

Cooperative random Lévy flight searches and the flight patterns of honeybees

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Abstract

The most efficient Lévy flight (scale-free) searching strategy for N independent searchers to adopt when target sites are randomly and sparsely distributed is identified. For $N = 1$, it is well known that the optimal searching strategy is attained when $\mu = 2$, where the exponent μ characterizes the Lévy distribution, $P(l) = l^{-\mu}$, of flight-lengths. For $N > 1$, the optimal searching strategy is attained as $\mu \rightarrow 1$. It is suggested that the orientation flights of honeybees can be understood within the context of such an optimal cooperative random Lévy flight searching strategy. Upon returning to their hive after surveying a landscape honeybees can exchange information about the locations of target sites through the waggle dance. In accordance with observations it is predicted that the waggle dance can be disrupted without noticeable influence on a hive's ability to maintain weight when forage is plentiful.

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1. Introduction

The scale-free movement patterns of some individual, independent, foragers [1–3] have aroused considerable interest because such patterns are known to constitute an optimal searching strategy when target sites are randomly and sparsely distributed and can be revisited [4]. Viswanathan et al. [4] considered an idealised model in which a searcher moves on a straight line towards the nearest target if the target site lies within a ‘direct vision’ distance, r , otherwise the searcher chooses a direction at random and a distance, l , drawn from a Lévy distribution, $P(l) \sim l^{-\mu}$ where $1 < \mu < 3$. It then moves incrementally towards the new location whilst constantly seeking for targets within a radius, r . If no target is sited, it stops after traversing the distance l and chooses a new direction and a new distance, otherwise it proceeds to the target. Viswanathan

et al. [4] then defined a search efficiency function $\eta(\mu)$ to be reciprocal of the mean distance travelled by a searcher before detection of a target site:

$$\eta = \frac{1}{N_l \langle l \rangle}, \quad (1)$$

where $\langle l \rangle$ is the mean length of a flight-segment and N_l is the mean number of straight-line segments traversed before arrival at a target site. When the distance between successive targets is approximated by the mean distance between successive targets, λ ,

$$\begin{aligned} \langle l \rangle &\approx \frac{\int_r^\lambda l^{1-\mu} dl + \lambda \int_\lambda^\infty l^{-\mu} dl}{\int_r^\infty l^{-\mu} dl} \\ &= \left(\frac{\mu-1}{2-\mu} \right) \left(\frac{\lambda^{2-\mu} - r^{2-\mu}}{r^{1-\mu}} \right) + \frac{\lambda^{2-\mu}}{r^{1-\mu}}, \end{aligned} \quad (2)$$

da Luz et al. [5] advocated the employment of a slightly more elaborate energy-weighted searching efficiency function $\eta_E(\mu) = \langle E \rangle / N_l \langle l \rangle$, defined as the ratio of the total energy

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gained in the sites visited to the total distance traversed. da Luz et al. [5] assumed that the mean net energy gained per site $\langle E \rangle = g - rN_l \langle l \rangle$ where g is the mean energy gained per site and r is the rate at which energy is lost per unit length during a search. The value of μ optimizing $\eta(\mu)$ will also optimize the energy-weighted searching efficiency $\eta_E(\mu)$ because $\eta(\mu)$ and $\eta_E(\mu)$ are linearly related. The optimal searching strategy would not be followed if it corresponds to $\langle E \rangle < 0$. Finding a food source close to the nest/hive is better than finding a food source further away, because the subsequent exploitation of that source is energetically more favourable. This desirable aspect of searching is captured by optimal Lévy-flight searching strategies. This is because such flights typically comprise of many, relatively short segments (comparable with the detection range of the searcher), punctuated by occasional longer segments. As a consequence, initial searches will tend to be localized relatively close to the nest/hive. More distant searches will arise only if sources are not detected during the initial search.

For a Lévy walk (here after referred to as ‘Lévy flight’ because of the focus on flights of honeybees) starting from an arbitrary point, x_0 in the interval $[-\lambda/2, \lambda/2]$, the average number of straight-line flight-segments traversed before first reaching a boundary (i.e., a target) is

$$N_L \sim ((x_0 + L)(L - x_0)/r^2)^{(\mu-1)/2}, \quad (3)$$

where $L = \lambda/2$ [6]. The searching efficiency is dependent upon the initial location of the searcher. Viswanathan et al. [4] considered two cases; so-called ‘destructive’ searching in which a searcher is initially located midway between adjacent targets (i.e., at $x_0 \approx 0$) and ‘non-destructive’ searching in which a searcher is initially located in the vicinity of a target site (i.e., at $x_0 \sim -L + r$). For sparsely distributed target sites ($\lambda/r \gg 1$), the searching efficiency for a non-destructive searcher is optimal when $\mu = 2$ [4]. This exponent characterises the foraging patterns of bumble bees [1], a species of African jackal [2] and wandering albatross [3]. These foragers do not appear to communicate location to each other [7]. The ability to communicate location may simplify an individual’s behaviour when foraging because only one of many foragers (rather than many individual foragers) needs to find forage and then communicate location to initiate subsequent exploitation by many foragers. In this Letter the optimal Lévy-flight (scale-free) searching strategy for many communicative searchers is established. These searchers undertake independent (and therefore not necessarily simultaneous) searches but communicate location after a target site has been located. A search is successful when one of many of these communicative searchers detects a target site. It is shown that the optimal Lévy-flight searching strategy for many communicative, non-destructive searchers ($\mu \rightarrow 1$) differs significantly from that of non-communicative, non-destructive searchers ($\mu = 2$). A similar distinction is found for non-communicative and communicative explorers which seek to maximize the territory covered during exploration. It is suggested that the orientation flights of honeybees [8] can be understood within the context of optimal cooperative random Lévy-flight (scale-free) searching/exploration strategies. Orientation flights are all the flights performed by a bee

before making her first ‘bee-line’ flight to and from a known forage location which may be located up to several kilometres from the hive. Orientation flights enable individual bees to acquire knowledge about the surrounding terrain. The orientation flights of honeybees may also contribute to the hive’s collective knowledge of the surrounding terrain because honeybees, unlike bumblebees, can communicate the location of forage patches through the waggle dance [9].

2. Effective searching strategies for communicative searchers

Here, the approach of Viswanathan et al. [4] is extended to establish the most effective searching strategy for many communicative searchers. This is achieved through a new derivation of mean first-passage time for Brownian walkers ($\mu = 3$) that is readily generalised to the case of many independent Brownian walkers. This analysis builds upon that of Nagar and Pradhan [10]. The mean first passage time of many independent Lévy flights ($\mu < 3$) is then examined in numerical simulations.

The probability, $p(x, t)$, that a Brownian walker with diffusivity K is located at some position, x , at time, t evolves according to

$$\frac{\partial p}{\partial t} = K \frac{\partial^2 p}{\partial x^2}. \quad (4)$$

When expressed in a Fourier-sine series the solution to (4) subject to the boundary conditions $p(\pm L, t) = 0$ and the initial condition $p(x, 0) = \delta_{x_0, x}$ is

$$p(x, t) = \frac{1}{L} \sum_{n=1}^{\infty} \sin \frac{(2n-1)\pi(x_0+L)}{2L} \sin \frac{(2n-1)\pi(x+L)}{2L} \times \exp \left(-K \left[\frac{(2n-1)\pi}{2L} \right]^2 t \right). \quad (5)$$

The probability that a Brownian walker is located within interval $[-L, L]$ at time t is just $q(t) = \int_{-L}^L p(x, t) dx$ and so the probability that a Brownian walker is absorbed between time t and time $t + \Delta t$ is $P(t) \Delta t = -\frac{dq}{dt} \Delta t$. Thus

$$P(t) = \frac{K\pi}{L^2} \sum_{n=1}^{\infty} (2n-1) \sin \frac{(2n-1)\pi(x_0+L)}{2L} \times \exp \left(-K \left[\frac{(2n-1)\pi}{2L} \right]^2 t \right). \quad (6)$$

Consequently the mean first-passage time, $\langle t_3 \rangle_1 = \int_0^{\infty} P(t) dt$, for a Brownian walker is, in accordance with Eq. (3), given by

$$\begin{aligned} \langle t_3 \rangle_1 &= \frac{16L^2}{\pi^3 K} \sum_{n=1}^{\infty} (2n-1)^{-3} \sin \frac{(2n-1)\pi(x_0+L)}{2L} \\ &\equiv \frac{1}{2K} (x_0 + L)(L - x_0). \end{aligned} \quad (7)$$

In the case of N independent Brownian walkers, the probability of absorption between time t and time $t + \Delta t$ is $P(t) \Delta t = -\frac{dq^N}{dt} \Delta t$. The resulting expression for the mean first-passage

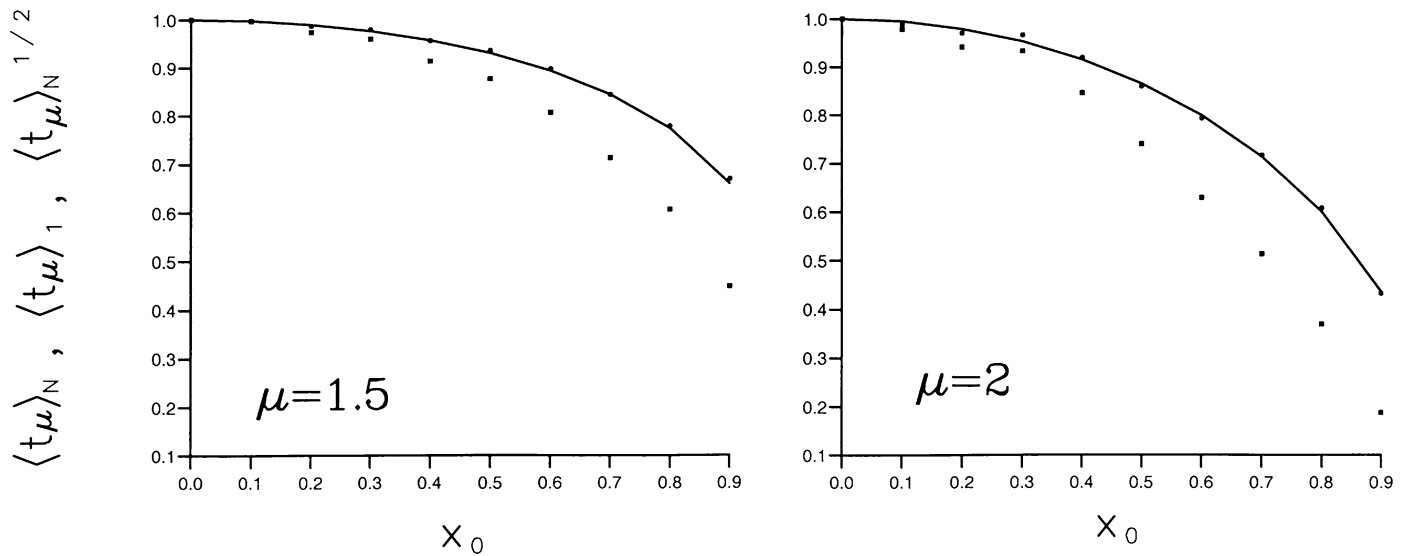


Fig. 1. The results of numerical simulations for the mean first-passage time, $\langle t_\mu \rangle_N$, of $N = 10$ Lévy flights with $\mu = 1.5$ (left) and 2.0 (right) and initially located at x_0 within the interval $[-1, 1]$ (■). Also indicated are $\langle t_\mu \rangle_N^{1/2}$ (●) and the analytic forms of the mean first-passage time, $\langle t_\mu \rangle_1$ (Eq. (3)), for $N = 1$ Lévy flights in the interval $[-1, 1]$ (solid-line). Comparable agreement between $\langle t_\mu \rangle_N^{1/2}$ and $\langle t_\mu \rangle_1$ was obtained for $N = 5$ and $N = 100$ (not shown).

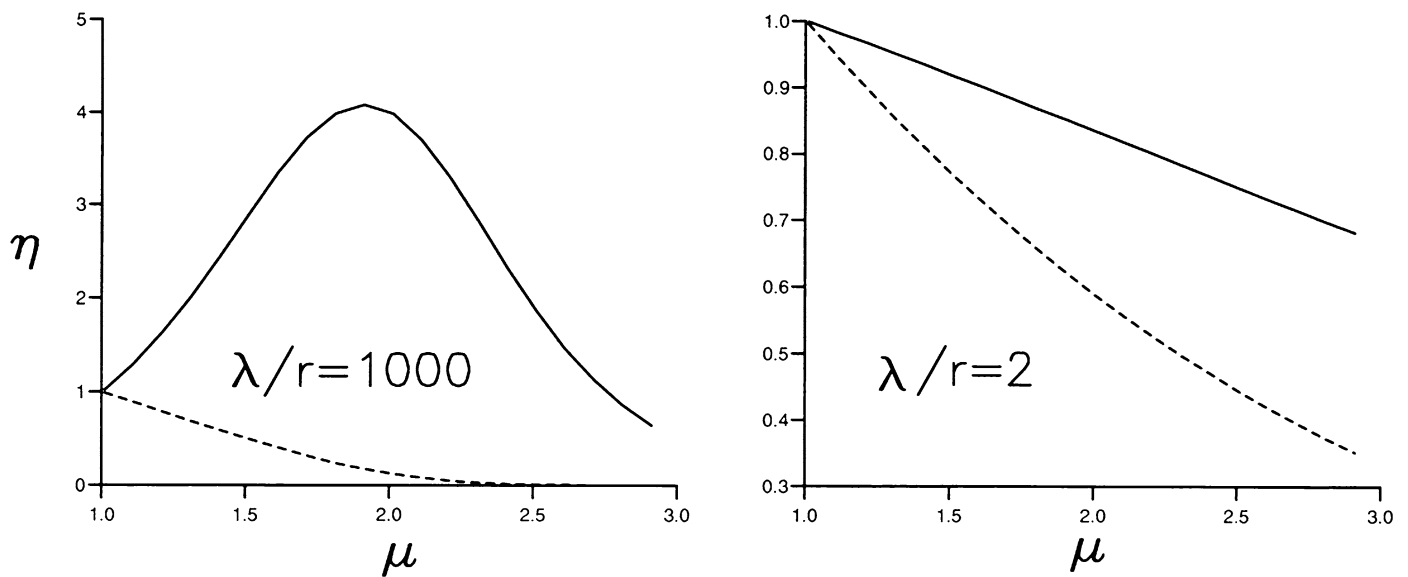


Fig. 2. Searching efficiencies of individual non-destructive searchers (solid-lines) and many ($N = 10$) independent non-destructive searchers (dashed-lines) when target sites are sparsely (left) and densely (right) distributed.

time, $\langle t_3 \rangle_N = \int_0^\infty q^N dt$, is readily computed numerically. It is found that $\langle t_3 \rangle_N \propto \langle t_3 \rangle_1^{\xi_N}$ where $\xi_N \approx 2$ for $N > 2$. The results of numerical simulations indicate that the mean first-passage times of N Lévy flights on the interval $[-L, L]$ have a similar scaling property, namely,

$$N_L \equiv \langle t_\mu \rangle_N \propto (x_0 + L)(L - x_0)^{\mu-1} \quad (8)$$

when $N > 2$. Some typical simulation data are shown in Fig. 1.

The associated searching efficiency (1), (2) and (8), $\eta = \frac{1}{N_L(L)}$ is just the reciprocal of the mean distance travelled by one of the searchers before a target site is first detected by any one of the searchers. Fig. 2 shows that the efficiency of non-destructive searching does not have a maximum when $N > 2$ but increases monotonically with decreasing μ so that the most effective

searching strategy arises as $\mu \rightarrow 1$. This remains the most effective searching strategy when $L/r \rightarrow \infty$ and $|x_0| \sim O(r)$ so that most flights terminate at only one of the two boundaries defining the interval $[-L, L]$. Consequently, $\mu \rightarrow 1$ constitutes an optimal scale-free searching strategy for the location of randomly and sparsely distributed targets sites and for the location of a single target site.

3. Effective exploration strategies for communicative explorers

The scale-free model of foraging is here adopted as a scale-model of exploration. A scale-free exploration is terminated when an explorer is first located at a distance R from its start-

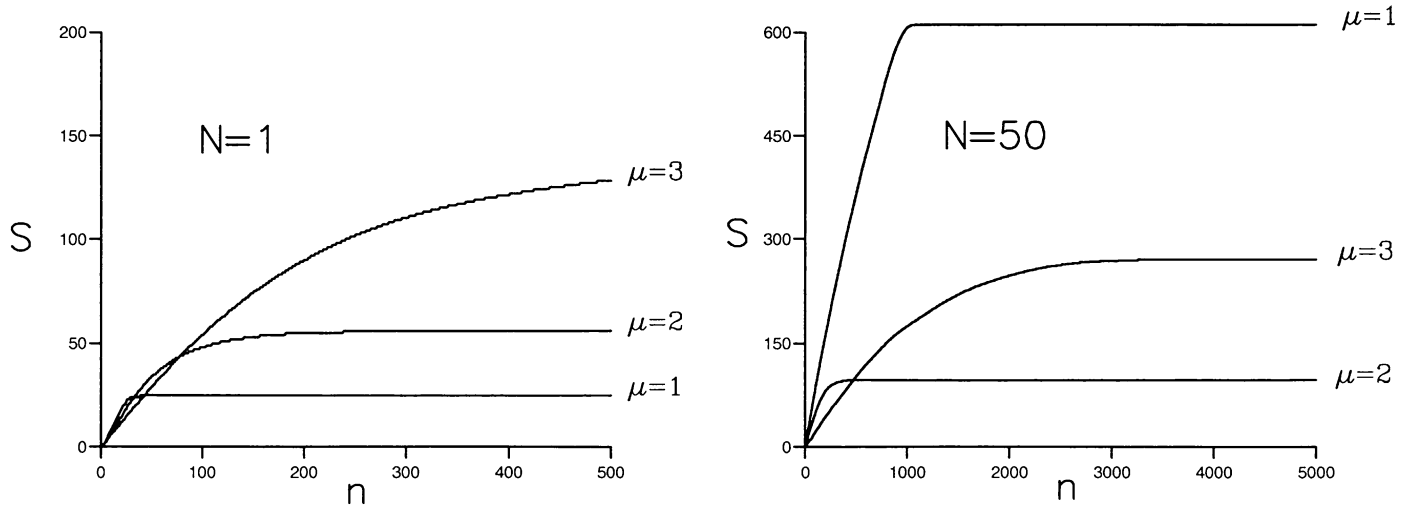


Fig. 3. The number, S , of distinct sites of area r^2 visited within a circular domain of radius $R = 25r$ by solitary ($N = 1$) explorers and by many ($N = 50$) independent explorers after n steps. These quantities pertain to the orientation flight patterns of bumblebees and honeybees. The number of distinct sites visited, S , is found to decrease monotonically with increasing μ when $N \geq 200$.

ing position. Non-communicative explorers seek to maximize their individual coverage of a territory and so effectively act as solitary explorers. Communicative explorers seek to maximize their collective coverage of a territory and thereby contribute to a collective rather than individual knowledge of a landscape. Predictions for the mean numbers of distinct sites of area r^2 visited by solitary (non-communicative) explorers and many independent (communicative) explorers were obtained from the results of numerical simulations. This facilitated the identification of optimal exploratory strategies, i.e., the identification of the values of the parameter μ that maximize the number of distinct sites visited by solitary explorers and by many independent explorers. The analysis complements that of Berkolaiko and Havlin [11] who considered the unbounded territory covered by N independent Lévy flights.

Some typical simulation data are shown in Figs. 3 and 4. For solitary explorers the optimal exploration strategy is seen to be attained when $\mu = 3$. In this case the increased coverage of a territory arising from the multiple loops and the associated delayed arrival at the domain boundary more than compensates for the repeated revisiting of sites. The revisiting of sites diminishes as $\mu \rightarrow 1$. The $\mu = 3$ strategy is also optimal for a small number ($N < N_c$) of independent explorers. The critical value of N_c is found increase with increasing values of R/r . For many ($N \geq N_c$) independent explorers, the optimal exploration strategy is seen to be attained as $\mu \rightarrow 1$. This typically corresponds to long, straight flights. Such flights promote the relative dispersal of many independent explorers and so reduce the likelihood that a site will be visited by more than one explorer. As the size of the search domain increases, flights comprising of two or more long, straight segments become more likely (see Fig. 4).

4. Discussion

It has been shown that when target sites are randomly and sparsely distributed the optimal Lévy-flight (scale-free)

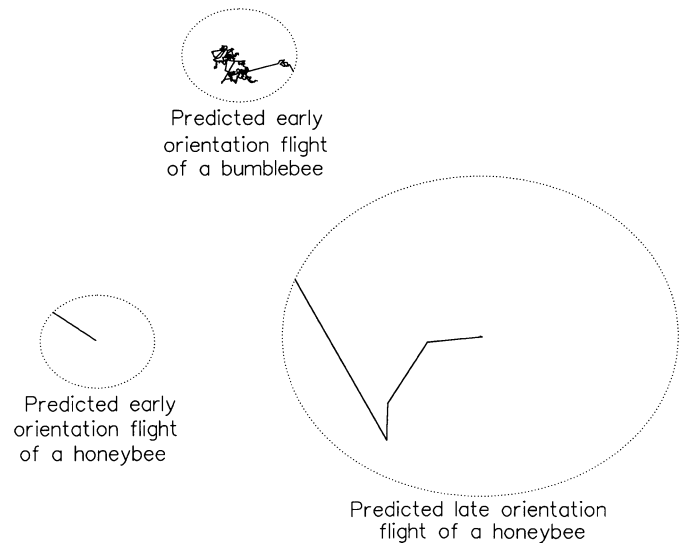


Fig. 4. Typical data for the optimal exploratory flights patterns of a solitary explorer ($\mu = 3$) and one of many independent explorers ($\mu \rightarrow 1$) within a search domain of radius $R = 25r$. Also shown is an example of a relatively rare multi-segmented optimal exploratory flight pattern of one of many independent explorers within a search domain of radius $R = 1000r$ (not to scale). All flights emanate from the centre of the domain and are terminated at the search domain boundary (dashed-lines). As the size of the search domain increases, flights comprising of two or more long, straight segments become more likely. This is consistent with observations of the orientation flights of honeybees [8].

searching strategy for many communicative, non-destructive searchers is distinctly different from the optimal scale-free searching strategy for non-communicative, non-destructive searchers. For many communicative, non-destructive searchers, optimal searching patterns comprise typically of long, straight flights ($\mu \rightarrow 1$) whilst for non-communicative, non-destructive searchers they comprise of multiple loops ($\mu = 2$). A similar distinction was shown to arise for optimal exploration strategies.

The movement patterns associated with optimal scale-free searching and explorations strategies (Fig. 4) for communicative searchers/explorers mirror closely the observed orientation flights of honeybees [8]. The first orientation flights typically comprise of relatively *straight* outward flights that extend between 10 and 300 m from the hive followed by return flights along routes that are often close to the outward ones. Capaldi et al. [8] observed flight lengths increased with the number of flights made by a honeybee. Some later (longer) flights comprised of several, relatively straight, long segments. The correspondence between optimal searching/exploration strategies and the observed ‘orientation flights’ of honeybees suggests that the honeybees may be motivated by a requirement to survey, in an optimal manner, the landscape in the vicinity of a hive and/or the need to locate and exploit nearby forage. Capaldi et al. [8] observed hairpin-shaped foraging flights within the vicinity of the hive. Capaldi et al. [8] reported that the orientation flights of honeybees rarely explored all quadrants around the hive. There was a bias towards occupancy of the two quadrants in front of the hive. This could be because naïve bees have made use of the hive’s collective knowledge of forage locations to limit their searching/exploration to sectors around the hive that contain useful forage. Simulation data (not shown) reveals that the optimal strategies for non-communicative free-ranging searchers/explorers ($\mu = 2$, $\mu = 3$) and for many independent communicative free-ranging searcher/explorers ($\mu \rightarrow 1$) remain optimal when the searchers/explorers are constrained to search/explore within just one or two quadrants.

When forage is plentiful the waggle dance can be disrupted without noticeable influence on a hive’s ability to maintain weight [12]. This is consistent with the optimal scale-free searching strategy for the location of plentiful forage being attained as $\mu \rightarrow 1$; irrespective of whether the foragers are

non-communicative or communicative (Fig. 2). This correspondence lends further support to the notion that optimal scale-free searching patterns underlie the orientation flights of honeybees.

The orientation flights of bumblebees have not yet been reported on in the literature and are predicted to comprise of multiple loops centred on the nest (Fig. 4).

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