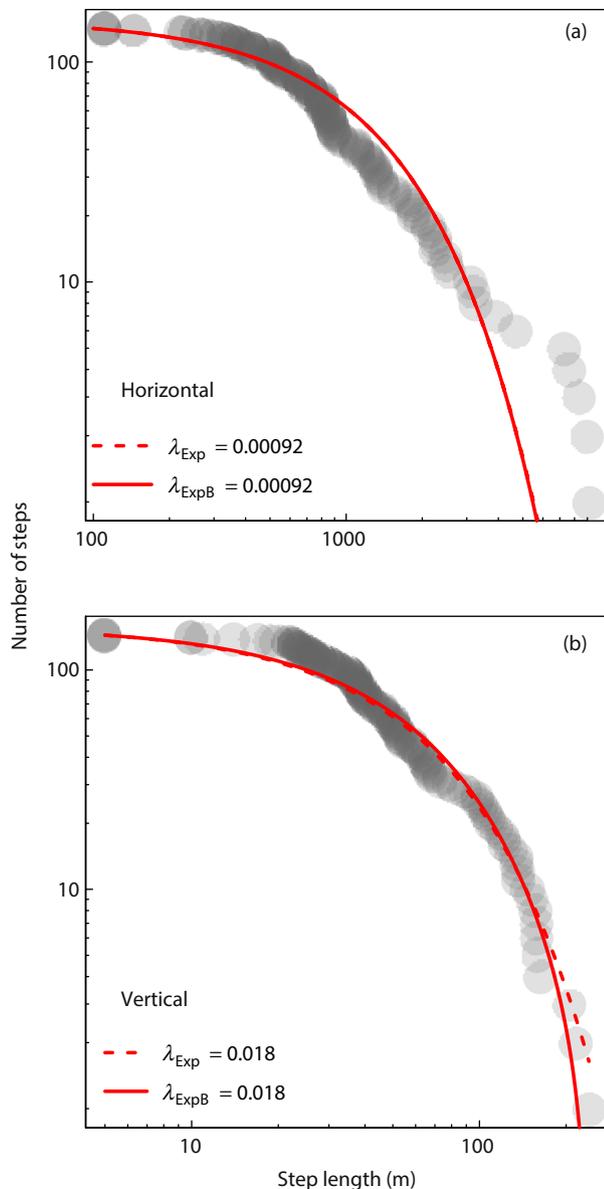
Figure 4. Rank–frequency distribution plots of the (a) horizontal and (b) vertical distribution of capelin. Model fits and parameter estimates of μ and/or λ are presented for best-fit exponential (Exp), bounded exponential (ExpB), power law (Lévy; PL) and bounded power law (Pareto-Lévy; PLB) models. Data derived from digitized Figure 3a in Davoren et al. (2006). Capelin were assumed to be benthic during the day.

foraging efficiency and future reproductive success. Tracks from naïve juvenile murres could provide insights into the presence of innate Lévy search behaviour; Lévy search should optimize the foraging success of juvenile murres since they lack knowledge of spatiotemporal dynamics of capelin patches.

Foraging decisions may, in some cases, be influenced by local enhancement, a process by which individuals cue in on the foraging activities of conspecifics within their visual range (Wittenberger & Hunt 1985). Game theory predicts that individuals will balance searching effort and competition by actively switching between 'producing' and 'scrounging'. Scrounging is expected to increase when prey patches are difficult to locate but decrease when competition is high (Beauchamp 2008). Thus, depending on circumstances, scrounging may be more efficient than searching or sampling mental maps, and vice versa. Because capelin shoals can be both persistent and ephemeral, a mixed strategy of memory and

local enhancement could be essential (Davoren et al. 2003). The scale and circumstances under which murres rely on each strategy depends on the resolution of cognitive maps and perceptual range (above and below water), as well as the spatial and temporal distribution of capelin and conspecifics. Working out such detail requires further research.

Conclusions

A central assumption of the LFF hypothesis is that predators are foraging for unpredictable resources (Viswanathan 2011). This strategy has been shown to be very efficient for predators searching for stochastic prey (Humphries et al. 2012). Violations of this assumption, however, are easily overlooked given the general assumption that marine predators are foraging for unpredictable resources. This is not always the case (sensu Weimerskirch et al. 2007); prey predictability is not uncommon; thus, the ability to retain information regarding the spatial and temporal distribution of prey patches should greatly improve foraging efficiency (Boyer & Walsh 2010). Moreover, many animals are capable of utilizing information gathered while foraging to strategically adjust foraging patterns (e.g. ARS; Fauchald 2009). Although little is known of the cognitive abilities of murres, they are capable of returning to previously visited sites. Of course, their knowledge of prey locations is not perfect; they appear to rely on ARS when information is sparse. This creates horizontal and vertical diffusion patterns similar to the distribution of their primary prey, capelin. It is therefore important to consider both prey predictability and cognitive skills when interpreting movement patterns.

Supplementary Material

Supplementary material for this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2013.06.008.

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