Ranging patterns of hamadryas baboons: random walk analyses

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ARTICLE INFO

Random walks have long been used to characterize animal movement patterns; recently, this practice has received renewed impetus via the application of Lévy walk models. Whilst such models have produced encouraging results, the methods applied have been inconsistent and often problematic; furthermore, primates remain under-represented in such studies. This paper addresses both of these problems via the explanation of a novel and robust analytical method as applied to an extensive primate data set. In a study of a band of hamadryas baboons at the Filoha outpost of Awash National Park, Ethiopia from March 2005 to February 2006, the baboons' location was mapped every 15 min during all-day follows using a handheld GPS unit, yielding over 3000 step lengths and waiting times documented across 105 complete follows. Both power law and exponential models were fitted to the step length and waiting time data via maximum likelihood procedures within a model selection paradigm facilitated by the use of an information criterion to distinguish between models. Results show that the step lengths were exponentially distributed, and thus consistent with a random distribution of resources in space. Waiting times, however, were power law distributed, and thus consistent with a power law distribution of patch sizes. We evaluate these results within a discussion of the extent to which random search algorithms are applicable to animals with extensive knowledge of their habitats.

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Animal ranging behaviour tends to occur within the context of foraging, and travel patterns are thus closely tied to the distribution of food resources (Kinnaird & O'Brien 2000; Milton 2000). The foraging demands of primates in particular may exceed those of other mammals because primates tend to be large-bodied and social and therefore must choose food patches that are sizeable and abundant in order to feed the whole group and minimize feeding competition (Janson 2000). When food and water resources are patchily distributed in both time and space, animals may need to structure their ranging and foraging strategies accordingly (Milton 1981; Oates 1987). Foraging may be enhanced by using strategies that increase the likelihood of encountering preferred feeding items, such as travelling in straight lines between them (Garber & Paciulli 1997; Menzel 1997; Milton 2000). Successful travel decisions incorporate information about various ecological factors, such as the location and patterns of changing resource abundance (Garber & Dolins 1996).

Prior research suggests that primates are able to perceive and remember patterns of resource availability and distribution and incorporate them into their travel decisions. The majority of such support

stems from experiments carried out in captive settings. Simulated foraging tasks have shown evidence for spatial memory in redtail monkeys, *Cercopithecus ascanius* (MacDonald & Wilkie 1990), Japanese macaques, *Macaca fuscata* (Menzel 1991), and longtailed macaques, *M. fascicularis* (Menzel 1996a, b). Experimental and naturalistic field studies of foraging behaviour in natural conditions have suggested the use of spatial memory in moustached tamarins, *Saguinus mystax*, saddle-back tamarins, *S. fuscicollis* (Garber 1989; Garber & Hannon 1993; Garber & Dolins 1996), white-faced capuchins, *Cebus capucinus* (Garber & Paciulli 1997) and brown capuchins, *C. apella nigritus* (Janson 1996, 1998). While much work on primate foraging and travel patterns has focused on arboreal frugivores, animals living in savanna environments, such as baboons, probably face similar foraging challenges.

Previous research has shown that home range use among baboons is affected by the spatial distribution of important resources (Barton et al. 1992), and that seasonal changes in their availability influence baboons' travel patterns (e.g. Kummer 1968; Altmann & Altmann 1970; Whiten et al. 1987; Barton et al. 1992). The resources that play the largest roles in determining baboons' home range use and travel patterns are (1) food (e.g. Devore & Hall 1965; Altmann & Altmann 1970; Barton et al. 1992; Henzi et al. 1992; Altmann 1998), (2) water (e.g. Altmann & Altmann 1970; Altmann 1974, 1998; Barton et al. 1992) and (3) sleeping sites (e.g. Devore & Hall 1965; Altmann & Altmann 1970; Anderson 2000).

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Hamadryas baboons, *Papio hamadryas hamadryas*, live in semi-desert habitats throughout the Horn of Africa (in parts of Ethiopia, Eritrea, Djibouti, Sudan and Somalia) and the Arabian Peninsula in Yemen and Saudi Arabia (Kummer 1968; Kummer et al. 1981; Biquand et al. 1992; Al-Safadi 1994; Zinner et al. 2001; Swedell 2002b, 2006). They are known for their flexible, multilevel social structure in which large groups (bands) break into smaller foraging parties (one-male units and clans) during daily travel. They have large home ranges and long daily path lengths compared with other primates, both of which are attributed to the sparse distribution of food and water in their habitats (Kummer 1968; Sigg & Stolba 1981; Swedell 2002b, 2006). Previous research suggests that this pattern of resource distribution influences hamadryas ranging behaviour. Kummer (1968, 1971) reported that the baboons spent a greater proportion of time in areas of their home range containing sleeping cliffs, water holes and Acacia trees than in areas without these resources. The baboons seemed to remember specific locations in their natural environment and appeared to travel between them via the shortest route. When in search of water sources, the baboons appeared to use least-distance strategies to travel from one location to another, and they sped up as they approached a water source even before it was in view (Kummer 1968).

Similarly, Sigg & Stolba (1981) reported several lines of evidence suggesting that hamadryas baboons know the spatial layout of their home range. First, they found a strong correlation between departure direction (from the sleeping cliff) and the location (relative to the sleeping cliff) of the midday water hole. Members of bands often split up after leaving the sleeping cliff but reunited at midday water holes, arriving from an assortment of directions and morning travel sequences (Sigg 1986). Second, the baboons reached frequently visited resources from a wider variety of departure directions than sites visited less commonly. In addition, the baboons' travel speed increased more frequently before reaching such resources than would be expected by chance, even when those resources were not in sight (Sigg & Stolba 1981).

The current study aims to expand on previous research by quantifying the movement patterns of hamadryas baboons within the framework of a random walk analysis. We present both a comprehensive empirical data set and a robust means of analysing that data set, developed from the growing literature within movement ecology on the use of quantitative, random walk characterizations of animal movement.

RANDOM WALKS

The use of random walk models has a long history in ecology and biology; such models have been used both to describe empirical data and as input to simulation models. What may be termed the 'original' or 'simple' random walk was first borrowed from physics by biologists of the 1950s who were interested in modelling the diffusion of organisms via mathematical means (Skellam 1951; Patlak 1953a, b; Reid 1953). All forms of random walk are composed of three basic sets of measurements: the step lengths, waiting times and turning angles, each of which can be characterized via a given statistical or probabilistic distribution (Berg 1983).

Simple random walks are ubiquitous in biological studies of animal movement (e.g. gophers: Benedix 1993; gazelles: Ward & Saltz 1994; wood mice: Blackwell 1997; caribou: Schaefer et al. 2000). The literature on theoretical advances in the study of random walks as animal search patterns is also continuously growing (e.g. Bartumeus et al. 2002, 2005, 2008; Benichou et al. 2006; Bradshaw et al. 2007; Borger et al. 2008; Codling et al. 2008). In addition to these basic forms, the use of Lévy walks to

model foraging is one of the foremost current trends in the mathematical treatment of movement data. The Lévy walk is simply a random walk in which the step lengths conform to a Lévy distribution, for which the probability of step of length l, $p(l)$, is given by

$$p(l) = cl^{-\mu}, \quad 1 < \mu < 3. \tag{1}$$

This distribution was established by Paul Lévy in the context of an expansive treatment of the addition of stochastic variables (Lévy 1937). Following the first published reference to Lévy walks in animal search behaviour (Shlesinger & Klafter 1986), empirical demonstrations of Lévy walk behaviour in the ecological literature appeared only periodically (e.g. Levandowsky et al. 1988a, b). However, spurred on by a series of landmark papers by Viswanathan et al. (1996, 1999, 2000, 2001, 2002), similar applications have appeared with increasing frequency over the past decade. Viswanathan and colleagues demonstrated via simulation that the Lévy walk is an optimal search pattern for a forager searching without prior information for randomly distributed, static, nondepleting food items at low density (Viswanathan et al. 1999). The simulation studies of Viswanathan et al. (1999, 2000, 2001, 2002) were complemented by empirical data on bumblebees and deer (Viswanathan et al. 1999), with both data sets showing Lévy walk behaviour and thus demonstrating what are thought to be optimal search strategies. These data were followed by additional data on reindeer (Mårell et al. 2002) and an extensive series of studies on search strategies in bees (Reynolds 2007, 2008; Reynolds & Frye 2007; Reynolds et al. 2007b, c) as well as papers reporting Lévy walk or Lévy walk-like behaviour in soil amoebas (Levandowsky et al. 1997), microzooplankton (Bartumeus et al. 2003), jackals (Atkinson et al. 2002), albatrosses (Fritz et al. 2003), arctic seals (Austin et al. 2004), moths (Reynolds et al. 2007a), elephants (Dai et al. 2007) and goats (de Knegt et al. 2007). In addition to these empirical studies a slew of papers highlighting theoretical advances pertaining to the interpretation and biological relevance of Lévy walks have appeared in the past decade (e.g. Ricotta 2000; da Luz et al. 2001; Alonso et al. 2002; Raposo et al. 2003; Hancock & Milner-Gulland 2006; Sims et al. 2006; Coscoy et al. 2007). Although doubts over the means of identifying Lévy walk behaviour have frequently surfaced (Benhamou 2007; Edwards et al. 2007; Sims et al. 2007), a recent and expansive study by Sims et al. (2008) demonstrating Lévy walks in sharks, sea turtles and penguins has hinted at their pervasiveness in the animal world.

The importance of the Lévy walk to the ecological study of movement is centred upon the finding that it is an optimal search algorithm (Viswanathan et al. 1999). In tune with many more traditional studies of optimal foraging theory, the finding of a Lévy walk pattern in the movement of a foraging animal suggests that, given certain assumptions about that animal's environment, it has evolved either an innate propensity or a cognitive capacity for adopting a strategy that will yield the greatest possible energetic return per unit time. The distinction between the evolved and the cognitive is a heuristic dichotomy we will return to in the discussion section below; suffice to say, however, that the findings of Lévy walk movement patterns in organisms as diverse as soil amoeba, bees and reindeer suggest the presence of convergent evolutionary pathways and thus a substantial adaptive advantage to this strategy. This advantage is almost certainly related to the resource structure upon which a given organism subsists. Whilst the movement described by a simple random walk equates to Brownian motion across a landscape, with step lengths defined by the finite mean and variance of the normal distribution, the 'super-diffusivity' of the Lévy walk, stemming as it does from a scale-free distribution with nonconvergent mean and variance, creates

a power law pattern that better approximates the distribution pattern of many primary resources (e.g. Palmer 1988; Loehle & Wein 1994; Loehle & Li 1996; Li 2000; Brown et al. 2002). Many plant species have been demonstrated to grow according to spatial power law distributions (see, e.g. Critten 1997; Escos et al. 1997; Alados et al. 2003, 2005; Dannowski & Block 2005) and thus it is logical to suggest that an animal subsisting on such flora would be well served by adopting a power law search pattern in the absence of information.

Random walk studies of primates remain scarce. Recently, however, Ramos-Fernández et al. (2004), studying the foraging patterns of a group of free-ranging spider monkeys in the forest of the Yucatan Peninsula, Mexico, demonstrated that the step lengths of this group show power law scaling, and are thus consistent with a Lévy walk. The expansion of Lévy walk studies to encompass primate foraging is of particular interest given the cognitive implications raised above. Given arguments concerning the presence of mental maps among many primates (e.g. Menzel 1973, 1979; Sigg & Stolba 1981; Boesch & Boesch 1984; Sigg 1986; Garber 1989, 2000; Janson 1996), it is reasonable to suspect that the assumption of no information postulated in the original simulations of Viswanathan et al. (1999) is violated. If the foraging animal has detailed prior knowledge of its home range, is the Lévy walk model still a likely approximation of the foraging pattern and,

if so, what does this imply about the animal's cognitive relationship with the environment?

TESTING FOR LÉVY WALKS

Most early research papers identifying Lévy or other power law distributions in animal movement data used least squares fitting methods on histograms. A frequently employed procedure has been to fit what is in effect a regression line to data graphed according to equation (1) or its logarithmic transformation,

$$\ln p(l) = \ln c - \mu \ln l, \tag{2}$$

the advantage of the latter being that, when either the data or the axes are logarithmically transformed, a sample of power law distributed data appears as a straight line of slope $-\mu$ (see Fig. 1a,b). It has often been assumed that presenting movement data plotted in this way and demonstrating the validity of the linear fit via a high value of the coefficient of determination is sufficient for a conclusion of Lévy walk behaviour. However, the deceptive simplicity of this technique hides a number of problems (see Fig. 1 for a graphical description of these). Below, we outline and extend an emerging consensus as to the most efficient and accurate means of testing for the presence of power laws in empirical data, and thus for Lévy walk mobility patterns in hamadryas baboons.
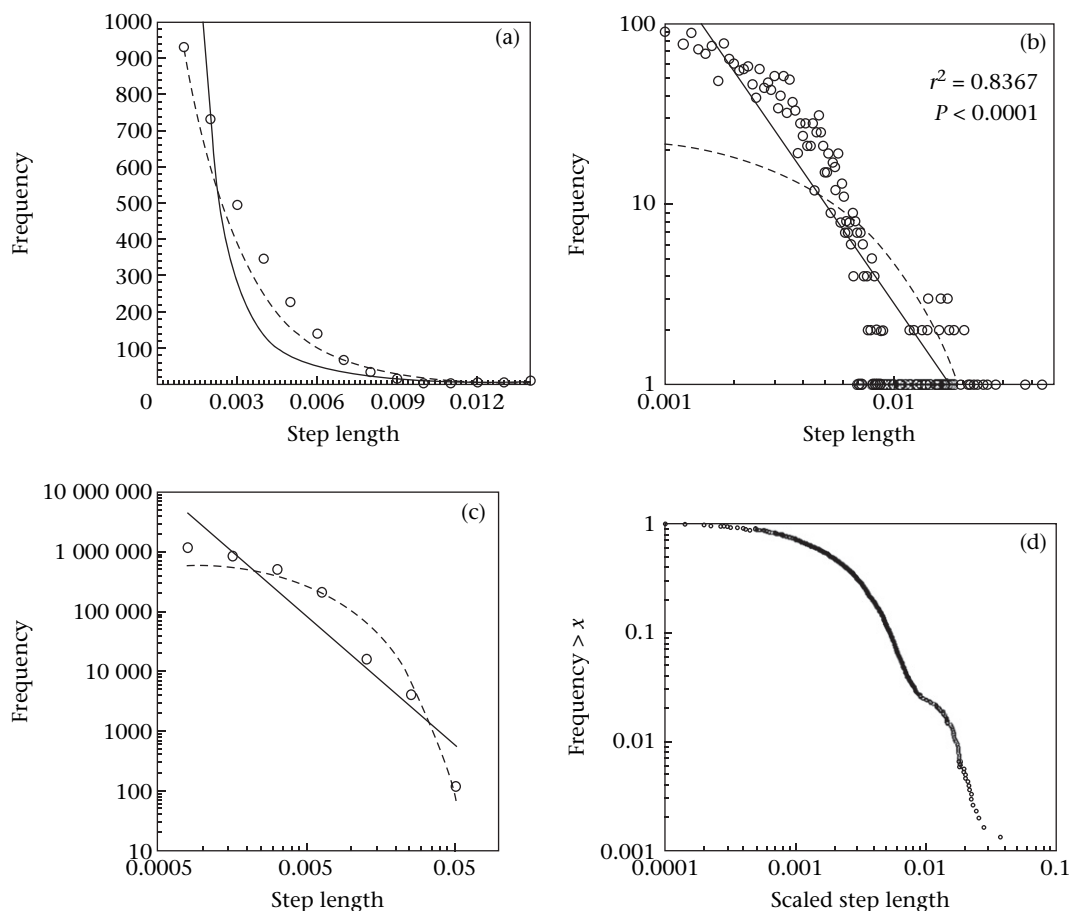

Figure 1. (a) Plot of the complete step length data of hamadryas baboons on linear scales with a bin size of 0.001; solid line: least squares regression (LSR) power law fit; dashed line: LSR exponential. (b) Log–log plot of the same data set with a bin size of 0.001 and the LSR power law and exponential fits as before. The coefficient of determination and significance level given are for the power law fit, indicating that this model would be firmly supported by the least squares method. (c) The data plotted according to the method of logarithmic binning; plotted in this way, the data clearly do not follow a straight line, and are better approximated by the exponential. (d) Relative frequency of cumulative density plot of the data, which avoids arbitrary binning of any kind and is an ideal visual starting point for the maximum likelihood method.

METHODS

Study Site and Subjects

Data on hamadryas ranging patterns were collected at the Filoha outpost of Awash National Park, Ethiopia (9°6′27′N, 40°0′50′E) from March 2005 to February 2006. The outpost is surrounded by about 2 km² of natural hot springs, doum palm trees (*Hyphaene thebaica*), swamp vegetation, and a 1.5 km long cliff (Swedell 2002b, 2006). Several bands of hamadryas baboons populate the Filoha region. The study group (Band 1) has been the focus of studies intermittently since 1996 (previously called 'Group 1': Swedell 2000, 2002a, b, 2006; Swedell & Tesfaye 2003). In February 2006, Band 1 consisted of approximately 210 individuals, including 24 leader males, 7 follower males, about 20 adult and subadult solitary males, 53 adult females, 13 subadult females, and at least 90 juveniles and infants.

Data Collection

In January 2004, A.S. visually characterized and mapped the Filoha region based on the dominant vegetation and topology, and described five habitat types: Acacia scrublands, palm forests, open grasslands, swamp vegetation and cliffs (Fig. 2). Acacia scrublands, open grasslands and cliffs are all typical of hamadryas habitat in other parts of their geographical range (Kummer 1968; Sigg & Stolba 1981; Biquand et al. 1992; Al-Safadi 1994; Zinner et al. 2001; Swedell 2006). The presence of palm forests and swamp vegetation, however, is unique to Filoha. There are at least four cliffs in the Filoha vicinity (Fig. 2), although the baboons predominantly slept on two: the Filoha cliff (about 200 m from camp) and the Wasaro cliff (about 4 km west of Filoha).

Data on ranging patterns derive from all-day follows of Band 1. Accompanied by a field assistant and/or an Ethiopian Wildlife Conservation Department scout, A.S. located the baboons at their sleeping cliff at 0600 hours and followed them until 1800 hours, or for as long as possible until we had to leave them in order to arrive at camp before dark. The band was followed on days when the baboons slept on the Filoha cliff the previous night, as well as on some days when they slept on the Wasaro cliff the previous night. During all-day follows, A.S. mapped the geographical centre of the band every 15 min (e.g. Sigg & Stolba 1981) using a Garmin etrex Legend handheld Global Positioning System (GPS) unit. The GPS unit provided positional coordinate readings to the ten-thousandth of a minute, and was accurate to within 10 m. Home range was defined as the total area used by the band over the course of the study period. It was calculated as the minimum convex polygon that included all recorded locations (from full and partial observation days) using ArcView GIS 3.1 software (Ostro et al. 1999). In this method, all points are connected by the smallest-area polygon with internal angles less than or equal to 180°.

Analyses

By far the majority of publications dealing with the issue of Lévy mobility in foraging animals have employed variations on
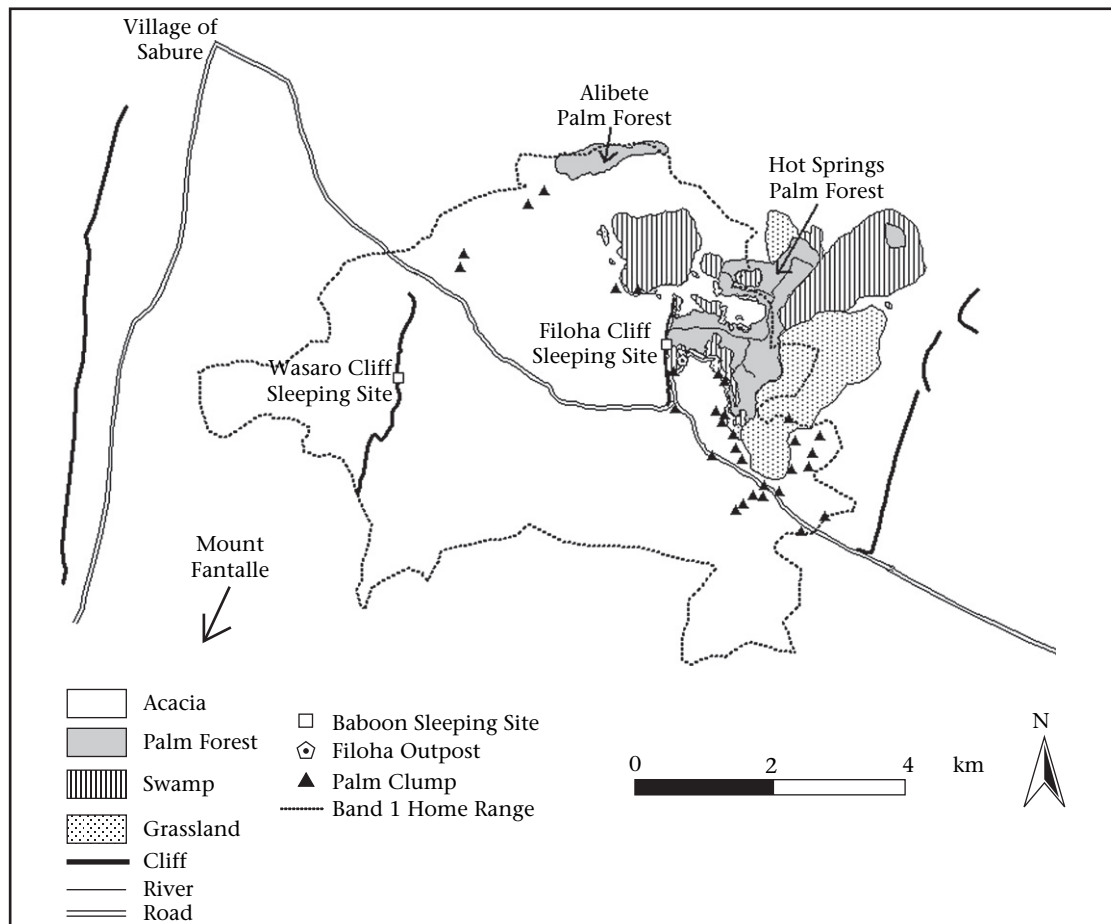

Figure 2. Map of Filoha region showing habitat types and the home range of hamadryas baboons in Band 1.

the flawed least squares methodology outlined above; however, recently a number of researchers in the ecological sciences have asserted the value of the maximum likelihood method (Newman 2005; Edwards et al. 2007; Edwards 2008). This development has been complemented by input from physical scientists offering refinements of the methods used in animal movement studies and the simulation models that have been formulated in parallel (Viswanathan et al. 2008; Raposo et al. 2009). Although maximum likelihood is not a graphical method, most researchers advocate the use of a relative frequency plot (also referred to as a cumulative density or survival function) to visualize the shape of the data. The relative frequency plot has the advantage of not using binned data; thus, the full shape of the data can be viewed in an unbiased format (see Fig. 1d). The method of maximum likelihood involves first calculating the exponent of the distribution, from which a log likelihood for the model can be calculated. In the current study we calculated exponents and likelihoods for both the power law, as a test of Lévy mobility, and the exponential, as a null model of randomly occurring move lengths. A third hypothesis, that the power law distribution arises as the result of 'composite Brownian walks' (Benhamou 2007), was not tested here as it was clearly incompatible with our findings regarding the two primary hypotheses stated above. The strength of the method lies in the comparison of these two models via an information criterion combined with the estimation of p values via a bootstrap simulation method (Clauset et al. 2009). To calculate step lengths, we first transformed our data from latitudinal and longitudinal coordinates into great circle distances between pairs of points using the haversine. Each step length, defined as the distance between two successive GPS fixes at 15 min intervals, is thus scaled to a consistent ratio that takes into account the curvature of the earth. Formally, the great circle distance between two points specified only by latitudinal (α) and longitudinal (δ) coordinates is given by Sinnott (1984) as

$$d = 2 \cdot \arctan\left(\frac{\sqrt{\text{hav}(\theta)}}{\sqrt{1 - \text{hav}(\theta)}}\right), \tag{3}$$

where

$$\text{hav}(\theta) = \left[\sin\left(\frac{\alpha_1 - \alpha_2}{2}\right)\right]^2 + \cos\alpha_1 \cos\alpha_2 \left[\sin\left(\frac{\delta_1 - \delta_2}{2}\right)\right]^2. \tag{4}$$

This correction produces only minor changes in the data set, but is nevertheless considered appropriate given that potential errors resulting from failure to apply the correction would not be systematic across the data set. Following this transformation of the whole data set, we then divided the step lengths into four groups based on the sleeping cliff at which the band began and completed their daily foraging route. Thus, we analysed the complete data set as well as four separate subsets where the band (1) started and ended at Filoha, (2) started and ended at Wasaro, (3) started at Filoha and ended at Wasaro and (4) started at Wasaro and ended at Filoha. The same procedure was followed for the waiting times, which were calculated as multiples of the 15 min periods used for sampling. For example, when the group was recorded as being in the same position for three subsequent observations, it was considered to have registered a waiting time of 30 min, with a general formula being the number of consecutive periods minus one multiplied by 15. This calculation provides minimum waiting times (in the example above, the group could have been stationary for a period approaching 45 min), but this potential discrepancy affects only the intercept (or constant) of the best-fit line, and has no effect on the exponent, which is the variable of interest. The waiting times

method therefore uses a discretized data set, requiring certain modifications to the maximum likelihood formulas, as outlined below.

To derive the model exponents for the step length data sets, we first calculated maximum likelihood estimates of the power law exponents, μ_{MLE}, as follows

$$\mu_{\text{MLE}} = 1 + n\left(\sum_{i=1}^{n} \ln\frac{x_i}{x_{\min}}\right)^{-1}, \tag{5}$$

where n is the total number of measured step lengths, and $x_{\min}$ is the minimum step length included in the analysis. When dealing with empirical data sets it is customary to fit the power law to the tail of the data only; thus values below a specified cutoff value at $x_{\min}$ will not be included. Clauset et al. (2007, 2009) provide a method for choosing the value of $x_{\min}$ by minimizing the value of the Komolgorov−Smirnov statistic measuring the maximum distance between the curve of the data and the best-fit power law model; however, given the hypothesis-testing framework used here we feel that optimizing the value of $x_{\min}$ for the power law would bias model comparisons towards validation of the Lévy hypothesis. It is imperative to the integrity of the model selection exercise that the power law and exponential models are compared over the same range of data; thus the solution of optimizing independently for each of the two models is not available to us. Given that the standard alternative involves simply estimating $x_{\min}$ by eye, we chose instead to employ two arbitrary values at 0.0001 and 0.001. The effects of these two cutoffs will be apparent from the Results and will be evaluated further in the Discussion. Following estimation of the exponent, the log likelihood for the power law model can be calculated as

$$L_{\text{pow}} = n(\ln(\mu_{\text{MLE}} - 1) - \ln x_{\min}) - \mu_{\text{MLE}} \sum_{i=1}^{n} \frac{\ln x_i}{x_{\min}}. \tag{6}$$

Similarly, the exponent of the exponential model, λ_{MLE}, is given by

$$\lambda_{\text{MLE}} = n\left(\sum_{i=1}^{n} (x_i - x_{\min})\right)^{-1} \tag{7}$$

with the log likelihood of the exponential model then calculated as

$$L_{\text{exp}} = n\ln\lambda_{\text{MLE}} - \lambda_{\text{MLE}} \sum_{i=1}^{n} (x_i - x_{\min}). \tag{8}$$

Since the waiting time data are discrete, when dealing with this data set we replace equation (3) with the following corrected formula (Clauset et al. 2009, page 667)

$$\mu_{\text{MLE}} \cong 1 + n\left[\sum_{i=1}^{n} \ln\frac{x_i}{x_{\min} - \frac{1}{2}}\right]^{-1}, \tag{9}$$

and equation (5) with the maximum likelihood estimates for the geometric distribution, which is the discrete analogue of the exponential

$$\lambda_{\text{MLE}} = \frac{n}{\sum_{i=1}^{n} x_i} = \frac{1}{\bar{x}}. \tag{10}$$

The log likelihoods for the waiting time models are calculated via equations (4) and (6), as per their continuous counterparts. The log likelihoods of the two models in both the step length and waiting time data sets can then be compared via the Akaike Information criterion (AIC), given as

$$\text{AIC}_i = -2L_i + 2K_i \qquad (11)$$

Where K_i is the number of free parameters in model i (for both the power law and the exponential models the exponent is the only free parameter, thus K effectively drops out). The model with the highest value of the Akaike weight, ω, is then the favoured model, with ω for model i given as

$$\omega_i = \frac{\exp\left(\frac{\text{AIC}_i - \text{AIC}_{\min}}{2}\right)}{\sum_{j=1}^{p} \exp\left(\frac{\text{AIC}_j - \text{AIC}_{\min}}{2}\right)}. \qquad (12)$$

When comparing two models, as in the current case, the Akaike weights are dichotomized as scores of 0 for the unsuccessful and 1 for the successful models. However, this dichotomy is not indicative of the actual distance between model fits. To demonstrate this distance, and to achieve a more traditional statistical validation of the model fits, we modified a simulation protocol outlined by Clauset et al. (2009) that provides bootstrapped p values via what is essentially a Monte Carlo method. After deriving the maximum likelihood estimates exponents and normalization constants for both models we calculated the following statistic for each model

$$D = \int_{x_{\min}}^{x_{\max}} |S(x) - P_i(x)| \qquad (13)$$

Where $S(x)$ is the cumulative distribution function of the empirical data, $P_i(x)$ is the cumulative density function of the model being tested and $x_{\max}$ is the maximum observed value in the data set. This is related to the Anderson–Darling test (Anderson & Darling 1952) in that it measures the area between the cumulative distribution function of the data and that of the model, rather than simply taking the maximum distance as would the Kolmogorov–Smirnov test. Although represented as an integral, it is in fact evaluated in discrete form, thus

$$D = \sum_{i=1}^{N} |S(x_i) - P(x_i)| \qquad (14)$$

over N bins of equal width $W = (x_{\min} - x_{\max})/N$. Importantly, N and W must be constant across models (i.e. models must always be compared across the same data range using the same bin width). This procedure is outlined in Fig. 3. The simulation procedure involves generating 1000 synthetic data sets via the transformation method with n, $x_{\min}$, and either μ (in the case of the power law) or λ (in the case of the exponential) identical to the best-fit model. Each synthetic data set is then fitted with its own model, and that model is evaluated via the statistic outlined above. The fraction of values of this statistic that is greater than the value for the fit of the model to the empirical data is given as the p value.

RESULTS

The home range of the baboons totalled 38.6 km², with daily path length averaging 8.3 ± 2.0 km ($N = 105$ complete paths, range 4.6–14.2 km). Mean daily path lengths differed as follows depending on the cliffs at which the group started and ended their daily route: Filoha–Filoha, 7.2 km ($N = 49$); Filoha–Wasaro, 9.6 km ($N = 29$); Wasaro–Filoha, 9.3 km ($N = 12$); Wasaro–Wasaro, 8.0 km ($N = 15$).

Step Lengths

Summary statistics for the step length data reflected differences between travel routes (mean $\pm$ SD step length and range (in km):
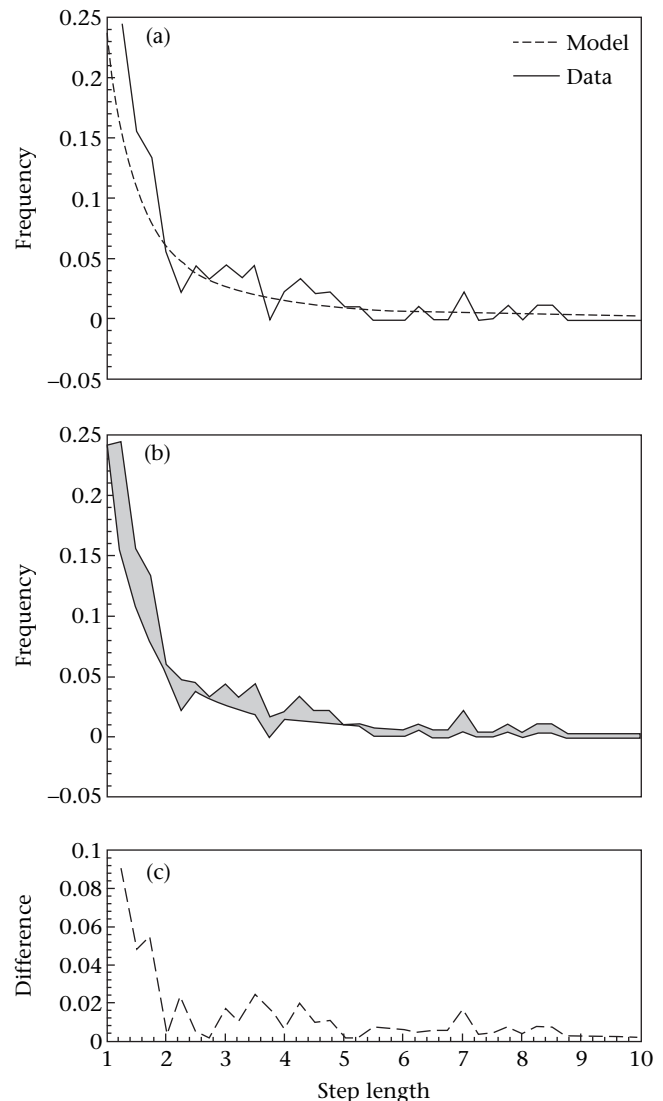

Figure 3. Schematic of the measure used to determine ranging patterns of hamadryas baboons during simulation for p values. (a) Plot of the model (in this case a power law) and the outcome of a single simulation. (b) Graphical calculation of the area between the model and the simulated data. (c) Absolute difference between the model and the simulated data. The decimal fraction of 1000 simulation runs in which this area is greater than that between the model and the empirical data is given as the p value; following Clauset et al. (2009), a model is ruled out if $p \leq 0.1$.

complete data set: 0.22 ± 0.25, range 0–0.96; Filoha–Filoha subset: 0.20 ± 0.24, range 0–0.96; Filoha–Wasaro subset: 0.25 ± 0.28, range 0–0.81; Wasaro–Wasaro subset: 0.19 ± 0.16, range 0–0.30; Wasaro–Filoha subset: mean $\pm$ SD $= 0.28 \pm 0.28$, range 0–0.50). Figure 4 shows the maximum likelihood power law and exponential models fitted to histogram presentations of the four subsets. Although there were some differences between the four subsets, this figure shows that their trajectories, once appropriately scaled, were similar in shape. The step length distribution of the entire data set showed a highly significant and favoured fit to a Lévy distribution with $x_{\min} = 0.001$, but was better approximated by the exponential distribution with $x_{\min} = 0.0001$ (see Table 1 for summary statistics). This result suggests that the former estimate of $x_{\min}$ better delineated the tail of the data, but was equivocal as regards the true distribution of the step lengths. Furthermore, according to the adopted simulation protocol for producing p values, both models reached significance for both values of $x_{\min}$. Of the site-to-site subset distributions, the Filoha–Filoha,
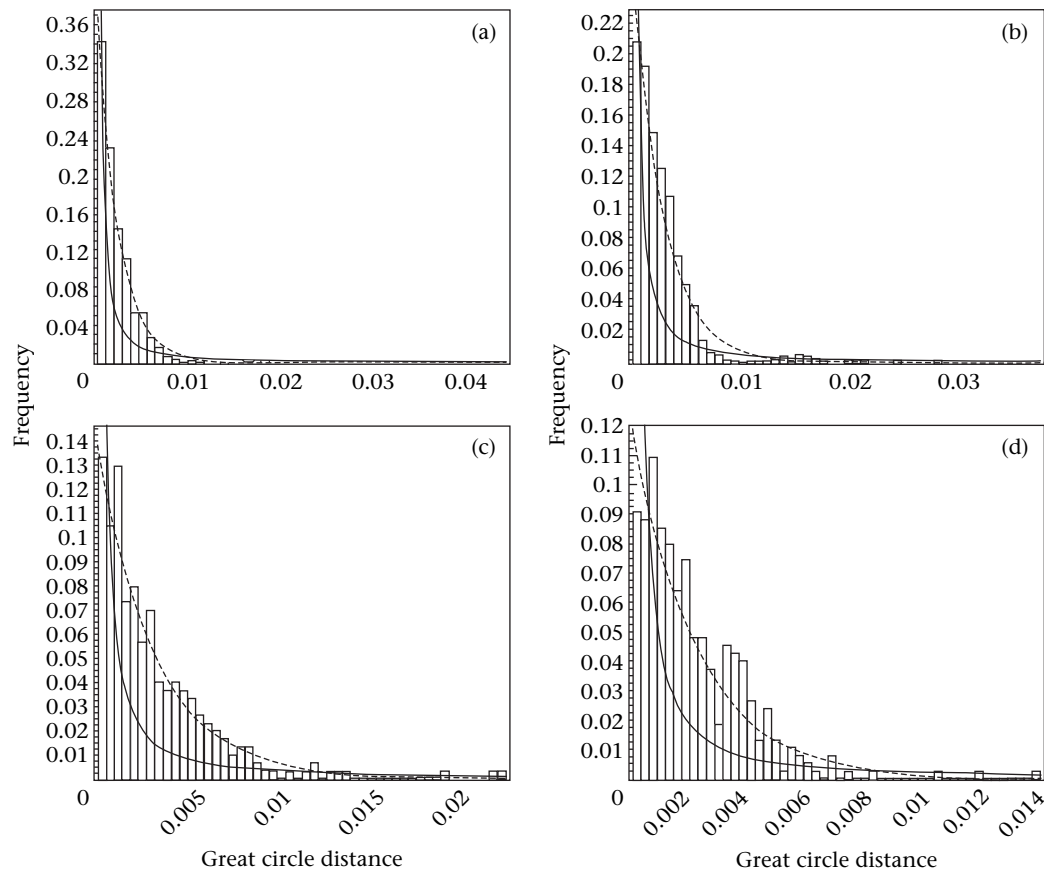
Figure 4. Step length best model fits. Histograms of (a) the Filoha–Filoha subset, (b) the Filoha–Wasaro subset, (c) the Wasaro–Filoha subset and (d) the Wasaro–Wasaro subset with maximum likelihood power law (black) and exponential (dashed) models fitted for comparison. Shown are the frequencies of the step lengths undertaken by hamadryas baboons in Band 1, measured as great circle distances between successive 15 min sampling locations.

Filoha–Wasaro and Wasaro–Filoha analyses comprehensively rejected the Lévy hypothesis, with the exponential providing a better model in each case, regardless of the value of x_{min} employed. Only the Wasaro–Wasaro data set was better approximated by a Lévy distribution, with this result occurring regardless of the value of x_{min} used. The p values for the subsets clearly supported the best model as identified by the AIC in each case, although in the case of the Wasaro–Wasaro data set both models achieved significance. Taken together, these results suggest that the first hypothesis, that the data are best approximated by an exponential distribution, should not be rejected for the step length data. Given the finding of an exponential distribution, a test of Benhamou's (2007) composite Brownian walks hypothesis is not

required, as the analyses he suggests are intended to distinguish between generating mechanisms in the case of a power law result.

Waiting Times

The results for the waiting times data were far more conclusive. Summary statistics reflected a similarity in the four separate subsets (mean ± SD waiting time and range (in min): complete data set: 29.44 ± 21.31, range 0–135; Filoha–Filoha subset: 29.57 ± 20.04, range 0–135; Filoha–Wasaro subset: 29.30 ± 22.10, range 0–120; Wasaro–Wasaro subset: 28.91 ± 22.18, range 0–90; Wasaro–Filoha subset: 29.61 ± 24.49, range 0–135). In each case, for both the entire data set and each of the four subsets, the data

Table 1
Maximum likelihood exponents, log likelihoods, Akaike Information Criterion values and Akaike weights for the hamadryas step length sample

	All data		Filoha–Filoha		Filoha–Wasaro		Wasaro–Wasaro		Wasaro–Filoha	
	x_{min}=0.0001	x_{min}=0.001	x_{min}=0.0001	x_{min}=0.001	x_{min}=0.0001	x_{min}=0.001	x_{min}=0.0001	x_{min}=0.001	x_{min}=0.0001	x_{min}=0.001
N	3058	2139	1489	973	892	670	375	265	302	231
μ_{MLE}	1.3599	2.0053	1.3760	2.0510	1.3427	1.9605	1.4108	2.0632	1.3344	1.8702
ρ_{pow}	0.264*	0.678**	0.045	0.051	0.098	0.087	0.512**	0.599**	0.083	0.094
ℓ_{pow}	13485.847	15445.640	6808.991	4870.818	3765.311	3233.631	1711.462	1342.611	1245.420	1065.945
λ_{MLE}	410.1261	417.3914	453.9817	445.4165	364.1743	384.7981	155.0230	123.9102	318.5702	325.4423
p_{exp}	0.280**	0.191*	0.452**	0.413**	0.512**	0.496**	0.451*	0.392*	0.449**	0.441**
ℓ_{exp}	15340.349	10767.778	7620.787	4961.336	4368.688	3318.322	1524.427	1019.822	1438.681	1105.378
AIC_{pow}	−26969.693	−30889.280	−13615.981	−9739.637	−7528.622	−6465.263	−3420.924	−2683.223	−2488.840	−2129.890
AIC_{exp}	−30678.698	−21533.556	−15239.573	−9920.673	−8735.377	−6634.643	−3046.854	−2037.644	−2875.361	−2208.755
ω_{pow}	0	1	0	0	0	0	1	1	0	0
ω_{exp}	1	0	1	1	1	1	0	0	1	1

* Denotes a significant model as determined by simulation; ** denotes a model that was both significant and the more likely of the two hypotheses, given the data.

were best approximated by Lévy distributions. Figure 5 shows the maximum likelihood power law and exponential models fitted to histogram presentations of the four subsets. The calculated *p* values consistently supported the best model as identified by the AIC, and in no case did the nonfavoured model reach significance (see Table 2 for summary statistics). In the case of the waiting times, therefore, the null hypothesis was comprehensively rejected, and the data followed Lévy distributions.

DISCUSSION

The following sections are based around three primary themes that emerge as a result of the work presented here. The first section examines the results of the analysis in light of the possible strengths and weaknesses of the methodology, stressing the importance of establishing accurate and reliable model selection criteria. The second section discusses what we might reasonably conclude about the resource structure of the habitat utilized by Band 1 given the results of the step length and waiting time analyses. Finally, the third section broadens the discussion to include previous work on spatial memory in primates and other animals, and examines the extent to which random search models are applicable to species that appear to have extensive knowledge of at least some aspects of their environments.

Model Fitting

The procedure employed in this paper involved the explicit comparison of two statistical distributions, the power law and the exponential, as models of both the step lengths and waiting times of a foraging baboon group. These were compared via Akaike's Information Criterion as calculated from maximum likelihood estimates of the model exponents, with overall model significance evaluated via a modification of a recently proposed simulation protocol (Clauset et al. 2009). We did not consider the turning angle distributions in the current paper as turning angles are ambiguous as regards the evaluation of the hypotheses of interest. In the literature on Lévy walks in the ecological sciences, neither maximum likelihood estimators nor model selection criteria are frequently used. There is, however, an emerging consensus among ecologists that such techniques are essential in arriving at accurate and faithful descriptions of animal behaviour. The underlying and often unstated rationale behind the promotion of such approaches relates directly to the very nature of the scientific method. The vast majority of papers to have tested for the presence of Lévy walks in animals have used standard least squares regression to do so, and have failed to posit an ecologically justified null model. In most of these cases, the analysis has involved testing the significance of a power law fit to the step length data: where the power law is shown to be significant, the animal is said to forage according to a Lévy walk pattern; where it is not significant, the conclusion is simply that a Lévy walk does not occur. This procedure leads to numerous shortcomings. Firstly, as highlighted above, the method of least squares is highly inaccurate for distribution-fitting purposes, and is essentially incapable of distinguishing between competing models, even when these are considered. Secondly, there are a series of failings in the way in which the tests are set up and carried out.
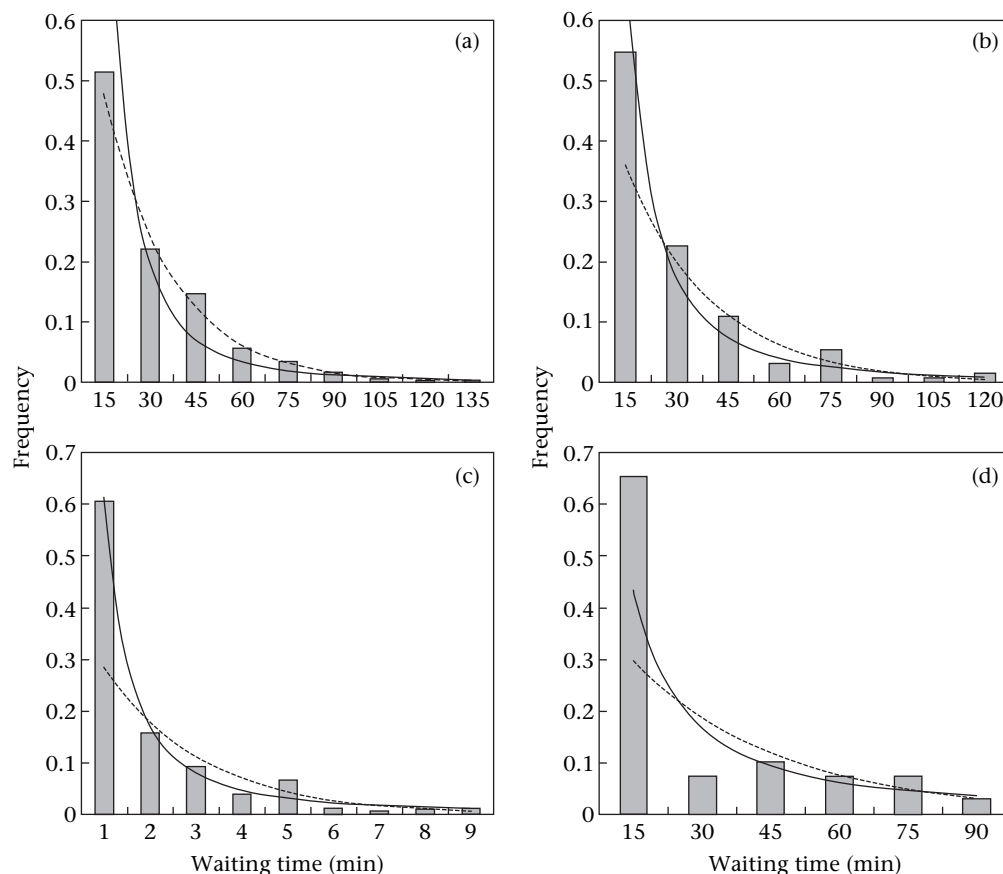

Figure 5. Waiting time best model fits. Histograms of (a) the Filoha–Filoha subset, (b) the Filoha–Wasaro subset, (c) the Wasaro–Filoha subset and (d) the Wasaro–Wasaro subset with maximum likelihood power law (solid) and exponential (dashed) models fitted for comparison. Shown are the frequencies of the waiting times seen among hamadryas baboons in Band 1, measured as the amount of time (in multiples of 15 min) that members of the band continually occupied a single sampling location.

Table 2
Waiting time summary statistics for hamadryas baboons in Band 1. Notation as per equations (5)–(12)

	All data	Filoha–Filoha	Filoha–Wasaro	Wasaro–Wasaro	Wasaro–Filoha
N	586	313	128	69	76
μ_{MLE}	3.091922236	3.00553247	3.12661197	3.321809357	3.225539771
p_{pow}	0.763**	0.667**	0.676**	0.634**	0.523**
ℓ_{pow}	−2020.525697	−1098.868288	−438.2402102	−227.4517385	−255.1608738
λ_{MLE}	0.069267139	0.068640351	0.069945355	0.071875	0.068468468
p_{exp}	0.098	0.089	0.086	0.067	0.092
ℓ_{exp}	−2150.493813	−1151.487785	−468.4852457	−250.6650478	−279.7850285
AIC_{pow}	4043.051393	2199.736576	878.4804203	456.903477	512.3217477
AIC_{exp}	4302.987625	2304.97557	938.9704914	503.3300956	561.570057
ω_{pow}	1	1	1	1	1
ω_{exp}	3.59389E−57	1.40489E−23	7.32399E−14	8.29064E−11	2.02239E−11

** Denotes a model that was both significant and the more likely of the two hypotheses, given the data (as per Table 1).

To begin with, proving that a particular hypothesis explains the data better than an associated null hypothesis is of little value relative to the evaluation of two or more mutually exclusive hypotheses, each of which is set up so as to be biologically relevant (Buckland et al. 1997; Hilborn & Mangel 1997; Johnson 1999; Anderson et al. 2000; Burnham & Anderson 2002). An unfortunate side effect of the impressive and valuable simulation work of Viswanathan and colleagues has been a short-sighted clamour for results confirming the Lévy hypothesis. The volume of literature thus produced has been facilitated by the apparently simple test procedure of assessing the validity of a straight line through the data on double logarithmic plots. Yet the most anomalous feature of much of this literature has been the distortion of the basic hypothetico-deductive framework. A truly scientific approach involves the establishment of a minimum of two alternative hypotheses; establishing a single hypothesis, with the null listed as simply the failure of that hypothesis, is only sufficient in situations where the null, thus established, is a viable hypothesis in and of itself. This is not the case in the current situation because the appropriate null model, that animals simply move randomly in either space or time, is described by the exponential distribution, not simply by the failure of the power law fit. This theoretical issue is exacerbated by the empirical fact that an exponential distribution can itself approximate a straight line on double logarithmic scales (see, e.g. Edwards et al. 2007).

The use of a viable alternative hypothesis, then, is a substantial methodological advance, and has been implemented recently by a number of researchers (e.g. Edwards et al. 2007; James & Plank 2007). Yet there still remain some potential weaknesses in even the most sophisticated applications of this research. Firstly, the maximum likelihood method involves the implementation of a lower bound, x_{min}, that can have a substantial effect on the results of the analyses. In the case of the step lengths analysed here, changing the value of the lower bound from 0.001 to 0.0001 reversed the findings of the analysis from a confirmation of the Lévy hypothesis to a result favouring the exponential. This raises fundamental questions about the determination and use of the lower bound. This is a particular concern given that x_{min} is often chosen via a visual examination of the relative frequency plot rather than a consistent statistical procedure.

A related issue involves biological, as opposed to statistical, validity. An accurate statistical characterization of a given movement pattern is of little or no use to us if it does not allow for an explicit and uniquely associated biological explanation. Both the power law and exponential models allow this, but when changing the lower bound also changes the result, and therefore the explanation, we must question how we approach the data, and what we hope to extract from it. It is clear that, in the current analyses, the higher value of x_{min} favoured the power law because it excluded a section of the data below 0.001 that formed a relatively flat line of

the relative frequency plot rather than forming a negative slope as would be expected given the equation of the power law. Including this section of the graph creates the appearance of a convex-down curvilinear plot that on double logarithmic scales is often indicative of an exponential. The question, then, is can we provide a biological argument for the inclusion or exclusion of this section of the data? In an examination of a data set detailing the foraging paths of a group of human hunter-gatherers, Grove (in press) suggested that competing models should be fitted to the complete data set, particularly in situations where the behaviour of the power law below x_{min} appears to directly contradict empirical frequencies. We face a similar situation in the current analysis, and must conclude that a model that accurately characterizes a greater proportion of the data is preferable.

Power Law Distributions and Resource Structure

Our analyses found that Band 1 conformed to a movement pattern in which step lengths are exponentially distributed whilst waiting times follow a power law. The most simplistic translation of this movement pattern into a characterization of the hamadryas resource base would be to suggest that patches utilized by the baboons are randomly distributed in space but power law distributed in size. As discussed below, this involves a number of simplifying assumptions about the baboons' intelligence and behaviour, but it also makes a number of more basic assumptions about the way in which the habitat is utilized.

The current analyses examine the overall movement pattern of Band 1 as well as their foraging movements in four specific subsets related to the use of two separate sleeping cliffs. Of interest is the fact that, among the separately analysed subsets, movement paths that both began and ended at the Wasaro cliff conformed to a Lévy distribution, whilst the other three subsets were better approximated by the exponential. This result held regardless of the value of the lower bound, suggesting that the habitat around Wasaro might be genuinely different from that around Filoha. If the environment around Wasaro were in some way conducive to power law distributed step lengths (i.e. if the patches were fractally distributed in space), we would expect support for the power law model, as given by the p values, to be greater in both the Wasaro–Filoha and Filoha–Wasaro subsets than in the Filoha–Filoha subset. As Table 1 shows, this was indeed the case, although the power law model was significant only for the Wasaro–Wasaro route. The potential differences between the habitat immediately surrounding Wasaro and that in the rest of the home range do, however, merit further investigation.

The tests of the Lévy hypothesis as performed in the current paper examine the distributions of two key elements of the mobility pattern, the step lengths and the waiting times. In attempting to reconstruct the nature of the habitat from these

distributions, we must be aware of the potential interplay between them, particularly given the ways in which they have been treated in previous studies. Many previous studies have concentrated on the step length distributions only; these are, after all, the most salient signature of movement available, measuring as they do the distances between individual feeding events. However, neglect of the waiting times can have a profound effect on the measured step lengths, particularly when the latter are measured as distance travelled per unit time, as is almost always the case. To see this, imagine an exceptionally simple, one-dimensional model environment in which patches are all equidistant from one another along a single line, and thus step lengths are all equal. Imagine also that these patches are power law distributed in size, as they were found to be in the current study. If the animal travels at a constant speed between patches and consumes at a constant rate within patches, then the step lengths will appear to be power law distributed when sampled at regular temporal intervals. This result, however, reflects the size of the patches rather than the distance between them. We must be aware of this potential confound when assessing research that fails to take waiting times into account, particularly given that studies of plant species have recently begun to find evidence of power law patch size distributions (Brown et al. 2002).

Information and Memory

Perhaps the most important development in the study of scale-free movement patterns was provided by the simulation studies of Viswanathan et al. (1996, 1999, 2000, 2001, 2002). From examinations of citations in subsequent work, it is clear that this body of research prompted numerous empirical studies of animal step length distributions, the majority of which explicitly tested the Lévy walks hypothesis. Although the emergence of this particular facet of movement ecology is hugely welcome, we feel it is time to recapitulate the limiting assumptions of the original simulations, and to assess the extent to which they could be said to accurately describe the study species considered here. The simulations carried out by Viswanathan and colleagues concluded that a Lévy walk with an exponent of close to two is an optimal search strategy for a forager searching without prior information for randomly distributed, static, nondepleting food resources at low density (Viswanathan et al. 1999). The major discrepancy with regard to hamadryas baboons, therefore, regards the assumed lack of prior information, and bears on the very distinction between search behaviour and the exploitation of a known environment.

The concept of search itself necessarily assumes a lack of prior information. There is, however, abundant evidence that primates' abilities to learn about and monitor aspects of their environments far exceed those of other animals (Shettleworth 1998). The extent to which the baboons in this study are exploiting a known environment is of considerable importance to our understanding of their movement patterns; optimal behaviours in familiar habitat will necessarily differ from those when true search is being employed.

The literature on spatial memory in primates reveals a variety of models, both empirically and theoretically derived, concerning how much animals know about the dynamics of their environments. The research in this area can broadly be divided into that which aims to reconstruct the kinds of spatial representations that primates hold concerning their resource distributions, and that which attempts to gauge the sensitivity of the animals to the temporal shifts in resource availability. Two particular models have emerged as conceptualizations of primates' spatial awareness, although it should be noted that these are umbrella terms and hide a raft of inconsistencies and disagreements. Broadly speaking, those that

believe primates employ egocentric maps propose a 'body-centred' coordinate system (Gallistel 1990; Gallistel & Cramer 1996; Potì 2000) in which the animals orient themselves relative to significant landmarks, topographic features, or habitually used paths (Poucet 1993; Janson 1998; Di Fiore & Suarez 2007; Noser & Byrne 2007a; Erhart & Overdorff 2008). Noser & Byrne (2007a) suggested that chacma baboons are unable to compute Euclidean relations between locations, and instead use 'network maps' to find their way between resources (see also Byrne 2000; Garber 2000). When baboon groups were diverted from a particular resource by the presence of another group, they were only able to navigate around the rival group and back to the resource if substantial landmarks were visible in the vicinity, suggesting that spatial relations between resources and the group could not be abstracted from their present situation.

The major alternative to the egocentric model is the geometric model, in which animals 'internally represent space, geometrically locate landmarks, use true distance and direction, and generate novel shortcuts to resources' (Erhart & Overdorff 2008, page 185). This is closer to the 'mental map' as traditionally construed (e.g. Milton 1981; Boesch & Boesch 1984). Normand & Boesch (2009) argued that, since chimpanzees in the Taï Forest approached the same resources from various directions during their study period, and showed no preferences for particular routes or paths, the most parsimonious explanation is that they possess detailed Euclidean maps of their environments, precisely the kind of abstractions that Noser & Byrne (2007a) argued are lacking in baboons. They noted, however, that this does not exclude the possibility that chimpanzees employ both egocentric and geometric maps (Normand & Boesch 2009, page 1200). This latter possibility was suggested by Gallistel (1990; Gallistel & Cramer 1996) to be the most efficient way of constructing a composite map suitable for navigational use.

As well as the question of determining the spatial layout of resources, however, there is also the question of monitoring when particular foods may be available. This rests not only upon the natural cycles of resource regeneration, but also upon previous depletion by the individual or group in question. Numerous studies have suggested that primates are able to monitor various aspects of phenology, and that they can retain information on the renewal status of patches long after they have been visited (e.g. tamarins: Garber & Hannon 1993; capuchins: Janson 1998; sakis: Cunningham & Janson 2007a; chacma baboons: Noser & Byrne 2007b).

The temporal aspect of primate environmental knowledge is also manifest at the shorter timescale of the daily foraging route. Garber (1989) suggested that tamarins can compare the distances and directions from their current location to a large number of potential foraging trees, and that this ability can be used to plot a profitable path through the forest. Cramer & Gallistel (1997; see also Gallistel & Cramer 1996) found that the next destination chosen by vervets was dependent on the distances to two further target patches beyond that destination, whilst Janson (2007) suggested that capuchins are able to plan paths to at least two subsequent foraging sites at a time, and Valero & Byrne (2007) found a similar capacity in spider monkeys. Noser & Byrne (2007b, page 265) suggested that baboons 'have a complex spatial mental representation of several important locations', and that this representation allows them to 'actively choose between alternative resource places even though they are out of sight'. Thus, advanced spatial knowledge and forward planning are both common facets of primate foraging, prompting some researchers to suggest that certain species possess episodic (or 'episodic-like') memory (chacma baboons: Noser & Byrne 2007b; capuchins: Janson 2007; sakis use 'elements of episodic-like memory': Cunningham & Janson 2007b, page 293), a form of memory

previously regarded as being unique to humans (Tulving 1983; but see Clayton & Dickinson 1998; Clayton et al. 2001, 2003).

We are justified in suggesting, therefore, that the baboons of this study possess a substantial knowledge about their habitat, and that they use this knowledge during foraging. This suggests that in fact baboons spend very little time 'searching' for their food; their environmental knowledge informs them of areas that are likely to be profitable, although it is impossible to gauge the extent of this knowledge from the current study. If baboons are searching only intermittently, at local scales, or not at all, the Lévy walk may not be an optimal strategy for resource acquisition, and we are therefore motivated to seek potential alternatives. A number of researchers have reported that groups simply move to the nearest available resource when leaving a depleted patch (Menzel 1973; Garber 1988, 1989; Janson 1998), although Menzel (1973) suggested that the 'least distance' principle in fact holds in relation to an overall foraging bout rather than individual patch-to-patch movements (see also Altmann 1974). A more useful approach may be to consider the optimal foraging strategy under complete information; both Menzel (1973) and Cramer & Gallistel (1997; Gallistel & Cramer 1996) found that primates (chimpanzees in the former case, vervets in the latter) can solve the 'travelling salesman problem'. This problem involves solving the shortest route along which one can visit a series of known locations. Menzel concluded that the achievements of the chimpanzees on a foraging analogue of this problem 'are a good first approximation of those at which an applied scientist would arrive from his real maps, algorithms, and *a priori* criteria of efficiency' (Menzel 1973, page 945). An interesting question then arises as to the nature of the optimal foraging algorithm when animals have partial knowledge of the locations of patches in their habitats; deficits in spatial awareness or memory could create this affect, as could the fact that many larger primates do not traverse their entire home range in a day, and may therefore not be aware of all changes taking place (Jetz et al. 2004; Carbone et al. 2005).

Acknowledgments

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