

Honeybees perform optimal scale-free searching flights when attempting to locate a food source

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Summary

The foraging strategies used by animals are key to their success in spatially and temporally heterogeneous environments. We hypothesise that when a food source at a known location ceases to be available, flying insects will exhibit search patterns that optimise the rediscovery of such resources. In order to study these searching patterns, foraging honeybees were trained to an artificial feeder that was then removed, and the subsequent flight patterns of the bees were recorded using harmonic radar. We show that the flight patterns have a scale-free (Lévy-flight) characteristic that constitutes an optimal searching

strategy for the location of the feeder. It is shown that this searching strategy would remain optimal even if the implementation of the Lévy-flights was imprecise due, for example, to errors in the bees' path integration system or difficulties in responding to variable wind conditions. The implications of these findings for animal foraging in general are discussed.

Key words: optimal search strategy, imprecise Lévy-flight, honeybee, *Apis mellifera*, harmonic radar tracking.

Introduction

The availability of food resources changes over time and space, and foraging animals are constantly faced with choices about how to respond when a resource becomes depleted. Foragers therefore benefit from employing flexible strategies for resource exploration and exploitation. Bees are 'central place foragers', exploiting resources by memorising routes from the nest/hive to profitable floral patches and then repeatedly visiting those locations. When a floral patch finishes blooming, or ceases to produce nectar and/or pollen, how do bees feeding at this site respond? Do they utilise knowledge of the landscape obtained during previous flights to locate a floral patch (Collett et al., 2006) or do they start searching anew? In the case of honeybees (*Apis mellifera* L.), there is also the option of returning to the hive and gathering information from other bees about resource locations, by means of the waggle dance (Biesmeijer and Seeley, 2005). In reality, the honeybee responses are likely to be a combination of the above strategies; Biesmeijer and Seeley showed that scouting and recruiting behaviour of individual honeybees is flexible such that one bee is not constrained to be a recruit or a scout but can perform either role, depending on circumstances (Biesmeijer and Seeley, 2005).

In addition to the resource depletion problem, slight navigational errors might also result in a bee arriving at a location slightly different from the actual location of known forage. In both of these scenarios, we might expect the bee to

perform a search strategy to re-find the known food source, or to find a new nearby source.

It is now possible to track individual flying bees as they forage, using harmonic radar (Riley et al., 1999; Riley et al., 2003; Riley et al., 2005), enabling us to investigate the search strategies used by bees when a forage source runs out. We hypothesise that when a food source at a known location ceases to be available, flying bees will spend some time in an optimised search of the vicinity for the resource in question before they (eventually) return to the hive (where they may or may not gather information on other resource localities from nest mates). These local search patterns are described mathematically, using Lévy-flight theory, in this paper.

Lévy-flights are comprised of random sequences of independent flight segments whose lengths, l , are drawn from a probability distribution function having a power-law tail, $P(l) \sim l^{-\mu}$, where $1 < \mu < 3$ [Bouchaud and Georges (Bouchaud and Georges, 1990) and references therein]. When $\mu \geq 3$, the distribution of the total length of any number of flight segments is Gaussian, by virtue of the central limit theorem, whilst $\mu \leq 1$ does not correspond to probability distributions that can be normalised. Lévy-flights have a remarkable statistical property: namely that distributions of the total length, L , of any number of flight segments have power-law tails, $P(L) \sim L^{-\mu}$. Consequently, Lévy-flights are said to be 'scale-free' because their statistical properties do not depend upon the observational scale. This absence of a characteristic scale makes Lévy-flights scale-

invariant fractals. Lévy-flights may have been observed in the movement patterns of wandering albatrosses, deer, foraging bumble bees (Viswanathan et al., 1996; Viswanathan et al., 1999), a species of African jackal (Atkinson et al., 2002), foraging spider monkeys (Ramos-Fernández et al., 2004) and *Drosophila* flying in a small circular arena (Reynolds and Frye, 2007). These *freely roaming* Lévy-flight movement patterns are known to constitute an optimal searching strategy for the location of randomly and sparsely distributed targets (Viswanathan et al., 1999). That is, they minimise the mean distance travelled before first encountering a target. Sub-optimal Lévy-flight searches with $\mu \neq 2$ and Gaussian (diffusive) searches ($\mu=3$) can be up to 10 times longer than optimal Lévy-flight searches (Viswanathan et al., 1999). Recently, Reynolds et al. reported that honeybees adopt $\mu=2$ Lévy-flight *looping* patterns when attempting to locate their hive and when deprived of navigational cues (Reynolds et al., 2007). In contrast to their freely roaming counterpart, Lévy looping flights extend out from and return back to a fixed location, around which the search is centred. Lévy looping flights with $\mu=2$ are optimal for the location of a single target location when the most likely location of the target is known or is presumed known (A.M.R., manuscript submitted). The equidistant spiral (Archimedean) search would be another alternative optimal pattern. If the bees were using this then it would be visible in the tracked flight patterns.

In this paper, we show how Lévy-flight looping patterns underlie the flight paths of honeybee foragers searching a local area for a known food source. These flight patterns can be associated explicitly with the adoption by the bees of an optimal scale-free searching strategy for the location of a single target. The theory of random Lévy-flight searching is advanced by the formal demonstration that these searches will remain optimal despite errors due to imperfections in the bees' navigation system.

Materials and methods

Experimental procedures

The data-set used in the present study comprised 39 tracks derived from an experiment, carried out in July–August 2003, to investigate honeybee flights in relation to the manipulation of landmarks (J. L. Osborne, A. D. Smith, D. R. Reynolds and N. L. Carreck, manuscript submitted). Consequently, an experimental arena of mown grass on an airfield at Wyton in Cambridgeshire, eastern England, was chosen for its lack of obvious landmarks and its horizon, which contained very few features that a honeybee's eye would have been able to resolve (Giurfa et al., 1996; Giurfa and Menzel, 1997). There was very little natural forage on the experimental site, and no honeybees were seen foraging in the vicinity prior to the start of our experiments. The honeybees to be tracked were foragers from a small colony of ~5000 workers, housed in a brood box mounted on a stand. The hive was fitted with a transparent Perspex® entrance tunnel with removable doors and roofs, enabling bees to be easily captured or returned to the hive or the hive to be completely closed. The front of the hive stand and the hive roof were painted white to aid visibility.

Bees were trained to a feeder, a glass jar containing 70% sucrose solution, inverted onto a grooved Perspex plate. The feeder was placed on a small wooden board 46 cm² in the grass. A visual resolution of 1–2° is possible for the bee compound

eye (Giurfa and Menzel, 1997) so the board would have been visible to the bee from a maximum distance of 18.6 m; and probably a lot less (7 m) since Giurfa et al. (Giurfa et al., 1996) suggest that 5° is a more realistic approximation of visual resolution once spectral contrast is taken into account. In the experiments, the feeder was removed in each of the test situations so that the bees were not responding to visual or olfactory cues from the feeder itself.

The feeder was positioned 210 m from the hive. In order to minimise the effect of navigational cues, such as any distant features, each evening after the end of the experimental work, the hive, and hence the entire experimental set-up, was moved 30 m to the east or west. This did not appear to affect the bees' ability to find the feeder or to find their way home. After moving the hive, no orientation flights were observed, and no bees were seen searching around the previous site of the hive or feeder the following morning.

The observations were carried out on marked bees that had been observed several times at the feeder and were therefore regular foragers. When one of these bees was about to leave the hive, she was captured and fitted with a harmonic radar transponder, as described by Capaldi et al. (Capaldi et al., 2000). The feeder (and the bees feeding on it) was removed from the experimental arena, and the bee with transponder was then released from the hive entrance. Her flight route was tracked using scanning harmonic radar (Riley et al., 1996; Riley and Smith, 2002). Only one such regular forager was tracked at a time and the transponder was removed when the bee returned to the hive. The errors in fixing positions of the bees were approximately ± 3 m in range and ± 1.3 m in azimuth (at a range of 300 m). Bees can be detected by the harmonic radar when flying below about 10 m (depending on range and terrain). We are unable to determine the precise height of flight but there is no evidence in this study or in others we have done (Reynolds et al., 2007) to suggest that bees fly higher when searching. Rather, the height of flight may be related to the maintenance of a certain optic flow (Riley et al., 1999).

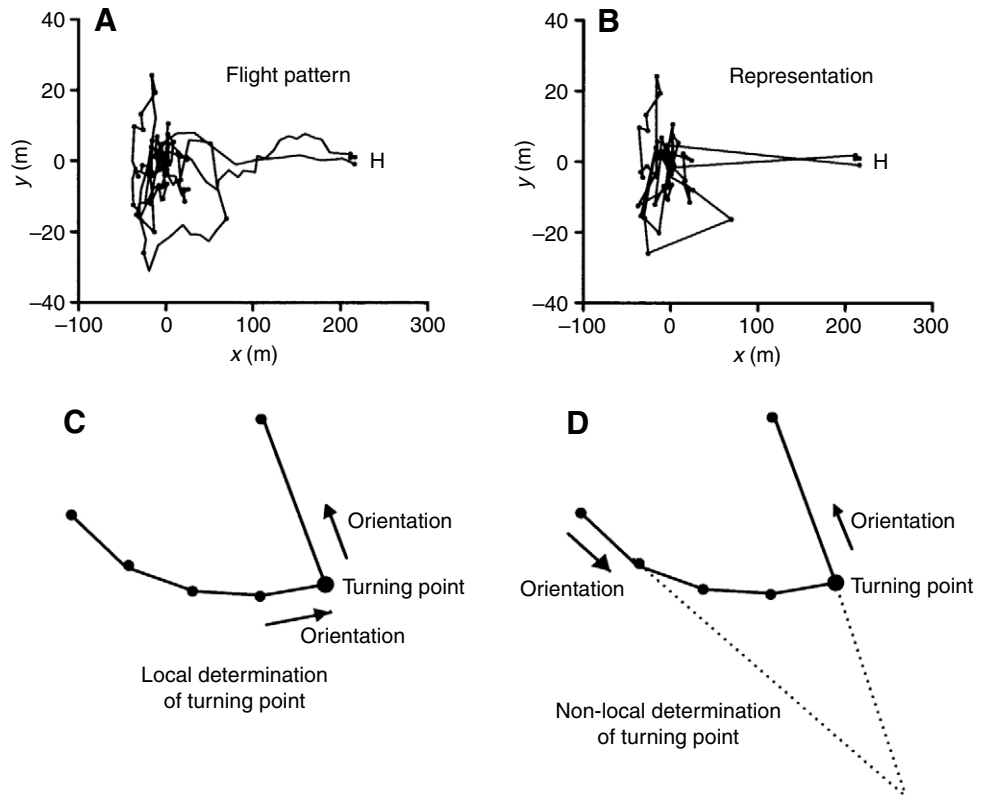
Some bees were trained to the feeder when a landmark (a white vehicle approximately 4 m long \times 2 m high) was positioned broadside-on either 150 m from the hive, but offset from the direct line between the hive and feeder by 12°, or 160 m from the hive on the direct line between the hive and feeder. In some cases, the landmark was removed when the feeder was removed.

Each of the 39 tracks used in this study comprised a 'vector' flight (Riley et al., 2003) from the hive to the vicinity of the former position of the feeder ('virtual feeder'), the ensuing searching flights and a return flight. A further 12 flights were excluded from the analysis either because the radar recordings were incomplete or because the bees flew around the hive rather than making an immediate vector flight towards the virtual feeder.

Analysis method for the honeybee search flights

After release, most bees flew immediately to the vicinity of the virtual feeder before engaging in long, looping flights indicative of searching. After a period of searching, most bees returned to the hive (see the example shown in Fig. 1). We carried out an analysis of the bees' flight tracks to determine

Fig. 1. (A) A typical flight pattern of a honeybee trained to an artificial feeder, which was then removed, resulting in a localized search around the former position of the feeder. The location of the honeybee was recorded every 3 s unless the radar failed to detect the radar transponder. The hive was located at $(x, y)=(210 \text{ m}, 0 \text{ m})$ and the feeder was located at $(x, y)=(0 \text{ m}, 0 \text{ m})$ (approximately). The flight begins and ends in the vicinity of the hive (marked with an 'H'). The locations where there are significant changes in flight orientation are indicated (\bullet). A significant change in orientation is taken to arise when the angle between the current flight segment (joining two successive recorded positions) and the flight segment immediately following the last change in orientation is less than 90° , i.e. when the current *non-local* flight orientation differs from proceeding flight orientation by more than 90° (Reynolds et al., 2006). (B) Representation of the honeybee flight in terms of straight-line flights and changes in flight orientation. The statistical properties of these representations do not differ significantly from representations in which *local* abrupt changes in orientation are taken to arise when the angle between two successive flight segments (i.e. between three successive recorded positions) is less than 90° . The close correspondence between these two [local (C) and non-local (D)] representations indicates that most changes in flight orientation occur abruptly rather than through the accumulation of small changes.



how they compared with what is known about optimal search strategies. To do this, we represented the flight paths as sequences of straight-line segments between the points at which significant changes in direction occur (see Fig. 1). A 'searching' flight is defined to be the entire flight pattern that arises after the first significant change in flight orientation and before the last significant change in flight orientation.

The representations of the searching flights (see Fig. 1) were analysed in detail by using 'random walk methods', which can detect the presence of long-term correlations. Our first analysis is based on the fact that the number of turning points occurring within the time intervals t to $t+\Delta t$ defines a time series, $u(t)$, and an associated net 'displacement':

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

If the values of $u(t)$ are completely uncorrelated and behave like 'white noise', then the root-mean-square displacement $F = \sqrt{\langle [n(t) - \langle n(t) \rangle]^2 \rangle} \propto t^\alpha$, where $\alpha = 1/2$ 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. Long-term power-law correlations, however, will generate α values $\neq 1/2$. Our subsequent analyses consist of a determination of the fractal dimension of the represented honeybee flight patterns and an

examination of the lengths and durations of the straight-line segments in those representations.

Results

Searching flights are consistent with an optimal Lévy flight search

Fig. 2C shows that, for most bees, the first significant change in flight orientation occurs in the vicinity of the virtual feeder; i.e. upon release from the hive most bees follow the expected beeline vector flights to the virtual feeder location (Riley et al., 2003). The vector flights to the virtual feeder made by three groups of bees (i.e. flights with no landmark present, and with the landmark in one of the two locations) are statistically indistinguishable. This suggests that the bee's 'vector navigation' system was accurate over these scales and was unaffected by the removal of the landmark during our experiment. The mean (\pm s.d.) duration of the searching flights was 249 ± 164 s. Fig. 2D shows that some, but not all, of the 'return' flights to the hive were beeline vector flights that emanated from the vicinity of the virtual feeder and approximately retraced the initial outward beeline vector flight. The figure also shows that some of the return flights over- or undershot the hive location and that these bees arrived at the hive location only after first having executed local looping flight manoeuvres.

The beeline vector flights were followed by searching flights that were centred on the location of the virtual feeder, as shown in Fig. 3, or were followed by return flights to the hive. There

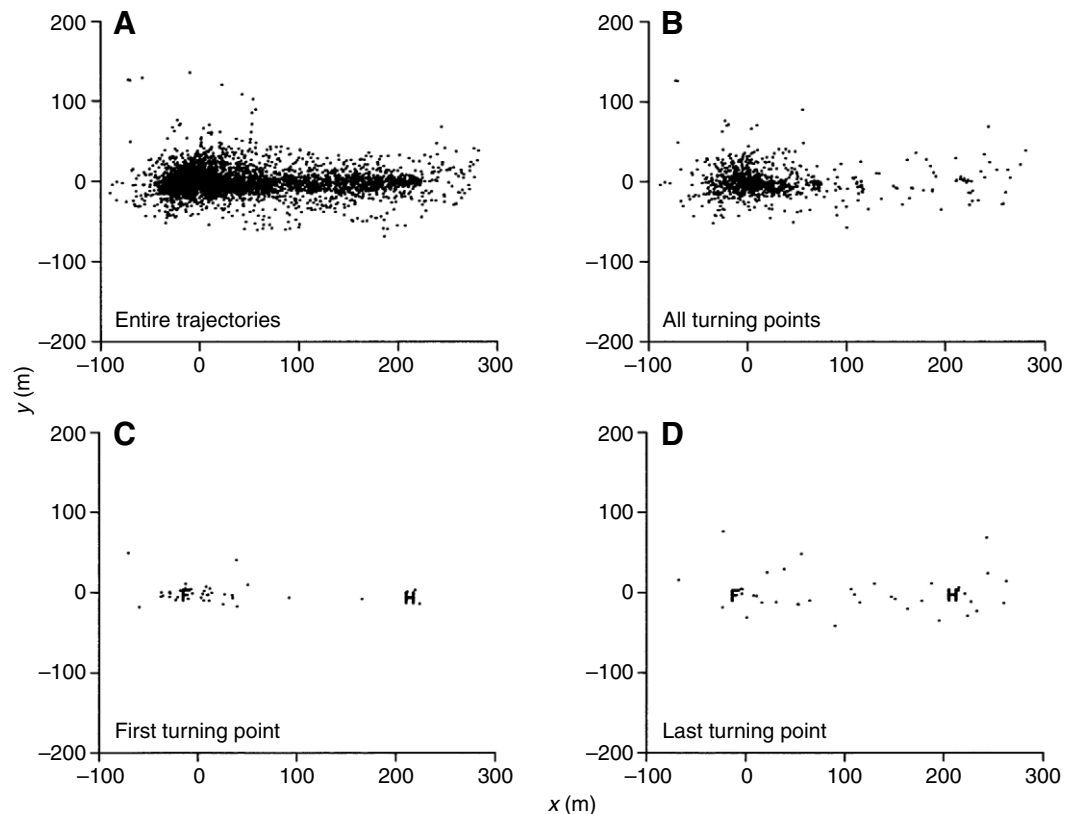


Fig. 2. (A) The recorded locations of the honeybee flights in an x - y coordinate system in which the virtual feeder (F) is located at the origin (0 m, 0 m), and the hive (H) is located at (210 m, 0 m). (B) The locations where the flights changed orientation. (C) The first significant change in flight orientation. It can be seen that this generally occurs in the vicinity of the virtual feeder. (D) The last significant change in flight orientation.

was more searching along the hive–feeder direction than at 90° to it. It is possible that the bees' navigation system was affected more by errors in range than by errors in angle. The directions, θ , of flight segments in the searching flights were, however, uniformly distributed between 0° and 360° (Fig. 4).

Fig. 5 shows that for our data the index α is equal to 0.85, and, as explained above, 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. The presence of this scale-free characteristic is confirmed by the fractal scaling property of the 'represented' honeybee flights shown in Fig. 6. Scaling properties of the first and second halves of the searching flights are statistically indistinguishable. This suggests that the search pattern does not change with time. The territory covered does, however, tend to increase with time.

The observed scale invariance of the representations of the honeybee flights can be understood within the context of a Lévy-flight (scale-free) model. In this model, the orientations, θ , of independent straight-line flights are, in accordance with observations (Fig. 4), drawn at random from a uniform distribution $P_\theta(\theta)=1/2\pi$ for $0\leq\theta<2\pi$. Flight lengths, l , are drawn at random from a Lévy-distribution $P=(\mu-1)l_0^{\mu-1}l^{-\mu}$ for $l\geq l_0$ and $P(l)=0$ for $l<l_0$ where $1<\mu<3$. Fig. 6 shows that the observed fractal scaling $D=1.3$ is close to the value of 1.2 predicted by the model when $\mu=2$ (Reynolds et al., 2007). Note that the fractal dimension of these finitely long Lévy-flights differs from the fractal dimension of infinitely long Lévy-flights, $D=\mu-1$ (Reynolds et al., 2007). Viswanathan et al. showed that such a model also reproduces the observed power-law scaling ($\alpha=0.85$) of the root-mean-square displacement, F

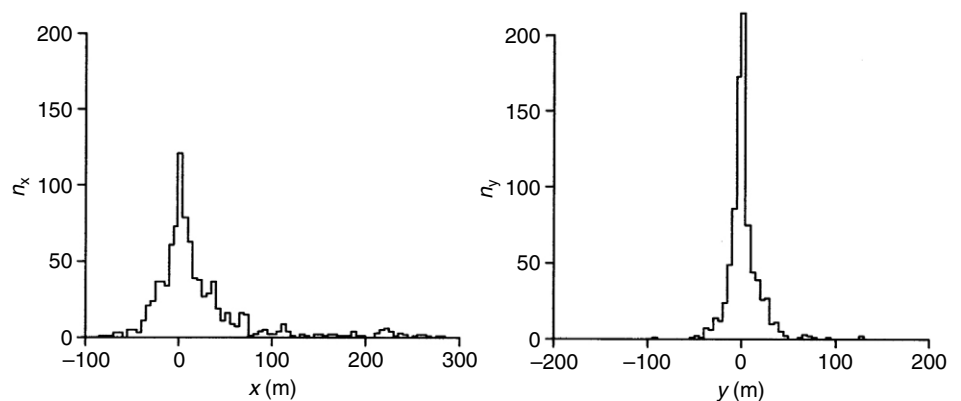


Fig. 3. The number of changes in flight orientation in an x , y coordinate system, showing that the search flights are centred on the location of the virtual feeder. The virtual feeder is located at the origin (0 m, 0 m), and the hive is located at (210 m, 0 m).

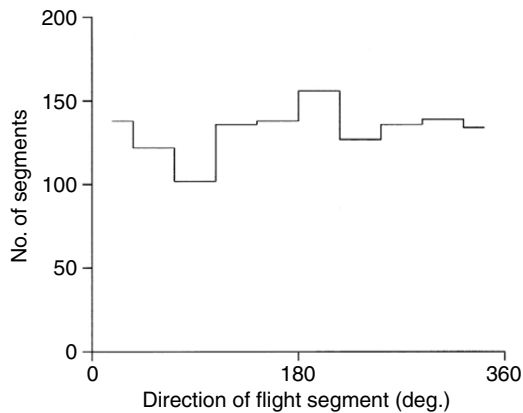


Fig. 4. Distribution of the directions, θ , of the flight-segments in the representation of the searching flights.

(Viswanathan et al., 1996). The lengths of the straight-line flights in the representations of the honeybee flights are seen in Fig. 7 to be distributed according to a Lévy stable distribution (Cauchy distribution). The tail of this distribution obeys an inverse-square law. This corresponds to $\mu=2$, the optimal value for the location of a single target (A.M.R., manuscript submitted). A Cauchy distribution of flight-segment lengths would arise if each of the Lévy flight-segments *resolved* by the analysis were actually comprised of many shorter *unresolved* Lévy flight-segments (Gnedenko and Kolmogorov, 1954). A Cauchy distribution may also arise if movement patterns were exclusively associated with the adoption of an optimal scale-free searching strategy. This is because a Cauchy distribution constitutes a least-biased choice for a distribution with an inverse-square-law tail (Alemany and Zanette, 1994).

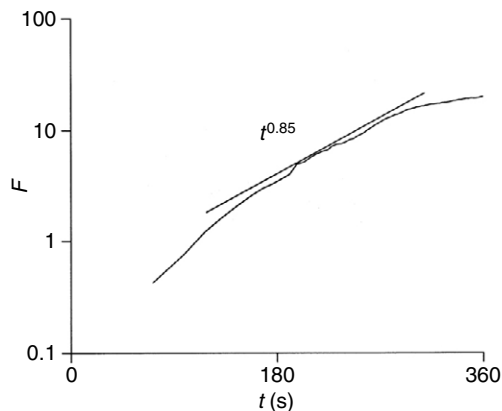


Fig. 5. Power-law scaling of the root-mean-square, F , net displacement indicative of the presence of long-range correlations, demonstrating that the honeybee flights are scale-free. The averaging is over the 'searching phases' of 39 bees. Approximate power-law scaling behaviour with $\alpha=0.85$ extending over about one decade is indicated (straight line). This scaling and others presented later are not sensitively dependent upon the presence or absence of four non-returning bee tracks within the averaging. The scaling exponent, α , does not change significantly when the angle (90°) between successive flight segments used to define a change in flight orientation is changed by $\pm 30^\circ$.

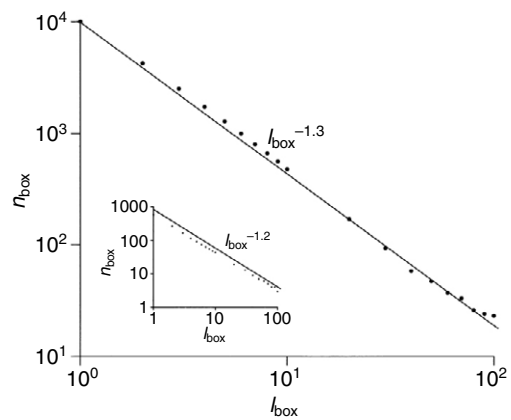


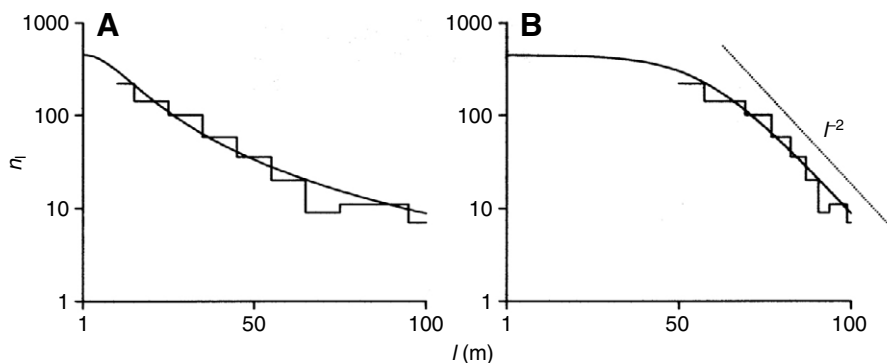
Fig. 6. The mean number, n_{box} , of boxes of size l_{box} required to cover the representations of the honeybee flights. Power-law scaling, $n_{\text{box}} \propto l_{\text{box}}^{-D}$ is indicative of a scale-free characteristic with fractal dimension D . Power-law scaling with $D=1.3$ obtained from a linear least-squares fit ($r^2=0.99$) is indicated. The insert shows the n_{box} of boxes of size l_{box} required to cover simulated Lévy-flights with $\mu=2$. The number of straight-line flights within the simulated Lévy-flights is equal to the mean number of straight-line flights in the representations of the honeybee flights. The model predicts that $D=1.2$. A similar level of correspondence between the fractal dimension of the representations of bee flights and simulated Lévy flights with $\mu=2$ is also attained when fractal dimensions are calculated using the method of dividers rather than the box-counting method.

Fig. 8 shows that relatively short flight segments tend to be associated with relatively slow speeds whilst longer flight segments tend to be associated with faster speeds. This correlation between flight-segment length and speed cannot be attributed to the effects of wind speed on flight speed because short and long flight segments are not executed along distinctly different directions. As a consequence of this correlation, bees spend more time searching in the location where the feeder is expected to be. If the search were to continue indefinitely then eventually it becomes advantageous to refrain from looping back to the origin of the search and instead adopt a freely roaming Lévy-flight searching pattern (A.M.R., manuscript submitted). The slow, shorter flight segments can then be associated with an 'active local searching phase' whilst the faster, longer flight segments can be associated with a 'relocation' phase where the bee moves to a new centre-of-search. Such intermittent searching has been observed in a diverse range of species (e.g. ground foraging birds, crickets, sea birds, octopi, planktivorous fish) (Kramer and McLaughlin, 2001). Lévy-flight models of intermittent searching predict that searching is optimal when $\mu=2$ and that, when the searching is optimal, the mean times within the searching and relocation phases obey the scaling relation $t_r \propto t_s^{2/3}$ (Reynolds, 2006). Fig. 9 shows that the honeybee flight patterns are consistent with this prediction and with observational data for many other species.

Imprecise Lévy-flight searching strategies

Here, it is shown that the $\mu=2$ scale-free searching strategy remains optimal when the execution of the Lévy-flight patterns is imprecise. Imprecise execution of a Lévy-flight pattern is an inevitable consequence of navigational errors. The simplest

Fig. 7. Number of straight-line flights, n_l , of length l in the representations of the honeybee flights (histogram) on linear-linear scales (A) and on log-log scales (B). A Lévy stable distribution (Cauchy distribution), $P(l) = (1/\pi)\gamma/(l^2 + \gamma^2)$, with scale parameter, γ , chosen to minimize the sum of the squared differences between the Lévy stable distribution and the data, n_l (solid line). The inverse-square law scaling of the high tail ($l > 10$ m) of the distribution, obtained from a linear least-squares fit of the distribution ($r^2 = 0.94$), is indicated (broken line).



scenario, and the one considered here, is that the intended and realized lengths of a flight segment are related by $l^* = l(1+s)$, where the random quantity, s , is the proportional error in flight length. The range of realised flight lengths increases with increasing length of the intended flight segment, thereby capturing the expected accumulation of flight errors with distance flown. The distribution of realised flights is determined by the convolution, $P_{l^*}(l^*) = \int P_l(l)P_s(s)\delta[l^* - l(1+s)]dl ds$, where $P_l(l)$ is the distribution of intended flight lengths and $P_s(s)$ is the distribution of proportional errors, s . If a bee seeks to adopt a scale-free searching strategy, then the distribution of intended flight lengths must have a power-law tail, $l^{-\mu}$. The tail of the distribution of realised flight lengths is then determined by $P_{l^*}(l^*) = l^{-\mu} \int (1+s)^{-\mu} P_s(s) ds \propto l^{-\mu}$. This tail coincides with the tail of the distribution of intended flights. It follows that the realised scale-free searching strategy will be optimal when the intended, perfectly executed, searching strategy is optimal.

Discussion

In our experiment, foraging honeybees were trained to an artificial feeder that was then removed, and the subsequent flight patterns of the bees were recorded using harmonic radar. After release, most bees flew immediately to the vicinity of the virtual feeder in straight, compass-directed 'vector' flights (Riley et al., 2003). Some of the vector flights took place in strong (5 m s^{-1}) and blustery cross-winds, which displaced the bees from a direct 'bee-line' flight path between hive and feeder. Nonetheless, the bees usually managed to get 'back on track' as they approached the hive or feeder location, demonstrating the impressive accuracy of the bees' path-integration system, at least on the landscape scale used in the present experiment. Cumulative

navigational errors are inevitable, however, and they could become large in long-distance foraging excursions. So, despite the use of other navigational aids, particularly landmarks (Collett, 1996; Collett et al., 2002; Chittka et al., 1995), it is quite conceivable that a foraging bee might initially arrive at a marginally incorrect location. The search strategies studied here would facilitate the relocation of a floral patch if the error was slight and the resource was close by. Moreover, if in the mean time the flowers in the patch had dropped or ceased to produce nectar and pollen, then the described strategy might also facilitate the finding of other resources in the vicinity. As with our tracked bees, foragers will give up searching after a time and return to the hive. Under normal circumstances, the bee may then start to gather information from other foragers dancing on the comb: Biesmeijer and Seeley showed that bees were more likely to follow dances after they had returned from a failed trip (without nectar and pollen) (Biesmeijer and Seeley, 2005). Local searching may also be required when honeybees are directed by the waggle dance to a new food source, because the dance communication system will not specify a food location with pinpoint accuracy (Riley et al., 2005).

We turn now to the precise nature of the search strategy as revealed by our experiments. At the end of its vector flight, the bee adopted a stereotypical flight pattern comprised of loops of ever-increasing size that start and end at the origin of its search and point in different azimuthal directions. This strategy ensures that the central area where the feeder is most likely to be is searched most extensively. We have shown that the looping flight patterns made by honeybees are consistent with their having adopted an optimal Lévy-looping searching strategy for the location of a single target when the most likely location of

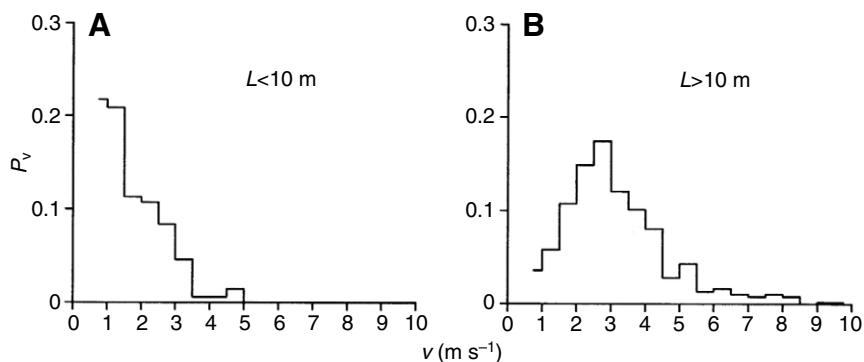


Fig. 8. The distribution of speeds associated with (A) short ($L < 10$ m) and (B) long ($L > 10$ m) flight-segments. The mean speeds are 1.6 m s^{-1} and 3.2 m s^{-1} . Distinctly different distributions are also obtained when the length scale L is increased or decreased by a factor of 2.

the target is known or is presumed known (A.M.R., manuscript submitted). This was done using a ‘random walk analysis’ of the turning points in the honeybee flight patterns, an examination of the fractal scaling properties of the flight patterns and a determination of the distribution of flight-segment lengths (Figs 5–7). The results of these independent analyses yield a consistent picture; namely that $\mu=2$ Lévy-flights underlie our recorded honeybee flight patterns. Some other reported instances of Lévy-flight animal movement patterns, most notably that of the wandering albatross (Viswanathan et al., 1999), are perhaps less secure because they are founded solely on the results of a single analysis. We also showed that the strategy remains optimal when the execution of Lévy-flights is imprecise due to the accumulation of navigational errors and unpredictable displacements by gusts of wind, i.e. when the execution of an optimal isotropic scale-free searching pattern is being compromised by flight errors (see section on Imprecise Lévy-flight searching strategies). In a Lévy-looping search, a searcher travels out from the origin of its search along a randomly orientated straight line whose length is drawn at random from a distribution with an inverse-square power-law tail. If the target is detected, the search ends – otherwise the searcher returns to the origin and then randomly chooses a new direction and distance before travelling out again. As a search progresses without success, the probability of finding the target at the origin decreases. Eventually it will become more profitable to desist from repeated returns to the original location and instead adopt a freely roaming Lévy-flight searching pattern. Such a strategy is not only optimal for the location of the original single target

(i.e. the hive or nest or nectaring plants), it is optimal for the location of sparsely and randomly distributed targets (i.e. food sources) that, once visited, are not depleted but instead remain targets for future searches (Viswanathan et al., 1999). This strategy minimizes the mean distance travelled, and so presumably the mean energy expenditure, before first encountering a target. Freely roaming Lévy-flight movement patterns may have been observed in a diverse range of organisms that includes the wandering albatross, an African jackal, spider monkeys and *Drosophila* fruit flies (Viswanathan et al., 1996; Viswanathan et al., 1999; Atkinson et al., 2002; Bartumeus et al., 2003; Reynolds and Frye, 2007).

The random Lévy-looping searching strategy is clearly less efficient than an equidistant spiral search pattern. A spiral search could, however, work only if the bees’ navigation were precise enough and their visual detection ability reliable enough to ensure that all areas are explored and that no intervening regions escape scrutiny. Should the objective be missed there would be no possibility of encountering it a second time because the flight path is an ever-expanding spiral. Relying on a spiral search pattern when attempting to locate the hive would therefore be disastrous where navigational systems are less than ideal; 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), in male ladybird beetles (*Adalia bipunctata*) after they encounter a conspecific female (Hemptinne et al., 1996) and in desert ants (*Cataglyphis*) returning to their nest after foraging beyond the range of their known landmark map (Wehner and Srinivasan, 1981) and if they are displaced by strong winds that have blown them off the ground (Wehner et al., 2002).

The case of *Cataglyphis* ants returning from foraging trips is interesting because it mirrors closely that of the honeybees searching at the end of their vector flights. In the *Cataglyphis* case, foragers that have moved beyond the range of their landmark map return to their nest using a path-integration (dead-reckoning) strategy (Wehner and Srinivasan, 1981). When adopting this strategy, an ant must continuously monitor its motion during foraging so that the mean vector pointing from its current position to its nest can be computed. Even small inaccuracies in this mode of navigation can result in large discrepancies between the end of the homing vector and the actual location of the nest. If a homing ant gets lost, it adopts a stereotypical search strategy that is comprised of loops of ever-increasing size that start and end at the origin of its search and point in different azimuthal directions (Wehner and Srinivasan, 1981). This strategy ensures that the central area where the nest is most likely to be located is searched most extensively. Müller and Wehner suggested that underlying the ant’s searching strategy is a spiral search programme that gets transformed into the observed pattern of loops by the ant’s idiosyncratic path integration system (Müller and Wehner, 1994). This search programme was described as a sequence of ever-expanding spiral movement patterns interspersed with reset episodes during which the ant returns to the origin. Our results for honeybees suggest that the searching patterns of homing desert ants are, in

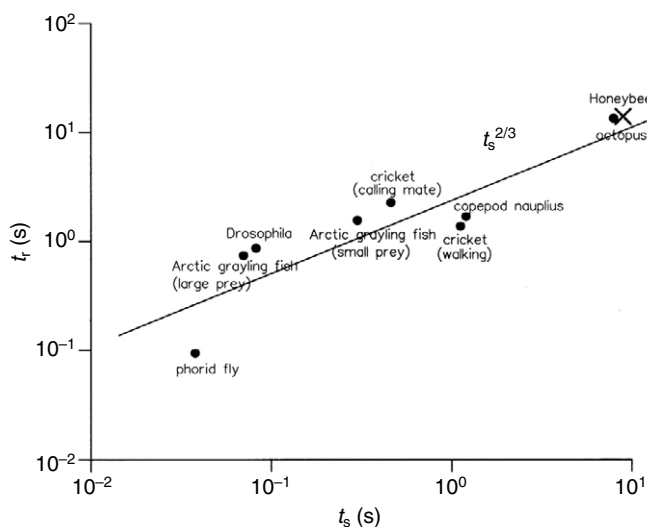


Fig. 9. Mean times in the local active searching phase, t_s , comprising short flight-segments having length $L < 10$ m, and in the relocation phase, t_r , comprising long flight-segments having length $L > 10$ m (X). Mean times do not change significantly when the length scale L is increased or decreased by a factor of 2. Mean times for a diverse range of intermittent foragers (●) [copepod nauplius, phorid fly, cricket, octopus, Arctic grayling fish (foraging for large and small prey) and freely flying *Drosophila* fruit flies] (Kramer and McLaughlin, 2001; Bénichou et al., 2005; Reynolds and Frye, 2007). The scaling relation $t_r \propto t_s^{2/3}$, predicted by the Levy-flight model of optimal searching (Reynolds, 2006), is shown (solid line).

fact, consistent with their having adopted an optimal 'Lévy-loop' searching strategy. Lévy-loop searches may also be adopted by other insects, including, for example, *Formica schaufussii* worker ants. Upon returning to a site at which food had previously been found, *F. schaufussii* workers adopt a fractal (i.e. Lévy-like) searching pattern and repeatedly return to the origin of their search (Fourcassié et al., 1992; Fourcassié and Traniello, 1994). Their searching patterns, like those of desert ants, become progressively more expansive. *F. schaufussii* show a greater tendency to return to, and search at, a site of a prior food find when offered a source of carbohydrate (sucrose solution) than when offered a source of protein (insect prey). That is, they search more persistently for resources that are renewed at a more or less regular rate (honeydew produced by homopterans), whereas they do not return as frequently to a rewarding site or give up their search rapidly when exploiting resources (e.g. dead arthropods) that have a high unpredictability in space and time (Fourcassié and Traniello, 1994). Our results with honeybees call for a re-examination of the movement patterns of these and other species as part of the development of a unifying theory of foraging patterns in animals. Indeed, our analysis (Fig. 9) suggests that this unification may extend well beyond insects and embrace a large class of animals. This is because the results presented in Fig. 9 support the conjecture that scale-free and intermittent behaviours are not manifestations of two distinctly different kinds of searching strategy but rather are constituent parts of a single, complex, widely adopted searching strategy (Reynolds, 2006; Reynolds and Frye, 2007).

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