

Foraging motivation favors the occurrence of Lévy walks

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ABSTRACT

Lévy walks are a property of random movements often observed among foraging animals (and humans), and they might confer some advantages for survival in an unpredictable environment, in comparison with Brownian walks. In animals with a nervous system, specific neurotransmitters associated with some psychological states could play a crucial role in controlling the occurrence of Lévy walks. We argue that incentive motivation, a dopamine-dependent process that in vertebrates makes rewards and their predictive conditioned stimuli attractive, has behavioral effects that may favor their occurrence: incentive motivation is higher when food is unpredictable and it strongly underpins foraging activity. An individual-based computer model is used to determine whether changes in incentive motivation can influence the probability that Lévy walks occur among foraging agents. Our results suggest that they are produced more often under an unpredictable than a predictable food access, and more often in strongly rather than weakly motivated foragers exposed to an unpredictable food access. Also, our motivational framework indicates that the occurrence of Lévy walks are correlated with, but not causally linked to, the number of food items consumed and the ability to store fat reserves. We conclude that Lévy walks can confer some advantages for survival in an unpredictable environment, provided that they appear in foragers with a high motivation to seek food.

1. Introduction

To find vital resources, such as food, foragers have to move within their environment when those resources are not directly available. When the environment contains a high density of food items (predictable access), foragers tend to adopt Brownian walks, characterized by a great number of short step lengths in random directions that maintain foragers in a small portion of the available space. In contrast, when the density of food items is low (unpredictable access), individuals tend to exhibit Lévy walks, where longer step lengths occasionally occur and relocate the foragers in the environment. In behavioral ecology, “predictable” access means that food is (relatively) abundant, suppressing any risk of starvation, while “unpredictable” access means that food is scarce and sometimes unavailable, causing a risk of starvation.

Lévy walks are scale-free motions observed in a large variety of animal species, from single cells to insects, birds and mammals (e.g., Atkinson et al., 2002; de Jager et al., 2014; Harris et al., 2012; Hays et al., 2012; Ramos-Fernandez et al., 2004; Reynolds et al., 2007; Sims et al., 2008), including human hunter-gatherers (Raichlen et al., 2014). Their occurrence requires that animals perform random search – i.e. observation and memory can only play limited role in an individual’s movements. Accordingly, Lévy walks have primarily been identified in

animals with low cognitive abilities (such as invertebrates) and/or little opportunity for sensory orientation (such as marine predators). To date, there is compelling evidence that doing Lévy walks optimize random search when the items are sparsely distributed (Bartumeus et al., 2005; Humphries and Sims, 2014; Viswanathan et al., 1999).

In this respect, the Lévy flight foraging hypothesis predicts that natural selection led to adaptations that favor their occurrence in unpredictable environments (e.g., Bartumeus et al., 2002; Bartumeus, 2007; Humphries et al., 2012; Humphries and Sims, 2014). However, the neurobiological mechanisms underpinning the execution of Lévy walks remain largely unknown. Reynolds et al. (2016) found that chaotic neuronal activity creates fractal movement patterns that optimize search success in mud snails (*Hydrobia ulvae*). But neuronal chaos is perhaps not the only cause of Lévy walks among phylogenetically distant zoological groups such as mud snails and spider monkeys or sharks (Sims, 2015). In addition to neuronal chaos, Reynolds (2015) suggested that Lévy walks could depend on specific brain neurotransmitters. We think that the idea that some neurotransmitters can influence the occurrence of Lévy walks is interesting, whether these walks support optimal foraging or not. But it is here important to realize that many neurotransmitters in the brain correlate with psychological processes, so that some of these processes may somehow be involved in the control of Lévy walks as well.

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A good candidate for an internal control of Lévy walks is incentive motivation, a dopamine-dependent process that makes rewards – such as food – and the conditioned stimuli (CSs) that predict their delivery, attractive, approached, and physically contacted (Berridge and Robinson, 1998; Blaiss and Janak 2009; Day et al., 2006; Flagel et al., 2007; Meyer et al., 2012; Robinson and Berridge, 2013). Dopamine has similar “positive” motivational/behavioral effects in all vertebrate classes and also in many invertebrate taxa (Barron et al., 2010).

A possible role of motivation in the occurrence of Lévy walks was envisioned (Reynolds and Rhodes, 2009), but it has never been tested – even though food deprivation was shown to extend run lengths in amoeboid cells (Van Haastert and Bosgraaf, 2009). Interestingly, food unpredictability is known to stimulate incentive motivation. When a CS is unpredictably followed by food or no food, mesolimbic dopamine release is increased compared to a situation in which the CS is predictably followed by food (e.g., Berns et al., 2001; Dreher et al., 2006; Fiorillo et al., 2003; Hart et al., 2015). Accordingly, behavioral response to an unreliable CS is higher than to a reliable CS (e.g., Anselme et al., 2013; Collins et al., 1983; Gottlieb, 2004), and rats are willing to cover a longer distance to reach an unreliable as opposed to a reliable CS (Robinson et al., 2014). These observations are potentially important for our purpose, given that the dopamine-dependent propensity of animals to approach CSs turns out to be positively correlated with exploratory activity in a novel environment (Beckmann et al., 2011; Dickson et al., 2015; Flagel et al., 2010), in which finding food is logically more unpredictable than in a familiar environment. If Lévy walks depend on dopamine release in the brain, then fluctuations in the motivation of foragers to seek food should influence their probability of occurrence.

In the present study, an individual-based computational model (e.g., Grimm and Railsback, 2005) was used to test the hypothesis that a higher motivation to forage on food items facilitates the occurrence of Lévy walks in an environment with unpredictable food access. The propensity of agents (or foragers) to explore their environment was a function of their motivational strength. Based on previous theoretical developments (Anselme, 2015, 2016), foraging motivation increased according to the physiological state (“hunger”) of foragers, and also as a function of CS unreliability and food scarcity. In Simulation 1, we analyzed the foraging patterns and successes in foragers exposed to a predictable or an unpredictable environment in order to determine whether our model is in line with current evidence that Lévy walks come with unpredictability of search targets. The idea is that food density alters foraging motivation, which controls seeking behavior. In Simulation 2, we studied the foraging patterns and successes only in foragers exposed to food unpredictability, for which the CS-detection radius or the probability of approaching a detected CS were gradually decreased – two consequences of a reduction in motivational strength. In Simulation 3, we also tested foragers exposed to food unpredictability, but included real-life factors such as predation risk, rest periods, and prey-handling costs. More foragers were assessed and they traveled a longer distance, so that there was a risk of starving to death during a simulation bout. Overall, our results suggest that a high motivation to forage strongly increases the probability that Lévy walks are shown, while their expression does not improve the chance of survival in itself. It is argued that, in nature, Lévy walks can confer some advantages for survival because they tend to appear in foragers with a high motivation to seek food. We show that our theoretical results are quite compatible with the behavioral patterns and foraging successes of albatrosses seeking food in the ocean (Humphries et al., 2012, 2013), and we provide some original predictions that could be tested in the future.

2. Materials and methods

2.1. Individual-based computer model

One single forager moved in a 2D environment (500 × 500)

according to a pseudorandom trajectory – generated by the Mersenne Twister algorithm of MATLAB (version 8.4.0, The Mathworks, Natick, MA). The environment contained CSs predictive of food items (CSs+), each providing the same amount of energy, and could also contain CSs without food items (CSs–). The terms CS+ and CS– simply denoted the presence and the absence of associated food, respectively, not two distinct stimuli. The CSs (and hence food) had a pseudorandom distribution as well – there were 0.25 million possible locations, most of them being empty. The forager could detect CSs from a distance (shorter or equal to the value of its detection radius) and approach them once detected (with a probability higher than for any other direction), but it had to reach the CS location to consume the food item possibly associated with that CS. This meant that the forager could locally modify its direction in order to reach the CS. But, unless another CS was also detected, the length of the step performed in the direction of the CS was random, and could therefore overcome the size of the detection radius. When a food item was consumed, it disappeared with its predictive CS, and a new CS-food pairing occurred anywhere else in the environment in order to hold food density constant. No more objects were present in the environment.

The forager’s movements were not governed by any form of spatial memory. The forager started in the middle of the environment, choosing between four directions with an equal probability (25%). Once a direction was selected, the probability to maintain that direction was a function of the forager’s motivational strength and the probability decreased after each new step (note that when the probability to move in one direction decreased, it increased simultaneously for the other directions – in total, the probability to move was always equal to 1). Then, a new direction was selected. Acting this way, the forager could explore larger portions of its environment when highly motivated to forage. In nature, the fact that animals show more extensive exploration of their environment when food is scarce suggests that they are more motivated to find food (e.g., Daunt et al., 2006; Hiraldo and Donazar, 1990; Kramer and Weary, 1991; Lovette and Holmes, 1995). This constraint did not make the occurrence of Lévy walks trivial, because it should logically lead highly motivated foragers to travel in straight lines only (no Lévy search) rather than to show disorganized movements interrupted by occasional straight lines (Lévy search). Approaching a border increased the probability to move in the opposite direction.

The energy accumulated from repeated consumption of food items represented the forager’s fat reserves. Fat reserves decreased constantly and gradually because of the energy costs related to the forager’s travels within the environment, and also occasionally because of prey-handling costs and rest periods without food. Thus, low fat reserves meant that the forager did not eat enough, and this increased its hunger-induced motivation (or “wanting”) to find food. Conversely, high fat reserves lowered “wanting” strength:

$$w = 1 - 0.0001 * E^4 \quad (1)$$

where w was “wanting” strength and E represented fat reserves (e.g., $E = 5$ caused an average w value of 0.5). In behavioral psychology, the motivational attraction of CSs and rewards is traditionally called “wanting” (Berridge and Robinson 1998). This psychological process mainly depends on dopamine release in the ventral striatum, a well-conserved brain structure across the evolution of vertebrates (Striedter, 2005; Yamamoto and Vernier, 2011). In the model, a higher (lower) “wanting” strength increased (decreased) the detection radius for new CSs and increased (decreased) the probability of approaching a detected CS (see Eqs. (3) and (4)). These effects were assumed to reflect two crucial psychological consequences of a higher incentive motivation: increasing sensory arousal levels (detection radius) and taking the potential opportunity to eat (approach probability).

A first memory buffer (m) allowed the forager to represent the sequence of the last 30 rewarded (CS+) and nonrewarded (CS–) prey-capture attempts or trials, which were coded 1 and 0, respectively. The

sequence of trials was stored and arithmetically averaged after each new trial in a cumulative way in order to calculate a “subjective” probability (p) of reward. The use of 30 trials offered some guarantee that the subjective probability was accurately computed while avoiding unrealistic (unlimited) memory capacities. The uncertainty (u) of reward encounter was $u = p(1-p)$, where $p = \frac{\sum_{i=1}^{30} m_i}{i}$. A second memory buffer allowed the agent to represent the sequence of the last 30 distances (measured as a number of step units) travelled between two rewarded trials. Variability in the number of step units was calculated as a coefficient of variation, $d = SD/mean$.

In a predictable (safe) environment, all the CSs were reliable predictors of food (CS +) and the actual density of food items (α) was equivalent to a predefined safety threshold value (π). Predictability of an environment simply meant that the forager did not detect/expect any food scarcity; an environment in which the perceived risk of starvation was nil. In contrast, an unpredictable (unsafe) environment contained CSs that were unreliable predictors of food (CS– mixed with CS +), and the actual density of food was lower than the safety threshold value. In this case, the forager detected/expected food scarcity; the forager perceived a risk of starvation. Indeed, a lower food density and the presence of unreliable CSs to inspect could potentially increase the delays between two rewarded trials, a situation that may imperil survival and may explain why animals often prefer short over long delays for food (e.g., Kacelnik and Bateson, 1996; Lea, 1979; Mazur and Biondi, 2009). Thus, when food access was unpredictable, we suggested that the forager did not just “want” food items, but that they also “hoped” for their obtaining – a term that refers to the forager’s excitement for possible “good news”. Incentive hope is assumed to occur when an individual “wants” a non-guaranteed reward (Anselme, 2015, 2016). This concept can explain the invigorating behavioral responses to CSs observed under partial reinforcement in Pavlovian conditioning more effectively than the concept of incentive salience (Berridge and Robinson, 1998) or that of frustration (Amsel, 1958). Here, it is extended to a broader ecological context, in which the forager not only “hoped” for CS reliability but also for short time intervals between food items (for details, see Anselme et al., 2017). The overall motivation to forage (γ) was described as follows:

$$\gamma = w \left[1 + c(p(1 - p)) + d \left(\frac{\pi}{\alpha} - 1 \right) \right] \tag{2}$$

where c is counterconditioning (set to 1 in the simulations below) and d is the coefficient of variation in the number of steps traveled between two rewarded trials. In this equation, we can see that variability in delays (d) was ignored when the food items were highly predictable ($\alpha = \pi$); the opportunity to obtain food sooner was unimportant. In contrast, variability in delays came to matter when the food items were scarcer ($\alpha < \pi$); obtaining food sooner became crucial for survival. In the simulations below, the presence of CSs– had no inhibitory effects on approach behavior (counterconditioning was maximal, $c = 1$). Along with “wanting”, incentive hope contributed to increase the detection radius, $R(D)$, as well as the probability of approaching the detected CSs, $P(A)$, according to equations:

$$R(D) = R(D)_{max} / (1 + e^{-4\gamma} + 4) \tag{3}$$

$$P(A) = (\gamma/k) * P(A)_{max} \tag{4}$$

For the calculation of the detection radius (Eq. (3)), a sigmoid function was used to reflect the great magnitude differences that exist in the ability to detect (pay attention to) stimuli depending on whether motivation is high or low. With respect to approach probability (Eq. (4)), we used constant $k = 1.5$ in order to keep $P(A)$ within realistic boundaries, especially in the absence of incentive hope – in a predictable environment, there is evidence that animals reject opportunities to feed ($P(A) < 1$), although they nevertheless do not starve ($P(A) > 0$; e.g., Brodin, 2007).

Additional factors allowed us to test our hypothesis (i.e., motivation to forage facilitates the occurrence of Lévy walks) in realistic ecological conditions. In the literature, mass-dependent predation risk denotes the detrimental effect of fat reserves in determining the agility and rapidity of birds, although small to moderate increases in fat reserves do not influence the ability to escape from predatory attacks (Brodin, 2001; Witter et al., 1994). Under constant predation risk, this effect is relatively linear (e.g., Pravosudov and Lucas, 2001). In the model, predation risk depended on body mass and its value increased linearly beyond a predefined value of energy (fat) level. Below that value, predation risk was equal to zero – although this rule was an oversimplification (Verdolin, 2006). Mortality risk, $M(R)$, induced by mass-dependent predation, was:

$$M(R) = (0.3 * E - 1) / 2 \tag{5}$$

An increase in predation risk increased the probability, $P(R)$, that the agent will take refuge after a fixed number of step units. Also, the actual food density (relative to the safety threshold π) contributed to increase $P(R)$ – although its influence was less pronounced when food was scarcer because then the forager had to take more risk to compensate for the low density of items. In the model, taking refuge meant that the forager suddenly lost a fixed amount of energy. The movement path was not interrupted. Therefore, $P(R)$ – and $M(R)$ even more directly – favored energy consumption, a phenomenon that has been observed (MacLeod et al., 2007) and captured by a similar version of the present model (Anselme et al., 2017). The equation governing the $P(R)$ value was:

$$P(R) = (M(R) + \alpha/\pi) / 2 \tag{6}$$

Finally, prey-handling constraints are known to induce some costs to real foragers (e.g., Stephens and Krebs, 1986). To represent them in the model, each time a CS was found or a food item consumed, the agent became insensitive to any new stimulus for a fixed number of step units and lost the amount of energy associated with those steps. So, the forager continued to move while insensitive, and the steps traveled did contribute to the movement path – whose length was fixed before the encounter with the CS. Therefore, the time/space/energy available to seek food over a fixed simulation bout was reduced (see Anselme et al., 2017).

2.2. Procedure

In Simulation 1, we tested whether our model could generate more Lévy walkers in an unpredictable than in a predictable environment, as reported in the literature, and we examined the impact of each environment on food consumption and fat reserves. Two groups of 10 foragers were assessed – with only one forager per run (inter-individual competition was not considered). In one group, the foragers were exposed to a predictable environment (500 × 500) that contained 1000 CS+ (α) and no CS– ($p = 1.0$); in the other group, they experienced an unpredictable environment (500 × 500) that contained 200 CS+ (α) and 200 CS– ($p = 0.5$). The food safety threshold (π) was fixed at a value of 1000 in both environments. This meant that more energy was necessary to reach food items in the unpredictable than in the predictable environment. Each run had an upper limit of 3000 step units (a step length could be composed of a variable number of step units). Each run started with $E = 5$, $P(A)_{max} = 1$, and $R(D)_{max} = 12$, although the moment-to-moment values for those factors could vary. All the foragers tested were kept for analysis.

In Simulation 2, the foragers were tested separately in the same unpredictability conditions as above, but the detection radius and the approach probability were manipulated independently, in order to determine the role they may have (as two consequences of motivational strength) in the occurrence of Lévy walks. Each change was assessed by means of a group of 10 foragers, all kept for analysis. In one (control) group, $P(A)_{max}$

was 1 and $R(D)_{max}$ was 12—as in Simulation 1. In three groups, probability was held constant ($P(A)_{max} = 1$) and radius was gradually decreased ($R(D)_{max} = 10, 8, 6$). In three more groups, radius was held constant ($R(D)_{max} = 12$) and probability was gradually decreased ($P(A)_{max} = 0.90, 0.75, \text{ and } 0.50$). Thereafter, these groups are denoted by referring to their $P(A)_{max}$ and $R(D)_{max}$ values – e.g., P1/R8.

The first two simulations considered the effects of motivation on the emergence of Lévy walks independently of other real-life factors, such as predation risk, rest periods, and handling costs. Also, the number of step units traveled was limited; all the foragers tested could survive the simulation bout. Finally, only 10 foragers per group were simulated – however, a number compatible with traditional experimental testing in psychology and behavioral ecology (we tested an individual-based model, not a dynamic model searching for optimized outcomes over thousands of runs). To remedy potential shortcomings, Simulation 3 was a partial replication of Simulation 2 with additional constraints. In one group, 20 foragers (instead of 10) with a high motivation to forage (P1/R12) were exposed to food unpredictability under predation risk, rest periods, handling costs, and the risk of starving to death. They were tested separately for 12,000 (instead of 3000) step units. Their performance was contrasted with that of 20 foragers tested under the exact same conditions, except that their motivation to approach detected food items was low in comparison (P0.5/R12). The effects of these additional factors were not assessed in themselves. The parametric values used in the three simulations can be found in Appendix A. Also, the justification for the small number of foragers per group (compared to many other studies) is described in Appendix B for Simulation 1 and in Appendix C for simulation 3.

2.3. Data processing

In most Lévy models, the step lengths are drawn from a statistical (Pareto-Lévy) distribution with a heavy power-law tail: $P(l_j) \approx l_j^{-\mu}$, where l_j is the step length and μ the power-law exponent. Here, we did not use any a priori function; the step lengths (composed of one or multiple step units) depended on motivational strength. To be characterized as a Lévy search, the distribution of step lengths implies that $1 < \mu \leq 3$ (Viswanathan et al., 1999): for $\mu \leq 1$, the distribution cannot be normalized and, for $\mu > 3$, it is equivalent to that of Brownian motions by virtue of the central limit theorem. But more thorough analysis is required to be sure that a specific motion has a true Lévy distribution (Humphries et al., 2013).

It was determined whether the movements of each forager described a Lévy (truncated power-law) or a Brownian (exponential) distribution using Maximum Likelihood Estimation (MLE) analysis. MLE is a method specifying the probability distribution that fits the observed data most likely (e.g., Myung, 2003). For that, the spatial (x,y) coordinates after any change in the forager’s trajectory were collected and analysed by means of a freely available software produced by the Marine Biological Association of the UK (Humphries et al., 2013). This software allowed us to categorize each dataset as “truncated power-law” (Lévy walks), “exponential” (Brownian walks) or “unclassified” (neither Lévy nor Brownian). The following parameters were selected: *Best fit Xmin*, *Coalesce*, and *Discrete*. With this software, a truncated power-law fit was only concluded when there was a valid Lévy exponent ($1 < \mu \leq 3$), but also when Akaike’s information criterion (AIC; Akaike, 1974) and the adjusted goodness of fit (GOF) supported the fitted truncated power-law over the exponential model (Humphries et al., 2013). Briefly, AIC is a measure of the relative quality of a statistical model over another for a given dataset. The GOF of a statistical model estimates how well it fits a dataset. The GOF value was computed from the Kolmogorov-Smirnov D statistic. The analyses were only carried out on the x dimension. Step units were coalesced into a single, longer step when they formed part of a contiguous movement in the same direction. As a result, foragers could turn at angles of 45°, 90°, 135°, and 180°, but turn angles were not analyzed. In Simulation 2, the energy gain per step was calculated as

$[\text{Number of food items consumed} * \text{Energy gain per food item}] / [\text{Number of step units traveled} * \text{Energy loss per step unit traveled}]$.

Data related to the number of food items consumed, the level of fat reserves, the radius of the detection field, and the probability of approaching a detected CS were systematically computed. Additional data (relative to predation risk, etc.) were also processed, as appropriate. Means and standard errors ($M \pm SE$) were reported, as if raw data had been generated by real animals. Data distributions were normal and homoscedastic. One-way ANOVAs with planned comparisons and t -tests for independent samples were computed. The effect sizes (partial eta-squared) were used to indicate the magnitude of the observed differences.

3. Results

3.1. Simulation 1

In the unpredictable environment, MLE analysis – i.e., examination of the μ value, comparison of the AIC value of the truncated Pareto-Lévy model with that of its exponential alternative, and GOF tests (see Humphries et al., 2013) – revealed that 90% of foragers showed Lévy walks (Fig. 1). The remaining 10% had an unclassifiable step-length distribution; they could not be qualified as Lévy or Brownian seekers. In the predictable environment, the same analysis provided a different pattern of results. Here, only 40% of foragers exhibited Lévy walks (Fig. 1), while the other 60% were unclassified.

Fig. 2 depicts the distribution of the step lengths for each forager, which is compared to the truncated power law (Pareto-Lévy) and exponential (Brownian) distributions in order to determine which one best fits the simulation data. When the environment was unpredictable (left panel), the average μ value among Lévy foragers was 1.678 (range: 1.250–2.063). The individual simulation data for all foragers (except individual B) fitted the Lévy distribution better than the Brownian distribution. Even the single unclassified individual had a μ value ($= 1.426$) within the appropriate Lévy range. In contrast, when the environment was predictable (right panel), the average μ value among Lévy foragers was more elevated (2.727; range: 2.608–2.905), close to the limit ($\mu \rightarrow 3$) where foragers’ movements cease to have a power-law distribution. Based on the exponent, the AIC, and the GOF analyses, most individual simulation data appeared incompatible with a Pareto-Lévy distribution (except individuals D, E, F, G).

The motivational strength of the foragers and its consequences in both environments were compared (Table 1). As a result of the model’s architecture, foraging motivation (γ factor) was significantly higher in the unpredictable than in the predictable environment. Thus, the radius of the detection field and the probability of approaching a detected CS

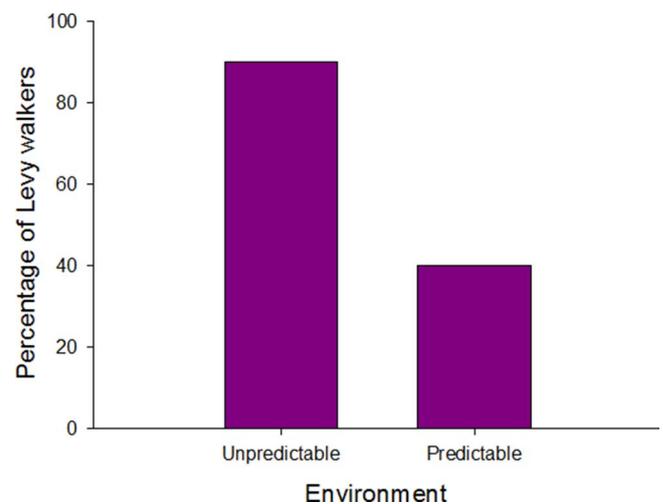


Fig. 1. Simulation 1: Lévy walks occur more frequently in an unpredictable than in a predictable environment.

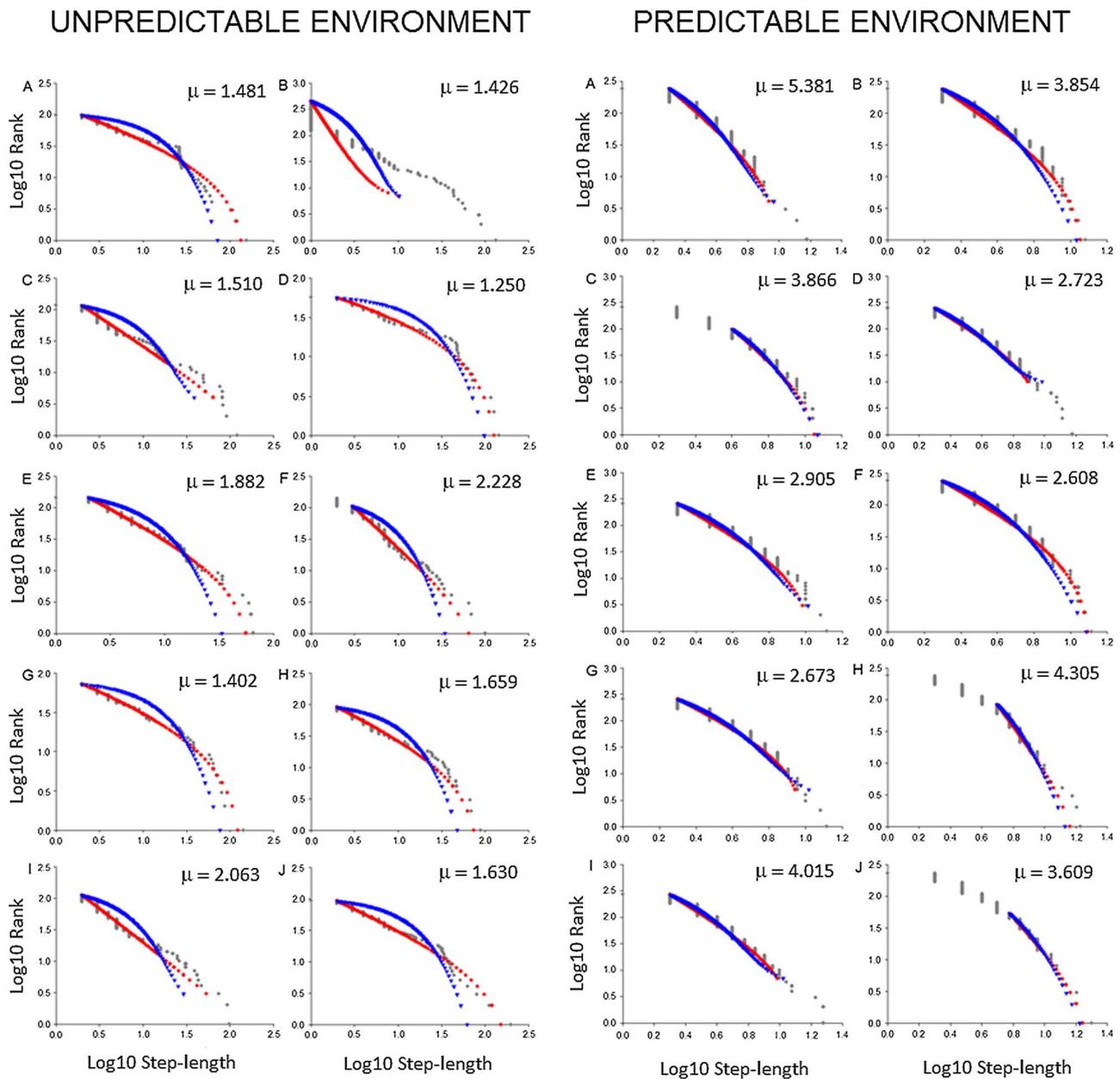


Fig. 2. Simulation 1: Representation of how individual computer data (grey) fit a truncated Pareto-Lévy distribution (red) or an alternative exponential distribution (blue). Left panel: Ten foragers tested in the unpredictable environment. All foragers show Lévy walks, except forager B. Right panel: Ten foragers tested in the predictable environment. Only four foragers (D, E, F, G) show Lévy walks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Simulation 1: Motivational strength (γ) and its consequences with respect to the ability to forage (detection radius and approach probability) and foraging successes (food items consumed and energy/fat stored). Legend: * Significant difference between the two conditions Unpredictable Environment and Predictable Environment; Mean (SE).

	U-env	P-env	P-value	Effect size
Motivational strength	6.947 (0.289)	0.810 (0.025)	< 0.001*	0.96
Detection radius	11.102 (0.453)	3.869 (0.229)	< 0.001*	0.92
Approach probability	0.950 (0.026)	0.540 (0.017)	< 0.001*	0.91
Food items consumed	24.700 (2.176)	20.900 (0.836)	> .05	0.13
Energy reserves	5.927 (0.366)	6.371 (0.232)	> .05	0.05

Table 2

Simulation 2: Values for approach probability and detection radius in the different groups; Mean (SE).

Group	Approach probability	Detection radius
P1/R12	0.975 (0.007)	11.534 (0.126)
P0.90/R12	0.884 (0.005)	11.643 (0.109)
P0.75/R12	0.715 (0.023)	11.160 (0.535)
P0.50/R12	0.491 (0.004)	11.669 (0.166)
P1/R10	0.982 (0.005)	9.678 (0.087)
P1/R8	0.938 (0.020)	7.304 (0.220)
P1/R6	0.973 (0.016)	5.776 (0.133)

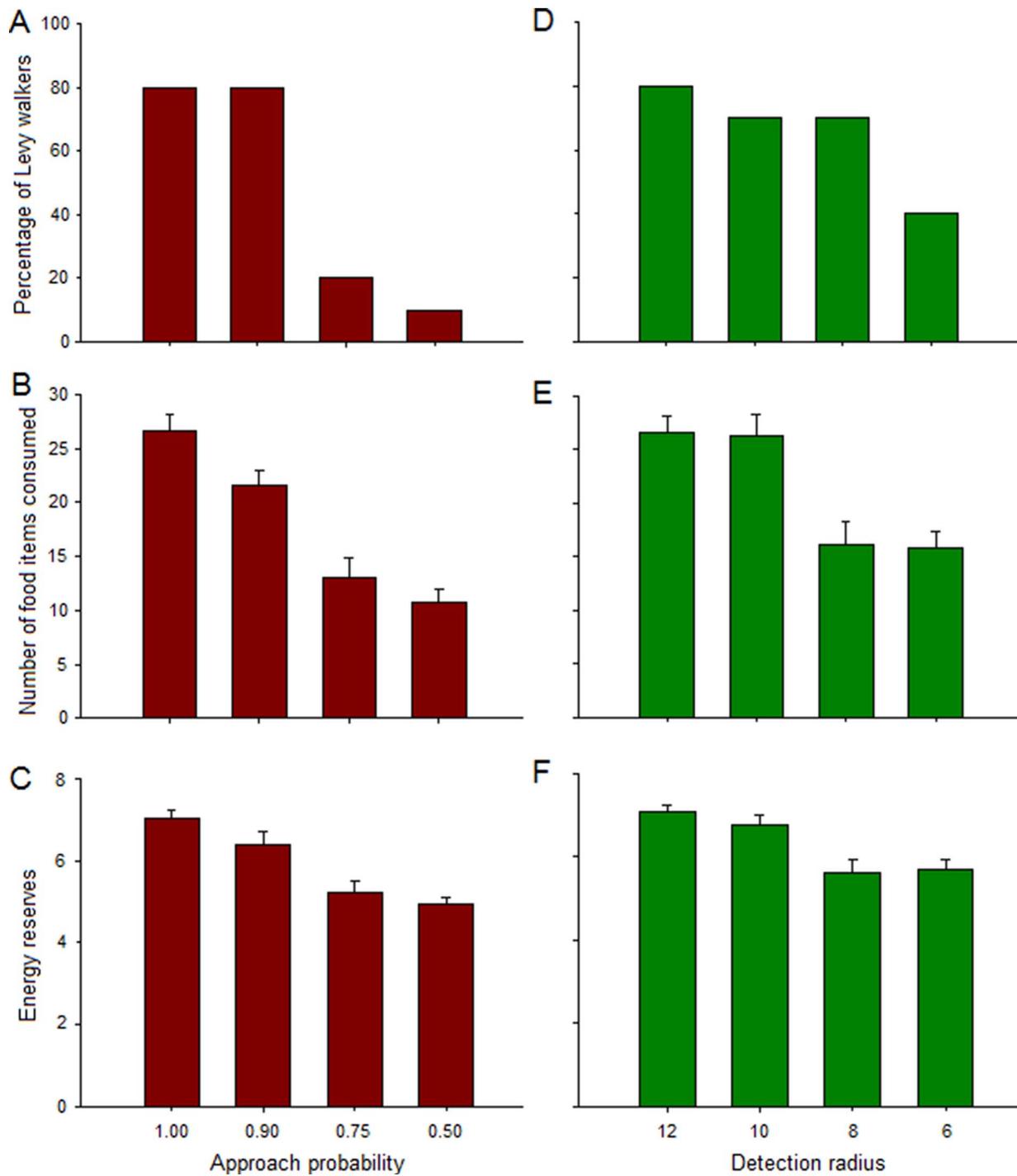


Fig. 3. Simulation 2: Effects of a gradual decrease in the approach probability (A–C) and in the detection radius (D–F) on the occurrence of Lévy walks, food ingested, and fat reserves. All foragers were exposed to an unpredictable environment. A gradual decrease in the approach probability decreases (A) the proportion of Lévy walkers (here, from 80% to 10%), (B) the number of food items consumed, and (C) the amount of energy (“fat”) stored. A gradual decrease in the detection radius decreases (D) the proportion of Lévy walkers (here, from 80% to 40%), (E) the number of food items consumed, and (F) the amount of energy (“fat”) stored. Probability and radius were decreased to the half of their initial (control) value. Note: the first bar in the two adjacent graphs ($P(A)_{\max} = 1.00$ and $R(D)_{\max} = 12$) designate the same foragers (P1/R12), representing the control condition. For the other histograms, radius was held constant ($R(D)_{\max} = 12$) in the left graphs (A–C), while probability was held constant ($P(A)_{\max} = 1$) in the right graphs (D–F).

were increased in the unpredictable environment. An examination of the number of food items consumed and of energy (fat) reserves indicated that foragers ate similar food amounts and had similar energy reserves in the two environments. In other words, a higher motivation to forage when food was both uncertain and scarce allowed the foragers to maintain their body weight (on average, they consumed even more items under unpredictable than under predictable foraging conditions).

Overall, these results are in accordance with the literature

concerning the evidence that Lévy walkers are more likely to appear in an unpredictable rather than in a predictable environment. However, because of design-induced constraints, it was not here possible to determine whether the occurrence of Lévy walks was the consequence of unpredictability itself or the consequence of the higher motivation to forage under food unpredictability. In the next simulation, we studied the foraging patterns and successes of foragers only exposed to unpredictable conditions, and whose detection radius or probability of

approaching a detected CS was gradually decreased.

3.2. Simulation 2

In each group, the average approach probability and the average detection radius were close to the maximum values fixed in advance (Table 2). There was a dramatic reduction in the occurrence of Lévy walks when the probability of approaching a detected CS decreased (Fig. 3A). In group P1/R12 (control), the step lengths fitted a truncated Pareto-Lévy distribution in 80% of foragers (range of μ values: 1.119–1.960). The remaining 20% had an unclassifiable step-length distribution. A small decrease in the approach probability (P0.90/R12) had no effect on the proportions of Lévy walkers (range of μ values: 1.212–2.377). A larger decrease in the approach probability (P0.75/R12) strongly limited the occurrence of Lévy processes since they were shown by only 20% of foragers (the two μ values were 1.100 and 1.540). Here, 50% of foragers travelled following Brownian walks (exponential distribution) and the remaining 30% were unclassifiable. Finally, in group P0.50/R12, Lévy walks emerged in only 10% of foragers, Brownian walks in 30% of foragers, and walks were unclassified in 60% of foragers (μ value for the unique Lévy walker: 1.653).

The number of food items consumed also decreased gradually with approach probability (Fig. 3B). The reduction of ingested food was significant between all probability values ($F(1,36)$'s ≥ 5.620 , p 's ≤ 0.023 ; $\eta_p^2 \geq 0.26$), except between $P(A) = 0.75$ and $P(A) = 0.50$ ($F(1,36) = 1.143$, $p = 0.292$; $\eta_p^2 = 0.05$). Fat reserves followed the same decreasing pattern as probability was lowered (Fig. 3C): the highest two probability values were significantly different from the lowest two probability values ($F = 42.240$, $p = 0.000$; $\eta_p^2 = 0.53$). But here there were no significant differences between $P(A) = 1.00$ and $P(A) = 0.90$ and between $P(A) = 0.75$ and $P(A) = 0.50$ (F 's ≤ 3.756 , p 's ≥ 0.060 ; $\eta_p^2 \leq 0.16$). In themselves, these results do not mean that consumption and Lévy search were causally related; at least, they were correlated together and depended on a common cause – the motivation to forage.

A gradual decrease in the detection radius also had a detrimental effect on the occurrence of Lévy walks (Fig. 3D). Compared to control foragers (group P1/R12), a small decrease in detection radius (P1/R10) reduced to 70% the proportion of Lévy walkers (range of μ values: 1.048–1.677), while 10% were Brownian walkers and 20% were unclassifiable foragers. Group P1/R8 also produced 70% of Lévy walkers (range of μ values: 1.004–1.852) and 30% of unclassified foragers. But in group P1/R6, only 40% of Lévy walkers were obtained (range of μ values: 1.067–1.651), and 60% of unclassified foragers. Taken together, these results indicate that the gradual disappearance of Lévy foragers was less pronounced after decreasing the detection radius than after decreasing the probability of approaching a detected CS to the half of their initial (control) value. Accordingly, the energy gain per step for P1/R12 foragers (2.428 ± 0.223 energy units) was significantly higher than for P1/R6 foragers (1.317 ± 0.130 energy units; $F(1,18) = 18.541$, $p = 0.0004$; $\eta_p^2 = 0.51$) and for P0.50/R12 foragers (0.893 ± 0.100 energy units; $F(1,18) = 39.450$, $p = 0.000$; $\eta_p^2 = 0.69$). It was also unsurprising that the energy gain per step was higher for P1/R6 than for P0.50/R12 foragers ($F(1,18) = 6.662$, $p = 0.019$; $\eta_p^2 = 0.27$). Fig. 3E indicates that the number of food items consumed was greater for the highest two ratio values than for the lowest two ratio values ($F(1,38) = 34.021$, $p = .000$; $\eta_p^2 = 0.47$), but no significant differences were shown between the highest values or between the lowest values ($F(1,36)$'s ≤ 0.024 , p 's ≥ 0.879 ; $\eta_p^2 \leq 0.05$). Similar effects were obtained with respect to fat reserves (Fig. 3F; $F(1,38) = 23.545$, $p = .000$; $\eta_p^2 = 0.38$).

3.3. Simulation 3

The first two simulations assessed the effects of foraging motivation on the occurrence of Lévy walks “in isolation”, regardless of any real-

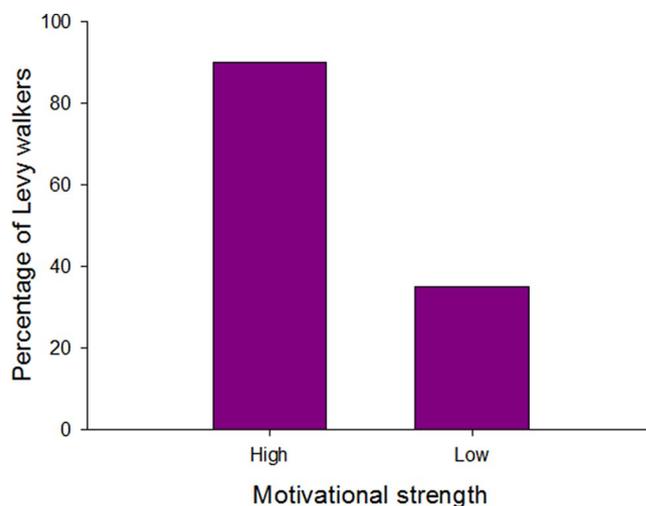


Fig. 4. Simulation 3: In an unpredictable environment, Lévy walks occur more frequently in foragers with a strong motivation to forage than in foragers with a weak motivation to forage (as measured in terms of the probability of approaching a detected CS). In each condition, the 20 foragers were exposed to mass-dependent predation risk, rest periods, prey-handling costs, and had a risk of starving to death.

life factors such as mass-dependent predation risk, rest periods, handling costs, and the risk of starving to death. Simulation 3 aimed to determine whether these additional constraints may impact the motivational control of Lévy walks in strongly vs. weakly motivated foragers exposed to an unpredictable environment.

Fig. 4 indicates that, under these conditions, the proportion of Lévy walkers was elevated (90%) when the probability of approaching a detected CS was maximal (P1/R12), along with only 5% of Brownian walkers and 5% of unclassified individuals. It is important to note that the two outsiders occurred within the first ten simulations, so that the present result is both compatible with the results obtained in Simulations 1 and 2—where Lévy foragers occurred in 90% and 80% of program runs, respectively. Thus, the addition of real-life constraints did not seem to have influenced the occurrence of Lévy walks in strongly motivated foragers. A much smaller proportion of Lévy walkers (35%) emerged when the probability of approaching a detected CS was low (P0.5/R12), along with 65% of unclassified individuals. Here, the additional real-life constraints might have had a boosting effect since, as shown in Simulation 2, the proportion of P0.50/R12 Lévy walkers was only 10% in the absence of such constraints.

In Fig. 5, the individual simulation data for the 20 strongly motivated foragers (high probability of approaching a detected CS) seeking food in an unpredictable environment are represented. Although the proportion of Lévy foragers was identical to that obtained in Simulation 1, even clearer evidence for Lévy search could be observed: in addition to fitting the Pareto-Lévy distribution, the simulation data here were more largely dissociated from the Brownian distribution (except for individuals B and H). This pattern is likely to be a consequence of the greater number of step units (12,000 instead of 3000) traveled by the foragers, because the distribution of step lengths gained in accuracy. Interestingly, the range of μ values among Lévy foragers (1.316–2.454; average = 2.250) was similar to the optimum shown in other studies (e.g., Atkinson et al., 2002; de Jager et al., 2011; Ramos-Fernandez et al., 2004; Viswanathan et al., 1999).

Fig. 6 shows the individual simulation data for the 20 weakly motivated foragers (low probability of approaching a detected CS) seeking food in an unpredictable environment. Here, the different distributions are difficult to distinguish, even among Lévy walkers (individuals C, D, F, G, P, Q, T). The μ values of Lévy walkers were elevated (range: 2.587–2.930; average = 2.784), similar to the values found in the predictable environment in Simulation 1. The contrast that emerged between the 20 strongly motivated foragers and the 20 weakly

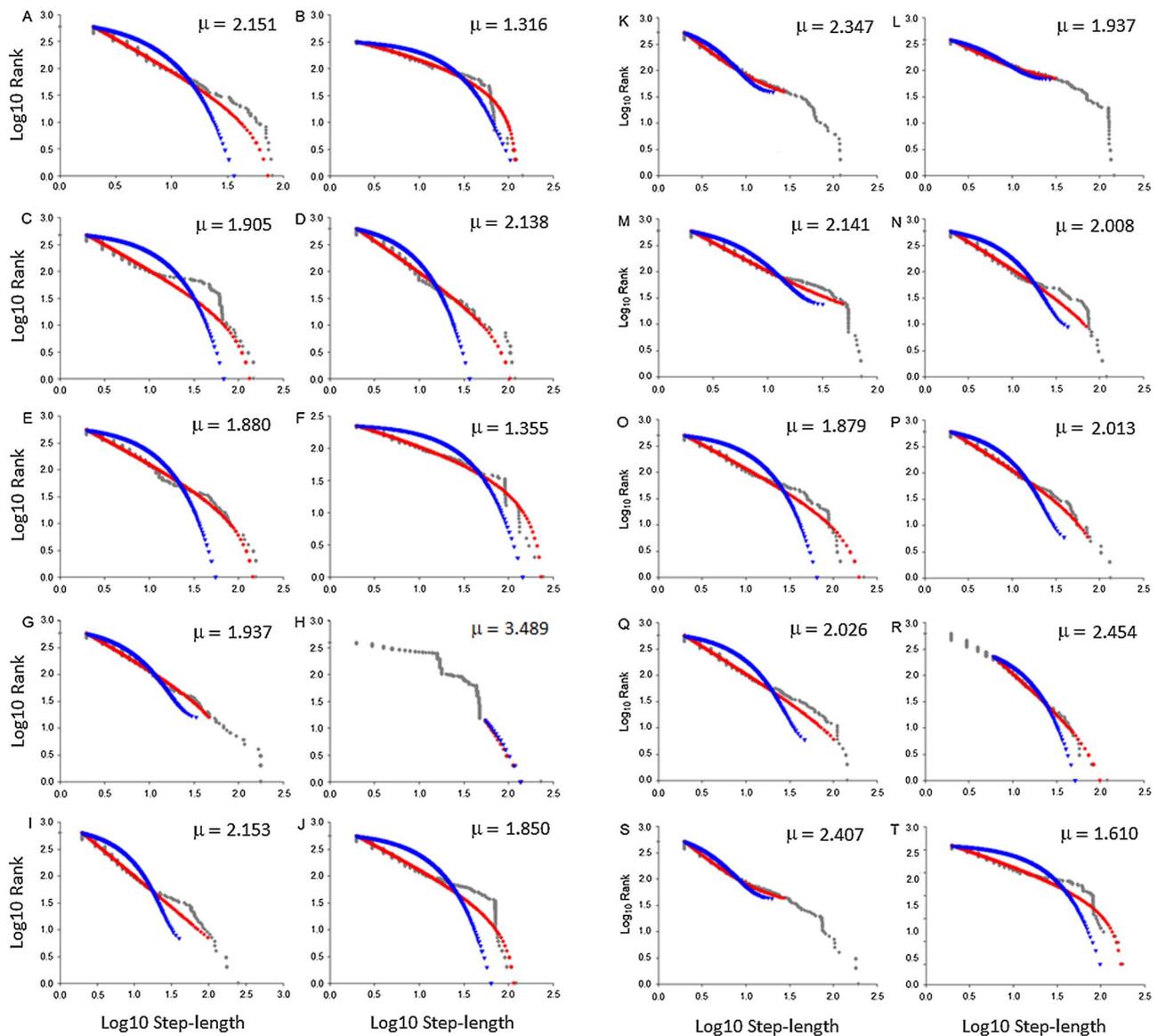


Fig. 5. Simulation 3: Strongly motivated foragers in an unpredictable environment. For most foragers (90%, but B and H), the distribution of computer data (grey) fits the prediction from the truncated Pareto-Lévy model (red) rather than that of the exponential model (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

motivated foragers suggests that motivation is a determining factor that modulates the emergence of Lévy walks in food-seeking animals.

Table 3 reports the consequences of a difference in motivational strength with respect to the number of food items consumed and energy (fat) reserves. It was observed that larger amounts of food were consumed and higher fat reserves were stored in the individuals with a strong motivation to forage compared to the individuals with a weak motivation to forage. But it is interesting to note that motivational strength also increased predation risk, the number of rest periods, and the ability to survive the 12,000 step units. Although a higher predation risk forced the foragers to take refuge (interrupted foraging) more often, 100% of the strongly motivated foragers survived – against only 40% of the weakly motivated foragers. The better chance of survival was likely to be due to the strong motivation of foragers rather than to the expression of Lévy walks in itself. Indeed, the two highly motivated individuals that showed no Lévy walks also survived. Also, only 2 of the 7 Lévy walkers with a weak motivation survived. This suggests that survival and the occurrence of Lévy walks may sometimes be correlated, but are not causally related (Reynolds, 2015). The causal factor that controls these two effects is the motivation to forage.

4. Discussion

The present results support our hypothesis that the propensity of foragers to exhibit Lévy walks is a consequence of their motivation to seek food items. This pattern occurs irrespective of the presence or the absence of real-life constraints that may impede foraging activity. Also, the number of food items consumed and the level of fat reserves increase in proportion to the percentage of Lévy walkers, although there is here no evidence that Lévy walks play a role in the optimization of food seeking – however, further studies including more agents are needed to possibly confirm this preliminary conclusion. Current results suggest that, if Lévy walks can confer some advantages for survival in nature, it is because they tend to appear in foragers with a high motivation to seek food. In this respect, most traditional models implicitly presuppose maximal motivation to find resources, since detected targets “are never missed and are always captured” (Reynolds and Rhodes, 2009, p. 880). Our results indicate that this presupposition has strong implications for the occurrence of Lévy walks when food access is unpredictable.

Our results show some similarities with the behavior of wandering

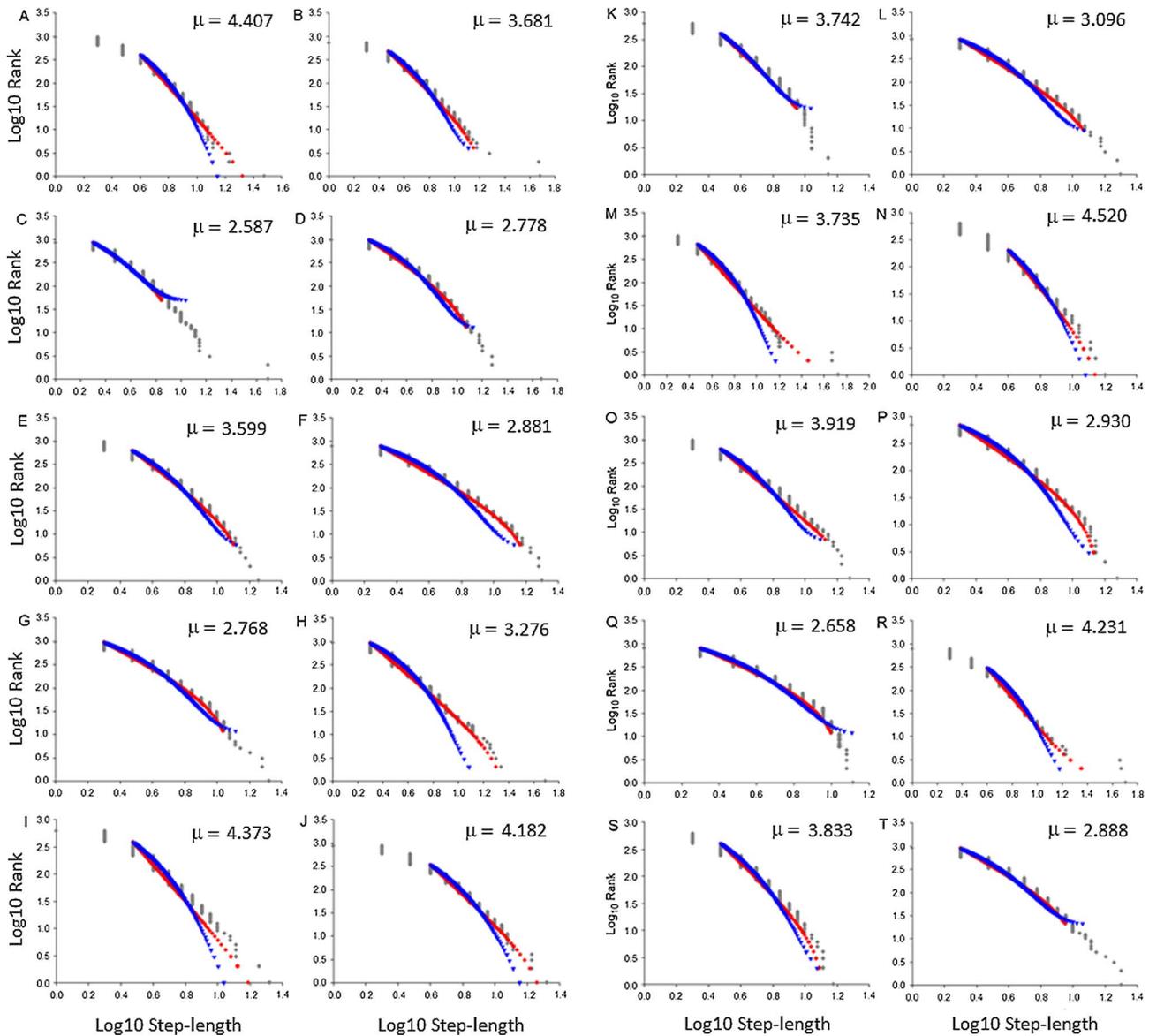


Fig. 6. Simulation 3: Weakly motivated foragers in an unpredictable environment. The distribution of computer data (grey) fits the prediction from the truncated Pareto-Lévy model (red) only in 35% of foragers (C, D, F, G, P, Q, T), while remaining very close to the prediction of the exponential model (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Simulation 3: Survival parameters correlated with the expression of Lévy walks, as a function of motivational strength (measured in terms of the probability of approaching a detected CS). Legend: * Significant difference between the two conditions Low Motivation and High Motivation; Mean (SE).

Variables	Low	High	P-value	Effect size
Food items consumed	23.05 (2.358)	62.15 (1.360)	< 0.001*	0.84
Energy reserves.	3.281 (0.132)	8.246 (0.149)	< 0.001*	0.94
Predation risk	0.107 (0.013)	0.737 (0.022)	< 0.001*	0.94
Rest periods	4.25 (0.522)	13 (0.615)	< 0.001*	0.75
Survival (%)	40 (11.239)	100 (0.000)	< 0.001*	0.43

and black-browed albatrosses (*Diomedea exulans* and *Thalassarche melanophrys*) seeking food – fish and squid – in the ocean. Initially, Humphries et al. (2012) found $\mu = 1.19$ for *D. exulans* (with only 4% of

Lévy walkers) and $\mu = 1.27$ for *T. melanophrys* (38% of Lévy walkers). But a follow-up study involving a more effective detection method showed 74% of Lévy walkers among *D. exulans*. Here, the average μ -value was 1.75–i.e., higher than previously obtained. These values were lower than the optimum for non-destructive search ($\mu \approx 2$), where the food sources can be revisited (Santos et al., 2004; Sims et al., 2012; Viswanathan et al., 2011). Destructive search does not prevent the occurrence of Lévy walks; in a 2D or 3D environment, the same locations are rarely revisited for foragers showing random, continuous directional changes (Reynolds and Bartumeus, 2009). But the μ values are typically lower ($\mu \rightarrow 1$) than in the case of non-destructive search. Because fish-prey disappear once captured or simply move below the water surface, albatrosses are likely to perform destructive search in the ocean. Our simulations were also carried out by means of an environment in which a food item disappeared once consumed – while a new one reappeared anywhere else, a simple property that could represent the dynamics of fish movements in the ocean. In Simulation 1, we found $\mu = 1.678$, a value that is not very different from that reported by Humphries et al. (2013). In Simulation 3, we obtained $\mu = 2.250$, a value very close to that allowing an optimal formation of tight clusters

in mussels (de Jager et al., 2011) and the search movements in other animal species (e.g., Atkinson et al., 2002; Ramos-Fernandez et al., 2004). Such a difference in the μ -values could intuitively suggest that food density was higher in Simulation 3 than in Simulation 1, but this was not the case. Explaining this difference is outside of the scope of the present study but should be investigated.

It has been argued that albatrosses use odor-related cues to orient while food-seeking (their movements are not random), and therefore that, like shearwaters (genus *Calonectris*), they do not perform Lévy walks (Reynolds, 2015; Reynolds et al., 2015). Although this is partly true, several studies suggest that a majority of prey encounters are random rather than based on prey odors (Nevitt et al., 2008; Humphries et al., 2012, 2013). In a sense, odor-like cues (CSs) were present in our model, but they could only influence a forager's trajectory very locally.

We observed that the approach probability altered the occurrence of Lévy foragers in a greater proportion than the detection radius (Simulation 2). This provides additional support for our hypothesis that motivation is a key factor here. As already noted, the propensity to approach a CS is typically used as an index of incentive motivation in real animals (e.g., Anselme et al., 2013; Blaiss and Janak, 2009; Day et al., 2006; Doremus-Fitzwater and Spear, 2011; Flagel et al., 2007; Robinson and Berridge, 2013). Also, approach behavior is correlated with exploratory activity (Beckmann et al., 2011; Dickson et al., 2015; Flagel et al., 2010), making room for a possible connection between motivation and Lévy search. Our model predicts that such a connection exists. Things are a bit different with respect to the detection radius. Lévy walks carry the forager outside of its initial perceptual range, irrespective of its size. Increasing or decreasing the detection radius should therefore have limited impact on relocations. So, the size of the detection radius might be more related to the ability to pay attention to the surroundings than to motivation per se. Nevertheless, even though the ability to detect a CS is a property of attention, its regulation

indirectly depends on an individual's motivation to do a task (Sarter et al., 2006).

Overall, our computer simulations indicate that unpredictability is a sufficient condition to produce Lévy walks in highly motivated foragers, but not in foragers whose motivation to seek resources are reduced. Based on these results, two lines of empirical research could be undertaken. Firstly, we predict that food deprivation enhances the propensity to show Lévy walks in an unpredictable environment. This hypothesis could easily be tested in the laboratory with small animals, such as invertebrate species (e.g., de Jager et al., 2011; Kölzsch et al., 2015; Van Haastert and Bosgraaf, 2009). Also, the foraging movements of birds previously fed or non-fed in aviaries might be compared after they are released in the wild, optimally midwinter – when resources are scarce. Secondly, it would be interesting to determine whether the accumulation of fat reserves in small passerine birds exposed to food unpredictability (in winter or in any unfavorable context, e.g., see Krams, 2000; MacLeod et al., 2007) is correlated with the expression of Lévy walks. For example, Gosler (1996) found that fatter great tits (*Parus major*) have a higher survival rate at the end of the winter season. But the question whether the fatter individuals perform more Lévy walks is unsettled.

Conflict of interest

We declare no conflict of interest.

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Appendix A

This section contains the definitions and values of the variables used in Simulations 1, 2, and 3. If the values were different in the predictable and the unpredictable environment, this is noted with the letters P and U between brackets. If different from one simulation (S) to another the values are separate as follows: S1 | S2 | S3. The main MATLAB files can be found as an online supplement in Anselme et al. (2017).

Maximal number of step units traveled: 3000 | 3000 | 12,000

Size of the 2D environment: 500 rows and 500 columns

Number of food items (α): 1000 (P) or 200 (U)

Number of CSs alone (CS-): 0 (P) or 200 (U)

Safety threshold (π): 1000 food items

Maximal probability to move toward a detected CS ($P(A)$): 1 | 1 – 0.9 – 0.75 – 0.5 | 1 – 0.5

Maximal radius of the detection field ($R(D)$): 12 | 12–10–8–6 | 12

E-threshold to compute mass-dependent predation risk: – | – | 3.5

Number of steps units required before checking the probability of taking refuge: – | – | 400

Energy lost while taking refuge: – | – | 0.05

Prey-handling cost (CS and food item): – | – | 6

Prey-handling cost (CS alone): – | – | 2

Last memory entries used to compute food probability: 30

Last memory entries used to compute the mean number of steps between two food items: 30

Energy decrease per step unit traveled: 0.001

Energy increase per food item consumed: 0.25

Decrement in the probability to change direction after each step unit: 0.0005

Initial energy level: 5 | 5 | 5.5

Initial value for the hunger-induced motivation (“wanting”): 0.5

Initial value for incentive hope: 0 (P) or 3 (U)

Initial value for the detection radius: 3 (P) or 12 (U)

Appendix B

Simulation 1: Variability within a group of foragers was low, despite a limited number of program runs (10 per group). Variability was assessed for the following dependent variables: number of different path lengths (which could be composed of one or multiple step units), total number of paths traveled (independently of their length), shortest and longest path length, and the percentage of space exploitation (for that, the environment was divided in 10 rows and 10 columns, forming 100 squares of 50 step units side; one square was counted provided that the forager entered that

square). The means and standard errors were calculated for each variable in the two groups (unpredictable and predictable environments). A comparison between the two groups for each variable indicated large significant effects (p -values) and large effect sizes (η_p^2).

SIMULATION 1					
	Number of different path lengths	Number of paths traveled	Shortest path length	Longest path length	Space exploitation (%)
Unpredictable environment	36	894	1	152	18
	34	1164	1	128	24
	35	1057	1	108	24
	34	1094	1	197	23
	38	858	1	127	29
	22	900	1	134	14
	20	779	1	84	5
	34	1107	1	85	16
	27	572	1	85	14
	35	798	1	100	14
Mean (SE)	31.50 (1.97)	922.30 (58.14)	1.00 (0.00)	120.00 (11.33)	18.10 (2.21)
Predictable environment	12	1668	1	14	6
	11	1613	1	11	8
	12	1477	1	12	4
	13	1489	1	13	8
	11	1572	1	12	5
	13	1351	1	18	5
	14	1356	1	15	9
	15	1175	1	19	5
	13	1317	1	18	4
	14	1221	1	14	6
Mean SE	12.80 (0.42)	1423.9 (52.58)	1.00 (0.00)	14.60 (0.90)	6.00 (0.56)
p-value	0.000	0.000	No variance	0.000	0.000
Effect size	0.83	0.69	No variance	0.83	0.61

Appendix C

Simulation 3: Variability within a group of foragers was low, despite a limited number of program runs (20 per group). Variability was assessed for the following dependent variables: number of different path lengths (which could be composed of one or multiple step units), total number of paths traveled (independently of their length), shortest and longest path length, and the percentage of space exploitation (for that, the environment was divided in 10 rows and 10 columns, forming 100 squares of 50 step units side; one square was counted provided that the forager entered that square). The means and standard errors were calculated for each variable in the two groups (strong and weak motivation to forage). A comparison between the two groups for each variable indicated large significant effects (p -values) and large effect sizes (η_p^2).

SIMULATION 3					
	Number of different path lengths	Number of paths traveled	Shortest path length	Longest path length	Space exploitation (%)
Strong motivation to forage	53	5409	1	103	45
	68	2512	1	144	41
	60	3619	1	148	57
	50	5339	1	118	62
	62	3888	1	156	41
	74	2314	1	246	31
	60	2094	1	178	40
	56	2094	1	231	38
	60	4154	1	173	42
	56	5049	1	153	49
	62	3523	1	145	54
	60	3997	1	168	46
	61	3776	1	158	43
	63	3813	1	223	42
	54	4240	1	161	48

	60	4100	1	143	45
	47	5089	1	124	44
	53	5226	1	185	42
	61	3536	1	178	36
	56	3675	1	120	37
Mean m(SE)	58.80 (1.36)	3959.10 (212.35)	1.00 (0.00)	162.75 (8.37)	44.15 (1.62)
Weak motivation to forage	16	6136	1	17	16
	18	5183	1	49	18
	16	5487	1	49	15
	17	6263	1	48	22
	16	6444	1	19	21
	15	5121	1	16	15
	14	6339	1	15	21
	15	7051	1	50	24
	14	4469	1	17	14
	17	5731	1	18	12
	14	4265	1	15	11
	17	6177	1	52	20
	14	4559	1	16	13
	19	6443	1	54	19
	15	4735	1	49	11
	15	4859	1	48	10
	16	5093	1	53	15
	13	4183	1	15	12
	14	5848	1	21	18
	18	6262	1	54	17
Mean (SE)	15.65 (0.36)	5532.40 (189.76)	1.00 (0.00)	33.75 (3.89)	16.20 (0.91)
p-value	0.000	0.000	No variance	0.000	0.000
Effect size	0.96	0.44	No variance	0.84	0.85

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