Prey field switching based on preferential behaviour can induce Lévy flights

Mathieu G. Lundy[1,2,3], Alan Harrison[4], Daniel J. Buckley[1,5], Emma S. Boston[1,5], David D. Scott[1,2], Emma C. Teeling[1,5], W. Ian Montgomery[2] and Jonathan D. R. Houghton[2,6]

[1]Centre for Irish Bat Research, Queen's University Belfast and University College Dublin, Dublin, Ireland
[2]School of Biological Sciences, Queen's University Belfast, 97 Lisburn Road, Belfast BT9 7BL, UK
[3]Agri-Food and Biosciences Institute, Fisheries Aquatic Ecosystems Branch, Newforge Lane, Belfast, BT9 5PX, UK
[4]Department of Zoology and Entomology, University of Pretoria, Pretoria 0028, South Africa
[5]School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland
[6]School of Biological Sciences, Queen's University Marine Laboratory, 12–13 The Strand, Portaferry, Co. Down, BT22 1PF, UK

Using the foraging movements of an insectivorous bat, *Myotis mystacinus*, we describe temporal switching of foraging behaviour in response to resource availability. These observations conform to predictions of optimized search under the Lévy flight paradigm. However, we suggest that this occurs as a result of a preference behaviour and knowledge of resource distribution. Preferential behaviour and knowledge of a familiar area generate distinct movement patterns as resource availability changes on short temporal scales. The behavioural response of predators to changes in prey fields can elicit different functional responses, which are considered to be central in the development of stable predator–prey communities. Recognizing how the foraging movements of an animal relate to environmental conditions also elucidates the evolution of optimized search and the prevalence of discrete strategies in natural systems. Applying techniques that use changes in the frequency distribution of movements facilitates exploration of the processes that underpin behavioural changes.

1. Introduction

Recent studies of animal foraging and search behaviour have focused on the detection of discrete movement patterns that optimize the efficiency of foraging movements [1–4]. Classically, animal foraging behaviour has been discussed in the context of optimal foraging theory [5]. Optimal foraging theory is founded on the idea that animals strive to acquire the greatest amount of resources per unit effort [6]. In response to variation in the distribution and availability of resources, distinct foraging strategies have evolved that vary in key characteristics such as prey capture rates, predator metabolic rate and dietary specialization [7–9]. The ability to optimize search strategies in response to changes in resource availability has marked consequences for individual fitness [10].

Different foraging strategies can have markedly different spatial properties, and the processes that generate them have been widely debated [11–15]. The characteristics of optimized search strategies, in relation to changes in resource availability, have highly contrasting properties [4,14]. Analysis of search movements in simulations and empirical studies identify discrete optimal patterns of movement, on the basis of the frequency distribution of distances travelled between reorientation events, referred to as movement steps [16–18]. Of these, Lévy search has received much attention, owing to the super-diffusive displacement rates compared with Brownian motion, and are suggested to have particular importance for the rapid spread of diseases or invasive species [15]. Lévy search patterns are characterized by a low frequency of long, dispersive movements and a high frequency of short, localized searches. The tail of the frequency distribution of movements generated by Lévy search follow a power-law or Pareto distribution, with infinite variance [19]. By contrast,

when movement steps are taken from a distribution with finite variance, a Brownian search pattern arises [20]. Search behaviours with rare long movements are considered a successful foraging strategy when the distribution of a resource is patchy and patches can be revisited [3,4,11], as it reduces return rates to areas already visited. However, modification of assumptions within simulated searching organisms can result in contrasting results [18].

Movement patterns other than Brownian motion have been indentified in a wide range of natural systems [20]. A highly efficient search strategy may also comprise a switch from a search based on intensive Brownian movement to straight line movement when the intensive Brownian search fails [21]. Patterns such as those generated by Lévy search can also arise from non-random processes, emerging from inherent spatial patterns within resource distribution and a forager's knowledge of this dispersion [22]. Predator behaviours in environments with heterogeneous prey are examined in the context of functional responses to changes in prey availability [23] and indeed prey preference [24]. These functional responses are considered central in maintaining predator–prey communities [24].

Plasticity of search strategies has been identified in animal search movements, represented by frequency distributions of movement step-lengths [4,15]. Understanding the determinants or covariates of different strategies greatly improves our understanding of the evolution of different movement strategies and their wider prevalence in diverse ecological processes. Different search patterns can be identified by fitting movement step-length data to competing distributions and assessing fit [1,25]. This method allows assessment of the relative fit of observed behaviour to discrete patterns of movement and facilitates investigation of the effects of environmental correlates on foraging strategies.

Flexible movement strategy of free ranging marine predators were identified by Humphries et al. [4] corresponding to spatial patterns of resource availability. For spatially restricted species, such as central placed foragers, knowledge of the environment and resource distribution may contribute to consistent spatial movement patterns over time. However, short-term temporal changes in resource distribution may occur in response to environmental change within the familiar range of a species [26,27]. Here, we examine how temporal changes in resource availability elicit a response in the movement patterns of a volant species, an insectivorous bat, Myotis mystacinus. We use the analytical framework that has been established for movement step lengths and apply this to tracking data for foraging bats. Insectivorous bats provide an interesting model to examine a change in movements in response to resource availability due to their high levels of mobility and the rapid changes in prey abundance that can occur within foraging periods. Active flight is a highly efficient means of travelling across a landscape but at an extremely high energy cost per unit time [28,29].

Boyles et al. [30] suggest that bats are among the most economically important, non-domesticated animal groups in North America, owing to the impact that they can have on insect populations. Nocturnal activity patterns of bats are considered to be synchronized with insect activity peaks resulting from variation in temperatures and light levels [31]. The densities and activity of airborne arthropod prey are related to meteorological factors such as wind and air temperature [32,33]. The abundance and distribution of insects can change on short timescales within homogeneous habitat patches [34]. We apply methods typically used to analyse movement step lengths for changes in inter-fix distances of radio-tracked bats to examine whether behavioural changes, in response to environmental conditions, are manifested in the frequency distribution of inter-fix distances. Sub-sampling animal movement paths has been shown to identify spurious patterns [35]. The ability to correctly identify different movement patterns using inter-fix distances is examined by simulating movement paths and sub-sampling these. We hypothesized that the movement strategies of bats change with the availability of insect prey and predicted movements with a heavy tail distribution when resources occur in dense patches that are distributed sparsely, i.e. at high variance in abundance at favourable meteorological conditions. Under such conditions, we predicted long exploratory movements to novel areas searching for patches of high prey density, coupled with multiple short-range movements within patches. Conversely, we expected a foraging strategy resembling Brownian motion, where high-density patches are rare and insect occurrence is less variable, at low overall abundance, owing to unfavourable meteorological conditions.

2. Methods

2.1. Tracking foraging movements of M. mystacinus

The Vespertilionidae range in size from 3.5 to 53 g [36]. At present, radiotelemetry is the only feasible method for tracking movements of micro-bats without impacting animal welfare [37]. Eighteen adults consisting of seventeen females and one male M. mystacinus were radio-tagged using 0.35 g PIP3 radio transmitters (Biotrack Ltd, Devon, UK) and tracked from a maternity roost and associated satellite roost in Co. Cork, Ireland (51°51′53″ N, 8°53′45″ W) during June–August 2009. Tagging and tracking were not carried out when female bats were in late stages of pregnancy, when dependent young were present in the maternity roost or during early lactation [37]. The activity of bats at the maternity roosts was monitored continuously for one week prior to tracking and throughout the study period, using ultrasonic recorders that logged activity to ensure that behavioural patterns were not disturbed. Bats were caught using harp-traps during the emergence period as they exited roosts. Myotis mystacinus have relatively low wing loadings (6.4 Nm^2) [38]; species with low wing loadings are capable of carrying tags up to 12 per cent of their body weight without impacting welfare, although avoiding this upper limit is advised [37]. Fitted tags represented a maximum of 7 per cent and mean of 6.4 per cent of the body mass of tracked bats. The tags were attached temporarily using a skin-bond surgical adhesive between the shoulder blades [37], allowing tags to drop off after a number of days (mean = 17.6 ± 7.6) [39]. Individual bats were held in cotton holding bags and processed immediately after capture. Bats were held in the hand during attachment of tags. All procedures were carried out under licence from the Irish National Parks and Wildlife Service (NPWS; licence no. 74 C/2008).

Each individual was tracked for up to five nights, starting 30 min after sunset and continuing until bats returned to roost.
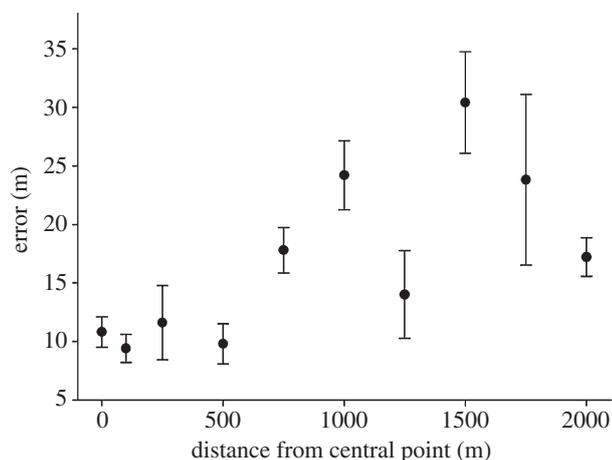
Figure 1. Location error assessed by triangulation of transmitters at known locations. Up to four bats were tracked at one time, using simultaneous triangulation from multiple positions.

Up to four bats were tracked at one time, using triangulation from multiple positions simultaneously. Coordination between multiple survey teams and tracking bats occasionally in disparate locations up to 2 km apart determined that positions of tracked bats could only be recorded every 30 min. It was necessary for teams to relocate to ensure strong signal contact in order to triangulate positions of tagged bats. The location of bats was calculated using 'locate' radiotelemetry triangulation software (http://www.locateiii.com). The Euclidean distance between consecutive fixes was calculated, excluding commuting movements, which were defined as movements that started or ended within close proximity to roosts (<100 m). Bats can be considered central placed foragers, using roosts for both rest during daylight hours and can return to rest for some portion of the night. We remove movements associated with roosting as these may introduce bias, such as long, directionally persistent movements between the central place and the foraging area. To assess the error of locations estimated by triangulation, the locations of transmitters, placed at known points, were calculated. Triangulation of these test locations was carried out from two fixed positions, 1 km from a central line, along which transmitters were positioned at intervals of 250 m from 0 to 2250 m. The average ($\pm$s.e.) accuracy of triangulation was 30.4 ± 4.3 m, at a distance of 1.8 km from transmitters (figure 1).

2.2. Resource availability

A model of insect activity (*Culicoides* sp. bite rate per 30 min (*br*)) was adapted from Carpenter *et al.* [32] to provide an estimate of insect abundance (figure 2). Air temperature ($^\circ$C), humidity (%) and wind speed (mps) were used within the model to predict insect activity. Solar radiation and variation in wind direction are required but were not available. Hence, these were maintained at 0 Wm^{-2} (darkness) and 13.3° (the average value recorded by Carpenter *et al.* [32]). The model was applied using both levels of the 'site' factor with a mean abundance calculated. Meteorological data were obtained from a weather recording centre ($51^\circ 50' 53'' $N, $8^\circ 28' 46'' $W) available from http://www.eurometeo.com recorded every 30 min. We used Taylor's power law to describe patch density change with increasing insect prey abundance [40]. Taylor's power law fits a linear relationship

of log mean abundance (*m*) to log variance in abundance (S^2). Taylor *et al.* [40] reported an average coefficient of 1.45 ± 0.39 for a range of taxonomic groups. Movements were divided into four categories using the modelled variance in abundance during which they occurred. The categories boundaries were defined by halving variance in abundance from the maximum predicted. The lowest category was extended to include the minimum variance predicted (figure 3).

2.3. Fitting probability density functions to foraging movements

Manual radio-tracking of multiple individual bats limited the frequency with which locations could be assessed. This restricted the interpretation of movements to an assessment of broad-scale foraging patterns at fixed time intervals, which may represent change in movement distance or movement speed. Probability density functions (PDFs) were fitted to subsets of movements occurring within discrete resource availability categories for movements pooled from all individual bats tracked. To account for individual behaviours, such as preference for movements of increased length in one animal, the movement lengths of individuals are rescaled to have the same mean length prior to analysis [41].

The distribution of inter-fix distances was examined using three PDFs: left-truncated Gaussian, gamma and a generalized Pareto. A Gaussian distribution represents random movement following Brownian motion, whereas the generalized Pareto distribution represents movements with a heavy tail caused by the occurrence of rare long movements. In cases previously identified to fit Pareto distribution forms, considered as Lévy movement, gamma distributions have been shown to be better descriptors of the frequency distribution of these movements [1], with an exponential decline in the frequency of longer movements. For a random variable x with a Gaussian distribution, the PDF $P(x)$ is characterized by its mean (α) and s.d. (σ):

$$P(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-1/2(x-\alpha/\sigma)^2} \quad -\infty \leq x \leq \infty. \quad (2.1)$$

If x cannot be observed below a certain value of $x(t)$, due to censoring or truncation, the resulting left-truncated Gaussian distribution occurs:

$$P(x) = \frac{f(x)}{\int_{xt}^{\infty} f(x)\mathrm{d}x}, \quad t \leq x \leq \infty, \quad (2.2)$$

where $f(x)$ is defined in equation (2.1). We use the minimum value within the observed data ($+1$) to set t. The gamma PDF are parametrized by a shape (k) and scale (θ) term. The gamma distribution allows a flexible range of distributions to be fitted including an exponential, where $k = 1$. A shifted gamma distribution was fitted with respect to t following the form

$$P(x) = \frac{\theta^k}{\Gamma(\theta)} (x-t)^{\theta-1} e^{-\theta(x-t)}, \quad x \geq t. \quad (2.3)$$

The generalized Pareto is parametrized by k, θ and t. The generalized Pareto distribution equates to an exponential distribution when $k = 0$; a value of $k > 0$ describes an infinite tail declining faster than exponential, while a value of $k < 0$
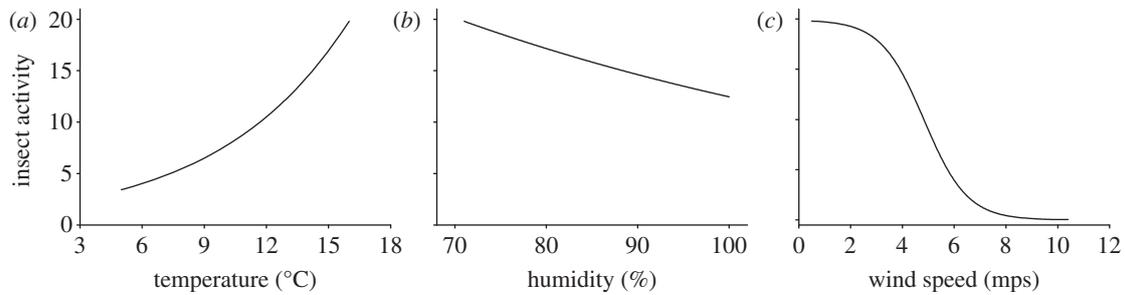
Figure 2. Modelled insect abundance in response to individual meteorological variables, adapted from Carpenter *et al.* [32]. For each variable—(*a*) temperature, (*b*) humidity and (*c*) wind speed, other variables in the model are maintained at optimal levels, which maximize insect abundance.
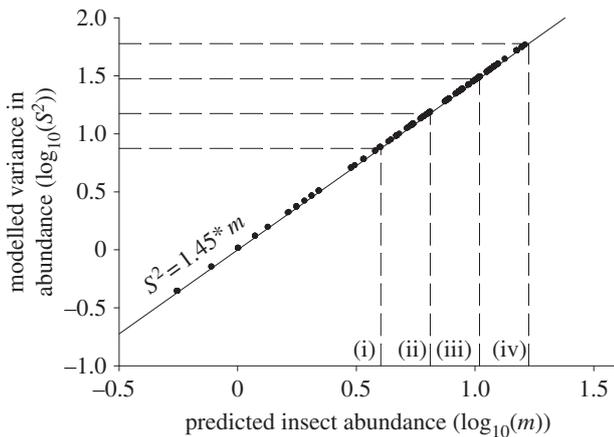

Figure 3. Modelled insect abundance (*m*) and variance in abundance (S^2) predicted by Taylor's power law [40]. Four categories are identified (i – iv) defined by abundance at which variance halves from the maximum-recorded. The lower boundary of category (i) is extended to minimum predicted variance. The points show modelled values of insect abundance from recorded weather data.

indicates a finite tail [42]. The generalized Pareto distribution is represented by:

$$P(x) = \begin{cases} \dfrac{1}{\theta}\left(\dfrac{1 + k(x - t)}{\theta}\right)^{\mu}, & k \neq 0; \\ \dfrac{1}{\theta}\exp\left(-\dfrac{(x - t)}{\theta}\right) & k = 0; \quad x \geq t \end{cases}, \qquad (2.4)$$

where the exponent (μ) is

$$\mu = \left(-1 - \frac{1}{k}\right), \quad x \geq t. \qquad (2.5)$$

All PDFs were fitted by the maximum-likelihood estimation using the '*fitdistr*' function in 'MASS' within program 'R' (http://www.r-project.com) for the gamma distribution, the 'Truncnorm' package to define the truncated Gaussian and '*fitgdp*' function in package 'POT' for the generalized Pareto. The minimum recorded movement within each subset of flights used as the threshold (*t*) in each case. Akaike information criterion, corrected for sample size (AICc), and Akaike weights (AICω) were calculated to assess the fit of each PDF [43]. For each candidate distribution, two parameters are considered to be fitted; α and σ for the truncated Gaussian, and k and θ for both the gamma and generalized Pareto. A Wilcoxon goodness of fit statistic (*W*) was used to test the fit of the selected distribution to each dataset. While these methods allow only identification of the best

of the fitted distributions, a behavioural change should still be represented by a change in the best-fitting distribution across categories of resource availability. Lévy search patterns are evident when the tail of a Pareto distribution has an exponent, μ, which ranges between 1 and 3. The exponent of fitted upper-truncated Pareto distributions was calculated for subsets of movements for which a generalized Pareto was selected as best fit using the R package 'VGAM'. The upper limit of truncated Pareto distribution was set as the maximum-recorded movement in each subset (*m*) and *t* identified by repeatedly fitting increasing values of *t* and selecting the best fit by AICc. The PDF of the truncated Pareto distribution is

$$P(x) = \frac{kt^k}{x^{k+1}(1 - (t/m)^k)}, \quad t \leq x \leq m. \qquad (2.6)$$

2.4. Simulation of foraging movements

To examine the ability of this method to accurately reflect inter-patch movements occurring at a faster rate, simulated movement step-length distributions were created. These simulated paths were re-sampled to reconstruct the movement paths that would be recorded if locations were determined using less-frequent sampling. One hundred replicates of three distributions were randomly generated, each consisting of $N = 600$ steps: left truncated Gaussian ($\alpha = 10$, $\sigma = 1$, $t = 1$), shifted gamma ($k = 2$, $\theta = 100$, $t = 1$), with k selected to give a right skewed distribution, and generalized Pareto ($k = 1$, $\theta = 100$, $t = 1$), for a generalized Pareto with $k > 0$ the tail is polynomial. A movement path consisting of these step lengths was created using randomly generated bearings. Each movement path was re-sampled and step lengths recalculated, using one in every two locations, rate $r = 1/2$ and, at one in every six locations, $r = 1/6$. Distributions were fitted to these sub-sampled distributions, as described earlier and the effect of changing sampling rates assessed by comparison of the fitted distribution parameters.

2.5. Movement direction

A central assumption of movement strategies such as Brownian motion and Lévy search is that movements are randomly orientated and result from random, Markovian, processes [12]. Searching for targets using a Lévy strategy is considered more efficient when the density of targets is low, as the return rate to previously visited areas is reduced as a result of the occurrence of extremely long step lengths [15]. To test the applicability of these assumptions to the tracking

Table 1. Simulated movement paths were generated using three distributions. These were re-sampled at two rates (r)—one in two locations (half) and one in six locations (one-sixth) and movement path recreated. The parameters (mean (α) and shape (k)) of re-fitted distributions to the paths generated by that distribution are given with 95% confidence estimates. The mean Akaike weight of the re-fitted distribution when compared with the fit of other distributions and percentage of correctly assigned distributions is presented.

original distribution	r = 1/2				r = 1/6			
	% correct	Akaike weight	α	k	% correct	Akaike weight	α	k
Gaussian ($\alpha = 10$, $\sigma = 1$)	100	1	20.3 (0.1)	—	77	0.748	47.6 (0.33)	—
gamma ($k = 2$, $\theta = 100$)	100	0.996	—	2.33 (0.03)	87	0.845	—	3.84 (0.11)
generalized Pareto ($k = 1$, $\theta = 100$)	100	1	—	1.95 (0.02)	99	0.984	—	0.56 (0.05)

data of *M. mystacinus*, the fix locations after long movements were compared with those after short movements in relation to the animal's characteristic foraging range. Kernel analysis was applied to all fixes of each individual to identify its core foraging area (50% kernel). For all movements made by an individual, the mean change in distance towards the centroid of the core foraging area was calculated as the proportion of total movement for short movements (movements comprising fifth percentile) and long movements (movements comprising 95th percentile). Significant movement towards or away from the centroid of short and long flights was compared using a Wilcoxon sign paired rank-test.

3. Results

Radio-tracking provided a total of 679 foraging locations, between which 548 Euclidean distances were calculated. The mean length ($\pm$s.e.) of all distances was 459 ± 426 m. The inter-fix distances were separated into four categories, based on the modelled abundance of insects during which the movements occurred (figure 3). The categories were defined by doubling variance in abundance with respect to Taylor's power law [40]: (i) $0br–4br$, (ii) $4.1br–6.5br$, (iii) $6.6br–10.4br$, (iv) $10.5br–16.8br$. The recorded inter-fix distances are provided in electronic supplementary material (SM1).

3.1. Simulated movement patterns

From simulated movements sampled at $r = 1/2$, all were identified as having best fit to that of the original distribution from which they were created. For movements sub-sampled at $r = 1/6$, there was greater misclassification of original distributions (table 1). The most common misclassification occurred for Gaussian distribution with 23 of 100 identified as gamma distribution. In two cases, a generalized Pareto distribution was identified spuriously, one from each of the predefined gamma and Gaussian distributions. The shape parameters of sub-sampled gamma distributions increased reflecting a perceived shift in frequency plot of the gamma distributions to the right. Additionally, a similar shift in α of Gaussian distributions was observed in sub-sampled distributions (table 1). Correct classification of simulated distributions provides strong support that the sampling rate permitted by radio-

tracking reflects the movement patterns occurring at a faster rate. However, deviation from original distribution parameters (i.e. mean and standard deviation) is likely.

3.2. Identified movement patterns

Fitting competing PDFs to flights within temperature bands revealed that no single PDF had the best fit to all subsets of data. A progression of fitted distributions from Gaussian, through gamma to generalized Pareto distribution, with a change from low- to high-modelled insect abundance and increased patch density was observed. Movements within the lowest activity categories were best characterized by the Gaussian PDF. The movements within the second category were described by a gamma PDF while a generalized Pareto distribution was best fit to those in the upper two categories (table 2 and figure 4). A Pareto distribution was fitted to sub-sets of movements in the upper two categories, with $t = 1510$ and $t = 800$ selected as best fit; the fitted Pareto distribution had $\mu = 1.26$ and $\mu = 2.44$.

Core foraging areas were calculated by Kernel analysis for all individuals, excluding the single male bat, which was only tracked for one night. The longest movements of individual bats ended significantly closer to the centroid of their core foraging area ($W = 126$, d.f. $= 17$, $p = 0.02$; figure 5).

4. Discussion

We show that changes in movements associated with foraging behaviour can be detected using analysis of the probability distributions of inter-fix movements. Our results are consistent with the hypothesis that movement behaviour of *M. mystacinus* bats is modified with prey aggregation density. The switch in movement patterns observed was consistent with the prediction that movement inter-fix distances conformed to a probability distribution with a truncated Pareto tail at highly variable resource availability. Indeed, the exponent of the Pareto distribution that was fitted to the tail of this distribution was within the indicative range of Lévy search, $1 < \mu < 3$. At the lowest category of resource variability in spatial abundance, when insect prey aggregations are at lowest densities, bat movements fitted a Gaussian frequency distribution.

Table 2. Fit of foraging movements of *Myotis mystacinus* to contrasting probability distribution functions. The log likelihood of each fit to each distribution, Akaike information criterion, corrected for sample size (AICc), the Akaike weight and parameters of the best fitting distribution are shown. The Wilcoxon fit (*w*) statistic is presented for the distribution of best fit, shown in bold.

modelled variance in insect abundance	distribution	sample size	log likelihood	AICc	Akaike weight	mean (α) ± s.d. (σ)	shape (k)	scale (θ)	Wilcoxon fit test (w)
<7.5	**Gaussian**	141	−1081.9	2168	**0.66**	**862 ± 515**			*W* = 11 378; *p* = 0.305
	gamma		−1197.8	2400	0		6.85	100	
	generalized Pareto		−1082.6	2170	0.33		−0.24	842	
7.5–15	Gaussian	118	−902.7	1809	0.03	859 ± 508			
	gamma		**−899.3**	1803	**0.96**		**2.62**	324	*W* = 9381; *p* = 0.215
	generalized Pareto		−904.3	1813	0.01		−0.31	1048	
16–30	Gaussian	194	−1504.5	3013	0	752 ± 565			
	gamma		−1630.5	3265	0		5.91	100	
	generalized Pareto		**−1472.6**	2949	**1**		**−0.12**	778	*W* = 17 897; *p* = 0.405
31–60	Gaussian	95	−781.1	1566	0	1087 ± 901			
	gamma		−962.2	1928	0		7.09	100	
	generalized Pareto		**−753.4**	1511	**1**		**−0.06**	1026	*W* = 4066; *p* = 0.347

The resolution of location data used in the present study was not sufficient to examine fine-scale foraging movements, such as searching for individual prey items, but reveals general patterns of search behaviour associated with foraging. Our simulations demonstrated that foraging movements occurring at a faster rate (e.g. twice and six times that recorded in the current study), indicative of inter-patch movements of every 15 or 5 min, would be correctly identified. Bradshaw *et al.* [44] demonstrated that relevant biological signals could be extracted from noisy data where errors are approximately one order of magnitude lower than that of the maximum observed step length. The small size of the study species limited tracking methodology to manual radio-telemetry. Although not possible at present, additional miniaturization of radiotelemetry devices may permit examination of search behaviour nested within foraging patterns and allow more detailed interpretation of environmental correlates of optimal foraging behaviour for small species. As technology advances, use of biosensors along with animal tracking may allow the interaction of physiological and behavioural traits to be addressed more fully [45]. Incorporating physiology into assessment of animal movement will allow the triggers for changes in movement strategies to be assessed in response to underlying metabolic and energetic requirements of foragers. For bats, the increased metabolic cost of heat loss during daylight dictates that diurnal flights are only undertaken when the relative energy gain is high [46].

Plank & Codling [35] showed that when using fixed sampling rates, it can be difficult to correctly determine the process generating the observed movements. Analysis of the locations of foraging bats after long movements suggested that individual bats may have knowledge of preferred locations in which to forage under optimal conditions. Higher insect abundance may facilitate increased encounter rates with insects and reduce 'en route' search efforts. Therefore, the long movements observed at higher temperatures may result from an accumulation of flights from a Gaussian distribution that are directionally persistent and temporally compressed. The occurrence of such movements may result in the misidentification of true non-Lévy flight as Lévy within animal movement data [12]. The long movements that occur during periods of high variation in abundance that we model in *M. mystacinus* could occur as a result of: (i) single long movements or (ii) an accumulation of movements occurring at a faster rate than at lower levels of variation in abundance. These uncertainties could be examined using high-resolution tracking, which could not be achieved in the present study. Further, a characteristic property of a Lévy walk is that movements are randomly orientated [12]. We found that long movements were in fact more likely to end closer to the core foraging area of individuals. This may be a common trait for centrally placed foragers, which have knowledge of how resource distribution changes within the limits of their familiar area. During periods of increased resource availability, a decision is made to make longer trips to optimal areas, while at reduced resource availability en route foraging in sub-optimal foraging areas results in punctuated movements.

Understanding species ecology is critical to valid interpretation of movement data, such as accounting for movements not associated with foraging such as commuting movements. Indeed, in some cases, it may be necessary to identify whether other resources, such as locations used for
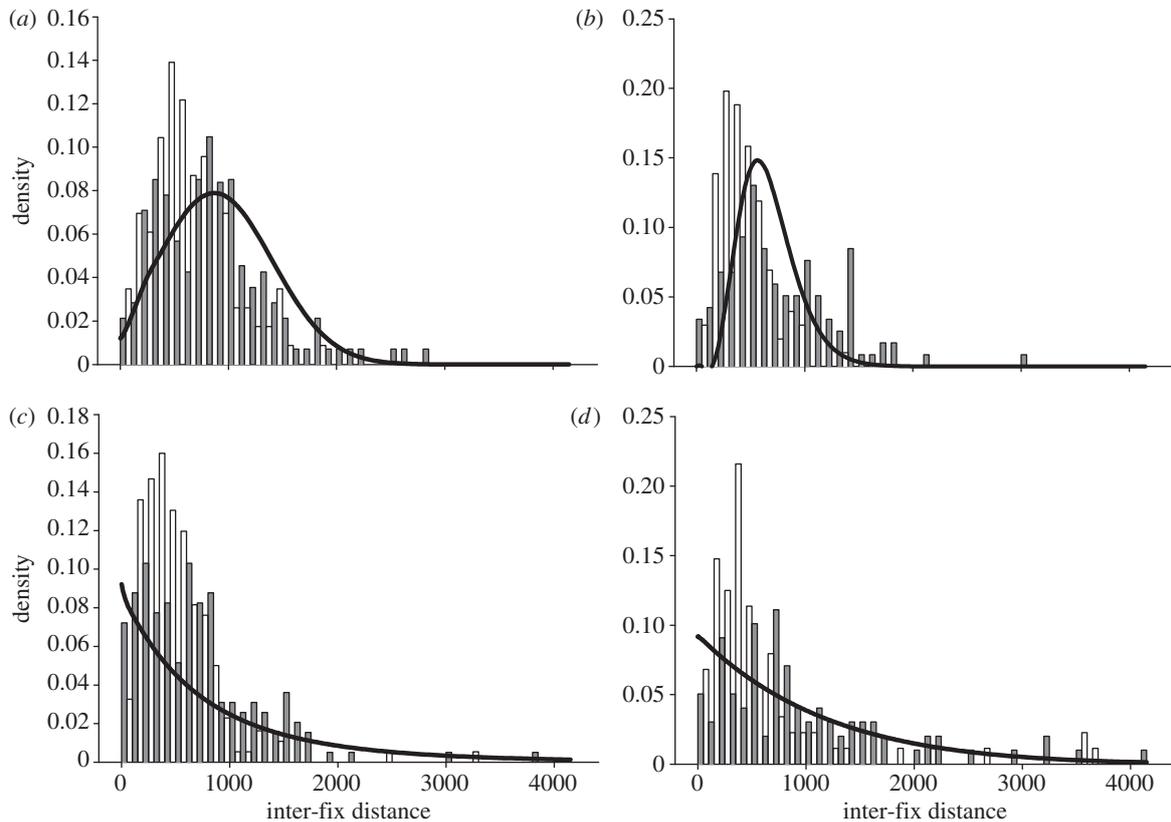
Figure 4. Histograms of inter-fix foraging (open bars) movements (*m*) of *Myotis mystacinus*, rescaled (grey bars) so that all individuals have equal mean movement length, in four categories (*a–d*) of modelled prey abundance, from low to high (figure 3). The best-fit probability distribution function is overlaid (line); (*a*), Gaussian; (*b*), gamma; (*c*) and (*d*), generalized Pareto.
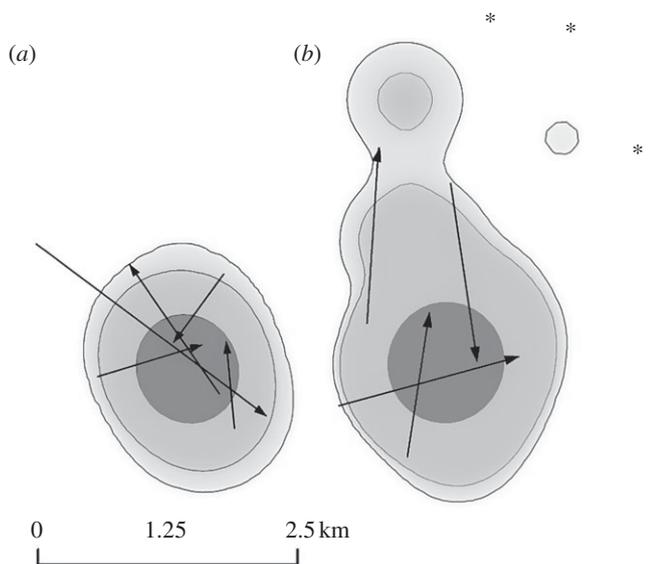

Figure 5. Examples of the longest movements (upper 10%) of two individual *Myotis mystacinus* (*a,b*). The core foraging area 50% identified by kernel analysis is shown in dark grey. The direction of movements is indicated by the arrowhead, see text for details. Roosts are marked with asterisks.

drinking or social behaviours, can create bias within movements. In free ranging animals, the knowledge of resource location is likely to be reduced in comparison with centrally placed foragers [47]. For central placed foragers, knowledge of the availability of resources may be increased particularly in highly predictable environments. This may allow Lévy

search patterns to emerge as a result of the spatial structure of the environment [22]. Predator preference for prey types is regarded as one mechanism through which different functional response forms can arise; preferences can change as the abundance of one prey species increases relative to others, known as prey switching [48]. We demonstrate a change in foraging movements with what appears to be an underlying spatial component. This may represent a form of prey switching, with a switch to familiar optimal areas at times of greater resource availability. At present, we cannot determine whether this behaviour results from prey preferences or from area preferences. Arguably, the foraging behaviour described here may be considered indicative of *M. mystacinus* having preference for familiar areas at times of highly variable resource availability. Long flights are highly efficient but expensive per unit time [29] and the ability to undertake such movements to optimal areas must be balanced against the potentially high returns of foraging within these areas. Bats foraging during cooler periods may have to make intermediate distance foraging movements to increase the encounter rate with lower density prey, more akin to foraging over much broader spatial scales [7].

Debate remains over the optimal search behaviour adopted by animals experiencing different environmental conditions [12–14]. Using techniques that use changes in step-length distributions allows the triggers of behavioural changes to be explored in a wide range of species and identify the processes that lead to these patterns more easily. Recently, different movement strategies have been examined in the environmental context of spatial resource availability [4]. In the present work, we demonstrate changes in the distribution

of inter-fix distances, and argue that these also relate to temporal variation in resource availability that drive spatial variability in localized prey fields. We combine the framework of optimal foraging theory and more contemporary movement rule analysis to examine the behavioural response of foraging animals to changing resource availability. Using a central placed forager, we demonstrate temporal flexibility of movement strategies in response to resource availability. The examination of inter-fix distances using analysis commonly applied to movement step lengths allows foraging strategies and responses to resource availability to be assessed in natural systems.

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