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Non-random walks in monkeys and humans

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Principles of self-organization play an increasingly central role in models of human activity. Notably, individual human displacements exhibit strongly recurrent patterns that are characterized by scaling laws and can be mechanistically modelled as self-attracting walks. Recurrence is not, however, unique to human displacements. Here we report that the mobility patterns of wild capuchin monkeys are not random walks, and they exhibit recurrence properties similar to those of cell phone users, suggesting spatial cognition mechanisms shared with humans. We also show that the highly uneven visitation patterns within monkey home ranges are not entirely self-generated but are forced by spatio-temporal habitat heterogeneities. If models of human mobility are to become useful tools for predictive purposes, they will need to consider the interaction between memory and environmental heterogeneities.

Keywords: movement ecology; home range; memory; human mobility;
capuchin monkeys; scaling laws

1. INTRODUCTION

Individual human displacements have a strong impact on many collective social phenomena, such as the spread of epidemics [1–3] or cultural traits [4]. The availability of quantitative mobility data has increased in recent years through the widespread use of global positioning systems [5] and the ability to track cell phones [6–8]. These new data show that human displacements do not follow memory-less processes, like the well-known Markovian random walk [9], rather they exhibit ultra-slow diffusion and unusual, long-lasting recurrence properties owing to the tendency of individuals to frequently revisit a small number of familiar locations [7,8].

Whether unifying principles that govern the movements of humans [8] and, more generally, of living organisms [10] exist is a hotly debated issue. As with the distribution of city sizes [11] or the dynamics of individual tasks [12], scaling laws prevail in human mobility data [5,8,13]. In physical systems, scaling laws are often the outcome of self-organization principles. Self-attracting or reinforced walks [14,15] are non-Markovian stochastic walks that tend to revisit with higher probability locations visited in the past. Recently, a new reinforced walk model with preferential return to previously visited

sites, in analogy with preferential attachment rules used in network science [16], could reproduce many empirical human visitation patterns [8]. However, it is also important to quantify the dependence of individual displacements on more complex external factors—for instance, transportation [1] and social networks [17], or the spatial distribution of facilities or resources [18].

In this contribution, we show that the scaling laws characterizing recurrence in human movements are similar to those exhibited by some foraging animals, which suggests that these patterns are not unique to humans and may be generated by a more generalized set of cognitive mechanisms. We present evidence that, like humans, other animals also live in heterogeneous habitats where some areas are more valuable to them than others. Recurrent patterns of movement, in particular home range behaviour, actually characterize the ranging of a very large number of animal species [19,20]. Here, we use radio telemetry data to show that the mobility and visitation patterns of capuchin monkeys (*Cebus capucinus*) foraging for fruit in a tropical forest are not only comparable to human cell phone users qualitatively, but also exhibit scaling laws that are strikingly similar in both the short and long time regimes. In addition, monkeys' movements are not entirely self-organized, but also strongly driven by spatio-temporal variations in resource distribution.
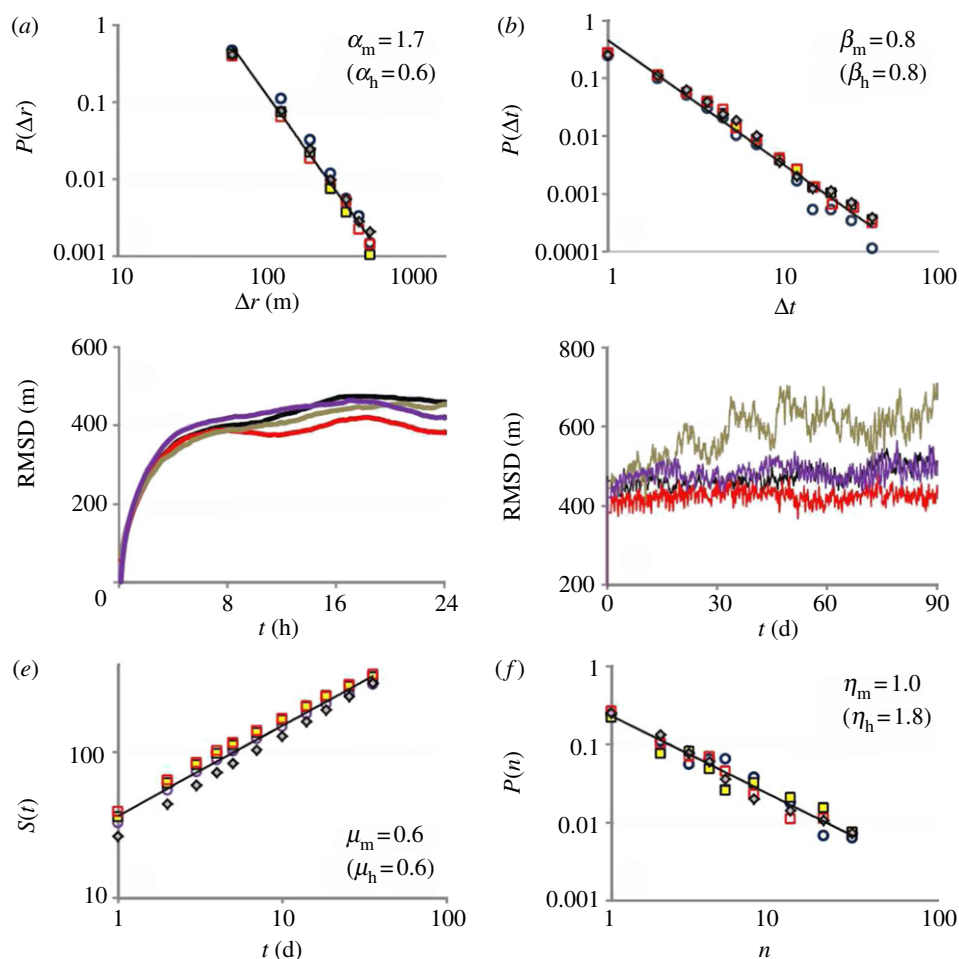
Figure 1. Comparison of monkey and human movement properties. Data for each of the four radio-collared capuchin monkeys were plotted separately. Monkey power-law exponents (subscript 'm') of the frequency distributions are estimated from pooled data using Bayesian Markov chain Monte Carlo estimation. These values are practically indistinguishable from the maximum-likelihood estimates (MLEs), which are not shown. Human power-law exponents from [8] (subscript 'h') are given in each plot for comparison. (a) Displacements between consecutive telemetry fixes (Δr in metres) showed a much steeper decay, $P(\Delta r) \sim (\Delta r)^{-1-\alpha}$ with larger α, than in humans but (b) waiting times (1 unit = 10 min) showed a power-law exponent close to humans. (c) RMS displacement $\langle (\mathbf{r}(t) - \mathbf{r}(0))^2 \rangle^{1/2}$ (in metres) rose quickly during the first day but (d) very slowly thereafter, with values always much smaller than the size of Barro Colorado Island (diameter ~ 5 km). (e) The number of distinct 50×50 m habitat cells visited, $S(t)$, as a function of time. (f) Like for humans, the probability that a cell received n visits within the six month time interval, $P(n)$, decays as a power-law, but with a smaller exponent. Estimation cut-offs for Δr, Δt and n were set, respectively, at 350 m, 12 h and 35 visits. In all cases, the bounded power-law model was a very good fit to the data ($R^2 \geq 0.98$), and the frequency distribution with MLE had an Akaike weight > 0.9999 when compared with the most likely exponential distribution. The sizes of the 95% CIs of the exponent values were always lower than 0.20. (Online version in colour.)

2. RESULTS

The data for our analyses come from a study on Barro Colorado Island, Panama, in which the movements of four radio-collared capuchin monkeys belonging to different social groups were tracked using an automated telemetry system over the course of a six month period, from November 2004 to April 2005 (see [21] for details). The locations for each individual were estimated every $\Delta t_0 = 10$ min and discretized into square cells of size 50×50 m, a scale that corresponds roughly to the measurement error and was taken as the spatial resolution. Unless indicated, we considered all available positions (night and day) in the analyses.

2.1. Basic movement properties

Short time-scale properties of monkey movement paths followed similar scaling forms as those of human cell phone users [8] (figure 1a,b). For example, the distributions of the displacement Δr between consecutive telemetry fixes are good fits to a power law, $(\Delta r)^{-1-\alpha}$ with $\alpha \simeq 1.7$ in the range of 50 m $< \Delta r < 350$ m, for all four individuals (sample sizes = 1619, 1998, 3072 and 2097). This exponent, as well as β and η below, was obtained by using a Bayesian Markov chain Monte Carlo simulation with uniform priors and the Metropolis–Hastings algorithm. For each measure, we evaluated the likelihood of a given value of the exponent of the bounded power law given the data. The exponent value is the average obtained from the posterior support distribution. We also calculated the maximum-likelihood estimate (MLE), obtaining practically the same value.

Similarly, the waiting time Δt, defined as the number of consecutive fixes found in the same 50×50 m cell multiplied by the temporal resolution Δt_0, follows a

power-law distribution, $P(\Delta t) \sim (\Delta t)^{-1-\beta}$ with $\beta = 0.8$, the same value as reported for humans [8,13] and other primates [22]. The exponents $\alpha < 2$ and $\beta \leq 1$ play central roles in continuous time random walk (CTRW) models of anomalous transport [13,23] and of biological Lévy flights [22,24,25].

However, as in the case of humans, monkey trajectories are incompatible with a random Lévy walk description at large timescales, as they exhibit strong recurrent patterns of movement. For example, the root mean squared displacement (RMSD) virtually asymptotes within one day, rather than following a classical power-law growth with time (figure 1c,d). This arrested or ultra-slow diffusion is a manifestation of home range behaviour [19,20]. Likewise, the average number $S(t)$ of distinct cells visited during a time interval t (figure 1e) increases through time as t^μ with μ smaller than the waiting time exponent β, which is what would have been expected for a CTRW [8,23]. One finds $\mu = 0.6$, remarkably close to what was measured by Song *et al.* for humans [8]. Another intriguing aspect of recurrence is the highly uneven visitation pattern among cells (figure 1f). Within the six month data collection period, the probability $P(n)$ of finding a cell that has received n visits by the same individual (i.e. has been entered n times) is not well described by a Poisson distribution or a bell-curve centred around a characteristic value. Instead, it follows a power law, $P(n) \sim n^{-\eta}$ with $\eta = 1.0$ ($\eta = 1.8$ in humans [8]). Whereas most sites were visited once or twice, it is not rare to find popular activity 'hotspots' or 'hubs', with 30 or more visits. In contrast, a random walker bounded in a closed domain would visit all sites more or less equally frequently. For all the properties described earlier, the four individual monkeys showed very similar exponent estimates. The number of distinct cells visited by the animals during the six-month period was 568, 488, 606 and 531, respectively.

2.2. Recurrence and environmental forcings

Like humans, many animals have sophisticated memory skills [26] and home ranges can emerge from frequent returns to previously visited locations [27]. In principle, home ranges could even be completely self-organized, arising as a result of the walker's history. Random walks biased towards the centre of mass of all previously visited sites, or such that, at each step, there is a finite probability of returning to a randomly selected site visited in the past, exhibit arrested or very slow diffusion [20,28]. In the context of human mobility, the results of figure 1 have been reproduced by assuming that the probability of choosing a given site is proportional to the number of previous visits to that site ('preferential attachment'), and assuming that the probability of taking a random step (to a unvisited site) decays algebraically with the number of sites already visited, $S(t)$ [8]. An advantage of this latter approach is that it builds up uneven visits and power-laws for the distribution $P(n)$.

What these models and those belonging to a much broader class based on preferential attachment mechanisms ignore is environmental heterogeneity. A mobile

agent may be inclined to visit a place not because it is familiar but because of some intrinsic quality of the location, (e.g. food content). Heterogeneity is implied in the relationship between the quality of habitat cells and the probability of cell revisit. Capuchin monkeys' home ranges typically contain millions of tree stems that belong to more than 200 species (M. C. Crofoot 2005, unpublished data), vary in size by two orders of magnitude [29] and only episodically produce fruit [30]. Consequently, the cells in our analyses varied widely in the content of monkeys' primary food, ripe fruit. During the day (from 04.00 to 20.00 h), animals are awake and active [21], and their primary activities are feeding and foraging with relatively rare periods of prolonged resting (M. C. Crofoot 2005, unpublished data). During the day, a waiting time of $\Delta t = \Delta t_0 = 10$ min (one fix, the minimum observable value) is assumed to correspond to a 'transit' through a cell. Given a series of consecutive fixes in a same cell, the time elapsed between the first and the last fixes, $\Delta t - \Delta t_0$, can be taken as a proxy of the ripe fruit content within the corresponding cell. An individual will tend to spend more time feeding in a tree that has more fruit and we consider $\Delta t = \Delta t_0$ as the threshold above which one can tell that a feeding event occurred. Figure 2 shows a positive correlation between the number n of daytime visits received by a cell and the average duration of a visit at that cell, $\langle \Delta t - \Delta t_0 \rangle_n$ (the average being taken over all visits among cells with n visits). The latter quantity can be approximated by a scaling law:

$$\langle \Delta t - \Delta t_0 \rangle_n \sim n^\gamma, \qquad (2.1)$$

with $\gamma \approx 0.3$. Although other functional relations may fit the data, the crucial point is that large n cells have, on average, longer waiting times and, most likely, higher food content. A similar, and even clearer, relationship is observed if all night and day positions are taken into account ($\gamma \approx 0.4$ in this case). Sleeping trees also represent resources, as not all trees are suitable for sleep at night.

Similarly, the time elapsed between two consecutive daytime visits to a site depends on the results of the initial visit. We denote $\text{MFRT}_{\Delta t}$ as the mean first return time to a cell where the waiting time was Δt at the last visit. As shown by figure 2b, the MFRT tends to decrease with increasing patch quality (Δt). For $\Delta t \leq 100$ min, it approximately follows the scaling law:

$$\text{MFRT}_{\Delta t} \sim (\Delta t)^{-\delta}, \qquad (2.2)$$

with $\delta \approx 0.3$. Note that the unaveraged first return time is a variable known to fluctuate widely in simple models such as the random walk [31]. Similarly, here the error bars in figure 2b increase with Δt, which may be due to the fewer available observations at larger Δt (figure 1b). Averages obtained from less than five observations were discarded.

These results show evidence that, in addition to being non-random, movement choices are driven by resource availability, with larger food patches visited more often. Equation (2.2) also holds if night and day positions are aggregated ($\gamma \approx 0.4$). Hence, a new
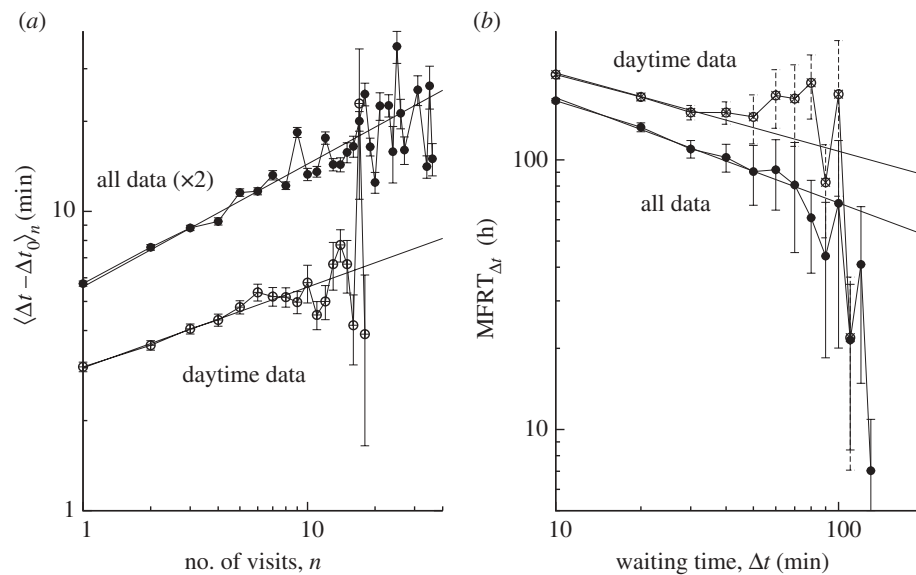
Figure 2. (*a*) Average visit duration at a cell that has otherwise received n visits during a time window corresponding to $S = 200$ distinct visited sites (about 2 week period). Each point represents an average over sites with n visits in one time window, over 12 different time windows and the four different monkeys. The curve obtained from all fixes ('all data') has been upscaled by a factor 2 for clarity. (*b*) Mean first return time to a cell as a function of the time spent on that cell during the last visit. Averages obtained from less than five observations were discarded. The solid lines are least-square fits and have slopes: 0.41 and 0.27 in (*a*) (all data and daytime data, respectively); -0.39 and -0.29 in (*b*) (all data and daytime data, respectively). In all cases, the probability that the variables are uncorrelated ($\delta = \gamma = 0$) is $p < 10^{-5}$.

waiting time is not randomly drawn at each cell visit, as assumed in CTRW models. Rather, the situation here is analogous to systems with quenched site disorder [31]. In trap models, though, the frequency of visits to a site by a memory-less random walker is independent of the waiting time ($\gamma = \delta = 0$).

Unlike supermarkets, gas stations or other human facilities, resources in natural ecosystems tend to be ephemeral. Trees produce fruit transiently and often asynchronously, with the fruiting periods of individual trees lasting from a few weeks to a couple of months [30]. Capuchin monkeys' hotspots, in particular, are not permanent. Figure 3*a* shows the positions of the 5 per cent most visited sites by a single individual during the day in successive non-overlapping time periods (of about two weeks) with $S = 200$ visited sites each. These cells are rarely the same from one time window to the other. The fluctuating cloud formed by the visited cells suggests a flexible use of space, despite the stability of the overall home range. Defining hotspots as the most frequently visited 10 per cent of sites, the probability $\Pi_{hs}(m)$ that a cell which is a hotspot during a time window i is also a hotspot during time window $i + m$ decays rapidly with m (figure 3*b*). The average number of visits $N_{hs}(m)$ received by a cell in time window $i + m$, given that this cell was a hotspot in time window i, also decays with m (figure 3*c*). Very similar curves are obtained if night and day data are aggregated.

3. CONCLUSIONS

We have shown that the individual movement patterns of humans are similar to those of capuchin monkeys. Most notably these patterns exhibit ultra-slow diffusion

(indicating the presence of a home range) and history-dependent recurrence properties obeying scaling laws. In monkeys, we have presented evidence that these non-random walks are caused by the use of memory, a behaviour that is not unique to humans nor evolutionary novel. These results suggest, but do not prove, that similar cognitive mechanisms may govern the movements of many animals. Testing such hypothesis would require data analysis for a variety of species.

Our analyses also indicate that monkey movements are driven by environmental heterogeneities. Monkey ranging patterns are thus not 'self-quenched' into a routine emerging from initially random movements that would be re-inforced and dominated at large time by frequent revisits to a small number of known locations, a mechanism proposed for human mobility [8]. Similarly, it is likely that human movements are not entirely self-organized, as this would imply that the locations of activity hotspots would be uncorrelated with environmental factors. In the real world, many hotspots would clearly be shared because of some intrinsic property of the location: e.g. schools, transit hubs or office buildings. A difference is that many human resources last over long timescales, such as homes and workplaces [6]. Yet, others are transient (such as restaurants, trendy night-clubs or fashionable shops) or seasonal (such as swimming pools and ski-resorts). A place can also be abandoned for another not because it is depleted but because the appetite for that resource has been temporarily sated.

Despite the similarities between human and monkey movements, there are important differences. In humans, the home range size fluctuates widely from one individual to another, ranging between 1 and 1000 km approximately [6,8]. In contrast, the nearly identical home range
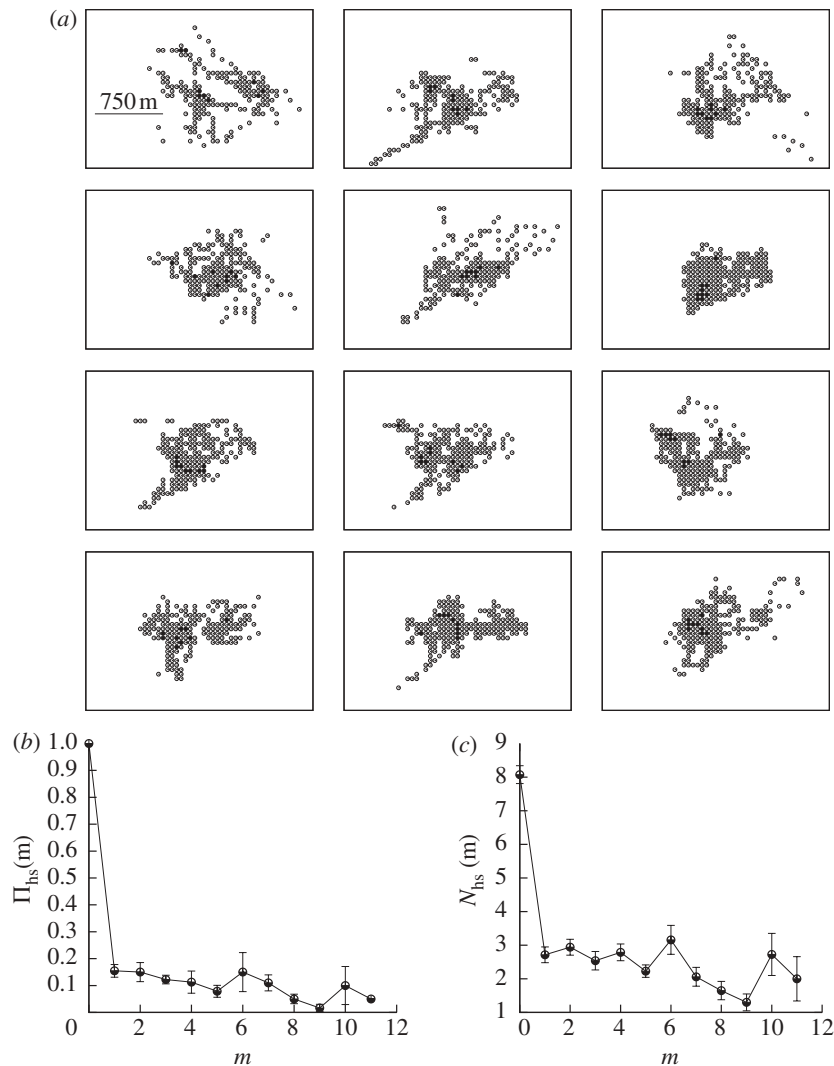
Figure 3. (*a*) Daytime (4.00–20.00 h) positions occupied by the same individual monkey during successive, non-overlapping periods each containing $S = 200$ visited sites. The black dots represent the 10 most visited cells during the day, for each time period. Chronological order goes from left to right and top to bottom. (*b*) Hotspot probability and (*c*) Π_{hs} mean number of visits to a hotspot N_{hs}, as a function of the separation m between time windows (see text).

sizes found for the four monkeys (figure 1*c,d*) suggest a narrow size distribution, probably owing to comparable habitats, energetic needs and locomotor capacities. This is consistent with the fact that the home range of a capuchin group overlaps with a relatively small number of other home ranges [21], which probably limits intergroup interactions to nearest neighbours or next-nearest neighbours. This property is not shared by all animal species, though. Territorial prides of Serengeti lions occasionally make long-range contacts with other prides as well as with nomadic individuals, producing a denser network of contacts with the 'small world' property that characterizes many human social networks [32].

Similar to random diffusion models of animal movements with intermittent central attraction [33], several models of human mobility with preferential return to home have been introduced recently, showing that recurrence can have marked effects on spreading processes in large populations [1–3]. These latter models typically assume a known set of locations that can be visited and Markovian, individual-dependent transition rates

between locations. Developing parallel modelling frameworks that adequately represent both self-organization and environmental forcing will be critical to the success of human movement models for purposes such as controlling the spread of infectious diseases. These alternate models should incorporate cognitive mechanisms that many vertebrates use, e.g. spatial representation mechanisms (cognitive maps or travel cost discounting) and temporal mechanisms (episodic memory) [34]. How scaling laws emerge from the interplay between memory and landscape features remains elusive.

del Ambiente, Panama and the Smithsonian Tropical Research Institute Institutional Animal Care and Use Committee. All research complied with the laws of the Republic of Panama and the United States.

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