

# The Lévy flight foraging hypothesis in a pelagic seabird

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## Summary

1. Lévy flight foraging represents an innovative paradigm for the analysis of animal random search by including models of heavy-tailed distribution of move length, which complements the correlated random walk paradigm that is founded on Brownian walks. Theory shows that the efficiency of the different foraging tactics is a function of prey abundance and dynamics with Lévy flight being especially efficient in poor prey fields.

2. Lévy flights have been controversial in some quarters, because they previously have been wrongly ascribed to many species through the employment of inappropriate statistical techniques and by misunderstanding movement pattern data. More recent studies using state-of-the-art statistical tools have, however, provided seemingly compelling evidence for Lévy flights. In this study, we employ these maximum-likelihood methods and their Bayesian equivalents by analysing both turning angles and move length distributions.

3. We tested, for compliance with Lévy flight foraging, a set of 77 independent foraging trajectories of Cory's shearwaters *Calonectris diomedea diomedea*. Birds were tagged with high-resolution GPS loggers in two Mediterranean colonies (Linosa and Tremiti) during both incubation and chick rearing.

4. We found that the behaviour of six birds was fitted by a correlated random walk; the movement of 32 birds was better represented by adaptive correlated random walks by switching from intensive to extensive searches; and the trajectories of 36 birds were fitted by a Lévy flight pattern of movement. The probability of performing Lévy flights was higher for trips during chick provisioning when shearwaters were forced to forage in suboptimal areas. This study supports Lévy flight foraging as an appropriate framework to analyse search tactics in this pelagic bird species and highlights that the adoption of a given search strategy is a function of biological and ecological constraints.

**Key-words:** Brownian motion, correlated random walk, foraging excursions, GPS tracking, Lévy flight, Scopoli's shearwater, searching behaviour

## Introduction

An important component of animal movement theory, which recently has received much attention, is represented as the search for resources (typically food or mating occasions). Random search is a widespread option when the location of resources is unknown or unpredictable to animals (Turchin 1998). Lévy flight foraging (LFF) represents an innovative approach for the investigation of animal search tactics (Viswanathan *et al.* 2011). As movement tactics based on Lévy flight (LF) can optimize

search efficiency, natural selection should have led to adaptations that allow animals to perform Lévy searches. The alternative view is that LF is an emergent property from the interaction of animal movement and environment. An even more basic concern is whether or not there are animals performing LF at all (Edwards 2011).

Lévy flight foraging represents animal movement as a distribution of discrete straight-line movements modelled by the Lévy exponent  $\mu$ . In a LF movement pattern, move lengths are drawn at random from a distribution with a heavy power-law tail. Lévy exponents lie in the range 1–3. The theoretical reason to assume that animals should perform LF is that Lévy search can be evolutionarily

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favoured (Preston, Pitchford & Wood 2010). This is due to Lévy search often being more efficient than Brownian or ballistic search, thus maximizing the number of targets encountered per unit time or search efficiency. Lévy search is useful when it is non-destructive and target density is low; 'Lévy flight foraging in high target density scenarios is as useful as eyesight in total darkness' (Viswanathan *et al.* 2011).

Reynolds *et al.* (2007) identified Lévy flying patterns in honeybees. Bazazi *et al.* (2012) showed intermittent movement and Lévy features in desert locusts *Schistocerca gregaria*, while Harris *et al.* (2012) showed that T cells used Lévy search to optimize the control of the pathogen *Toxoplasma gondii*. Sims *et al.* (2008) and Humphries *et al.* (2010) used huge data sets of marine predators and showed that the adoption of a Lévy search was typical in poor environmental conditions, while Brownian motion is typical in rich habitats. Focardi, Montanaro & Pecchioli (2009) found LF in solitary but not in social fallow deer *Dama dama*. Sims *et al.* (2012) demonstrated the intraindividual variability in the search strategies of white sharks *Charcharodon carcharias*, where LF is observed in poor conditions and Brownian motion is seen in rich habitats. Humphries *et al.* (2011) showed that, in poor prey fields, wandering and black-browed albatrosses *Thalassarche melanophrys* perform LF landing patterns and that LF were also characterized by an efficiency comparable to those of a Brownian search on rich prey fields. Despite this evidence, some studies (Benhamou 2007; Edwards *et al.* 2007; Edwards 2008, 2011; Jansen, Mashanova & Petrovskii 2012) highlighted the importance of robustly testing for the power-law distributions of step-lengths and testing for competing alternative model distributions.

According to Turchin (1998), an appropriate parameterization of animal movement in a 2-dimensional space can be performed by discretizing the path and then measuring the turning angle ( $\alpha$ ) and the distance, move ( $y$ ), between two successive changes of directions (reorientations). The set  $(\alpha_t, y_t)$  ( $t = 1, 2, \dots$ ) approximates the actual path. The critical point is to determine the distance travelled between biologically meaningful turns, rather than between successive (arbitrarily defined) recordings (Reynolds *et al.* 2007).

It is useful to highlight some limitations of previous analyses of LF. (1) Most authors considered move length distribution but not angular distribution and overlooked problems arising from inappropriate path discretization. (2) Some analyses (Focardi, Montanaro & Pecchioli 2009; Edwards 2011; Reynolds 2012a) have pointed out the relevance of using truncated Lévy distributions instead of unbounded distributions as performed in the earlier studies; Humphries *et al.* (2011) re-analysed the wandering albatross *Diomedea exulans* data of Edwards *et al.* (2007) and showed that a truncated power-law distribution indeed fitted these data. (3) Recently, Miramontes, Boyer & Bartumeus (2012) pointed out that data used by Humphries *et al.* (2011) were based on sea-landing patterns and not on

flying patterns. Hence, the observed Lévy distribution could be the by-product of a fractal distribution of prey, and thus, it is necessary to distinguish between movement and prey detection statistics, because we might have exponential displacements but Lévy detections.

To summarize a rich debate that produced > 200 papers in the last five years, different cases are possible: (i) Lévy flight distributions are the by-product of unreliable statistical approaches, (ii) Lévy distributions are actually present in the data, but they are determined by processes other than animal search and (iii) animals actually perform LFF as a method to optimize target provisioning.

Correlated random walk (CRW) represents the reference model for animal movement and assumes correlated turning angles,  $\alpha$  (i.e. organisms 'persist' in their movement direction so that the  $\alpha$  distribution is clustered around zero), while distances are drawn from distributions with finite variance, such as the exponential. With respect to CRW, a LF appears to be characterized by more linear trajectories interleaved by areas of intense search (Viswanathan *et al.* 2011), which is a feature that makes the LF quite attractive to biologists because the existence of area-restricted search (ARS) (Kareiva & Odell 1987) is well documented (e.g. Weimerskirch 2007). However, Brownian motion, CRW and LF appear to the ethologist's eye as too rough portraits of animal movement, so a number of more realistic movement tactics have been introduced. Benhamou (2007) proposed that alternating ARS and straight displacements can be explained by adaptive CRW (ACRW), a model where movement parameters depend on the habitat. Bartumeus & Levin (2008) assumed that animal movement is in its essence discrete, and a continuous flow of movement, described by a CRW model, is interrupted by abrupt reorientations. In this Lévy-modulated CRW (LMCRW), the time intervals between reorientations are assumed to be Lévy distributed, while reorientation angles are uniformly distributed. Both models produce trajectories with some degree of biological realism and are good candidate models for a first analysis of field data.

In this context, breeding pelagic (i.e. foraging in open sea) birds represent appropriate biological models. Their foraging trips, in fact, encompass both deterministic (at large scales, typically  $10^2$ – $10^3$  km) and random searches (at short scales 1–10 km) (Weimerskirch 2007). During their excursions, birds alternate their ARS by switching from intensive to more extensive searching, because predators adapt and respond quickly to changes in prey clumping (Weimerskirch 2007). Bartumeus *et al.* (2010) showed that power-law distributions could fit the movement of shearwaters in the western Mediterranean, while Reynolds (2012b) showed that, in pelagic birds, LF may represent an emergent property of using fishy-scented odours to locate the prey.

We analysed the flying patterns of a pelagic seabird by tracking breeding adults of Cory's shearwater *Calonectris*

*diomedea diomedea* using GPS loggers during both incubation and chick rearing. During incubation, breeding birds generally perform long trips before standing in for the partner to exploit rich fishing areas far from colony (Cecere *et al.* 2013). In contrast, after hatching, chicks need to be fed frequently, which constrains the parents to taking much shorter trips. During chick rearing, adults are engaged in a dual-foraging strategy (Magalhães, Santos & Hamer 2008) by alternating between long-lasting excursions where they refill their own reserves and short ones devoted to chick provisioning. We expect Cory's shearwaters to adopt different movement strategies in the two phases, with breeding birds forced to maximize the efficiency of their short foraging trips during chick rearing. Further, movement strategies can differ among birds from different colonies as a response to variable environmental conditions.

A total of 77 foraging excursions of Cory's shearwaters were tested for compliance with LFF and (1) we classified, for the first time to our knowledge, foraging tactics taking into account both angles and move lengths distribution; then, we assessed whether (2) LF are present in the studied populations and (3) if this is the case, the probability of having LF is higher during foraging trips performed for chick provisioning. Finally, (4) we evaluated differences between colonies.

## Materials and methods

The tracking of Cory's shearwater was carried out during the breeding seasons of 2008–10 in two Italian colonies (Fig. 1): (i) Linosa island (35°51'33" N; 12°51'34"E), located between Sicily, Tunisia and Libya, hosts an estimated 10 000 breeding pairs. Field work was carried out during both the incubation (June 2008) and chick rearing (July–August 2008 and 2009). (ii) Tremiti Archipelago (42°08'19"N; 15°30'52"E) has approximately 400 breeding pairs. There, field work was carried out on the islet of Capraia during the incubation period only, in June 2009 and 2010.

Breeding birds were tagged with a mini GPS logger (Earth & Ocean Technologies, Kiel, Germany and Technosmart, Guidonia, Italy) attached to the back feathers using 3–4 strips of Tesa® marine cloth tape. Total handling time was kept below 10 min, and birds were immediately returned to their nests. We monitored nests once per day. When tracked birds returned to their nest, they were recaptured and the GPS loggers were removed. Device weight was < 3% of the bird's weight. GPS loggers were set to record one fix every 10 min.

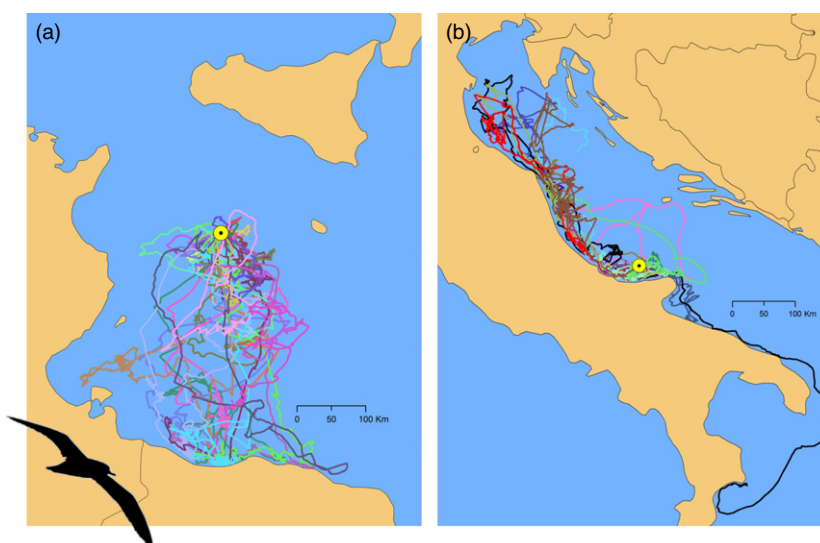
## DATA SETTING

Only one foraging trip per bird was used for analyses with the departure from the nest considered as the beginning of the trip and either the return to brood guarding during incubation or the first return to the nest during the chick rearing period considered as the end of the trip.

Trajectories were checked for the presence of gaps in data collection caused by device malfunction. When the interruption was < 60 min, the last and the first positions were interpolated by estimating a fix each 10 min. When a gap was > 60 min, the animal was retained, but the distance and the angle between the two points were not considered. Trajectories characterized by more than two long gaps were removed from the analyses. Sometimes, the animal returned to the colony without standing in for the partner and later, it continued its trip at sea; distances and angles between locations on the island were not considered. Overall, we had 1.42% ( $\pm$  0.04 SD) of interpolated data. In 54 of 77 trajectories, we did not perform any interpolation. Depending on whether GPS loggers recorded the first location when the bird was at sea after leaving the colony, we introduced a correction to locate the first fix in the colony. A total of 86 birds were tracked, but nine of them were removed from the analyses. Thus, we analysed 44 birds from Linosa (14 incubation, 40 chick rearing) and 23 birds from Tremiti (incubation).

## STATISTICAL ANALYSIS OF ANGULAR DISTRIBUTIONS

Let us denote  $\alpha(t)$  as the turning angles recorded each 10 min. We compared three different *a priori* models. Eqn (1) represents



**Fig. 1.** (a) Position of Linosa island, located between Sicily (Italy), Malta, Tunisia and Libya, and tracks recorded both during incubation and chick rearing by birds breeding on the island. (b) Position of Tremiti Archipelago, located in the Adriatic Sea, and tracks of birds tagged during incubation. Each coloured line represents a single bird.

a mixing of a wrapped Cauchy distribution (WCD) (with weight  $w$ ) with uniform angular distribution (with weight  $1-w$ ):

$$F_1 = w \frac{1 - \rho^2}{2\pi(1 + \rho^2 - 2\rho \cos(x))} + \frac{(1-w)}{2\pi} \quad \text{eqn 1}$$

The second model assumes a simple WCD:

$$F_2 = \frac{1 - \rho^2}{2\pi(1 + \rho^2 - 2\rho \cos(x))} \quad \text{eqn 2}$$

The third model is represented by a mixture of two WCD with concentration parameters  $\rho_1$  and  $\rho_2$  and weights  $w$  and  $(1-w)$ , respectively:

$$F_3 = w \frac{1 - \rho_1^2}{2\pi(1 + \rho_1^2 - 2\rho_1 \cos(x))} + (1-w) \frac{1 - \rho_2^2}{2\pi(1 + \rho_2^2 - 2\rho_2 \cos(x))} \quad \text{eqn 3}$$

By convention,  $\rho_1$  and  $\rho_2$  indicate the smallest and highest  $\rho$  of each trajectory, respectively.

Other circular distributions, such as the von Mises and the circular normal ones, could be appropriate as well. However, the WCD is especially useful because it can be written in closed form (Ravindran & Ghosh 2003).

$F_2$  generates a uniform angular distribution for  $\rho = 0$ , and  $F_3$  generates  $F_1$  for  $\rho_2 = 0$ , while  $F_1$  reduces to  $F_2$  for  $(1-w)$  tending to 0.  $F_1$  is coherent with the LMCRW (Bartumeus & Levin 2008), and  $F_2$  is coherent with the simple CRW (Turchin 1998) or Brownian motion (when  $\rho = 0$ ), while  $F_3$  is coherent with an ACRW (Benhamou 2007).

Following Morales *et al.* (2004), eqns 1–3 were fitted using a Monte Carlo Markov Chain (MCMC) (PROC MCMC in SAS 9.3, SAS Institute 2011). The procedure maximizes the log likelihood of distributions. As priors, we used the uniform distributions for both  $w$  and  $\rho$ , denoting  $\hat{w}$  and  $\hat{\rho}$  as the estimated variables. MCMC was checked by trace plots and convergence diagnostics focusing on the probability of the Geweke diagnostic to verify the stability of the chain and on the Monte Carlo Standard Errors compared with the posterior standard deviation (MCSE/SD). Further details can be found in Chen (2009). Equations  $F_1$ ,  $F_2$  and  $F_3$  were compared using the deviance information criterion (DIC), which is the Bayesian equivalent of the AIC representing the trade-off between explained deviance and model complexity. DIC was used to compare models that did not present problems of convergence because a poor convergence indicates that the specified model is not appropriate for tested data.

#### STATISTICAL ANALYSIS OF MOVE LENGTHS

Assuming a LMCRW process, the method used to locate reorientation events is illustrated in the Supporting Information. A move is the straight-line distance between consecutive reorientations; thus, once it is determined when a reorientation occurs, we may determine the length of moves. The tests for compliance with a power-law distribution were performed following the guidelines of Clauset, Shalizi & Newman (2009): (i) we selected a threshold minimal distance  $y_{\min}$ ; (ii) we used AIC values and evidence ratios to select the appropriate model among a set of candidate

models; (iii) we estimated model parameters; and (iv) we tested goodness-of-fit for the selected models.

A power-law reads as:

$$P(y) = Cy^{-\mu}$$

for  $y > 0$ ,

where  $y$  is the move length,  $C = (\mu - 1)y_{\min}^{\mu-1}$  is a constant and  $\mu$  is the Lévy scaling parameter.

To estimate  $y_{\min}$ , we used method 2 proposed by Clauset, Shalizi & Newman (2009). A preliminary inspection of data showed that  $y_{\min}$  should be around 500 m. Thus, the range between 0 and 3000 m by steps of 25 m was explored. For each  $y_{\min}$ , all  $y < y_{\min}$  were discarded, then the PL model was estimated (see below and Supporting Information), and a Kolmogorov–Smirnov test was performed computing the statistics  $D^+(y_{\min})$  for each tested  $y_{\min}$ . Finally, the  $y_{\min}$  minimizing  $D^+$  was retained.

Following Edwards (2011), four different models (see Supporting Information) were tested: power-law unbounded (PL), power-law bounded (PLB), exponential (EXP) and bounded exponential (EXPB). The formulas for computing the log likelihood of the four models are reported in the Supporting Information. Estimation was performed by PROC NLMIXED (SAS Institute 2011) using the dual quasi-Newton algorithm to perform the numerical optimization of the likelihood (Supporting Information). For data displaying, the rank–frequency plots were used (Benhamou 2007). Models were compared using the AIC. To verify that the selected model effectively fitted the data better than the second model, we used a likelihood ratio  $\chi^2$  test via a Monte Carlo estimation of exact  $P$ -values using 10 000 resamplings (PROC FREQ, SAS Institute 2011). To visualize fitting, we computed the distribution of residuals and QQ plots. Residuals were computed using the cumulative distribution functions (see Supporting Information). In a model characterized by a good fitting, one expects that the residuals averaged zero and were normally distributed.

Another relevant point raised by Benhamou (2007), Reynolds (2010), and Jansen, Mashanova & Petrovskii (2012) is that multi-exponential distributions of move length generated by ACRW could resemble LFs (but see Gautestad 2012, for a different approach). To deal with this problem, we used rank–frequency plots. Depending on whether experimental rank–frequency distribution is linear on the log–log scale, we may conclude that a Lévy distribution is the appropriate model, and when it exhibits a hump, it is likely that the process is multi-exponential. Evaluation of the linearity of a rank–frequency plot is not trivial because actual data are characterized by high-frequency oscillations, which tend to hide the underlining pattern we are interested in. We used a sequential linearity test (Supporting Information) to find the position of an eventual hump on the plot. If the hump is observed at long moves, it presumptively represents the truncation; if it is shifted towards small move lengths, it may represent the signature of a multi-exponential process. For each trajectory, the fraction of consecutive experimental points exhibiting a linear pattern was determined. When at least 80% of the consecutive points showed a linear pattern, we concluded that the assumption of linearity was reasonably met.

Finally, we can classify each foraging excursion in one of four different types: (A) simple Brownian or CRW for animals shown to exhibit a fit with the  $F_2$  angular distribution, (B) ACRW for birds fitted by a  $F_3$  angular distribution, (C) Lévy intermittent for animals with a  $F_1$  angular distribution and a PL or PLB move

length distribution, and (D) Gaussian intermittent for birds with  $F_1$  angular distributions and EXP or EXPB move length distributions.

Through the text, we report mean values  $\pm$  standard error.

## ECOLOGICAL ANALYSES

The dual foraging strategy was already recorded in the Linosa population of Cory's shearwater (Cecere *et al.* 2013). According to Magalhães, Santos & Hamer (2008), we divided each chick-rearing trip into 'short' ( $\leq 4$  days) and 'long' ( $\geq 5$  days). These two classes together with the colony (Linosa and Tremiti) and breeding stages (incubation and chick rearing) were used as independent variables, while the foraging tactics (A to D above) represented the dependent variable. *A priori*, we decided to pool tactics A, B and D vs. tactics C and to compute the probability of performing a LF. To estimate general linear models, we used the PROC GENMOD of SAS 9.3 (SAS Institute 2011) with a logit link function and a binomial distribution.

## Results

The best model for the angular distribution of the analysed 77 birds is provided in Table 1. We found that the  $F_1$  model fits the data of 36 birds,  $F_2$  the data of nine birds, while 32 birds exhibit a  $F_3$  angular distribution. We found a difference in the angular distribution between the periods for Linosa birds ( $\chi^2_2 = 6.4$ ,  $P = 0.04$ ) with an occurrence of  $F_1$  during chick rearing (52.5%) higher than that recorded during incubation (21.4%). Moreover, we found a between-colony difference during incubation ( $\chi^2_2 = 10.3$ ,  $P = 0.006$ ), because the frequency of  $F_1$  is higher in Tremiti birds (52.1%) than in Linosa ones (21.4%).

In Fig. 2, we plotted the empirical distributions of  $\rho$  values characterizing the different angular models  $F_1$ ,  $F_2$  and  $F_3$  (note that for  $F_3$  we separated the histograms relative to  $\rho_1$  and  $\rho_2$ ). The value of  $\rho$ s of models  $F_1$  and  $F_2$  and of  $\rho_2$  for  $F_3$  are quite similar ( $\chi^2_2 = 3.08$ ,  $P = 0.2$ ) and large ( $\bar{\rho} = 0.84 \pm 0.01$ ), indicating that birds performed highly correlated linear movements. On the other hand, the difference between  $\rho_1$  ( $0.30 \pm 0.03$ ) and  $\rho_2$  ( $0.85 \pm 0.02$ ) is significant ( $\chi^2 = 31.5$ ,  $P < 0.001$ ).

Half of the estimated  $y_{\min}$  values (Table 2) were lower than 1 km, 30.5% were between 1–2 km and 19.5% were higher than 2 km. No significant differences were detected either between incubation (average = 1.08 km) and chick rearing (average = 0.82 km) in Linosa (Wilcoxon test:  $Z = 0.61$ ,  $P = 0.54$ ) or between Linosa and Tremiti (average = 1.7 km) during incubation (Wilcoxon test:  $Z = -1.01$ ,  $P = 0.33$ ).

The comparison of the four models considered is reported in Table 2 for each bird. It is clear by the large  $\Delta AIC$  values that the PLB model is selected with a large amount of evidence with respect to the competing models. The fact that PLB was always better than PL and that EXPB was better than EXP (with the exception of one bird) suggests that truncation is a necessary ingredient in data analysis. The rank–frequency, residual distribution

and QQ plots for each bird are reported in Fig. S4. Here, we present some examples of the observed patterns (Fig. 3). Bird T75239 represented a pattern expected by a power-law with an abrupt truncation. One can note that the PLB prediction curve overlaps fairly well with experimental points, while the predicted bounded exponential curve is quite different with a larger-than-observed frequency at small distances and a smaller-than-observed frequency at large distances. The likelihood ratio test reported in Table 3 shows that, for this bird, PLB fits data much better than EXPB. For bird TB0524, the PLB curves fit data well until 10 000 m; but for larger move lengths, experimental points appear to better conform to an exponential decay, and the likelihood ratio test (Table 3) shows that there is no significant difference between the two functions. A total of six of 36 birds showed this kind of pattern (Table 3). In bird TB0524, the step in experimental points around 10 000 m was also suggestive of some motivational change. The third case is that of bird TE1339, where a large estimated  $y_{\min}$  (2.15 km) excludes 93 moves, leaving a sample size too small for a good estimate. Indeed, experimental points are well fitted by the PLB curve, but given the small sample size, the likelihood ratio test is not significant (Table 3). On the whole, for the 36 analysed birds, we found a good compliance with the PLB distribution (Fig. S4).

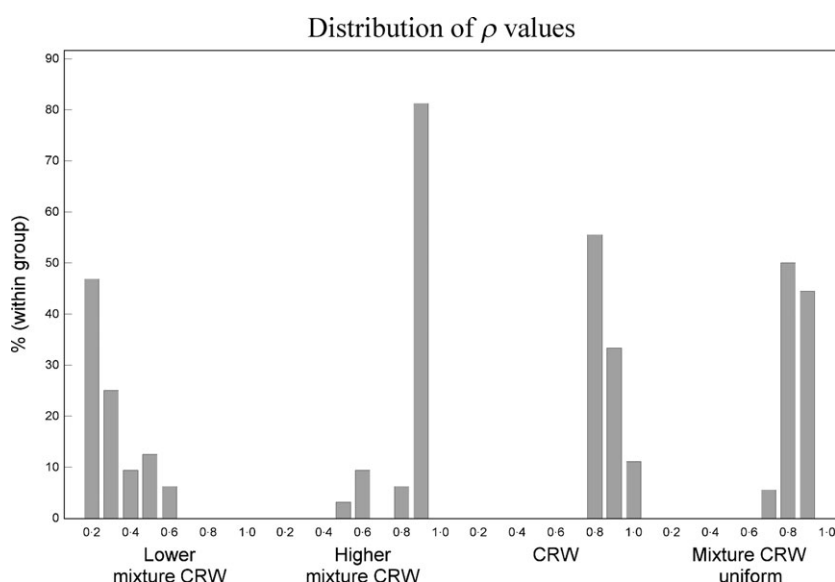
The second diagnostic analysis refers to residuals. An appropriate model should generate an unbiased and Gaussian distribution of residuals (Table 3). However, 11 of 36 cases resulted in a relevant distortion in the distribution of residuals. To enlighten this point, we reported in Fig. 3 the distribution of residuals and QQ plots of the three birds discussed above. The distribution of residuals was symmetric for bird T75239, and its QQ plot did not show any bias with respect to the expected normal distribution. The case of TB0524 was characterized by some distortions in the distribution of residuals, which was not normal. Indeed, its QQ plot showed unexplained high-frequency oscillations. Finally, bird TE1339 did not show any distortions in its distribution of residuals. In Fig. S4, other examples with distortions in the residual distribution are reported.

Figure 4 represents the amount of linearity in the rank–frequency plots of the sample. We observed that there are 26 trajectories where the linearity of the rank–frequency plot was clear, while for four birds, the assumption of linearity was weak, and for the remaining six birds, the results were intermediate. Looking at the rank–frequency plots in Fig. S4, one can note that in most cases, points are well aligned on the PLB prediction curve, but also that some jumps and irregularities are present, which corresponds to outliers in the residual distribution.

In Fig. 5, we reported an analysis of the probability of performing a LF distribution as function of colony, breeding period and the duration of the foraging excursion. The model was significant ( $\chi^2_5 = 21.5$ ,  $P < 0.001$ ). The difference between short and long excursions at

**Table 1.** Best-fitting distributions of turning angles for 77 Cory's shearwaters in two Mediterranean islands during chick rearing or incubations according to DIC. Three different mixtures of angular distribution have been compared: a mixture of wrapped Cauchy and uniform distributions ( $F_1$ ), wrapped Cauchy ( $F_2$ ) and a mixture of two wrapped Cauchy distributions ( $F_3$ )

| Bird   | Period        | Colony  | Distrib. mixture | Bird   | Period        | Colony  | Distrib. mixture |
|--------|---------------|---------|------------------|--------|---------------|---------|------------------|
| T75239 | Incubation    | Linosa  | $F_1$            | TH7183 | Incubation    | Linosa  | $F_2$            |
| T97769 | Incubation    | Tremiti | $F_1$            | TH8040 | Incubation    | Linosa  | $F_2$            |
| TB0524 | Incubation    | Tremiti | $F_1$            | T73735 | Chick rearing | Linosa  | $F_2$            |
| TC7507 | Incubation    | Tremiti | $F_1$            | TH8522 | Chick rearing | Linosa  | $F_2$            |
| TC7509 | Incubation    | Tremiti | $F_1$            | TJ1651 | Chick rearing | Linosa  | $F_2$            |
| TC7510 | Incubation    | Tremiti | $F_1$            | TJ1677 | Chick rearing | Linosa  | $F_2$            |
| TC7511 | Incubation    | Tremiti | $F_1$            | TC7503 | Incubation    | Tremiti | $F_3$            |
| TC7514 | Incubation    | Tremiti | $F_1$            | TC7505 | Incubation    | Tremiti | $F_3$            |
| TC7519 | Incubation    | Tremiti | $F_1$            | TC7506 | Incubation    | Tremiti | $F_3$            |
| TC7522 | Incubation    | Tremiti | $F_1$            | TC7524 | Incubation    | Tremiti | $F_3$            |
| TE1339 | Incubation    | Tremiti | $F_1$            | TC7525 | Incubation    | Tremiti | $F_3$            |
| TE1341 | Incubation    | Tremiti | $F_1$            | TC7527 | Incubation    | Tremiti | $F_3$            |
| TE1347 | Incubation    | Tremiti | $F_1$            | TC7529 | Incubation    | Tremiti | $F_3$            |
| TH1871 | Incubation    | Linosa  | $F_1$            | TC7533 | Incubation    | Tremiti | $F_3$            |
| TH8412 | Incubation    | Linosa  | $F_1$            | TE1342 | Incubation    | Tremiti | $F_3$            |
| T73783 | Chick rearing | Linosa  | $F_1$            | TE1343 | Incubation    | Tremiti | $F_3$            |
| T74321 | Chick rearing | Linosa  | $F_1$            | TE1345 | Incubation    | Tremiti | $F_3$            |
| T75215 | Chick rearing | Linosa  | $F_1$            | TH1759 | Incubation    | Linosa  | $F_3$            |
| T75237 | Chick rearing | Linosa  | $F_1$            | TH1863 | Incubation    | Linosa  | $F_3$            |
| T75402 | Chick rearing | Linosa  | $F_1$            | TH7179 | Incubation    | Linosa  | $F_3$            |
| TH2729 | Chick rearing | Linosa  | $F_1$            | TH7185 | Incubation    | Linosa  | $F_3$            |
| TH4334 | Chick rearing | Linosa  | $F_1$            | TH8438 | Incubation    | Linosa  | $F_3$            |
| TH4335 | Chick rearing | Linosa  | $F_1$            | TH8444 | Incubation    | Linosa  | $F_3$            |
| TH7203 | Chick rearing | Linosa  | $F_1$            | T75298 | Chick rearing | Linosa  | $F_3$            |
| TH8447 | Chick rearing | Linosa  | $F_1$            | T75409 | Chick rearing | Linosa  | $F_3$            |
| TH8518 | Chick rearing | Linosa  | $F_1$            | TH4336 | Chick rearing | Linosa  | $F_3$            |
| TH8560 | Chick rearing | Linosa  | $F_1$            | TH4398 | Chick rearing | Linosa  | $F_3$            |
| TH8636 | Chick rearing | Linosa  | $F_1$            | TH8450 | Chick rearing | Linosa  | $F_3$            |
| TJ1655 | Chick rearing | Linosa  | $F_1$            | TH8510 | Chick rearing | Linosa  | $F_3$            |
| TJ1662 | Chick rearing | Linosa  | $F_1$            | TH8530 | Chick rearing | Linosa  | $F_3$            |
| TJ1664 | Chick rearing | Linosa  | $F_1$            | TH8534 | Chick rearing | Linosa  | $F_3$            |
| TJ1666 | Chick rearing | Linosa  | $F_1$            | TH8535 | Chick rearing | Linosa  | $F_3$            |
| TJ1672 | Chick rearing | Linosa  | $F_1$            | TH8544 | Chick rearing | Linosa  | $F_3$            |
| TJ1673 | Chick rearing | Linosa  | $F_1$            | TH8559 | Chick rearing | Linosa  | $F_3$            |
| TJ1674 | Chick rearing | Linosa  | $F_1$            | TJ1659 | Chick rearing | Linosa  | $F_3$            |
| TJ1675 | Chick rearing | Linosa  | $F_1$            | TJ1665 | Chick rearing | Linosa  | $F_3$            |
| TE9522 | Incubation    | Linosa  | $F_2$            | TJ1670 | Chick rearing | Linosa  | $F_3$            |
| TH4333 | Incubation    | Linosa  | $F_2$            | TJ1676 | Chick rearing | Linosa  | $F_3$            |
| TH7178 | Incubation    | Linosa  | $F_2$            |        |               |         |                  |



**Fig. 2.** The interindividual distribution of estimated  $\rho$  values. For the mixture of two wrapped Cauchy distributions ( $F_3$ ), we reported separately the lower and the higher values observed.

**Table 2.** Model selection for move length relative to 36 Cory's shearwaters exhibiting angular distributions of type  $F_1$ . The models studied are exponential (EXP), bounded exponential (EXPB), power-law (PL) and power-law bounded (PLB). The  $\Delta AIC$  value is relative to the second best model. For model PLB, we also reported the estimate of minimal distance ( $y_{\min}$ ) and the Lévy index  $\mu$

| Bird (it lives). | $y_{\min}$ (m) | EXP       | EXPB      | PL        | PLB       | $\Delta AIC$ | $\mu$ (SE)   |
|------------------|----------------|-----------|-----------|-----------|-----------|--------------|--------------|
| T73783           | 500            | 13357.29  | 13356.6   | 12946.34  | 12843.31  | 103.03       | 1.58 (0.037) |
| T74321           | 225            | 59458.42  | 59452.15  | 55439.93  | 54725.87  | 714.06       | 1.29 (0.013) |
| T75215           | 875            | 16473.07  | 16454.42  | 16378.42  | 16111.65  | 266.77       | 1.33 (0.038) |
| T75237           | 325            | 68135.48  | 68135.46  | 67350.25  | 66595.26  | 754.99       | 1.32 (0.012) |
| T75239           | 2000           | 106838.06 | 106837.99 | 104029.24 | 103593.31 | 435.93       | 1.69 (0.014) |
| T75402           | 300            | 63114.2   | 63111.22  | 62386.67  | 61635.51  | 751.16       | 1.42 (0.015) |
| T97769           | 1425           | 142511.31 | 142511.25 | 141933.03 | 141598.94 | 334.1        | 2.19 (0.017) |
| TB0524           | 2225           | 42102.28  | 42073.05  | 42536.88  | 41931.01  | 142.04       | 1.44 (0.028) |
| TC7507           | 550            | 268183.96 | 268179.23 | 263197.61 | 261090.09 | 2107.52      | 1.57 (0.008) |
| TC7509           | 1575           | 149321.97 | 149309.31 | 148970.87 | 147856.17 | 1114.7       | 1.73 (0.014) |
| TC7510           | 1175           | 40375.25  | 40370.16  | 40093.63  | 39730.13  | 363.5        | 1.6 (0.025)  |
| TC7511           | 1575           | 119825.47 | 119825.24 | 117111.3  | 116767.74 | 343.56       | 2 (0.016)    |
| TC7514           | 1950           | 17399.68  | 17389.5   | 17291.15  | 17131.43  | 159.73       | 1.73 (0.048) |
| TC7519           | 1875           | 913251.83 | 913240.07 | 903325.67 | 898016.73 | 5308.94      | 1.7 (0.005)  |
| TC7522           | 275            | 46659     | 46658.97  | 44701.02  | 44443.32  | 257.7        | 1.6 (0.017)  |
| TE1339           | 2150           | 2432.17   | 2430.29   | 2415.41   | 2387.7    | 27.7         | 1.54 (0.116) |
| TE1341           | 2750           | 222746.45 | 222745.61 | 222468.49 | 221845.34 | 623.14       | 2.21 (0.014) |
| TE1347           | 2500           | 119205.45 | 119203.08 | 117343.2  | 116943.56 | 399.65       | 2.1 (0.019)  |
| TH1871           | 975            | 256905.98 | 256900.97 | 250884.36 | 248394.41 | 2489.95      | 1.39 (0.007) |
| TH2729           | 1450           | 12331.47  | 12330.86  | 12060.77  | 11980.86  | 79.91        | 1.66 (0.044) |
| TH4334           | 2150           | 14075.34  | 14070.83  | 13945.53  | 13837.16  | 108.37       | 1.78 (0.052) |
| TH4335           | 150            | 82923.41  | 82918.77  | 80763.17  | 79165.56  | 1597.6       | 1.16 (0.01)  |
| TH7203           | 25             | 4827.84   | 4822.93   | 4573.31   | 4448.1    | 125.21       | 1.07 (0.038) |
| TH8412           | 275            | 9148.85   | 9148.47   | 8683.18   | 8625.82   | 57.36        | 1.59 (0.044) |
| TH8447           | 525            | 10803.37  | 10802.81  | 10327.54  | 10253.04  | 74.49        | 1.58 (0.041) |
| TH8518           | 375            | 175142.58 | 175142.58 | 169122.16 | 167659.4  | 1462.75      | 1.35 (0.007) |
| TH8560           | 2150           | 10317.12  | 10314.76  | 9998.99   | 9953.6    | 45.39        | 2.02 (0.065) |
| TH8636           | 2150           | 41321.4   | 41317.61  | 40636.72  | 40416.15  | 220.57       | 1.87 (0.03)  |
| TJ1655           | 1850           | 7032.64   | 7032.21   | 6734.88   | 6712.25   | 22.63        | 2.02 (0.072) |
| TJ1662           | 500            | 36144.69  | 36144.62  | 33690.94  | 33571.24  | 119.69       | 1.74 (0.023) |
| TJ1664           | 1650           | 4288.64   | 4261.34   | 4328.02   | 4221.4    | 39.94        | 1.2 (0.103)  |
| TJ1666           | 50             | 6686.72   | 6679.82   | 6459.53   | 6297.64   | 161.89       | 1.11 (0.037) |
| TJ1672           | 200            | 133301.78 | 133301.63 | 131112.1  | 129354.28 | 1757.82      | 1.28 (0.008) |
| TJ1673           | 225            | 5355.79   | 5354.73   | 5157.21   | 5095.24   | 61.98        | 1.4 (0.052)  |
| TJ1674           | 50             | 29513.98  | 29513.97  | 22706.18  | 22629.84  | 76.35        | 1.47 (0.016) |
| TJ1675           | 1650           | 12698.03  | 12694.52  | 12679.77  | 12537.36  | 142.41       | 1.48 (0.045) |

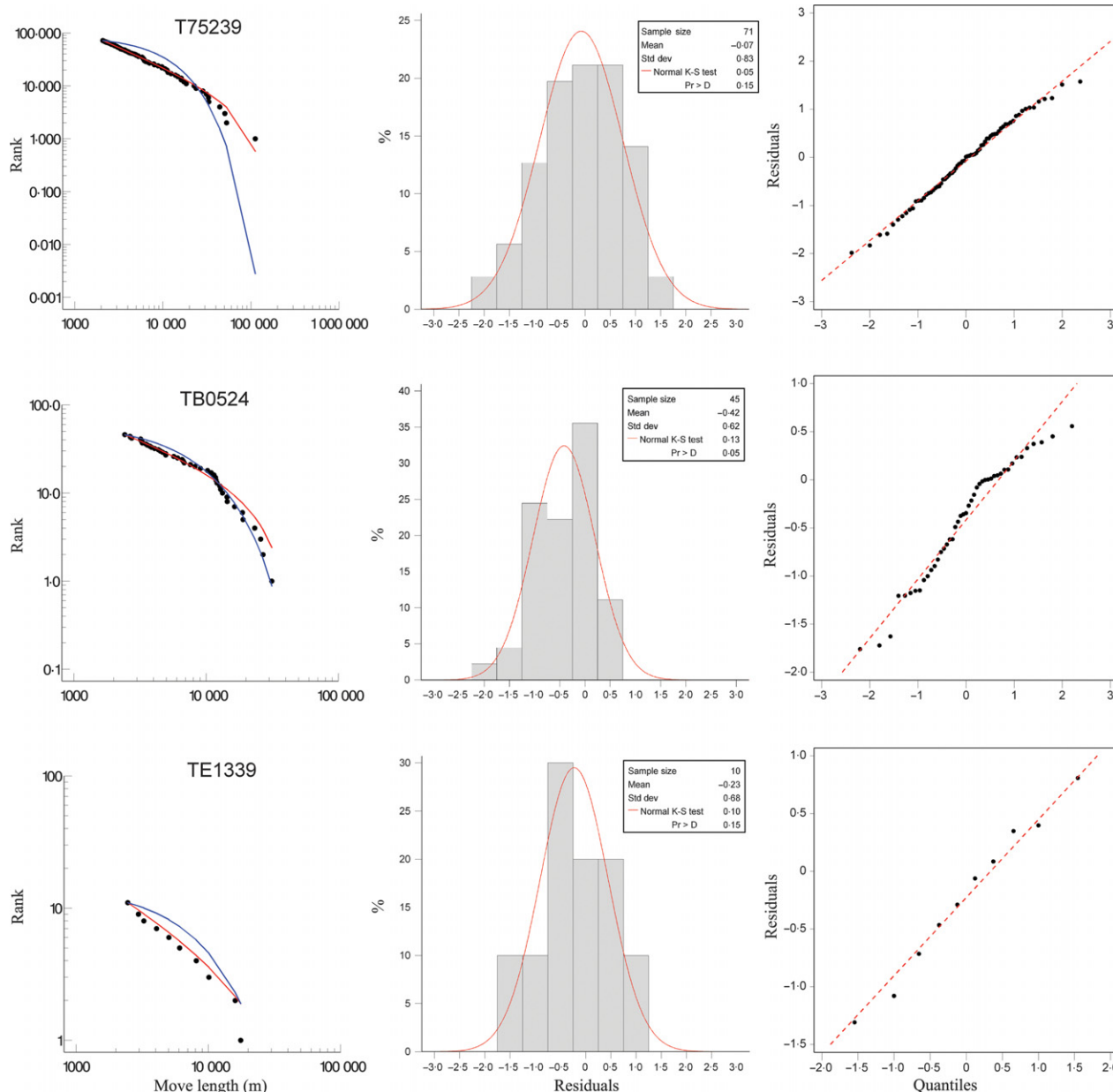
Tremiti had an almost significant result (Wald  $\chi^2 = 3.55$ ,  $P = 0.06$ ). At Linosa, the probability of performing a LF was significantly higher for short excursions during chick rearing than for the other groups (Wald  $\chi^2 = 5.23$ ,  $P = 0.02$ ). So, on the whole, the probability of adopting a PLB distribution of move length was higher for short than for long excursions, and PLB was quite likely if short excursions were performed during chick rearing.

## Discussion

The debate about the presence of LF under natural conditions has given a strong push to analyse search strategies in animals. Indeed, the original result of the study by Viswanathan *et al.* (1999), that is, that actual animals perform LF with  $\mu = 2$  optimize food search, has suggested the presence of an important unification principle able to describe animal movements under a large set of different environmental conditions. However, successive refinements

of the analyses have marked several weak points in this initial attempt.

A result that emerges through this study as well as by others (Humphries *et al.* 2010; Sims *et al.* 2012) was the modulation caused by environmental and biological conditions. The basic theoretical prediction that animals should perform LF in poor habitats and Brownian motion in rich ones (Viswanathan *et al.* 2011) was in fact confirmed. In Linosa, during chick provisioning (short-lasting trips), Cory's shearwaters were forced to fish in suboptimal areas close to the colony; while performing long-lasting trips during chick rearing, birds managed to reach more profitable waters (Cecere *et al.* 2013). Accordingly, we demonstrated that the probability of LF was significantly higher for Linosa birds in short-lasting trips at chick rearing than during self-provisioning trips during both chick rearing and incubation. We were not able to evaluate their predation success (as done in albatrosses by Humphries *et al.* 2011), but our findings are strongly suggestive that Cory's



**Fig. 3.** Model fitting of 3 different birds. In the left column, we report the rank–frequency plot of experimental values (dots). The expected PLB distribution (red) and the expected EXPB (blue) distributions are included for comparison. In the central column, we display the histogram of quantile residuals. The black line represents the expected normal curve. In the inset, we report sample size, mean (expected value: 0) and standard deviation (expected value: 1), the statistics  $D$  of a Kolmogorov–Smirnov goodness-of-fit test and the probability value under  $H_0$ . Right column: QQ plots. The red line represents the expected distribution on the assumption of a normal distribution. Methods to compute residuals and expected PLB and EXPB distributions are reported in section S9 of *Supporting information*.

shearwaters adopt LF to improve search efficiency in poor habitats. While differences between breeding stages were evident, contrary to expectations, differences in LF occurrence between colonies were scarce.

In black-browed and wandering albatrosses, Humphries *et al.* (2010) found  $< 2$   $\mu$  values (1.27 and 1.19, respectively), which were explained as destructive foraging in scarce prey fields. In our study, we found  $\mu$  values around 1.6 (but recall our estimates are biased a bit low, cf. Fig S5). There are several factors that may explain the observed values: (1) following James, Plank & Edwards

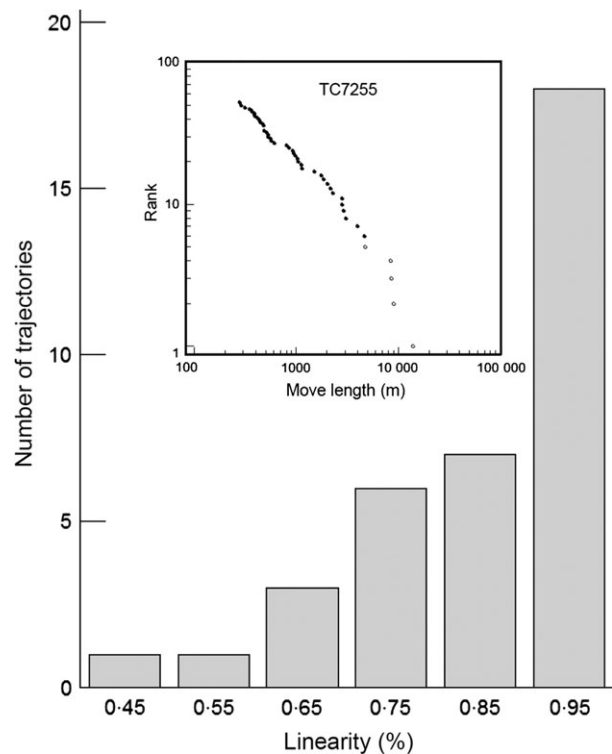
(2011) and Ferreira, Raposo & Viswanathan (2012), we might conjecture that the prey of Cory's shearwater form loose patches in the Mediterranean, (2)  $\mu$  values  $< 2$  might also be a by-product of trajectory subsampling (Reynolds 2008), or (3)  $\mu$  values close to  $3/2$  are consistent with reorientation or landing in response to peak fluctuations in concentrations of background fishy odours (Reynolds 2012b). The optimal  $\mu = 2$  holds when the energetic cost of travel is independent of the direction of travel. However, moving upwind or downwind might determine whether  $\mu$  is lower than 2.

**Table 3.** For any bird tested for compliance with LFF, we computed the likelihood ratio  $\chi^2$  test between PLB and EXPB models, using Monte Carlo estimation of exact  $P$  values with 10 000 resamplings. We report the mean  $\pm$  standard error of quantile residuals and the Student's test for the difference from 0, the  $A^2$  statistics of the Anderson–Darling goodness-of-fit test for the empirical normal distribution and its probability ( $*P < 0.05$ ,  $**P < 0.01$ )

| Bird   | $\chi^2$ | $P$     | Mean $\pm$ SE    | $t$   | $P$    | $A^2$  |
|--------|----------|---------|------------------|-------|--------|--------|
| T73783 | 6.13     | 0.013   | -0.32 $\pm$ 0.21 | -1.54 | 0.14   | 0.63   |
| T74321 | 166.5    | < 0.001 | -0.36 $\pm$ 0.1  | -3.62 | < 0.01 | 0.37   |
| T75215 | 22.45    | < 0.001 | -0.62 $\pm$ 0.16 | -3.86 | < 0.01 | 0.76*  |
| T75237 | 8.75     | 0.003   | -0.27 $\pm$ 0.09 | -2.91 | < 0.01 | 1.33** |
| T75239 | 79.26    | < 0.001 | -0.07 $\pm$ 0.1  | -0.75 | 0.45   | 0.17   |
| T75402 | 44.48    | < 0.001 | -0.38 $\pm$ 0.12 | -3.21 | < 0.01 | 1.2 ** |
| T97769 | 2.36     | 0.125   | 0.02 $\pm$ 0.09  | 0.18  | 0.86   | 0.51   |
| TB0524 | 0.75     | 0.387   | -0.42 $\pm$ 0.09 | -4.54 | < 0.01 | 0.72   |
| TC7507 | 248.3    | < 0.001 | -0.18 $\pm$ 0.07 | -2.44 | 0.02   | 0.73   |
| TC7509 | 48.81    | < 0.001 | -0.22 $\pm$ 0.1  | -2.35 | 0.02   | 0.91*  |
| TC7510 | 8.47     | 0.004   | -0.22 $\pm$ 0.12 | -1.92 | 0.06   | 0.45   |
| TC7511 | 174.3    | < 0.001 | -0.04 $\pm$ 0.1  | -0.41 | 0.68   | 0.27   |
| TC7514 | 7.55     | 0.006   | -0.22 $\pm$ 0.14 | -1.58 | 0.13   | 0.51   |
| TC7519 | 713.8    | < 0.001 | -0.19 $\pm$ 0.06 | -3    | < 0.01 | 1.73** |
| TC7522 | 58.67    | < 0.001 | -0.08 $\pm$ 0.11 | -0.74 | 0.46   | 0.41   |
| TE1339 | 0.78     | 0.376   | -0.23 $\pm$ 0.21 | -1.07 | 0.31   | 0.14   |
| TE1341 | 15.77    | < 0.001 | -0.04 $\pm$ 0.09 | -0.42 | 0.67   | 1.36** |
| TE1347 | 49.77    | < 0.001 | -0.12 $\pm$ 0.11 | -1.07 | 0.29   | 0.44   |
| TH1871 | 380.1    | < 0.001 | -0.29 $\pm$ 0.07 | -4.05 | < 0.01 | 0.95*  |
| TH2729 | 8.34     | 0.004   | -0.27 $\pm$ 0.22 | -1.23 | 0.23   | 0.59   |
| TH4334 | 4.68     | 0.031   | -0.13 $\pm$ 0.14 | -0.94 | 0.35   | 0.22   |
| TH4335 | 118.4    | < 0.001 | -0.66 $\pm$ 0.08 | -8.35 | < 0.01 | 1.25** |
| TH7203 | 3.47     | 0.063   | -1.21 $\pm$ 0.2  | -6.05 | < 0.01 | 0.79*  |
| TH8412 | 11.21    | < 0.001 | -0.3 $\pm$ 0.24  | -1.23 | 0.23   | 0.69   |
| TH8447 | 11.95    | < 0.001 | -0.28 $\pm$ 0.23 | -1.24 | 0.23   | 0.67   |
| TH8518 | 173.5    | < 0.001 | -0.25 $\pm$ 0.09 | -2.85 | < 0.01 | 1.23** |
| TH8560 | 5.6      | 0.018   | -0.24 $\pm$ 0.24 | -1.01 | 0.33   | 0.86*  |
| TH8636 | 28.19    | < 0.001 | -0.1 $\pm$ 0.12  | -0.86 | 0.39   | 0.31   |
| TJ1655 | 8.87     | 0.003   | -0.05 $\pm$ 0.23 | -0.23 | 0.82   | 0.25   |
| TJ1662 | 76.06    | < 0.001 | -0.22 $\pm$ 0.17 | -1.29 | 0.2    | 0.31   |
| TJ1664 | 1.52     | 0.217   | -1.17 $\pm$ 0.24 | -4.89 | < 0.01 | 1.09** |
| TJ1666 | 5.83     | 0.016   | -0.93 $\pm$ 0.16 | -5.93 | < 0.01 | 0.54   |
| TJ1672 | 91.75    | < 0.001 | -0.38 $\pm$ 0.08 | -4.63 | < 0.01 | 1.54** |
| TJ1673 | 6.6      | 0.01    | -0.44 $\pm$ 0.25 | -1.74 | 0.1    | 0.59   |
| TJ1674 | 122.3    | < 0.001 | -0.09 $\pm$ 0.16 | -0.55 | 0.58   | 0.42   |
| TJ1675 | 1.03     | 0.311   | -0.25 $\pm$ 0.12 | -2.03 | 0.05   | 0.22   |

Several papers published in recent years (Benhamou 2007; Edwards *et al.* 2007; Edwards 2011) have provided an impressive improvement in data analysis using likelihood and information criteria to select among competing models. However, a number of statistical problems in the detection of LF remain open, and even an approach based on likelihood cannot be sufficient for a sure discrimination between LF with  $\mu \approx 4/3$  and continuous time CRW (Reynolds 2012c). Five birds analysed in this study showed a Lévy exponent close to  $4/3$ . Thus, in principle, we cannot exclude that these birds performed a CRW.

As recommended by Clauset, Shalizi & Newman (2009), we determined the value of the minimal distance to find out the tail of the move length distribution. There are

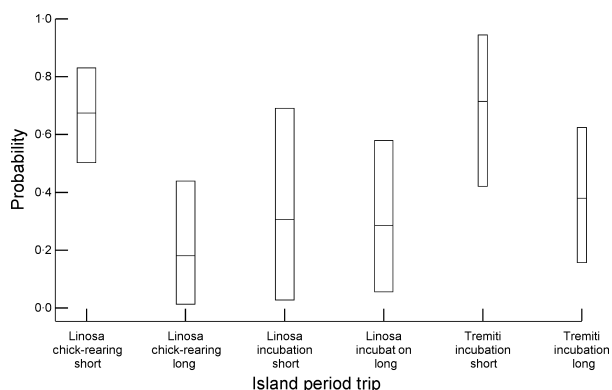


**Fig. 4.** Inset: a rank–frequency plot. For each point characterized by a move length  $y_i$ , we considered all points with distance  $\leq y_i$  and we computed whether these points are better modelled by a linear (black dot) or quadratic (black circle) regression. In the example of TC7522, all points except the largest ones exhibit a linear pattern. The nonlinear largest points represent the truncation. Linear points represent 90% of data for TC7522. The grey histogram represents the distribution of this value for the whole sample ( $N = 36$ ).

some concerns in using the  $y_{\min}$  values selected when looking at the empirical distribution of minimal move lengths. In our case, minimal distances showed a peak around 500–1000 m (also observed by Humphries *et al.* 2011). Bartumeus *et al.* (2010) (Supplemental Information) have suggested that to correctly identify the  $y_{\min}$ , sequential pointwise tests can represent a useful alternative to Clauset, Shalizi & Newman (2009).

The decision to test for ACRW was based on the evidence that this pattern might be confused with LFs (Benhamou 2007; Reynolds 2010). The use of LMCRW was necessary for the sake of realism, because we cannot expect that birds can fly perfectly straight. As a matter of fact, the estimated  $\rho$  values indicated fairly straight movements between reorientation events.

This study introduces two advances in the study of search strategies, which could be of general interest. First, we used flying patterns instead of prey detection patterns to eliminate the possibility that a Lévy's distribution of moves is determined by a fractal distribution of preys (Miramontes, Boyer & Bartumeus 2012). This adds credibility to the hypothesis that observed LF represents a search strategy, which is an opinion strengthened by the



**Fig. 5.** Least square probability to adopt a power-law distribution of move length as estimates of the function of colony, breeding phase and duration of trajectory of Linosa birds (large boxes) and Tremiti birds (thin boxes). Central line of boxes indicates the least square estimate, and box size represents its 95% Wald confidence interval.

presence of predictable variations in the use of LF in the two breeding phases (incubation and chick rearing). Secondly, we performed a set of analyses encompassing both turning angles and move length. *Per se*, turning angles are a relevant aspect of animal movement as they determine path sinuosity and hence animal diffusion through the environment. The use of both statistics helps in falsifying hypotheses and strengthening conclusions.

We found that Cory's shearwater trajectories were characterized by significantly different angular distributions and that only a small fraction of the studied birds showed an angular distribution compatible with a simple CRW. This occurrence is consistent with our expectation because Paiva *et al.* (2010b) showed ARS in this species. The pattern of angular distributions observed in 32 of 77 analysed birds is consistent with the model of ACRW proposed by Benhamou (2007). Most of these birds were tagged during incubation, and they foraged far from the colony. Under this scenario, birds move towards patch concentrations, probably known from previous experience, and once they are in the good area, they perform a CRW with a small  $\rho$  value to locate patches of food.

The mixture of uniform and Cauchy distribution is compatible with a LMCRW (Bartumeus & Levin 2008). To test for a power-law distribution of move length, we were obliged to define the reorientation events along the trajectories. The method presented here is simple, and simulations showed that the bias should be of the order of 7% for our estimated values of  $\rho$  and  $\mu$ , which is a bias we consider reasonably low. It is noteworthy that all birds that showed a mixture of uniform and Cauchy angular distribution also resulted as being characterized by a PLB distribution of move lengths. The coherence between the results of the angular and move length analyses, both consistent with the LF model, supports our conclusions.

However, the fitting of move length to PLB was imprecise for some animals. This fact could be due at least to two different factors. First, the number of moves recorded

could be too small for some birds, especially during short-lasting trips. The second factor is the use of too simple models to fully explain animal behaviour. Indeed, Sims *et al.* (2012) showed that white sharks shifted among different movement modes. In a few of our rank-frequency plots, there is a suggestion of a behavioural switching. In the rank-frequency plots of several trajectories fitted by a PLB model, we have noted some irregularities, jumps and outliers. This is probably due to different processes overlapping into a basic LFF. When comparing actual and simulated trajectories (Fig. 1 and Fig. S2), we can observe differences. At large- and meso-scale, seabirds may be able to head to known favoured and profitable foraging areas such as shelf edges, frontal zones and upwelling (Weimerskirch 2007). Further, actual movements are influenced by the exigency, for these central place foragers, to return to the colony. This would probably produce more complex angular distributions of moves – of Cory's shearwaters (present study) and bees (Reynolds *et al.* 2007) – producing possible ramifications for the interpretation of the LF-like patterns in terms of the execution of an optimal foraging strategy. We are aware that this point needs to be addressed by future research as recently suggested by Gautestad (2011).

This work and other recent studies, which overcome the statistical problems which affected earlier work, suggest that LFF is an appropriate paradigm to investigate search strategies in wild animals. Lévy flight foraging unifies both power-tailed and Gaussian distributions of move length and puts this pattern in relation to the kind of prey fields encountered by animals. Our analyses showed consistency between adopted movement tactics and the biological needs within the breeding period where birds were forced to exploit environments characterized by low prey availability.

In our opinion, a topic that emerges from the rich debate on LFF is to use a model complex enough to grasp the important features of animal movement and ignore higher-order effects – which are definitely present under natural conditions – but which are not really relevant. The use of more complex models might yield better fits, as proposed by Jansen, Mashanova & Petrovskii (2012), but the risk is to 'throw the baby out with the bath water'. Maybe in future research, the use of the coarse-graining test proposed by Gautestad (2012) will be useful to face this problem.

To our knowledge, there is no theoretical explanation for using Brownian movements in rich habitats when a Lévy flight should be as appropriate. However, this and other studies (Humphries *et al.* 2010; Sims *et al.* 2012) have consistently found a behavioural shift between poor and rich habitats. We stress that, from a behavioural point of view, discriminating between continuous vs. discrete movement models is relevant for understanding habitat use by animals and for improving animal management and conservation, which was the starting point from which the project on Cory's shearwaters was built upon (Cecere *et al.* 2012).

An approach using *a priori* mechanical statistics models may appear to be in contrast with a mechanistic data-driven approach. This last approach has contributed to understanding human mobility and is applied in many studies motivated by commercial purposes or by traffic regulation (Renso, Spaccapietra & Zimányi 2013). However, Viswanathan *et al.* (2011) made a point that the movement of different organisms, which are led by completely different biological processes, may appear very similar when observed 'from a certain distance'. If this is true, then a limited number of basic models may account for a large set of different movement patterns. In other words, one loses in details but gains in universality. As noted by Gautestad (2013), 'the statistical mechanical approach implies paying closer attention to the classes of meso- and macro-scale laws that emerge from mechanistic micro-scale interactions but where these interactions are analysed from the perspective of a coarser observational scale'.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Fig. S1.** (A) The pdf of a wrapped Cauchy distribution (red) with a concentration parameter of  $\rho = 0.9$  and of an uniform distribu-

tion (green) are plotted as a function of turning angle  $\alpha$ .  $\theta$  indicates the angular threshold. (B) The reorientation (red) occurs when  $\alpha > \theta$ .

**Fig. S2.** We display two simulations obtained with  $\mu = 1.4$ ,  $\rho = 0.70$  (left), and  $\rho = 0.95$  (right). The black point represent the origin of simulation.

**Fig. S3.** (A) The bias of  $\hat{\rho}$  is plotted as a function of the assigned  $\rho$  values. (B) The bias of  $\hat{w}$  is plotted as a function of the assigned  $\rho$  values. (C) The bias of  $\hat{\rho}$  is plotted as a function of the assigned  $\mu$  values. (D) The bias of the recovered  $\hat{w}$  is plotted as a function of the assigned  $\rho$  values. Vertical bars represent standard errors.

**Fig. S4.** The fraction of successful identifications of reorientation angles is shown for (A)  $\rho$  and (B)  $\mu$  values.

**Fig. S5.** The recovered  $\mu$  values are reported as a function of the assigned  $\mu$  values.

**Fig. S6.** In blue we represent the recorded trajectory; in red we connect the point where we identify a reorientation event with a straight line. We reported bird identification. The suffix  $_{L}$  and  $_{T}$  indicate the colony (Linosa and Tremiti, respectively), the suffix  $_{i}$  and  $_{c}$  the phase of the breeding period (incubation and chick-rearing, respectively).

**Fig. S7.** Model fitting. Bird identification. The suffix  $_{L}$  and  $_{T}$  indicate the colony (Linosa and Tremiti, respectively), the suffix  $_{i}$  and  $_{c}$  the phase of the breeding period (incubation and chick-rearing, respectively).