

Fishery Discards Impact on Seabird Movement Patterns at Regional Scales

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Summary

Human fishing activities are negatively altering marine ecosystems in many ways [1, 2], but scavenging animals such as seabirds are taking advantage of such activities by exploiting fishery discards [3–5]. Despite the well-known impact of fisheries on seabird population dynamics [6–10], little is known about how discard availability affects seabird movement patterns. Using scenarios with and without trawling activity, we present evidence that fisheries modify the natural way in which two Mediterranean seabirds explore the seascape to look for resources during the breeding season. Based on satellite tracking data and a mathematical framework to quantify anomalous diffusion phenomena, we show how the interplay between traveling distances and pause periods contributes to the spatial spreading of the seabirds at regional scales (i.e., 10–250 km). When trawlers operate, seabirds show exponentially distributed traveling distances and a strong site fidelity to certain foraging areas, the whole foraging process being subdiffusive. In the absence of trawling activity, the site fidelity increases, but the whole movement pattern appears dominated by rare but very large traveling distances, making foraging a superdiffusive process. Our results demonstrate human involvement on landscape-level behavioral ecology and provide a new ecosystemic approach in the study of fishery-seabird interactions.

Results and Discussion

Fishery Discards: A Human-Induced Experiment on How Resource Predictability Impacts Seabird Foraging Strategies

Fishery activities have long-term negative effects on seabird populations via their impact on marine food webs (e.g., habitat destruction and resource overexploitation) [1, 2]. Nevertheless,

it has been demonstrated that the availability of supplementary foraging resources in the form of fishery discards strongly modifies seabird population biology [5, 7, 9, 10], enhancing short-term breeding and survival performances [9]. The latter is especially true in some marine areas, such as the western Mediterranean, where trawling fisheries provide scavenging seabirds with a naturally unavailable trophic resource (i.e., demersal fish) that can be acquired with more predictability than their natural prey (e.g., small pelagic fish) [9–12]. This finding raises a key question about how fishery discards impact on seabird foraging strategies by modifying resource availability and predictability at regional scales.

To characterize how the presence of fishery activities modifies the foraging strategies of seabirds during the breeding season, we analyzed and modeled satellite tracking data (Argos system) covering 10 foraging trips of breeding Balearic shearwaters (*Puffinus mauretanicus*) and 26 trips of breeding Cory's shearwaters (*Calonectris diomedea*) in the northwestern Mediterranean during the period 1999–2005. The foraging trips usually lasted less than two days, the total distances traveled per foraging trip ranging from 10 to 1000 km, and the maximum distances between two successive locations being about 300 km. The foraging range of these species is delimited by the isobath of 1000 m, including the continental shelf as well as the area within the shelf break [13–15] (Figure 1). Within these areas, shearwaters feed on small shoaling pelagic fish and squids, particularly mobile prey whose availability is unpredictable in space and time [16, 17], but they can also feed on trawling discards that show predictable temporal and spatial dynamics (e.g., [11]). Across the entire western coast of Spain, trawlers operate approximately 12 hours per day from Monday to Friday, departing from harbors early in the morning and returning in the late afternoon. Fisheries target demersal species with hauling and discarding procedures occurring at approximately the same hours each day ([18] and references therein). From each harbor, captains choose specific fishing grounds based on weather conditions, distance to other fishing grounds, and their expectation of other trawlers' activities. Such potential variability is however strongly suppressed because the fishing grounds of one harbor are limited in space by the fishing grounds of the neighboring harbors. There are no fishery activities during the weekend, calendar holidays, and trawling moratorium days, except for a few coastal artisanal boats, which generate negligible discards. Poaching is nonexistent because both fishing guilds and conservation agencies control the fleets and prevent boats from operating during fishery closure periods.

In the present work, we characterize movement patterns within the 1000 m isobath and consider the presence or absence of trawling activities according to whether or not these displacements occur during weekends, calendar holidays, and trawling moratorium days [18] (see [Supplemental Results](#) and [Table S1](#) available online).

A Generalized Random Walk Model for Seabird Movements
Based on a sequence of recorded locations in the xy plane, a moving animal can be quantitatively characterized by means

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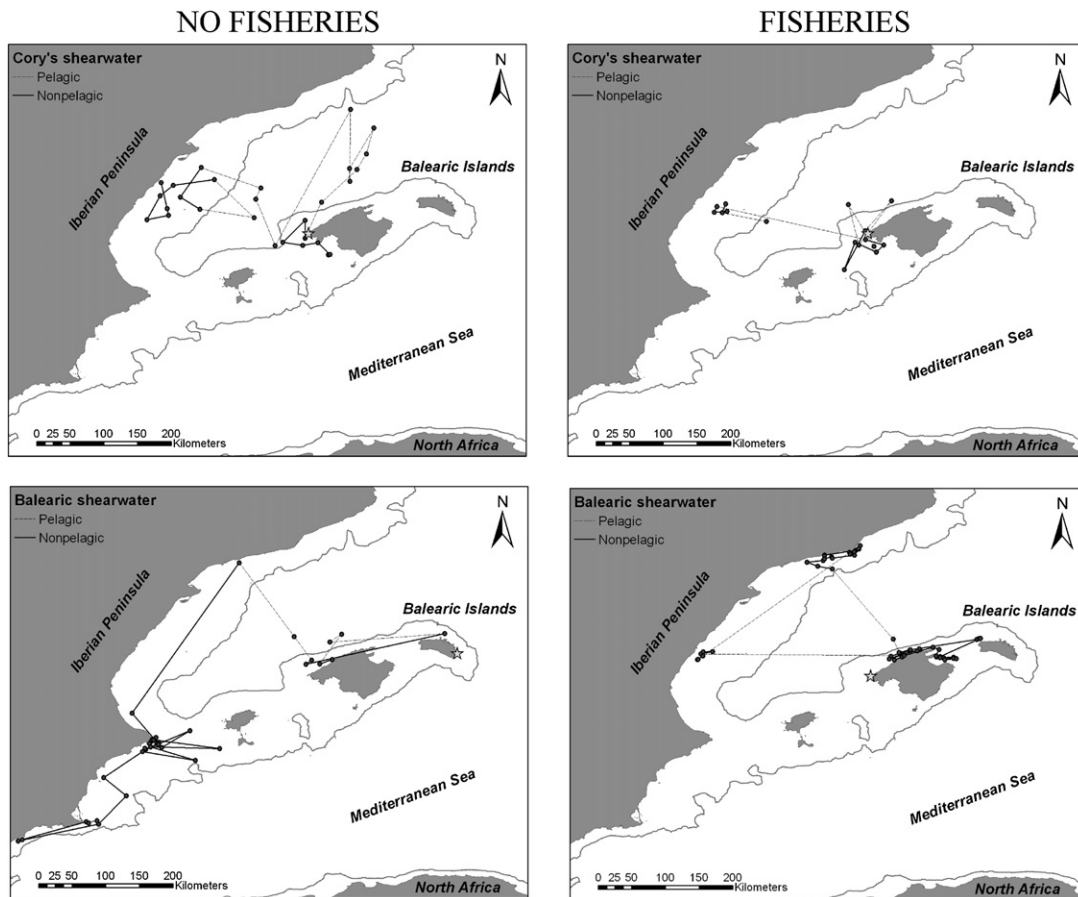


Figure 1. Shearwater Foraging Trajectories in the Western Mediterranean Region

Examples of single trajectories for the Cory's shearwater (upper panels) and the Balearic shearwater (lower panels). For illustrative purposes, we have assigned each of the trajectories to one of the two possible scenarios under study: absence (left panels) or presence (right panels) of fishery activity. For a given trajectory, if less than 50% of the total number of locations occurred in the presence of fishery activities, we considered that trajectory as a “no fisheries” trajectory; otherwise, the trajectory was considered as a “fisheries” trajectory. For the four trajectories shown, the percentage of locations occurring in the presence of fishery activities are 16% (upper left), 68% (upper right), 37% (lower left), and 65% (lower right). The percentage differences among trajectories are not great, but they are large enough to recover the average behavior of the spatial kernels measured in the presence and in the absence of fisheries when pooling the flying segments at the population level. Pelagic and nonpelagic flights are characterized by dashed lines and bold solid lines, respectively. The limit of the foraging grounds is at the isobath of 1000 m, represented here by a continuous line. Breeding colonies are indicated by stars. It can be observed that large, nonpelagic displacements are more prone to occur in the two trajectories associated with periods with no fishery activity (left panels) than in the two periods with more fishery activity (right panels). For more details on the data set, see [Figure S1](#) and [Table S1](#).

of a random walk model [19, 20]. The fractional diffusion equation (FDE) [21–25] is a powerful mathematical framework to describe the stochastic movement of objects in space and time. The FDE assumes that motion results from a random series of displacement and pausing periods, and it requires the computation of a spatial and a temporal kernel. The spreading behavior of seabirds while searching for food is built up from the displacement and the pause distributions. Sub- or superdiffusion regimes can be identified depending on whether the spreading rates are smaller or larger than in normal diffusive processes (e.g., [22, 23]).

We show that in a two-dimensional FDE, the temporal kernel is proportional to $t^{-1-\alpha}$ ($0 < \alpha \leq 1$), whereas the spatial kernel is proportional to $|z|^{-\mu}$, where z represents either of the two Cartesian coordinates and μ is the Lévy index ($1 < \mu \leq 3$) [21, 22]. A temporal kernel or a pause-time distribution from a data set that does not show explicit pauses (Argos satellite tracking) is obtained by estimating a site fidelity kernel $S_A(t)$. $S_A(t)$ is defined as the probability of observing a seabird within

a square area $A = L^2$ as function of time t , and its theoretical shape can be derived from the FDE itself. The relevance of $S_A(t)$ is doubly important: (1) it can be estimated from Argos tracking data, directly connecting empirical records to the temporal kernel of the FDE, and (2) it has a straightforward biological interpretation as a measure of the local intensity use of particular sites by an animal ([Supplemental Experimental Procedures](#)).

Looking at the long-time limit behavior of $S_A(t)$, i.e., $S_A(t) \sim t^{-\beta}$, it is possible to determine the exponent α characterizing the scaling of the temporal kernel in the FDE. Once the spatial kernel $F(r)$ and the site fidelity kernel $S_A(t)$ are reconstructed from the empirical data, one is able to estimate their respective exponents μ and β and finally recover the value α , i.e., the scaling exponent of the temporal kernel. Assuming finite displacement speed, it is possible to compute the exponent γ in the expression $\langle r^2 \rangle(t) \propto t^\gamma$, which characterizes the spreading behavior of the seabirds [26, 27]. The exponent γ determines different qualitative regimes of spreading

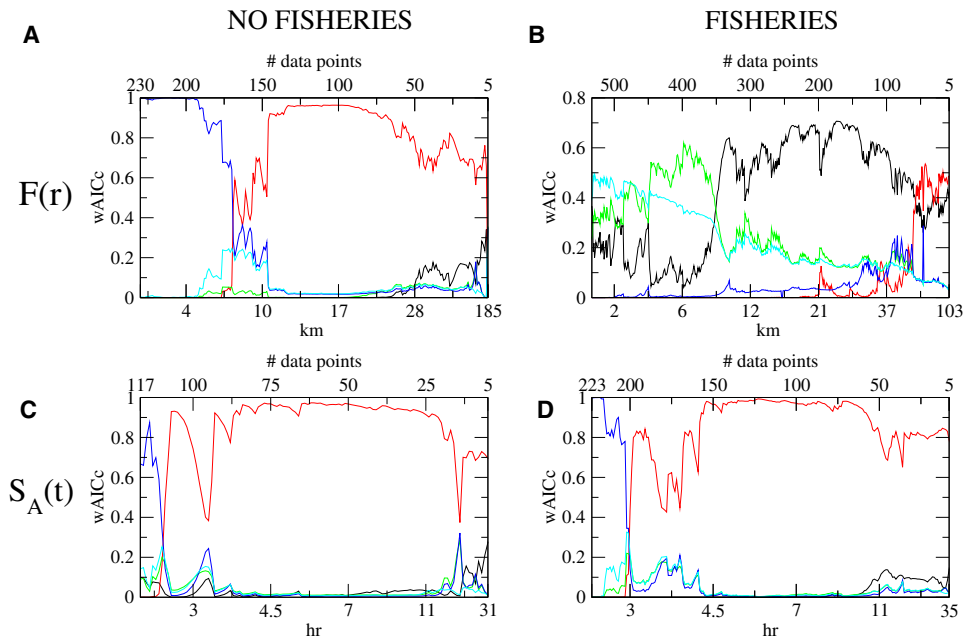


Figure 2. Sequential Pointwise Model Comparison

We contrast the exponential (black), truncated power-law (red), gamma (green), lognormal (dark blue), and stretched exponential (light blue) distributions for both the spatial kernel (i.e., $F(r)$, A and B) and the site fidelity kernel (i.e., $S_A(t)$, A = 50 km × 50 km, C and D) observed in the absence (A and C) and in the presence (B and D) of fisheries. A value of corrected and weighted Akaike information criteria (wAICc) = 1 gives the maximum weight of evidence in favor of one of the models that are compared. Upper x axis shows the number of data points used in each comparison; lower x axis shows the approximate value of each data point labeled in the upper x axis. Different x_{\min} values were successively chosen from the minimum to the maximum value (without the last five values) of the observed traveling distances (A and B), and site fidelity times (C and D). For further sequential pointwise statistical analyses, see [Figures S2 and S3](#).

behavior: subdiffusion (or superdiffusion) corresponding to $\gamma < 1$ ($\gamma > 1$), and normal diffusion corresponding to $\gamma = 1$ [21, 22] (Supplemental Experimental Procedures).

Estimating the Spatial and Temporal Movement Kernels from the Data Set

To model seabirds' movement at regional scales (10–250 km), we need to reconstruct the asymptotic behavior of the spatial and temporal kernels in the FDE, that is, to quantify the tail behavior of $F(r)$ and $S_A(t)$ from the empirical data. We first showed that the observed patterns for $F(r)$ and $S_A(t)$ were not an artifact of the noise and/or the irregularities of the tracking system (Supplemental Experimental Procedures; [Figure S1](#); [Table S1](#)). Second, we fit probabilistic tail models to the functions $F(r)$ and $S_A(t)$ in the presence and absence of trawling activities. We use two tail model selection tests: (1) a sequential pointwise model comparison based on Akaike information criteria (AIC) weights [28–30] ([Figure 2](#); wAICc-based SPWMC), and (2) a sequential pointwise model validation based on Kolmogorov-Smirnov goodness-of-fit tests ([Figure 3](#); KS-based SPWGoF). Based on the results shown in [Figure 2](#) and [Figure 3](#), we selected, fit, and statistically validated a tail model for each scenario (i.e., with fisheries and without fisheries) and each kernel (i.e., spatial and temporal) (see [Table 1](#) and [31]). Finally, we calculated the cumulative distributions and normalized log-binning histograms of $F(r)$ and $S_A(t)$ for each scenario ([Figure 4](#); [Figure S4](#)).

In the absence of trawling activity, the wAICc values show evidence for truncated power-law behavior in $F(r)$ ([Figure 2A](#)) when traveling distances are larger than 13 km. In particular, we found that the spatial kernel behaves asymptotically as

$F(r) \sim r^{-\mu}$ with a scaling exponent $\mu \cong 2.09 \pm 0.25$ ([Table 1](#)). When trawlers are operating, the wAICc values give support to an exponential tail behavior for $F(r)$ ([Figure 2B](#)), specifically when traveling distances are larger than 9 km ([Table 1](#)). In the latter conditions, the spatial kernel behaves asymptotically as $F(r) \sim \exp(-r/\lambda)$, where $\lambda \cong 24 \pm 3$ km ([Table 1](#)). An exponential distribution of traveling distances implies that movement patterns rapidly converge to Brownian statistics (in terms of the Lévy index, a traveling distance distribution with $\mu \geq 3$) [21]. Both fitted models (truncated power law and exponential) are statistically validated by the SPWGoF tests ([Figures 3A and 3B](#)). We inferred the quantitative features of the temporal kernel for each scenario, estimating $S_A(t)$ as a function of time for an area $A = 50$ km × 50 km, that is, of the same order of magnitude as the average trawling activity domain ([Figures 2C and 2D](#); [Figures 3C and 3D](#); [Supplemental Experimental Procedures](#)). Similar results were obtained for 40 km × 40 km < A < 200 km × 200 km (e.g., [Table 1](#)). SPWMC and SPWGoF tests show that $S_A(t)$ is best fit by a truncated power-law tail for data beyond 3–5 hr both in the presence and in the absence of trawling activities ([Figures 2C and 2D](#); [Figures 3C and 3D](#)). Maximum likelihood estimations of the asymptotic regime $S_A(t) \sim t^{-\beta}$ lead to slightly larger scaling exponents β in the presence of fisheries than in their absence, implying a higher probability of leaving a localized area during trawling activity ([Table 1](#)). In addition to the indirect model comparisons (exponential versus truncated power law) shown in [Table 1](#), we performed direct model comparisons ([Table S2](#)) and additional statistical tests ([Figure S2](#)) to further rule out other competing models (see [Supplemental Results](#)). We conclude that, overall, the exponential and the truncated

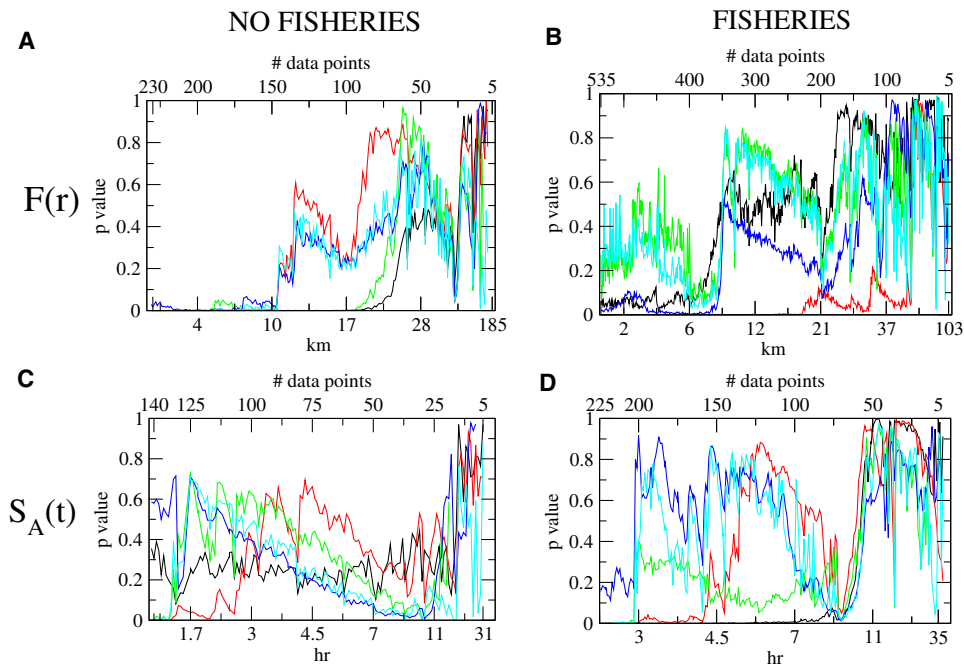


Figure 3. Sequential Pointwise Goodness of Fits

Goodness of fits are based on Monte Carlo replicates and the computation of Kolmogorov-Smirnov tests as in Clauset et al. [30]. Statistical validation was performed for exponential (black), truncated power-law (red), gamma (green), lognormal (dark blue), and stretched exponential (light blue) distributions for both the spatial kernel (i.e., $F(r)$, A and B) and the site fidelity kernel (i.e., $S_A(t)$, A = 50 km × 50 km, C and D) observed in the absence (A and C) and in the presence (B and D) of fisheries. For each data point, if the p value is much less than 1 (i.e., $p < 0.1$), it is unlikely that the subset of data including all of the values above that point is drawn from the corresponding model; therefore, the tail model can be ruled out. For further sequential pointwise statistical analyses, see Figures S2 and S3.

power-law models are good enough probabilistic models to describe our data beyond some threshold values (Figure 4; Figure S4). These results allow us to use the FDE modeling framework to statistically characterize seabird movements within the fitted range of spatiotemporal scales, that is, from 10 to 250 km and from 3 to 40 hr.

Similar quantitative behavior for $F(r)$ and qualitative behavior for $S_A(t)$ were observed when considering the two seabird species separately, indicating that, in statistical terms, trawling activities similarly affect the movement patterns of both species (Figure S3 and Table S3). Our results suggest that closely related species might respond similarly to trawling activities on marine ecosystems.

From the fitted β values $S_A(t) \sim t^{-\beta}$, one can determine the exponent α characterizing the scaling of the temporal kernel in the FDE through the relations $\beta = 2\alpha/\mu - 1$ when $F(r)$ decays as a power law, and $\beta = 2\alpha$ when $F(r)$ is an exponential (see Supplemental Experimental Procedures and Supplemental Results). We computed different estimates for the temporal scaling exponent α based on the central values of μ and β and their 95% confidence intervals. We then averaged these over the two areas A used for the calculation of $S_A(t)$ (see Table 1) to finally obtain the values $\alpha = 0.9 \pm 0.25$ when trawlers operate and $\alpha = 0.3 \pm 0.25$ when trawlers are absent (note the nonoverlapping confidence intervals). The exponents μ and α , obtained from $F(r)$ and $S_A(t)$, respectively, can thus be employed to estimate the spreading behavior of seabirds during their foraging or, equivalently, how the mean square displacement $\langle r^2 \rangle(t) \propto t^\gamma$ grows over time with $\gamma < 1$ ($\gamma > 1$) corresponding to subdiffusion (or superdiffusion) [21, 22, 32, 33]. Averaging the maximum likelihood estimations for μ and α and

their confidence intervals, and averaging also the results obtained for the two areas (A1 and A2) used to compute the site fidelity kernel (Table 1), we obtain the values $\gamma = 1.26(1.23 - 1.44)$ and $\gamma = 0.91(0.65 - 1.19)$ in the absence and in the presence of trawling activity, respectively. In both cases, γ values are close to 1, indicating that seabird foraging patterns generate statistical properties at the edges of normal diffusion. Our results suggest that the behavioral change between an opportunistic search in the presence of fisheries and an active search in its absence can be accompanied by a statistical transition from diffusive or even subdiffusive motion ($\gamma_{\text{mean}} = 0.91$) to superdiffusive motion ($\gamma_{\text{mean}} = 1.26$).

From the series expansion in powers of t of $S_A(t)$ (Supplemental Results), it is also possible to determine the generalized diffusion constants $D_{\alpha,\mu}$ for the case $\mu = 3$. Such constants can be used to compute the daily (12 hr) area explored by a seabird in the foraging grounds, giving an average value of 200 km² per day, consistent with the observed seabird movement scales over a breeding month [34].

Fishery Activities Modify Seabird Movement Patterns at Regional Scales

It is conceivable that the observed change in seabird movement patterns at regional scales may be reflecting a corresponding change in the spatiotemporal pattern of the exploited resources, in this case, natural prey (small pelagic fish) versus discards (demersal, benthic fish) [35–39]. The foraging movements of seabirds exploiting discards are Brownian-like and mainly depend on the activities of trawlers, which in turn should resonate with the distributions of the prey targeted, i.e., demersal fish. Demersal fish live in particular

Table 1. Maximum Likelihood Parameter Estimation of the Selected Tail Models

	Fitted Model	x_{\min}	Parameter (CI)	n (Tail)	Range	GOF1	GOF2
No fisheries	$F(r) \sim r^{-\mu}$	13.21 km	2.09 (1.84–2.35)	130	13.21–254 km	0.567*	0*
	$S_{A1}(t)/t \sim t^{-\beta}$	3.3 hr	1.63 (1.31–1.96)	78	3.3–41.50 hr	0.406*	0.101*
	$S_{A2}(t)/t \sim t^{-\beta}$	3.3 hr	1.67 (1.38–1.97)	95	3.3–41.50 hr	0.725	0.158
Fisheries	$F(r) \sim e^{-r/\lambda}$	9.16 km	24.39 (21.73–27.02)	333	9.16–165 km	0.639*	0*
	$S_{A1}(t)/t \sim t^{-\beta}$	3.73 hr	1.85 (1.6–2.12)	122	3.73–55.44 hr	0.843*	0.002*
	$S_{A2}(t)/t \sim t^{-\beta}$	5.27 hr	1.98 (1.70–2.27)	135	5.27–55.44 hr	0.484*	0.019*

Maximum likelihood fits of the probabilistic tail models selected through sequential pointwise model comparison and goodness of fits in the absence and in the presence of fishery activities for $F(r)$ and $S_A(t)$ (i.e., $A1 = 50 \text{ km} \times 50 \text{ km}$ and $A2 = 100 \text{ km} \times 100 \text{ km}$). x_{\min} , lower bound (in km or hr); parameter, maximum likelihood estimator of λ (exponential model) and β (truncated power-law model); CI, 95% confidence interval; n, number of data points at the tail used for the fit; range, range of values fitted; GOF1, goodness of fit for the fitted model; GOF2, goodness of fit for the competing model. In all cases, the lower bounds (x_{\min}) of the tails were chosen to be those generating the best (lowest) Kolmogorov-Smirnov statistic in the data fits [30]. A truncated power law was assumed as the competing model for the exponential fit (i.e., fisheries; $F(r)$). Exponential tail models are assumed as the competing models of the truncated power-law fits. In all cases, p values were obtained from 2500 Monte Carlo replicates. Asterisks (*) indicate statistically significant p values that do not rule out the fitted model but rule out the competing model. The competing models were tested covering the same range of values as the fitted models. For further statistical results, see [Tables S2 and S3](#).

productive marine areas such as canyons or continental slopes, whereas the main natural prey of Mediterranean shearwaters, i.e., small pelagic fish and squid, are relatively elusive given that they are very mobile and are not heavily targeted by trawlers or any other fishery [6, 11, 40, 41]. Similarly to the foraging movements of Mediterranean shearwaters on days without trawling activity, purse seiners that target small pelagic fish along the Peruvian coast produce Lévy trajectories [42, 43]. In complex and dynamic marine environments, however, it is difficult to know whether such movement

patterns represent a tight (unambiguous) mapping of the spatial resource distribution or whether they represent part of an efficient behavioral strategy to explore highly unpredictable environments [44, 45]. Also noteworthy is the fact that a Lévy (fat-tailed) spatial kernel can emerge either as a result of a change in the average behavior of the population or as a result of the emergence of a few superspreaders responsible for the largest traveling distances [46]. Although we cannot determine the underlying mechanism, it is notable that a highly heterogeneous spatial redistribution kernel favors

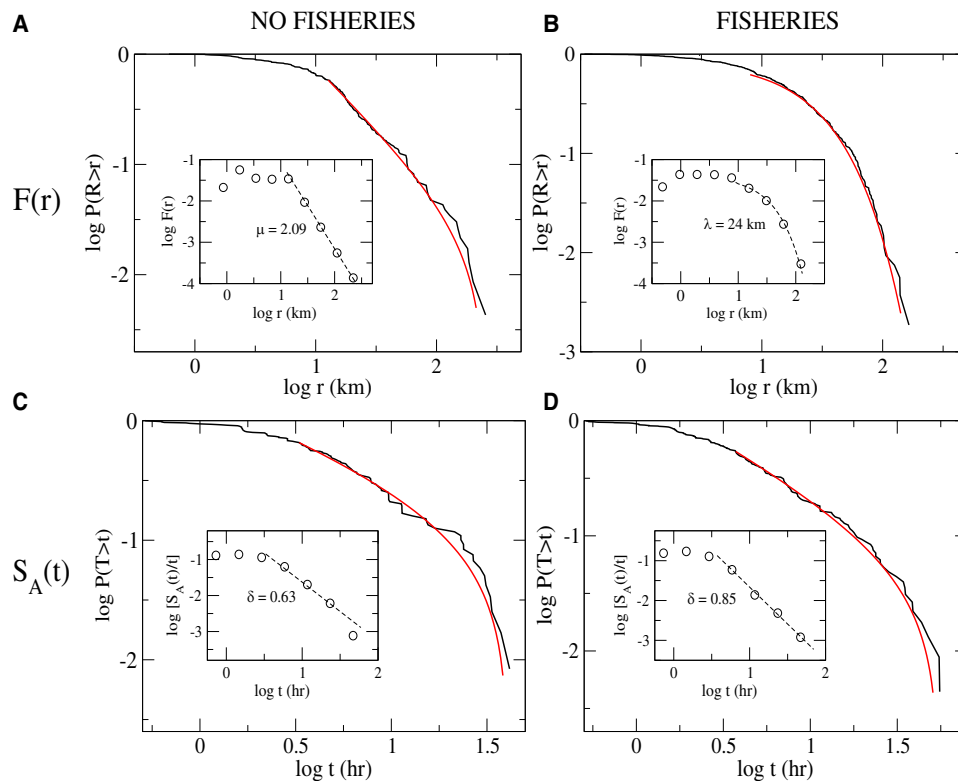


Figure 4. Cumulative and Probability Density Distribution Plots

Cumulative probability distribution plots for the spatial kernel (i.e., $F(r)$, A and B) and the site fidelity kernel (i.e., $S_A(t)$, $A = 50 \text{ km} \times 50 \text{ km}$, C and D) in the absence (A and C) and in the presence (B and D) of fishery activities. Insets show log-binned, normalized plots of the behavior of the probability density functions. Red and dashed lines illustrate the behavior of the best fits (see [Table 1](#)) for the tail of the distribution in both the cumulative and the probability density forms. The exponent of the site fidelity kernel density function is $\delta = 1 - \beta$ because $S_A(t) \sim t^{-\beta}$. See also [Figure S4](#).

efficient searching in complex and unpredictable environments [45, 47–50].

Within their foraging grounds, most seabirds restrict their searches to particular environments where prey are more abundant [13, 44, 51]. Such strong site fidelities suggest that seabirds “know” where to find food, probably from previous experience. The local area intensity of use and the amount of time spent within each of these high-resource-density areas (“hot spots”) must be correlated to both local resource availability and predictability patterns [44, 51]. In the western Mediterranean, the hot spots overlap with the trawling fishing areas of relative high marine productivity, where small pelagic fishes are also abundant [10, 13, 16]. We show that the probability of observing an animal in a localized area (supposedly a hot spot) at different time intervals decays faster (i.e., has a larger scaling exponent) in the presence of trawlers than in their absence. Hence, when trawlers are operating, the foraging fidelity to hot-spot areas probably decreases because seabirds become much more efficient, via fishery discards, in fulfilling their energetic requirements. On the contrary, in the absence of trawling activity, seabirds may spend much more time looking for prey or prey cues, most probably in the same highly productive marine areas [10]. Larger site fidelities in the absence of trawlers produce, in terms of the FDE model, larger pause probabilities, i.e., smaller scaling exponents in the temporal kernel. Because discard availability improves the breeding performance of Mediterranean shearwaters ([4–6], but see also [52]) but decreases their fidelity to hot spots, we hypothesize that in the presence of trawling activities, shearwater breeding populations may take advantage of the extra time available to increase the frequency of return trips to the colony (these displacements are not taken into account in this study) [10, 53–55]. In seabird populations that breed on islands, trips to and from the richer areas of the mainland coast might be strongly competing with lengthy exploration trips within the foraging grounds. To the extent that human activities produce more predictable resource patterns, the investment effort in large displacements should be biased more toward trips to and from the colony than toward lengthy exploration displacements within the foraging grounds. If trawlers are operating, seabirds may trust previous experiences about the time and energetic costs of finding and exploiting resources in successive feeding trips. In the absence of trawling activities, food availability and predictability become more uncertain. Seabirds may need more time to successfully exploit the hot spots within the foraging grounds [40], and, provided a high uncertainty about future foraging success, “good enough” spots might be less prone to being underexploited. However, seabirds seem to be able to overcompensate for the slow dispersal due to strong site fidelity effects via very large albeit rare flights, which can lead to a free-range type of exploration. Such a strategy generates a fast and highly heterogeneous spreading over the seascape, minimizing potential unsuccessful site fidelities on commonly exploited areas and maximizing encounters with new (known or unknown) high-resource patches. The nontrivial algebraic laws and the statistical changes observed in both the traveling distances and the site fidelity kernels clearly illustrate the complexity of patch-use dynamics by the seabirds. Such results should be taken as a call to incorporate new landscape-level behavioral ideas into optimal foraging models [56, 57]. Further investigations and higher-resolution data would be needed to gain a complete mechanistic

understanding of the regionally scaled seabird movement patterns identified in the present work.

Conclusions

Understanding how animal behavior generates varying spatio-temporal movement patterns at different scales is a classic problem in ecology [19, 20]. Our approach to understanding the impact of human fishing activities on seabird movement patterns has been based on three steps: (1) assuming that, at regional scales, the search for food follows a FDE model; (2) estimating the FDE model’s free parameters directly (i.e., μ) and indirectly (i.e., α is obtained via the computation of β in $S_A(t)$) from the empirical data; and (3) interpreting the FDE model and its diffusive properties (i.e., γ) in biological terms. Our work bridges the existing gap between animal ecology and anomalous diffusion phenomena and illustrates how human activity impacts on landscape-level behavioral ecology by modifying the availability and predictability patterns of resources.

Experimental Procedures

Breeding individuals were equipped with satellite transmitters (Microwave Telemetry, Inc.) [34]. Tracking data for Balearic shearwaters were recorded from breeders from two colonies in the islands of Mallorca and Menorca (1999–2000) and for Cory’s shearwaters from three colonies in Mallorca, Menorca, and Corsica (2003–2005). Trajectory series ranged from 7 to 147 locations (mean value of 35), and our final data set consisted of 1402 locations. The time interval between successive positions spanned from 15 min to 48 hr, although 80% of the time intervals were less than 24 hr. The median sampling interval was 3.65 hr, giving an average rate of 6.5 positions per day. Traveling distances were computed as geodetic distances (km) based on the implementation of Vicenty’s algorithm made available as a MATLAB script by M. Kleider (<http://www.mathworks.com/matlabcentral/>). Statistical computations were performed with R version 2.2.0 (<http://www.r-project.org>) and the “bbmle” R package, made available by B. Bolker (<http://www.zoology.ufl.edu/bolker/>; see also [58]). The **Supplementary Information** provides a detailed explanation of the statistical procedures, a formal description of the fractional diffusion equation and the site fidelity kernel, and an extended set of statistical results supporting the main conclusions of our work.

Supplemental Information

Supplemental Information includes four figures, three tables, Supplemental Experimental Procedures, and Supplemental Results and can be found with this article online at doi:10.1016/j.cub.2009.11.073.

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