DISPLACED HONEY BEES PERFORM OPTIMAL SCALE-FREE SEARCH FLIGHTS

ANDREW M. REYNOLDS,[1,4] ALAN D. SMITH,[1] RANDOLF MENZEL,[2] UWE GREGGERS,[2] DONALD R. REYNOLDS,[3] AND JOSEPH R. RILEY[1]

[1]*Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ United Kingdom*
[2]*Freie Universität Berlin, FB Biologie/Chemie/Pharmazie, Institut für Biologie - Neurobiologie, Königin-Luise-Str. 28/30, 14195 Berlin, Germany*
[3]*Natural Resources Institute, University of Greenwich, Chatham, Kent ME4 4TB United Kingdom*

Abstract. Honey bees (*Apis mellifera*) are regularly faced with the task of navigating back to their hives from remote food sources. They have evolved several methods to do this, including compass-directed "vector" flights and the use of landmarks. If these hive-centered mechanisms are disrupted, bees revert to searching for the hive, but the nature and efficiency of their searching strategy have hitherto been unknown. We used harmonic radar to record the flight paths of honey bees that were searching for their hives. Our subsequent analysis of these paths revealed that they can be represented by a series of straight line segments that have a scale-free, Lévy distribution with an inverse-square-law tail. We show that these results, combined with the "no preferred direction" characteristic of the segments, demonstrate that the bees were flying an optimal search pattern. Lévy movements have already been identified in a number of other animals. Our results are the best reported example where the movements are mostly attributable to the adoption of an optimal, scale-free searching strategy.

Key words: flight pattern; harmonic radar; honey bees; Lévy flights; optimal searching strategy; scale-free.

INTRODUCTION

Understanding animal movement patterns in terms of characteristic scales is a long-standing goal of ecological research (Levin 1992). Shlesinger and Klafter (1986) were the first to suggest that the movement patterns of some animals may have so-called Lévy-flight characteristics, named after Paul Pierre Lévy, the French mathematician. Lévy flights consist of sequences of independent, randomly oriented steps with lengths, l, drawn at random from a probability distribution function having a power-law tail, $p(l) \sim l^{-\mu}$ where $1 < \mu < 3$. Lévy flights have no characteristic scale because the variance of $p(l)$ is divergent and are therefore said to be "scale free." Instead, frequently occurring but relatively short moves are punctuated by more rarely occurring longer moves which in turn are punctuated by even more rarely occurring even longer moves, and so on. Over much iteration, a Lévy flight will be distributed much farther from its starting position than a Gaussian (i.e., Brownian) random walk of the same length. The scale-free and super-diffusive properties of Lévy flights can lead to advantages over Gaussian motions in search scenarios (Bartumeus et al. 2005). Lévy flights can, for example, increase random encounter success when searching for scarce targets or for those with a patchy

distribution. Viswanathan et al. (1999) demonstrated that $\mu = 2$ constitutes an optimal Lévy-flight search strategy for the location of randomly and sparsely distributed targets i.e. the mean distance traveled before a target is encountered, is minimized. It is assumed in Viswanathan et al.'s analysis that the searcher is exclusively engaged in searching, has no prior knowledge of target locations and that the mean spacing between successive targets greatly exceeds the searcher's perceptual range. Lévy flights with $\mu = 2$ have subsequently been found to characterize the movement patterns of a diverse range of animals including, microzooplankton (Bartumeus et al. 2003), albatrosses, deer, bumblebees (Viswanathan et al. 1996, 1999), jackals (Atkinson et al. 2002), and spider monkeys (Romas-Fernández et al. 2004). Even human hunter-gatherers perform Lévy flights (Brown et al. 2007).

Many central-place foragers, and foragers with preferred feeding grounds, adopt a different stereotypical search strategy that begins at the location where the forager initially expects to find the target, and is comprised of loops of ever-increasing size that start and end at this location, and are directed in different azimuthal directions (Wehner and Srinivasan 1981 [and references therein], Hoffman 1983, Fourcassié and Traniello 1994). This strategy ensures that the area where the target is expected to lie is searched most intensively. (We can show that this strategy is optimal for the location of a single target when the lengths of the loops are distributed according to an inverse-square

power-law (A. M. Reynolds, *unpublished manuscript*), and that it corresponds to "looping" Lévy flights with μ = 2.) However, if the search progresses without yielding the target, the probability that it is in the vicinity of the start point decreases and eventually it would become advantageous to abandon looping back to the origin, and instead adopt a freely roaming, Lévy-flight searching pattern (A. M. Reynolds, *unpublished manuscript*). The presence or otherwise of Lévy-flight characteristics in the movement patterns of central place foragers has hitherto not been established, but the advent of scanning harmonic radar (Riley et al. 1996, Riley and Smith 2002) able to record the flight patterns of honey bees (*Apis mellifera*) over hundreds of meters means that it is now possible look for these characteristics.

Honey bees are regularly faced with the task of navigating back to their hives from remote food sources, and they have evolved several methods to do this. They use path integration while foraging for new sources (Collett and Collett 2000, Collett et al. 2006), and once one is found, they travel in straight, compass-directed "vector" flights, to and fro, between the food source and hive (Riley et al. 2003). Landmarks may also be used, particularly on long flights (Collett et al. 2002). However, impressive though these methods are, they are not perfect. For example, the bees' path-integration system will always be subject to cumulative errors, especially on long-range flights over unfamiliar terrain, and particularly if compass information is made less precise by heavy overcast. The strong winds and limited visibility associated with sudden summer thunderstorms, for example, may induce navigational errors, and the question arises, how do honey bees find their hives when their usual navigation methods fail to bring them home? It has been known for 80 years that if bees' hive-centered navigational mechanisms are artificially disrupted, they adopt what appear to be looping, searching flights, and usually manage to (eventually) find their hives (Wolf 1927). In this paper, we investigate the search strategy that they use in these circumstances. To do this, we analyzed records of the flight paths of bees that had been captured, artificially displaced, and then released. As expected, the paths showed that the bees initially tended to make long looping flights away from the release point, as though they were searching systematically for their hive, and our paper presents evidence that these were "looping" Lévy-flight patterns.

The flight records were obtained from harmonic radar observations (Riley et al. 1996, Riley and Smith 2002) that were carried out in the course of recent studies of other aspects of honey bee navigation that are described elsewhere (Riley et al. 2003, 2005, Menzel et al. 2005).

METHODS

The experimental arena

The flight observations were made over a carefully selected (Chittka and Geiger 1995), large area of mown pastureland, approximately 1 × 1.5 km, where the terrain was unusually flat and free from obstacles that would have obscured the radar's field of view. The radar was set up on the southern edge of the arena, so that it overlooked the hive and three release points (R1, R2, and R3) set up 200 to 250 m from it (Menzel et al. 2005). Of these, R2 lay on a linear landscape feature formed by adjoining areas of unequally mown grass that crossed the observation arena and passed through the position of the hive (Menzel et al. 2005). Some brightly colored tents were also placed in the arena to act as artificial landmarks, for separate navigation experiments (Menzel et al. 2005).

Empirical data and flight experiments

Honey bees were trained to a feeder that was moved around the hive on a radius of 10 m at two to three revolutions per day. This movement suppressed the establishment of vector flights along any fixed compass direction to and from the feeder. Individual honey bees were caught when they left the feeder, fitted with a harmonic radar transponder (Riley and Smith 2002), and carried in an opaque tube to one of the three release points. The bees, which had no opportunity to use their path integration capabilities during this displacement, were then released, and subsequent flight trajectories were recorded using harmonic radar (for experimental details, see Menzel et al. 2005).

A path was created from records of the bee's position that were normally made every 3 seconds. However, if the bee flew through an area of radar "shadow" or climbed temporarily above the horizontally scanning radar beam, the missing interval was spanned by joining the last recorded position to the first one to be acquired after the interval. Analyses were based upon 60 recorded flight patterns. Fifty-six flights terminated in the immediate vicinity of the hive. Flight durations ranged from 128 to 7286 s. Flight lengths ranged from 341 m to 14 187 m, and had a mean of 2153 m.

Basis of analysis

Statistical analyses were based on data that were pooled for the three release points. The results are not significantly different from those of analyses (not reported on) undertaken separately for each of the three release points. We tested for the presence of Lévy-flight patterns, and to do this, we followed Bartumeus et al. (2005) and represented the flight paths as sequences of straight-line movements between the points at which significant changes in direction occurred. These representations were then examined for the presence of Lévy-flights characteristics. A significant change in flight direction is deemed to have arisen when the direction of the current flight segment (joining two successive recorded positions) and that of the flight segment immediately following the last deemed change in direction, is more than 90° (see Fig. 1 and caption). Statistical properties of these representations do not change significantly when the critical angle, 90°, is changed by ±30°. Furthermore, the statistical
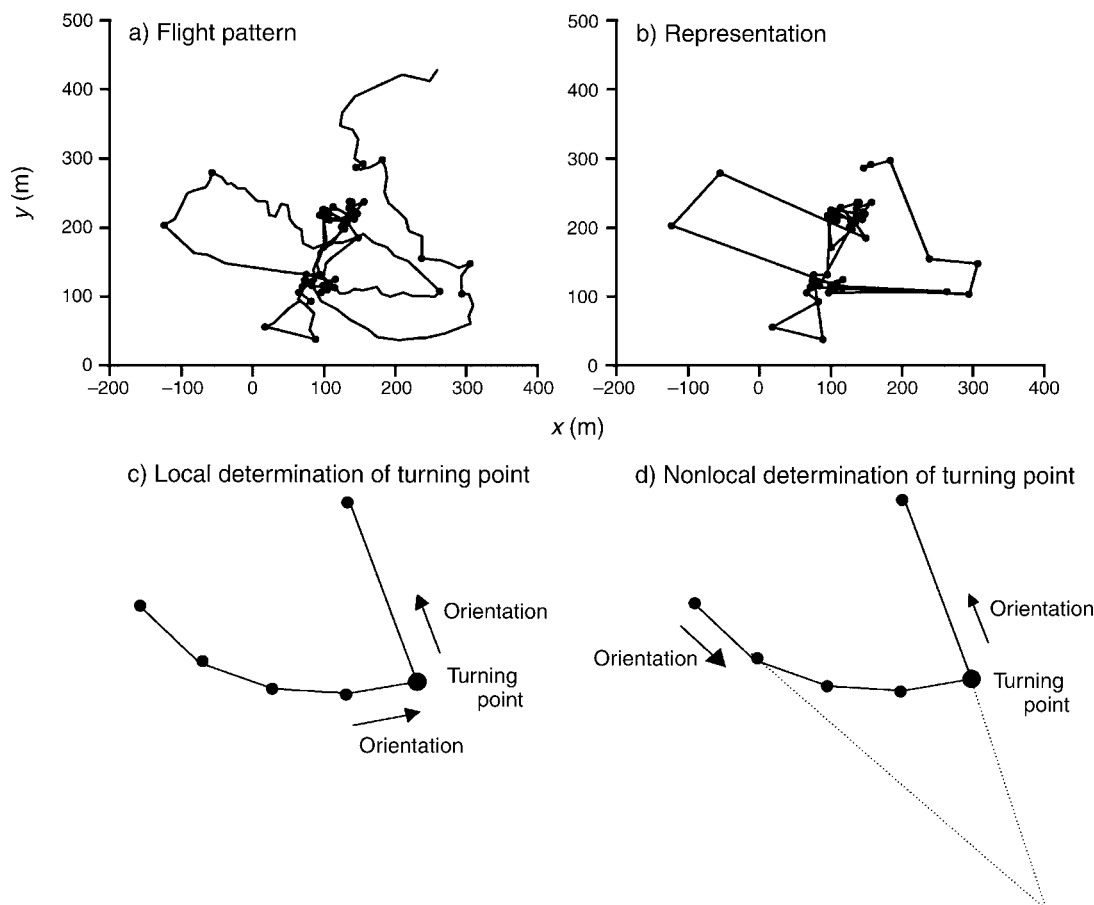
FIG. 1. Representation of the flight paths. (a) An example flight path of a honey bee after being displaced and then released. A change in flight direction is deemed to have arisen when the direction of the current flight segment (joining two successive recorded positions) and that of the flight segment immediately following the last deemed change in direction is less than 90° (i.e., when the interior angle of the turn is acute). The locations of these direction changes are marked (with solid circles). (b) Representation of the flight path as straight-line movements between the positions at which changes in flight direction occurred. (c) Local determination of the turning point using three successive recorded positions. (d) Nonlocal determination of the turning point used in the analysis. The statistical properties of representations are not dependent on the method used to locate turning points.

properties of these flight representations do not differ significantly from those in which direction changes are deemed to have arisen where the direction between two successive flight segments (i.e., between three successive recorded positions) is more than 90°. The close correspondence between these two (nonlocal and local) representations indicates that most changes in flight direction occur abruptly rather than through the accumulation of small changes.

Only around 6% of the changes in flight direction occurred within 5 m of any one of the tents used as artificial landscape features, so the vast majority of turns cannot therefore be attributed to the presence of these landmarks.

<div align="center">RESULTS</div>

<div align="center">*Analysis of flight paths*</div>

A preliminary examination of the flight paths revealed that the distribution of flight lengths has an inverse-square power-law tail rather than an exponential or Gaussian one, and that the occurrence of an inverse-square power-law tail is not dependent on the critical angle used to define a turning point (Fig. 2). Fig. 3 shows that the directions of flight segments are uniformly distributed between 0° and 360°. Our next examination used the fact that the number of turning points occurring within time intervals t to $t + \Delta t$ define a dimensionless time series, $u(t)$, and an associated running sum,

$$n(t) = \sum_{i=0}^{N} u(i\Delta t).$$

If the values of $n(t)$ are completely uncorrelated and behave like "white noise," then the root-mean-square value of the running sum $F = \sqrt{\langle [n(t) - \langle n(t) \rangle]^2 \rangle} \propto t^{\alpha}$ where $\alpha = 0.5$ and where the angular brackets denote an ensemble average over all flights in the data set (Peng et al. 1995). Short-term correlations in the data may cause the initial slope of a plot of $\log(F)/\log(t)$ to differ from 1/2, although it will still approach 1/2 at longer times.
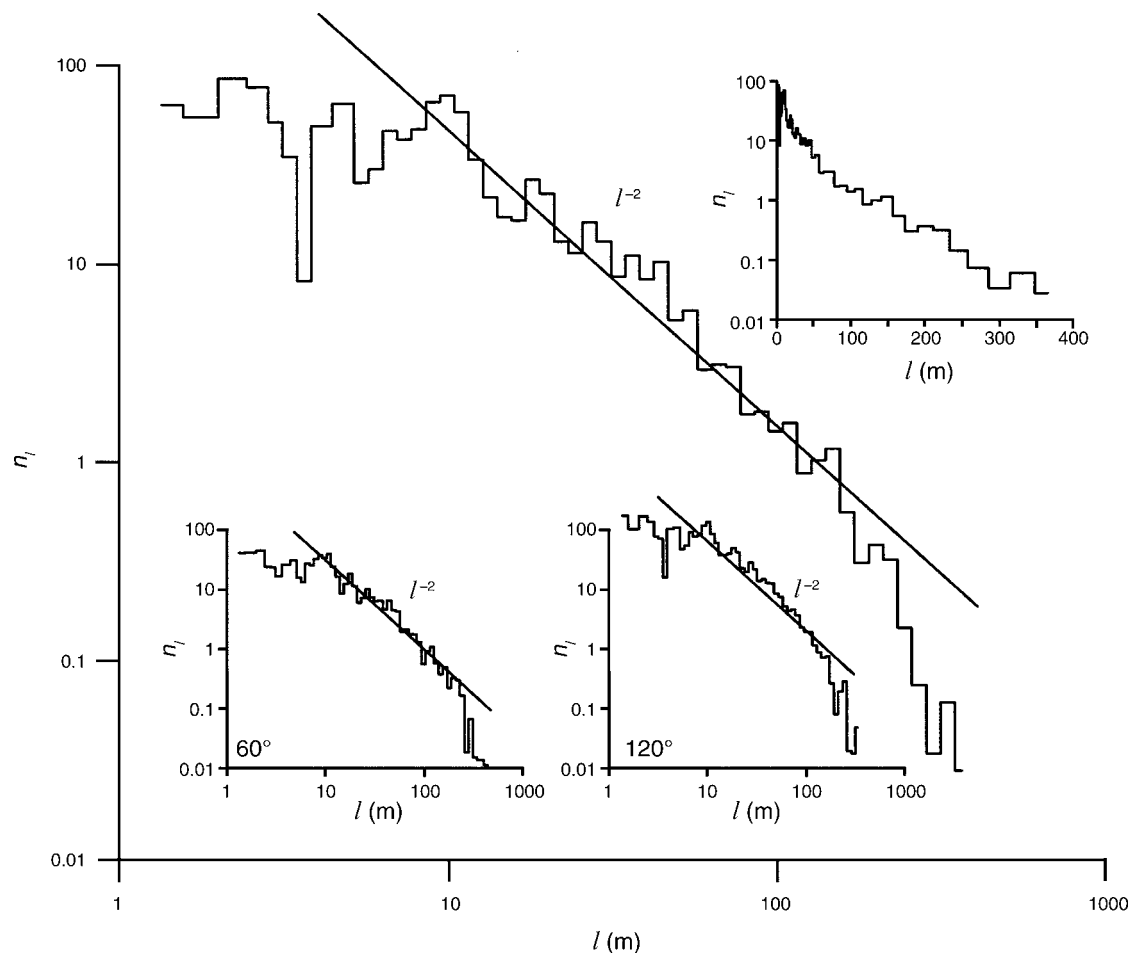
FIG. 2. The distribution, n_l, of lengths, l, of "straight-line flight segments." The sizes of the data collection bins are logarithmically distributed, and numbers of straight-line flight segments have been normalized by the bin sizes. The inverse-square-law scaling of the high tail ($l > 10$ m) of the distribution, l^{-2}, obtained from a linear least-squares fit of the distribution ($r^2 = 0.94$), is indicated. The upper inset shows the same data on log-linear scales. The lower insets show the distribution, n_l, of lengths, l, of "straight-line flight segments" when the critical angle used to define a turning point is taken to be 60° or 120° rather than 90° as in the main plot.

Long-term power-law correlations (Peng et al. 1995) however, will generate α values $\neq 0.5$. Fig. 4a shows that for our data $\alpha = 0.85$, and this implies that long term power-law correlations exist in the data, or in other words, the bee flight patterns were similar on all temporal scales. This scale-free, Lévy-flight-like characteristic is confirmed by the power-law dependence of the ensemble-averaged power spectrum (Buldyrev et al. 1995) of the time series $u(t)$ shown in Fig. 4b. The spectrum is seen to approximately follow a power-law scaling with $S \propto f^{-\beta}$ where $\beta = 0.7$, a result that is consistent with $\alpha = 0.85$ because $2\alpha = 1 + \beta$ (Buldyrev et al. 1995). The power spectrum is distinctly different from that of white noise (where $\beta = 0$) which has no temporally correlated behaviour, and is akin to "1/f" noise found in scale-invariant systems with long-range correlations. The exponents did not change significantly when the 90° angle used to define a change in flight direction, was altered by ±30°. To investigate the
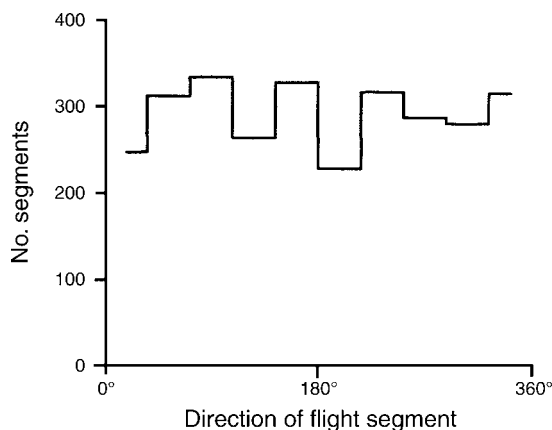

FIG. 3. Distribution of the directions of the flight segments in the representation of the bee flights.
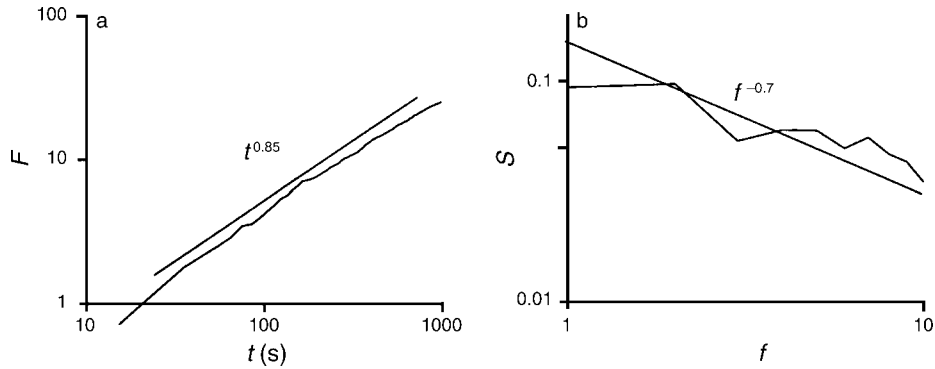
FIG. 4.   The net root-mean-square value of the running sum, F, and the power spectrum of the time series $u(t)$. (a) F is plotted as a function of elapsed time, t, measured in seconds from the moment at which the radar first detected each released bee. The straight line with $\alpha = 0.85$ constitutes a linear least-squares fit to the data (correlation coefficient, $r^2 = 0.90$). (b) The ensemble-average of the power spectrum $S(f)$ of the time series $u(t)$. The straight line with $\beta = 0.70$ constitutes a linear least-squares fit to the data (correlation coefficient, $r^2 = 0.90$).

possible origin of this scale-free behavior further, we determined the fractal dimension, D, of the flight paths. This was done by calculating the average number, n_{box}, of boxes of size l_{box} required to enclose the representations of the flights. A power-law relationship of the form $n_{box} \propto l_{box}^{-D}$ would be indicative of a scale-free characteristic with fractal dimension D. Fig. 5 shows that $D = 1.2$.

The scaling properties of the first and second halves of the flight patterns were statistical indistinguishable, as were those of the first and last quarters of the flight patterns. This indicates that the scale-free characteristics of the flight paths do not change during the course of the flights.

Correspondence with Lévy flights

The inverse-square power-law distribution of flight lengths is indicative of the presence of Lévy flights with $\mu = 2.0$. Their presence is supported by the occurrence of
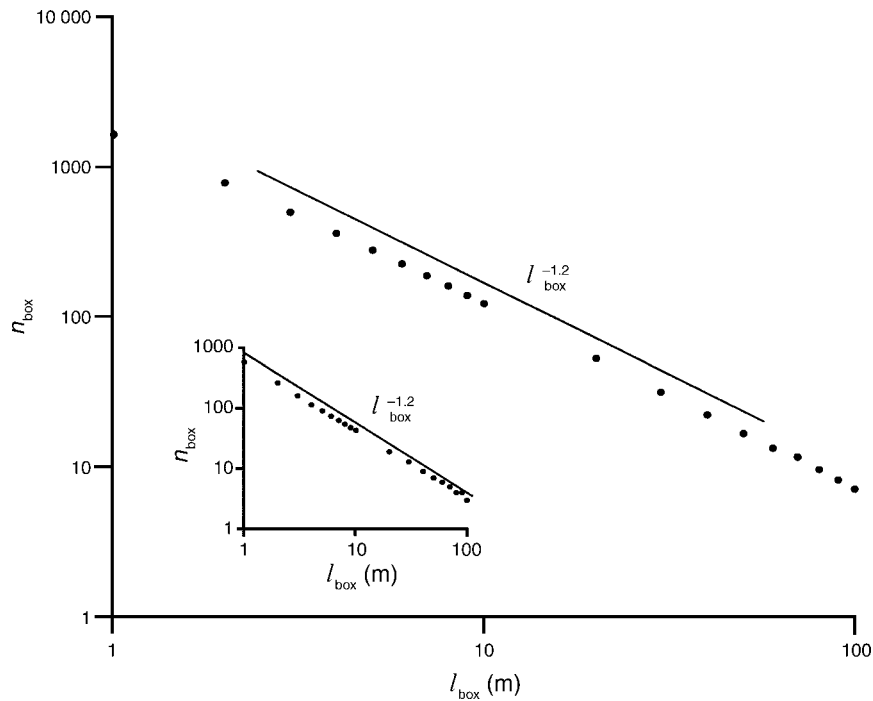

FIG. 5.   Assessment of the fractal dimension associated with the representations of the bee flights. The average number, n_{box}, of boxes of size l_{box} required to enclose the representations of the honey bee flights is plotted against l_{box} (solid circles). A power-law relationship of the form $n_{box} \propto l_{box}^{-D}$ would be indicative of a scale-free characteristic with fractal dimension D, and here, a linear least-squares fit shown by the straight line indicates that $D = 1.2$ ($r^2 = 0.99$). The inset shows the same plot for a series of simulated Lévy flights with $\mu = 2$.

long-range power-law correlations in the time series data for turning points and by power-law scaling of the corresponding spectra. This is because the scaling exponents $\alpha = 0.85$ and $\beta = 0.7$ can be produced by finitely long Lévy flights with $\mu = 2.0$ (Viswanathan et al. 1996). Fig. 5 shows that the fractal scaling, $D = 1.2$, found from our observations, can also be reproduced by truncated Lévy flights with $\mu = 2$. It can be shown that α approaches the limit $2 - \mu/2$ and that D approaches $\mu - 1$ asymptotically for sufficiently long sequences (Viswanathan et al. 1996).

DISCUSSION

Our harmonic radar data reveal that displaced bees adopt a stereotypical search strategy when attempting to locate their hive. The search begins at the location where the bees initially expect to find the hive, and is comprised of loops of ever-increasing size that start and end at this location, and are directed in different azimuthal directions. This strategy ensures that the area where the target is expected to lie is searched most intensively. We tested whether these flights represented an optimized search pattern, and found that they had all the characteristics of an optimal looping Lévy-flight searching strategy (A. M. Reynolds, *unpublished manuscript*). In this strategy, the lengths of the loops are distributed according to an inverse-square power law, and are directed in different azimuthal directions. If such a search progresses without success, it eventually becomes advantageous for the searcher to refrain from repeatedly returning to the origin and to instead adopt an optimal freely-roaming Lévy-flight searching strategy (Viswanathan et al. 1999). The bees in our study did exactly this.

Freely roaming Lévy flights have been found to characterize the movement patterns of a diverse range of animals including, albatrosses, deer, bumble bees (Viswanathan et al. 1996, 1999), jackals (Atkinson et al. 2002), microzooplankton (Bartumeus et al. 2003), spider monkeys (Ramos-Fernández et al. 2004), and even human hunter-gathers (Brown et al. 2007). Our results are the first reported example of optimal looping Lévy-flight searching.

The random Lévy-looping searching strategy is clearly less reliable than an equidistant (Archimedian) spiral search pattern. Such a spiral search could, however, work only if the bees' navigation were precise enough and their visual detection ability were reliable enough, to ensure that all areas are explored and that no intervening regions escape scrutiny. Should the hive be missed, there would be no chance of encountering it a second time because the flight path is an ever-expanding spiral. Relying on a spiral search pattern would therefore be disastrous where navigational and detection systems are less than ideal, and even then, this method could be used only for short searches before the inevitable cumulative navigational error became too large to allow a true spiral to be maintained. Switching from spiral to random looping search paths has been observed in the desert isopod

Hemilepistus reaumuri when it gets lost after an excursion from its burrow (Hoffman 1983) and in desert ants (*Cataglyphis*) returning to their nest after foraging beyond the range of their known landmark map (Wehner and Srinivasan 1981). The same strategy is also adopted by *Cataglyphis* ants if they are displaced by strong winds that have blown them off the ground (Wehner et al. 2002). These situations are not dissimilar to that of the displaced honey bees in our study, and it is therefore possible that the random looping searching patterns of desert ants, of desert isopods, and of other central place foragers, all constitute an optimal looping Lévy-flight searching strategy. This possibility is the subject of an ongoing investigation.

Our analysis of the flight patterns of displaced bees showed that their Lévy-flight searching strategy can occasionally and temporarily be disrupted when the bees encounter localized landscape features but that the overall flight paths remain close to the optimal search pattern. In particular, upon encountering a linear landscape feature that passed through the hive position, most bees flew repeatedly back and forth along a portion of it before arriving at the hive, or resuming an off-feature flight pattern which usually brought them back to the hive. One release point, R2, was actually on the linear feature, and most bees released from this point flew back and forth along it before eventually traveling far enough along it to arrive at the hive. Nevertheless the scaling exponent characterizing the time series of turning points, the associated power-spectra, and the fractal dimension characterizing these flights emanating from R2 did not differ significantly from those characterizing two-dimensional flights beginning from the off-feature release points, R1 and R2. These results are consistent with the hypothesis that an inverse-square power-law distribution of move lengths is universal; independent of the dimensionality of the searching and robust with respect to short-term effects, including effects on the organisms' behaviour and physiology (Viswanathan et al. 1999, Bartuemeus et al. 2003). The results also illustrate that the behavioral plasticity of the bees allows them to adapt their random searching strategy to widely different environmental scenarios.

Finally we note that the walking patterns of some ants (*Formica schaufussi, Pogonomyrmex occidentalis*), beetles (*Eleodes extricata, E. obsoleta, E. hispilabris*), grasshoppers (*Opeia obscura, Psoloessa delicatula, Xanthippus corallipes*), and spider mites (*Tetranychus urticae*) may exhibit a scale-free or fractal property (Dicke and Burrough 1988, Fourcassié et al. 1992, Wiens et al. 1995), which is consistent with optimal Lévy-flight searching patterns. We hope that our study will motivate ecologists to reexamine in this context the movement patterns of these and other insects.

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