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Exploring the interplay between small and large scales movements in a neotropical small mammal

E. Brigatti^{1*}, B. Ríos-Uzeda^{2,3} and M. V. Vieira²

Abstract

We record and analyze the movement patterns of the marsupial *Didelphis aurita* at different temporal scales. Animals trajectories are collected at a daily scale by using spool-and-line techniques and, with the help of radio-tracking devices, animals traveled distances are estimated at intervals of weeks. Small-scale movements are well described by truncated Lévy flight, while large-scale movements produce a distribution of distances which is compatible with a Brownian motion. A model of the movement behavior of these animals, based on a truncated Lévy flight calibrated on the small scale data, converges towards a Brownian behavior after a short time interval of the order of 1 week. These results show that whether Lévy flight or Brownian motion behaviors apply, will depend on the scale of aggregation of the animals paths. In this specific case, as the effect of the rude truncation present in the daily data generates a fast convergence towards Brownian behaviors, Lévy flights become of scarce interest for describing the local dispersion properties of these animals, which result well approximated by a normal diffusion process and not a fast, anomalous one. Interestingly, we are able to describe two movement phases as the consequence of a statistical effect generated by aggregation, without the necessity of introducing ecological constraints or mechanisms operating at different spatio-temporal scales. This result is of general interest, as it can be a key element for describing movement phenomenology at distinct spatio-temporal scales across different taxa and in a variety of systems.

Keywords Movement patterns, Spatio-temporal scales, Lévy flight, Brownian motion, Marsupials

Introduction

In the last 2 decades the analysis of a large amount of biological data related to animal displacements has shown that the distribution of the movement single steps can be well characterized by the use of heavy tailed distributions [1–7]. Even if some concerns about these results have been raised [8], and the risk of describing such a variety of behaviors and strategies with an oversimplified theoretical framework can exist, nowadays it seems evident that stochastic processes which can generate such type of behaviors must be included in the indispensable toolbox for modeling animal movements. These processes, generally known as Lévy processes [9, 10], present some specific traits which are very different from those of ordinary

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Brownian processes. In fact, they produce trajectories with a peculiar geometry, marked by abrupt long jumps that connect clusters of frequent short displacement, which generates a characteristic scale-invariant structure. Moreover, such Lévy processes trigger super-diffusive behavior [11–13], which means that the mean squared displacements of individuals are a super-linear function of time and the limiting distributions of the total traveled distances present power law behavior. These features lead to an efficient way of exploring the space, in contrast to the slowness of standard diffusive behavior. In fact, Lévy flights have been suggested to be the best option for solving the problem of random search [1, 14], and, for this reason, the optimal choice for describing searching and foraging movements, specifically for environments with homogeneous and scarce resources [15].

Lévy flights, similarly to ordinary random walks, can be defined as a sum of independent identically distributed random steps. In this case, the step distributions present power law tails which generate divergent variances. For this reason, the central limit theorem does not apply, and the limiting distributions of the total traveled distances present power law behaviors [13].

The fact that the single step distributions present infinite variance can discourage their use, as in ecological systems an unavoidable cutoff is always present. In fact, the step movement of an individual is evidently limited because of natural, physical and energetic constraints. Moreover, a realistic animal movement is characterized by physiological and circadian rhythms which cause direct limits on the maximum step length. For this reason, the power law behaviour can hold only in a limited spatial range, and some type of cutoff must be considered. These facts suggest the use of truncated power laws [8, 16], an important element taken into account in different studies [8, 15, 17–20].

The presence of the cutoff means that the variance is finite and, in principle, it should cause the convergence to a Gaussian behaviour. But this convergence, in general, is slow and it is reached only after a very large number of steps [20]. In these conditions, the distribution of the total traveled distances maintain statistical properties indistinguishable from the ones generated by Lévy flights. Only increasing the number of realized steps, a crossover between Lévy and Gaussian regimes is observed, which depends on the cutoff and the exponent values of the Lévy flights [20]. Therefore, an open question is when such large number of steps are achieved in the movements of specific organisms, causing a change from a Lévy to a Gaussian regime.

These theoretical results have been registered in some empirical studies. Two distinct modes in the walking behaviour of aphids was recorded by Mashanova et al.

[17]. Similarly, in the case of human mobility, the heavy-tailed behaviours have been reported within a certain region, but not on a global scale [18, 21]. The relationship between Lévy and Gaussian regimes in movement paths could therefore depend on the scale of the tracking data. The same organism could present a Lévy regime at fine-scale movements that could change to Gaussian as the interval between locations increases. This interesting question remains still open, as empirical studies which describe the movements of the same species at pronounced different scales are sparse [22–24]. Fryxell et al. [22] studied elks over different orders of magnitude in time (minutes to years) and space (meters to 100 km). This study is based on descriptive statistics and qualitatively shows and characterizes elk shifts from dispersive to home-ranging phases. At the finest scales, elk used area-restricted search while browsing, and less sinuous paths when not browsing. The study by Kazimierski et al. [24] studied the movements of a small american marsupial qualitatively characterizing the shape of the small scales trajectories and estimating the speed of movement, the daily home range (less than 100 m²) and its exploration by using the large-scale dataset.

The main purpose of our study is to characterize the movement patterns of a Neotropical marsupial at different temporal scales. In a first experimental set, animal trajectories were mapped continuously and in detail, during a tracking that lasts up to one night of activity (ca. 8 h). These data were used to estimate the single step distribution $P(\ell)$, where the step ℓ is defined as the distance between two successive turning points. In a second field work, based on radio-tracking locations, positions of animals were recorded at larger time intervals, of the order of weeks. Animals were released in the same site of capture, and their location was determined every night, for several nights. From these measurements it was possible to estimate the total traveled distances distribution $P(r)$, where r is the geographical distance traversed in a week time. The statistical properties of these two distributions were analysed, showing the presence of a truncated Lévy flight for $P(\ell)$, with parameters that generate a total traveled distances distribution $P(r)$ with a Brownian character, for large temporal scales. The number of steps necessary for reaching such distribution is estimated, allowing a consistency check between the distinct movement characteristics present at different scales.

Materials

These experiments were conducted in the Iconha and Guapi-Macacu river basins, which are part of the municipalities of Guapimirim and Cachoeiras de Macacu, in the Rio de Janeiro State, Brazil.

For describing the features of animals movements at different temporal scales we use two complementary approaches: with spool-and-line devices and with radiotracking. The experiments of the first set, with spool-and-line devices, were conducted in the Serra dos Órgãos National Park, PARNASO, the largest continuous Atlantic Forest remnant in the State of Rio de Janeiro (20,020 ha), southeastern Brazil (22.479° S, 42.988° W, datum WGS84), between 500 and 700 m altitude. The forest is part of the montane rainforest complex, in an old-growth successional stage (details in [25]).

The experiments of the second set, with radiotracking, were conducted in a nearby location, in forest fragments varying from 5 to less than 10000 ha area, immersed in a matrix of pastures near the Reserva Ecológica Guapiaçu - REGUA (22°25' S, 42°44'W). Linear distances between opposing edges of forest fragments varied between ca. 200 m to dozens of kilometers. The original forest of these fragments was disturbed by different degrees of anthropogenic activities. Canopy is 20 m high approximately, but varying in continuity between forest fragments. Subcanopy is fairly open (details of the structure of forest fragments in [26]).

The first experiment recorded movements of *Didelphis aurita*, a small marsupial released in the forest of PARNASO. Individuals were equipped with a spool-and-line device [27], which consisted in a bobbinless cocoon, containing up to 480 m of thread, wrapped in a PVC film. This device was glue to the back of animals with synthetic resin, and the end of the thread was attached to a mechanism [28] which marked the starting point of the animal path. Trajectories were tracked following the thread and measuring the azimuth angles corresponding to a pronounced change in the direction of motion (a deviation greater than 5°), and the distances between these turning points. Note that the use of a spool-and-line device is a better replacement for GPS tracking when, as in our case, the considered species lives in region of dense forest and intricate topography, which cause low reliability in GPS positioning.

In the second experiment, performed in REGUA, individuals of *D. aurita* were equipped with a radiotracking device, released at the same site of capture, and tracked for one night every week. Individuals were captured-recaptured from 2014 to 2015 as part of a population ecology study in forest fragments near REGUA [29]. A total of 14 *D. aurita* (subadults or adults of both sexes) were selected for tracking based on good physical condition. The chosen individuals were taken to the laboratory of the REGUA located in the study area, and kept in a plastic cage (41 × 34 × 18 cm) for no more than 24 h, with ad libitum food and water, and covered to reduce disturbance and stress. Early in this 24 h

period the individual had a radiotag tracking device with an active sensor (VHF radio tracking, Telenax inc.) attached on its back at a point just below the scapulas. The radiotag was fixed with flexible and water-resistant glue (Super Bonder Power Flex, Loctite™), and ranged between 4 and 10 g, depending on the animal weight, representing a maximum five percent of its total weight. After receiving the radiotag, the individual remained under observation overnight to detect any apparent disturbances in behavior, and to evaluate if the radiotag was fixed and working properly. Animals were released the next day on the same site of capture. After release, they were tracked for a whole night once a week using the homing-in technique [30]. As marsupials are nocturnal, monitoring took place mainly during the night, when signal location was determined every two hours. A receiver TR-4 and an antenna RA-14K (Telonics, Mesa, USA) were used to detect and close in the signal of individuals until we were sure the animal was less than 5 m away, based on the quality and intensity of the signal. Only when an individual moved more than 20 m a new location was georeferenced. Individuals were monitored until their radiotag fell, the animal died, or the signal was lost for two consecutive weeks. From these data, the geographical distances traversed in a week time were extracted.

A graphic representation showing the typical spatial scales covered by the two experiments is shown in Fig. 1.

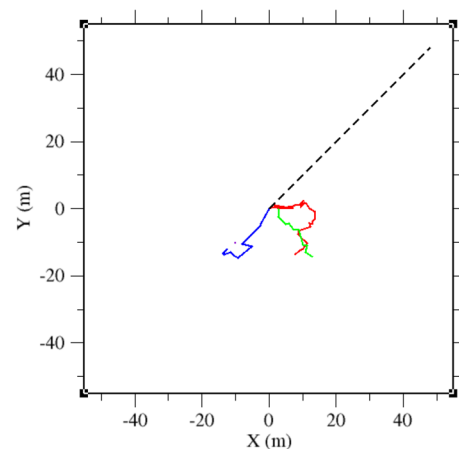


Fig. 1 Colored continuous curves represent some trajectories tracked at small scales with the spool-and-line technique. The black dashed straight line represents the mean distance travelled by an individual after 1 week, as estimated from the dataset obtained using radiotelemetry techniques. The typical animals size is comparable with the width of this line

Methods

Small scales

For the data collected during one night of activity, we quantify the distribution of the step-lengths ℓ , defined as the distances between two successive turning points of a given trajectory. The turning points can be identified as the points with a change in the direction of motion larger than a fixed minimal angle. However, such an ad-hoc discretization is arbitrary and the estimated distribution $P(\ell)$ would strongly depend on this choice [31]. We overcome this problem following a recent approach introduced in [2]. In analogy with that procedure, a trajectory is projected on one axis and the projected step is defined as the distance between two inversions in the direction of the movement of the projected trajectory. It was analytically proven that in the presence of a power law distribution for the original path in 2D, the distribution for the projected paths preserves the same power law relationship [2]. In the case of an exponential distribution, the projected data maintain the exponentially decaying behaviour. Following this method, we are able to rigorously investigate the shape of the $P(\ell)$ distribution using a segmentation procedure which does not depend on any arbitrary choice. As pointed out in [2, 31], there is only an important detail to be taken into account. The operation of projection causes the proliferation of spurious data corresponding to steps similar or even smaller than the smallest step-length present in the original dataset. These data must be excluded from the final analysis. Moreover, as the last measured step-length can have a length influenced by the ending of the spool, they were eliminated from the data set too.

Once obtained $P(\ell)$, we look for the best supported model for describing our data. We are interested in distinguish if the distributions present power law or exponential behaviors. For the power law behaviour we consider the Pareto distribution: $f(x) = (\mu - 1)a^{\mu-1}x^{-\mu}$, for $x \geq a$, and the truncated Pareto distribution, defined as: $g(x) = (1 - \mu)/(b^{1-\mu} - a^{1-\mu})x^{-\mu}$, for $a \leq x \leq b$. Finally, the exponential distribution is defined as: $h(x) = \lambda \exp(\lambda a) \exp(-\lambda x)$, for $x \geq a$. As already commented in the introduction, the use of a truncated Pareto distribution is essential. In fact, the direct physical limits characteristic of a realistic animal movement produce inevitable truncation effects. For this reason, it is important to consider an upper limit for the ℓ values.

The best estimation of the parameters of these distributions can be obtained using the Maximum Likelihood Estimation (MLE) technique. This technique has shown to be the most reliable compared to classical least squares methods [16, 32, 33]. For the truncated Pareto distribution, the estimation of the μ parameter must be realized numerically; details can be found in [19, 33, 34].

Finally, a quantitative selection between the three considered fitting models is obtained using the Akaike information criterion (AIC), which compares models likelihoods, penalizing models with more parameters [35]. The AIC is defined as: $AIC = 2K - 2L$. L corresponds to the maximum log-likelihood, which is estimated following Edwards [8]; K is the number of parameters of the model, which is 2 for the exponential and Pareto distribution and 3 for the truncated Pareto. The best supported model is the one which displays the lowest AIC.

Large scales

The data collected during the radiotracking field study were filtered, considering only movements of individuals which do not leave the fragment where they were first detected. In fact we considered only the movement behavior of settled animals, disregarding animals that left the forest fragment for dispersal. We measured the geographical distance between the first animal position (the vector \bar{x}_1) and the secondary location (\bar{x}_2), measured 1 week later: $r = |\bar{x}_2 - \bar{x}_1|$. From these data it is possible to quantify the frequency of traveled distances of individuals as a function of geographical distance r . Our aim is to distinguish if the data are better described by a classical distribution expected for a normal diffusive behaviour, or by a distribution generated by Lévy walks.

The first situation corresponds to a Rayleigh distribution, which is the one expected for a Brownian process. The distribution has the following aspect:

$$P(r) = \frac{r}{\sigma^2} \exp(-r^2/2\sigma^2), \tag{1}$$

and the best estimation of its single parameter is obtained using the Maximum Likelihood Estimation technique. A simple calculation gives: $\sigma_{MLE} = [\frac{1}{n} \sum_{i=1}^n r_i^2 / 2]^{1/2}$, where n is the sample size, and its approximate variance is: $\sigma_{MLE}^2 / 4n$.

For testing if the data are well described by distributions generated by Lévy walks, we should consider the family of L-stable distributions, characterized by power-law tails [13]. Unfortunately, most members of the L-stable family have no closed form and they are characterized by four parameters. For these reasons, they are not well suited for a direct goodness-of-fit test. However, in order to consider the L-stable family as an alternative model, the crucial aspect is to demonstrate that data present a clear power law upper tail. In fact, it is the tail the most important portion of the distribution for determining if the central limit theorem applies or not. For this reason, it is reasonable to focus on determining how heavy is the upper tail of the distribution. If we assume that our distribution decays as $F(x) \propto x^{-\alpha}$ for $x > M$, where M is the

median of the distribution and $\alpha > 0$, the distribution is heavy-tailed if $\alpha < 3$. The estimation of the tail index α is obtained by using the conditioned maximum likelihood estimator introduced by Hill [36].

This approach has some important advantages over popular models comparison or specific test based on general distributions. In fact, distributions with two power law tails are used in the literature [37, 38], but, despite they may present some convenience in the statistical description of the dataset, these general probability distributions do not have any plausible theoretical connection with movement models. Moreover, in general, a comprehensive fitting of the data has the greatest descriptive power for the central region, but it says less about the tails of the distribution.

Exploring the connection between small and large temporal scales

Based on the results of the analysis of the data at small and large scales, we will explore the connections between these two regimes. Our aim is to test the robustness of our results and to clarify the relationships linking the two scales. In particular, we want to show how it is possible to obtain the principal statistical features of the large scale distribution as an emergent behavior generated by the properties of the small scale walks. For achieving these goals, we implement some simulations, based on discrete walks, for synthetical reproducing the empirical $P(r)$ distribution. The discrete walks are parametrized using the results obtained from the analysis of the small scale data of *Didelphis aurita*. Fixed the number of steps n , for each walk, we calculate the related traveled distance r_i . By generating a large amount of walks we can obtain the distribution $P_n(r)$. In dependence of n , this distribution presents very different characters. In fact, a small n generates a distribution with a well defined heavy upper tail; increasing the n value produces a shape change towards a typical Rayleigh distribution. This evolution in the shape of the distribution can be described by measuring the tail index α defined previously. Alternatively, we can measure the maximum of the log-likelihood of the dataset of the r_i , which are generated by the simulations, considering a Rayleigh distribution ($L(r_i|\sigma_{MLE})$) and the maximum of the same log-likelihood of a dataset of equal size, but composed by independent, identically-distributed draws (d_i) from a Rayleigh distribution with the same parameter σ ($L(d_i|\sigma_{MLE})$). For our setting, the ratio $R = \frac{L(r_i|\sigma_{MLE})}{L(d_i|\sigma_{MLE})}$, will be very close to one when the distribution of the r_i is practically represented by a Rayleigh distribution, and it will decrease towards zero the more the distribution $P_n(r)$ departs from this shape. Note that we do not use the logarithm of the likelihood-ratio but the ratio of the log-likelihoods because its numerical

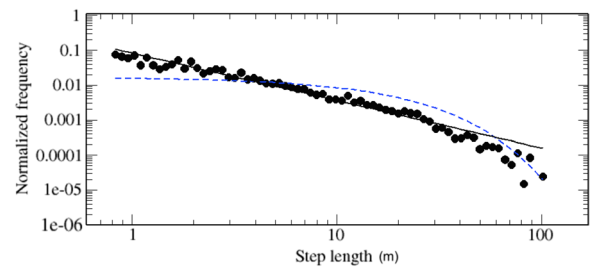


Fig. 2 Log-binned data with the best estimated Pareto-truncated distribution (continuous lines) and exponential distribution (dashed line). Step-lengths are expressed in meters. Analyzed data consider steps coming from the projections onto the two axis (x and y) together. In fact, as expected, the two projections present indistinguishable behaviors

Table 1 Models selection between Pareto-truncated, Pareto and exponential distribution. ΔAIC is the difference of the AIC values and $wAIC$ is the weighted value of the AIC of the considered models

	Pareto-truncated	Pareto	Exponential
Loglikelihood	-6712	-6937	-6965
AIC	13431	13879	13934
ΔAIC	0	448	503
$wAIC$	1	0	0

output can more easily provide a rough description of the similarity between the two distributions.

Finally, we will shed light on the diffusion properties of these stochastic walks depicting the dependency of the typical value of these distributions on n .

Results

Small scales

We analysed 141 different trajectories, where each trajectory is the whole track of a single individual movement. These data generated a sample size of 2239 steps, which corresponds to the number of regressed data after eliminating the spurious l . The calculation of the AIC values shows that the Pareto-truncated distribution presents the lowest AIC, which indicates that it is the best model for the description of the data (see Table 1). This fact can be visually appreciated in Fig. 2, where we plot the data with the best estimated model. The Pareto-truncated distribution obtained using the MLE approach is quite satisfactory. The exponent μ of the Pareto-truncated distribution is equal to 1.36 ± 0.02 and the parameter a and b are respectively 0.8 and 103.1 meters.

Large scales

The histogram of the collected data with the best estimated Rayleigh distribution is plotted in Fig. 3. A visual

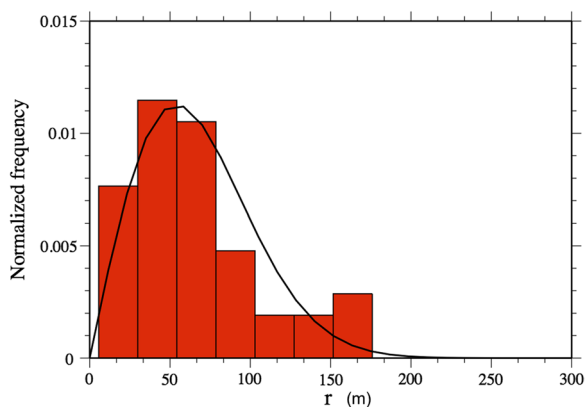


Fig. 3 Histogram of $P(r)$ as obtained from the telemetry measurements, with the best estimated Rayleigh distribution (continuous line). The sample size is 43, which corresponds to the number of 1-week distances measured, combining data from all individuals

inspection suggests that data are well described by this model, in particular considering that the Rayleigh distribution depends only on a single parameter. The best estimated parameter obtained by means of the MLE is: $\sigma_{MLE} = 54 \pm 4$ m. A Kolmogorov–Smirnov test of our observations against the fitted Rayleigh distribution gives a p value of 0.166, which suggests that we cannot reject the hypothesis that the field data come from the fitted distribution.

The estimation of the tail index α , as obtained using the Hill’s estimator, obviously depends on the fraction of observations used in the tail estimation. For every subset of observations which satisfies $r > M$, the estimated α is always greater than 3, and it increases with decreasing subsets, rejecting the hypothesis of a power law tail (α should be < 3). In particular, a subset corresponding to the largest 58% of the original dataset gives $\alpha = 3.3 \pm 0.5$. Diminishing the subset size the tail index increases, reaching 4.1 ± 0.9 when the 30% of the observations are used.

Exploring the connection between small and large temporal scales

Individual movements are simulated performing a discrete walk which implements a Pareto truncated step-length distribution with isotropic directions of motion. Once fixed the number of steps n , we measure the distance r_i between the starting point and the final individual position. We run 200,000 different simulations of the walk and we obtain the histogram of the r_i for that n . We can observe that by changing the value of n , these histograms undergo a change in their shape. When the

number of performed steps is small, a power law tail is clearly recognizable, but increasing the number of steps it disappears, generating a distribution characterized by a Rayleigh-like shape. This phenomenon is well described in Fig. 4, where we plot the tail index α and R , as measured from the different distributions $P_n(r)$. In this case, the α are measured selecting an upper-order statistics corresponding to the 40% of the original dataset. This value is chosen because it produces a consistent estimations of α for small n . For $n < 40$, α is smaller than 3, which implies the presence of heavy upper tails. This fact finds a correspondence in the small R values, which suggests that a Rayleigh distribution is a poor description of the data. In contrast, for $n > 40$, α is larger than 3, revealing the disappearance of the power law tail. The R value comes close to 1, suggesting that now the Rayleigh distribution can well approximate our data. For values of n larger than 100, effectively $R \approx 1$ and $P_n(r)$ becomes indistinguishable from a Rayleigh distribution.

These simulation data can also characterize, in a clear and intuitive way, the diffusion properties of these walks. In Fig. 4 we display the typical value $r_n^{t.v.}$ of the $P_n(r)$ as a function of n . For n large enough, the behaviour predicted by the central limit theorem, where $r_n^{t.v.} \sim n^{1/2}$, is recovered. In this regime r is the sum of a sufficient large number of ℓ and the maximum values reached by these ℓ are directly determined by the cut-off value b . For small n , we can observe a superdiffusive behaviour ($r_n^{t.v.} \sim n^k$, with $k > 1/2$). In this regime the number of sorted step lengths ℓ is reduced. It follows that the maximum values reached by these ℓ are generally small compared to the cut-off and its effect can be partially neglected. If we could effectively forget the cut-off and consider the distributions as power laws with exponent δ , the typical values should grow as $n^{1/(\delta-1)}$ [13]. As in our case the cut-off is very sharp and the μ exponent is relatively close to 1, even if a power law can be detected, it is difficult to robustly estimate the corresponding exponent. The transition between the two regimes is quite smooth and the progressive convergence towards the normal diffusion set in for n close to 100, in accordance with the previous analysis of the $P_n(r)$ shape.

Finally, we estimated the best n value which reproduces the $P(r)$ of the field work dataset. This is determined by looking for the σ_{MLE} value which best approximates the one of the empirical data. For a number of steps fixed to 68, $\sigma_{MLE} = 54$, exactly the same of the empirical case. In Fig. 5, it is possible to appreciate how the histograms of the simulated and experimental dataset are effectively very similar.

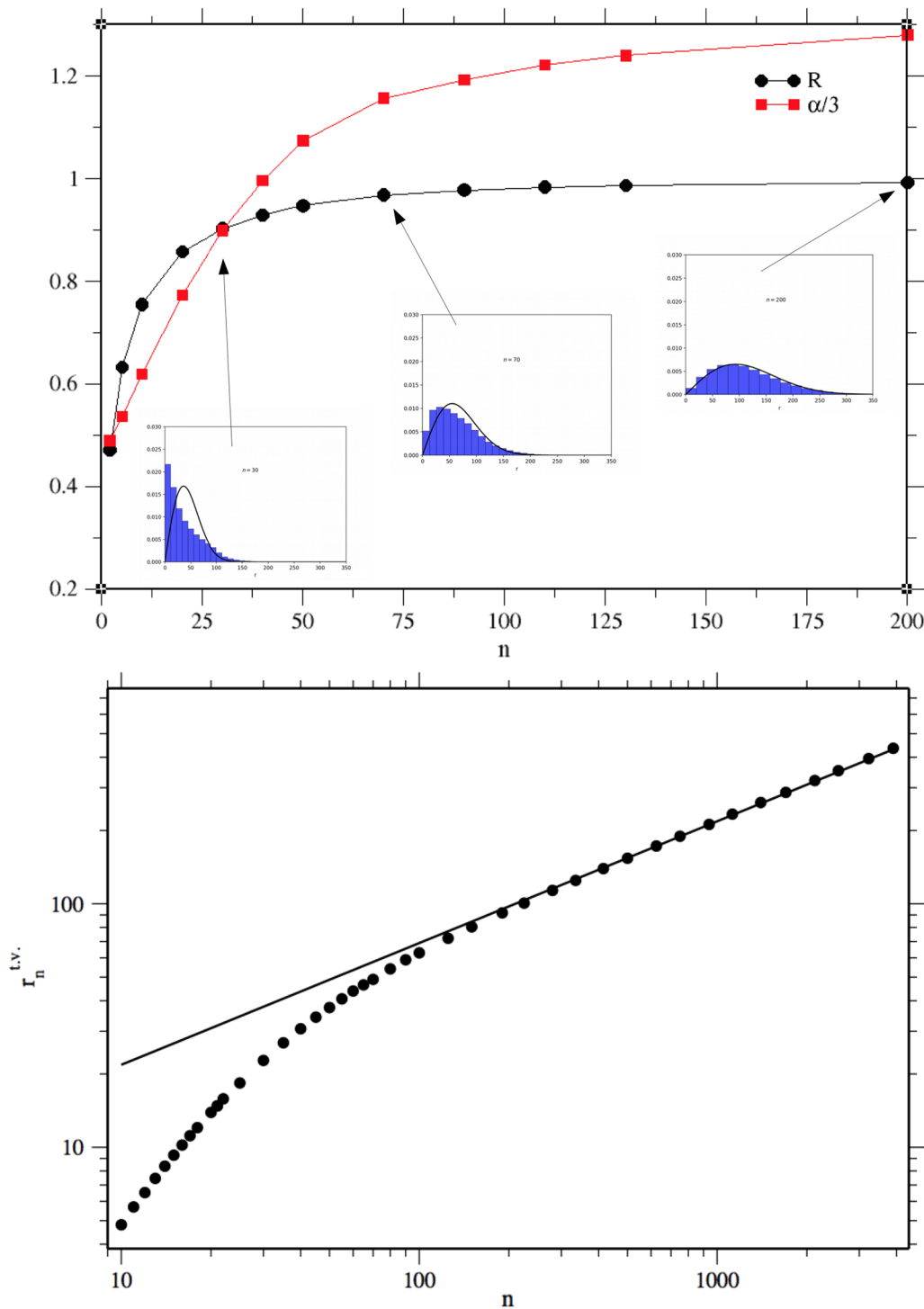


Fig. 4 Top: Tail index α normalized by 3, and R , as measured from the different distributions $P_n(r)$. Continuous lines are just a guide for the eyes. In the inboxes, the histograms represent the $P_n(r)$ for $n = 30, 70, 200$, as obtained from the simulation of 200,000 different walks. The continuous lines are the corresponding best estimated Rayleigh distributions. Bottom: typical values of the $P_n(r)$ as a function of n . As a measure of typical value we use the geometric mean, which better characterizes the distributions when they are close to power laws. For large n we can observe that $r_n^{t.v.} \sim n^{1/2}$ (continuous line)

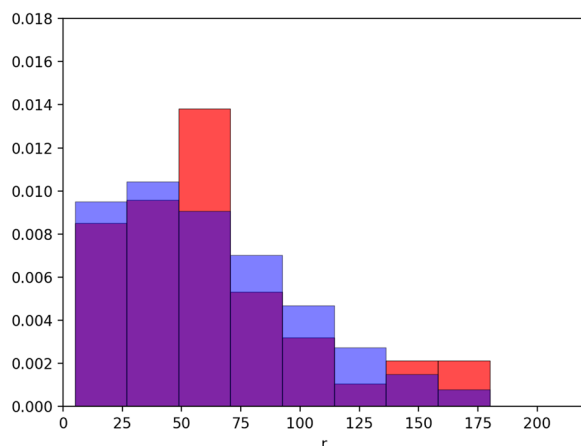


Fig. 5 The blue histogram represents the distances r generated by a simulation which uses a Pareto truncated distribution with the parameters calibrated from the empirical dataset when it implements walks of 68 steps. Data are obtained from 200,000 different walks. The red histogram illustrates the field data as obtained from the telemetry measurements

Discussion

In the literature it is common to find works which describe the geometry of paths followed by different species of animals, characterized by a variety of body sizes and, conversely, geographical scales. In general, these analysis collect data on short temporal scales (hours or daily scales) and use different specific methods of tracing and segmentation of the paths. When large temporal scales are considered, studies are more interested in describing dispersion properties, and, for illustrating long-distance migration and dispersal, other methodologies, like biotelemetry techniques and satellite tagging, are typically used. In contrast, analyses which focus on a single species and describe movements at all relevant scales, relating the small to the large ones, are few [22–24]. These studies are very important for the development of the movement ecology paradigm [39], which presents the goal of unifying organismal movement research also from the perspective of temporal scales: from a single step toward the entire lifetime track, eventually characterizing the presence of different movement phases. In this work we have explored these ideas from a particular point of view. We do not emphasize the importance of different biological processes, but we just scrutinize the statistical effects generated on movements by crossing through different temporal scales, without introducing any scale-dependent ecological effect or mechanism.

In order to fully describe the statistics of general movements, in principle, it would be necessary to typify the distribution of the movement steps at every time scale; in fact, the distribution of the daily steps could be different

from the weekly or monthly ones. In simplified cases, it is possible to reconstruct the distributions corresponding to large time scales only knowing the one describing the short time scales. In fact, from a theoretical perspective, if the short time scale distributions are Gaussian or Lévy ones, the situation is particularly favorable. In this case, as these distributions are stable, at all time scales the step distributions will be described by the same stable law, with their parameters values appropriately tuned. This well known result can be generalized to the case when movement steps are summed from independent distributions with finite variance. Then, the central limit theorem assures that the distribution describing long times steps converges towards a Gaussian, if the number of steps is sufficiently high. Depending on the rate of convergence, this result can be of greater or lesser interest, and, for example, a Lévy flight with truncation can lead to Gaussian behaviors.

These theoretical results can be applied to real-world data, implying that whether a truncated Lévy flight or a Brownian motion apply will depend on the scale of aggregation of the paths of the considered animals. By resampling at smaller scales and retesting the model at each scale, discernible truncated Lévy or Brownian modes may come into focus at the appropriate scale. In our case, at the scale of 1-day paths, a truncated Lévy flight fits very well steps length data. Zooming out, however, we would expect a truncated Lévy flight model to be falsified when the scale matches a sufficient large sum of steps. Indeed, our analysis shows that the Lévy truncated distribution which characterizes the daily movements of *Didelphis aurita* converges towards a Brownian model after only 1 week. This means that the effect of the rude truncation present in the daily data generates a fast rate of convergence towards Brownian behaviors. For this reason, Lévy flights become of scarce interest in describing the dispersion properties of these animals inside the considered fragments, which result described by a normal diffusion process, and not a fast, anomalous one. This result has a clear ecological relevance, as normal diffusion processes produce shorter typical translation distances than the anomalous ones, generated by Lévy flights. This implies a lower propensity to explore regions further away from the origin of the movement.

Our study presents some connections with the current growing interest in describing the crossover from superdiffusive to normal-diffusive dynamics in different particles systems such as, for example, in actively moving biological cells. However, with the exception of a study on aphids [17], this phenomenon has not yet been quantitatively recorded in the case of animal movements. Note that this crossover is generally characterized by looking at the temporal dependence of the mean squared

displacement. A linear dependence corresponds to the normal diffusion law; super-linear relations, in the form of a power-law, correspond to superdiffusive behaviors. In our study we are not able to describe this phenomenon by looking directly at the mean squared displacement since our trajectories did not present temporal tracking and did not entirely span the considered time scales.

Finally, it is important to note that the effect of summation of enough different steps is sufficient for generating the Rayleigh distribution. Here it is not necessary to introduce other biological or ecological constraints, such as fragment size, aversion to densely occupied regions, feeding spots, and home range, nor to typify a variety of ecological processes operating at diverse spatio-temporal scales, for producing different movement phases [39]. In this way we are able to predict movements over large temporal scales through simulations calibrated from empirical results obtained over short time periods [40, 41], without the necessity of introducing other effects. Of course, ecological constraints on movement behavior do exist, in general and for *Didelphis aurita* in particular [27–29]. Home range area and location is frequently considered one such ecological constraint, that could limit superdiffusive movement, generating subdiffusive or normal-like diffusion (review in [42]). However, home range actually is more a consequence of interactions between individual behavior and their environment, not an environmental factor itself. Our results suggest that factors determining home ranges are more likely to be affecting short term responses, manifest in the distributions of step lengths and turning angles. Long term normal-like diffusion could be just a consequence of these short-term effects.

This study shows how very simple models like traditional discrete walks may be adequate for describing movement data at many temporal resolutions, producing results that are not obvious, but can be easily interpreted. Even when a Lévy flight results not to be appropriate for describing large scales behaviors, it provides a reference point for a parsimonious explanation of the overall process of movement. In this sense a Lévy flight can be seen, together with the Brownian motion, as an appropriate null model, which acts as a more useful starting point than other more elaborated models.

Lévy processes have been accepted as appropriate models describing movement paths of a variety of organisms [43], but conflicting views remains on the processes they represent. Some argue that they are mostly limited to describe movements at large spatial scales, and Lévy processes would be a result of a series of random walk processes acting at different spatial scales [42, 44]. Conversely, truncated Lévy processes may approximate random walks, or Brownian motion, as the number of steps

increases between points where positions are registered [20]. Our results presents evidence that the latter occurs in nature, in the paths of the marsupial *Didelphis aurita*. More than one mechanism could result in a Lévy process [43]. The realization of this connection between Lévy and Brownian regimes in the modeling of animal paths is essential to understand what mechanism is determinant in a particular system.

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Author contributions

E.B., B.R.U. and M.V.V. conceived the paper and interpreted the results; data were collected by the team of B.R.U. and M.V.V.; B.R.U. preprocessed the dataset; E.B. and B.R.U. analysed the data; E.B. analysed the models; E.B. and M.V.V. wrote the manuscript.

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Availability of data and materials

Data can be found at <https://doi.org/10.6084/m9.figshare.25446214>.

Declarations

Ethics approval and consent to participate

Trapping and handling conformed to guidelines sanctioned by the American Society of Mammalogists [45], and was approved by IBAMA/MMA (Authorization numbers 87/05-RJ, 099/06-RJ, 13861-1, 13861-2, 16703).

Conflict of interest

The authors declare no conflict of interest.

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References

1. Viswanathan GM, Afanasyev V, Buldyrev SV, Murphy EJ, Prince PA, Stanley HE. Lévy flight search patterns of wandering albatrosses. *Nature*. 1996;381:413–5.
2. Sims DW, Southall EJ, Humphries NE, Hays GC, Bradshaw CJA, Pitchford JW, et al. Scaling laws of marine predator search behaviour. *Nature*. 2008;451:1098–102.
3. Shaffer CA. Spatial foraging in free ranging bearded sakis: traveling salesmen or Lévy walkers? *Am J Primatol*. 2014;76:472–84.
4. Ramos-Fernández G, Mateos JL, Miramontes O, Cocho G, Larralde H, Ayala-Orozco B. Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behav Ecol Sociobiol*. 2004;55:223–30.
5. Atkinson RPD, Rhodes CJ, Macdonald DW, Anderson Atkinson RM, Rhodes RP, Anderson DW, et al. Scale-free dynamics in the movement patterns of jackals. *Oikos*. 2002;98:134–40.
6. Focardi S, Montanaro P, Pecchioli E. Adaptive Lévy walks in foraging fallow deer. *PLoS ONE*. 2009;4: e6587.
7. Hays GC, Bastian T, Doyle TK, Fossette S, Gleiss AC, Gravenor MB, Hobson VJ, Humphries NE, Lilley MKS, Pade NG, Sims DW. High activity and Lévy searches: jellyfish can search the water column like fish. *Proc R Soc B*. 2012;279:465.
8. Edwards AM. Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals. *Ecology*. 2011;92:1247–57.

9. Shlesinger MF, West BJ, Klafter J. Lévy dynamics of enhanced diffusion: application to turbulence. *Phys Rev Lett*. 1987;58:1100–3.
10. Shlesinger MF, Zaslavsky GM, Klafter J. Strange kinetics. *Nature*. 1993;363:31–7. <https://doi.org/10.1038/363031a0>.
11. Bartumeus F, Catalan J, Fulco U, Lyra M, Viswanathan G. Optimizing the encounter rate in biological interactions: Lévy versus Brownian strategies. *Phys Rev Lett*. 2002;89:1–4.
12. Viswanathan GM, Raposo EP, da Luz MGE. Lévy flights and superdiffusion in the context of biological encounters and random searches. *Phys Life Rev*. 2008;5:133–50.
13. Metzler R, Klafter J. The random walks guide to anomalous diffusion: a fractional dynamics approach. *Phys Rep*. 2000;339:1–77.
14. Lomholt M, Tal K, Metzler R, Joseph K. Lévy strategies in intermittent search processes are advantageous. *Proc Natl Acad Sci USA*. 2008;105:11055–9.
15. Viswanathan GM, Buldyrev SV, Havlin S, da Luz MGE, Raposo EP, Stanley HE. Optimizing the success of random searches. *Nature*. 1999;401:911–4.
16. Clauset A, Shalizi C, Newman M. Power-Law distributions in empirical data. *SIAM Rev*. 2009;54:661–703.
17. Alla Mashanova, Oliver Tom H, Jansen Vincent AA. Evidence for intermittency and a truncated power law from highly resolved aphid movement data. *J R Soc Interface*. 2010;7:199.
18. Rhee I, Shin M, Hong S, Lee K, Kim SJ, Chong S. On the Lévy-walk nature of human mobility. *IEEE IEEEE/ACM Trans Netw*. 2011;19:630.
19. Ríos-Uzeda B, Brigatti E, Vieira MV. Lévy like patterns in the small-scale movements of marsupials in an unfamiliar and risky environment. *Sci Rep*. 2019;9:2737.
20. Mantegna RN, Stanley HE. Stochastic process with ultraslow convergence to a Gaussian: the truncated Lévy flight. *Phys Rev Lett*. 1994;73:2946.
21. Gonzalez MC, Hidalgo CA, Barabasi L. Understanding individual human mobility patterns. *Nature*. 2008;453:779–82.
22. Fryxell JM, Hazell M, Börger L, Dalziel BD, Haydon DT, Morales JM, McIntosh T, Rosatte RC. Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proc Natl Acad Sci*. 2008;105:19114–9.
23. Torney CJ, Grant J, Hopcraft C, Morrison TA, Couzin ID, Levin SA. From single steps to mass migration: the problem of scale in the movement ecology of the Serengeti wildebeest. *Philos Trans R Soc B Biol Sci*. 2018;373:20170012.
24. Kazimierski LD, et al. Trajectory assessment of the vulnerable marsupial *Dromiciops gliroides* in the Patagonian temperate forest. *Mamm Biol*. 2021;101:715–27.
25. Finotti R, Vieira MV, Freitas SR, Cobra P, Rezende N, Cerqueira R. Climatic influences on leaf fall seasonality in the Atlantic Forest (Serra dos Órgãos National Park - RJ -Brazil). *Oecol Aust*. 2020;24:406–19.
26. Finotti R, Kurtz BC, Cerqueira R, Garay I. Variação na estrutura diamétrica, composição florística e características sucessionais de fragmentos florestais da bacia do rio Guapiáçu (Guapimirim/Cachoeiras de Macacu, RJ, Brasil). *Acta Bot Bras*. 2012;26:464–75.
27. Cunha A, Vieira MV. Support diameter, incline, and vertical movements of four didelphid marsupials in the Atlantic forest of Brazil. *J Zool*. 2002;258:419–26.
28. Forero-Medina G, Vieira MV. Perception of a fragmented landscape by neotropical marsupials: effects of body mass and environmental variables. *J Trop Ecol*. 2009;25:53–63.
29. Uzeda BR. Movement and dispersal of small mammals: predictive models based on biological traits, and Lévy walks by marsupials in a landscape of fragmented Atlantic Forest. Unpublished Ph.D. dissertation, Universidade Federal do Rio de Janeiro, Brazil, 2017.
30. White GC, Garrott RA. Analysis of wildlife radio-tracking data. San Diego: Academic Press; 1990.
31. Humphries NE, Weimerskirch H, Sims DW. A new approach for objective identification of turns and steps in organism movement data relevant to random walk modelling. *Methods Ecol Evol*. 2013;4:930–8.
32. Edwards AM. Using likelihood to test for Lévy flight search patterns and for general power-law distributions in nature. *J Anim Ecol*. 2008;77:1212–22.
33. White EP, Enquist BJ, Green JL. On estimating the exponent of power law frequency distributions. *Ecology*. 2008;89:905–12.
34. Aban IB, Meerschaert MM, Panorska AK. Parameter estimation for the truncated Pareto distribution. *J Am Stat Assoc*. 2006;101:270–7.
35. Anderson DR, Burnham KP, Thompson WL. Null hypothesis testing: problems, prevalence and an alternative. *J Wildl Manag*. 2000;64:912–23.
36. Hill BM. A simple general approach to inference about the tail of a distribution. *Ann Stat*. 1975;3:1163–74.
37. Van Houtan KS, Pimm SL, Halley JM, Bierregaard RO Jr, Lovejoy TE. Dispersal of Amazonian birds in continuous and fragmented forest. *Ecol Lett*. 2007;10:219–29.
38. Schwämmle V, Queirós SMD, Brigatti E, Tchumatchenko T. Competition and fragmentation: a simple model generating lognormal-like distributions. *New J Phys*. 2009;11:093006.
39. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. A movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci*. 2008;105:19052–9.
40. Revilla E, Wiegand T, Palomares F, Ferreras P, Delibes M. Effects of matrix heterogeneity on animal dispersal: From individual behavior to metapopulation-level parameters. *Am Nat*. 2004;164:E130.
41. Rocha ÉG, Brigatti E, Niebuhr BB, et al. Dispersal movement through fragmented landscapes: the role of stepping stones and perceptual range. *Landsc Ecol*. 2021;36:3249–67.
42. Benhamou S. Of scales and stationarity in animal movements. *Ecol Lett*. 2014;17:261–272.
43. Reynolds AM. Current status and future directions of Lévy walk research. *Biol Open*. 2018;7.
44. Pyke GH. Understanding movements of organisms: it's time to abandon the Lévy foraging hypothesis. *Methods Ecol Evol*. 2015;6:1–16.
45. Sikes RS, and the Animal Care and Use Committee of the American Society of Mammalogist. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J Mammal*. 2016;97:663–88.

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