How unpredictable access to food increases the body fat of small passerines: A mechanistic approach

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ABSTRACT

Unpredictable rewards increase the vigor of responses in autoshaping (a Pavlovian conditioning procedure) and are preferred to predictable rewards in free-choice tasks involving fixed- versus variable-delay schedules. The significance those behavioral properties may have in field conditions is currently unknown. However, it is noticeable that when exposed to unpredictable food, small passerines – such as robins, titmice, and starlings – get fatter than when food is abundant. In functional terms, fattening is viewed as an evolutionary strategy acting against the risk of starvation when food is in short supply. But this functional view does not explain the *causal mechanisms* by which small passerines come to be fatter under food uncertainty. Here, it is suggested that one of these causal mechanisms is that involved in behavioral invigoration and preference for food uncertainty in the laboratory. Based on a psychological theory of motivational changes under food uncertainty, we developed an integrative computational model to test this idea. We show that, for functional (adaptive) reasons, the excitatory property of reward unpredictability can underlie the propensity of wild birds to forage longer and/or more intensively in an unpredictable environment, with the consequence that they can put on more fat reserves.

1. Introduction

The effects of reward unpredictability on behavioral decisions have long been studied in psychology. When the presentation of a conditioned stimulus (CS) is unreliably followed by food delivery (unconditioned stimulus, UCS), rats respond more vigorously – and a larger number of rats respond – to the CS compared with rats exposed to a CS that predicts food on each trial (Anselme et al., 2013; Boakes, 1977; Robinson et al., 2015; in pigeons, see Collins et al., 1983; Gottlieb, 2004). Also, an unpredictable delay between response and food reward is chosen more often than a fixed delay: starlings prefer to receive five food items after a variable delay (2.5 or 60.5 s with a 50% probability) than after a fixed delay of 20 s (Bateson and Kacelnik, 1995), a propensity also notably demonstrated in pigeons (Ahearn and Hineline, 1992; Cicerone, 1976) and jays (Ha et al., 1990).

Formal models in psychology are crucial tools to explain and predict how animals decide to react to specific situations, and some of them attempt to capture how reward unpredictability influences behavior (e.g., Amsel, 1958; Bateson and Kacelnik, 1995; Gibbon et al., 1988; Mazur, 1987; Pearce and Hall, 1980). But psychological models are often limited to accounting for the responses of animals confined within experimental setups that imperfectly represent real environmental conditions. It is important to show how they can be used to account for

phenomena described and analyzed by ethologists and behavioral ecologists. In nature, unpredictability is everywhere and animals must deal with it, especially when related to the distribution of food and the presence of predators. It is therefore likely that the abovementioned experimental results reflect some adaptations in the response animals provide to uncertain significant stimuli in this wild.

Hundreds of studies indicate that small passerines exposed to an environment with an unpredictable food access have increased fat reserves (e.g., Bauer et al., 2011; Cresswell, 1998; Cuthill et al., 1997; Ekman and Hake, 1990; Gosler, 1996; Hurly, 1992; Lundberg, 1985; MacLeod et al., 2007, 2008; Polo and Bautista, 2006; Pravosudov and Grubb, 1997; Pravosudov and Lucas, 2001; Ratikainen and Wright, 2013; Rogers, 1987; Witter and Swaddle, 1995). For example, Cresswell (2003) found that some individual blackbirds (*Turdus merula*) have a predictable access to food because they are good foragers (high feeding rate without competitors), while other individuals have a more unpredictable access to food because they are poor foragers (low feeding rate without competitors). Interestingly, poor foragers put on more fat (about 19 g) than good foragers (about 9 g) over the winter. This magnifying effect of food unpredictability on body fat has been observed whether in the field or in captivity. Such a phenomenon may seem counterintuitive in the sense that a sparse distribution of food should have a detrimental effect on the ability to find edible items, and

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hence to get fatter. However, ethologists and behavioral ecologists argue that when food is unpredictable, birds have to accumulate more fat because large fat reserves are an insurance against starvation.

This functional explanation sheds light on the adaptive solution shaped by natural selection to improve the chance of survival under unfavorable environmental conditions. But it does not aim to identify the *causal mechanisms* behind this adaptation. In other words, functional theories explain why animals decide to perform specific actions (to eat or not to eat), but not *how* individuals make their decisions to act. Here, we think that there is room for complementary analysis from psychological models, which attempt to capture the processes controlling – the "how" of – behavior. It is argued that the study of motivational changes under reward uncertainty (Anselme, 2015, 2016) can help understand fattening in small birds. An agent-based computer model is developed to test whether the theory is computationally tenable. This computer model represents the behavior of a small bird foraging on bugs in a lawn, where the distribution of food items is random. Predictability of food depends on the reliability of conditioned cues (holes, colors, noises, odors, etc.) associated with the presence of specific prey, as well as on food density. This model provides a mechanistic explanation to phenomena traditionally captured by functional models (for reviews, see Brodin, 2007; Houston et al., 1993). Overall, we show how fat regulation can be influenced by variables such as foraging motivation, rest periods, handling costs, food quality, initial fat level, and predation risk. Before, we provide a brief survey of the ecological and psychological literature related to food unpredictability.

2. Seeking behavior and the starvation-predation tradeoff

Fattening under harsh environmental conditions occurs during winter and, more generally, in any environment where food density has declined. In some cases, an increase in food consumption is observed (Bauer et al., 2011; Dolnik, 1967; Haftorn, 1976; King and Farner, 1965; Pravosudov and Grubb, 1997; van Balen, 1980), although most studies report correlational data only. Metabolic factors independent of food consumption may also play a role in fattening, but they are not considered here (e.g., Cornelius et al., 2017; Cuthill et al., 2000; Fokidis et al., 2012).

Exposure to unpredictable food supplies is known to act as a stressor, which increases systemic levels of glucocorticoids (Homberger et al., 2014; Marasco et al., 2015; Pravosudov, 2003; Wingfield et al., 1997). The stress response makes small birds behaviorally more active (Fokidis et al., 2012), and is likely to be related to the observed increase in time and energy spent seeking scarce food items (Lahti et al., 1998; Lovette and Holmes, 1995; in non-passerine species, e.g. see Daunt et al., 2006; Hiraldo and Donázar, 1990). Seeking food for longer and/or more intensively does not necessarily lead to an increase in consumption – and hence in fat reserves. Indeed, during a foraging bout, animals can decide to limit their consumption, caching most items for later use (Bartness et al., 2011; Cabanac and Swiergiel, 1989; Hurly, 1992; Lucas, 1994; Shettleworth et al., 1995). But it is important to realize that enhancement of seeking behavior is required to obtain more food, whether that food is consumed or cached. In this article, we only focus on food consumption and examine whether an increase in seeking behavior may contribute to a greater fat deposition.

Functionally, putting on more fat in unpredictable environments is an adaptation against the risk of starvation (Lima, 1986). For example, when beech-mast was not available, great tits (*Parus major*) that had been fatter during winter had a better survival rate than leaner individuals (Gosler, 1996). In winter, the number of food items available is likely to be reduced in comparison with the summer, because many insects have died or are difficult to find, and because part of the seeds produced during the spring are already consumed, cached, or degraded. Snow cover may also temporarily render many food items inaccessible to small birds. Of course, animals can only increase their fat reserves

provided that the amounts of food available remain sufficient. But the reduced density of food may cause unsuccessful foraging bouts on some days, increasing the risk of starvation.

The influence of predation risk on body mass is complex and may have opposite effects depending on the environmental conditions – a phenomenon referred to as risk allocation (Ferrari et al., 2009; Higginson et al., 2012; Lima and Bednekoff, 1999). Mass-dependent predation risk typically decreases the body mass of small passerines because leaner birds are faster and more agile in their ability to escape from predators (e.g., Gosler et al., 1995; Krams, 2000; Lima, 1986; McNamara and Houston, 1990) – although small to moderate increases in fat reserves have no effect on the success of predatory attacks (Brodin, 2001; Witter et al., 1994). Thus, contrary to the risk of starvation, the risk of predation tends to cause a downregulation of body fat (Lima, 1986). But mass-dependent predation risk may also increase – rather than decrease − the body mass of birds (Fransson and Weber, 1997; Lilliendahl, 1998; Pravosudov and Grubb, 1998; MacLeod et al., 2007). The presence of predators has the effect of interrupting foraging, and those interruptions reduce the time available for birds to meet their daily budget. In favorable environments, birds compensate for this waste of time by foraging more when predators are absent. As a result, birds become fatter in response to predation risk – they react as if the presence of predators increased the unpredictability of food access. In poorer environments, however, birds have no opportunity to interrupt foraging and respond to the potential threat by losing body mass in order to remain fast and agile. Alternatively, birds may need to interrupt foraging at some points and, consequently, lose body mass owing to the difficulty of finding enough food items during the safe periods. Finally, it must be noted that habitat structure is used by animals to predict the presence or the absence of predators, even if no one has been detected (Verdolin, 2006).

The validity of the functional explanation of fat regulation based on predation-starvation tradeoffs cannot be denied. But as Pravosudov (2007) pointed out: "the literature on fat regulation in birds has paid little attention to the mechanisms regulating fattening processes" (pp. 440–441). The reason is that functional models can fruitfully account for the available data without having to consider causal mechanisms (Sherry and Mitchell, 2007). Identifying causal mechanisms may fail to predict new significant facts, however, their identification is the only way of explaining how foraging works (McNamara and Houston, 2009; Pravosudov and Smulders, 2010).

3. The excitatory properties of food unpredictability

The need for a psychological approach to foraging has been pointed out by many authors (e.g., Bateson and Kacelnik, 1995; Cabanac, 1992; Kamil, 1983; Lea, 1979; McNamara and Houston, 1985; Ollason, 1980; Pravosudov and Smulders, 2010). None of them has specifically tried to explain how food uncertainty influences animal behavior, while uncertainty is perhaps the major problem that organisms have to manage in order to survive in nature.

First, birds and mammals are sensitive to the uncertainty with which a CS predicts UCS delivery. They respond more to unreliable CSs, predicting food occasionally, than to reliable CSs, predicting food consistently (e.g., Anselme et al., 2013; Boakes, 1977; Collins et al., 1983; Gottlieb, 2004; Pearce et al., 1985; Robinson et al., 2014). Frustration- and learning-based theories (Amsel, 1958; Pearce and Hall, 1980) are relatively unsatisfactory to account for this phenomenon (Anselme, 2015, 2016). Instead, some findings suggest that increased conditioned responding under uncertainty results from increased incentive motivation – the psychological process that makes rewards attractive, approached, and physically contacted (Berridge and Robinson, 1998) – for the CSs. For example, rats trained under reward uncertainty accept to approach and interact with a lever CS located at a longer distance from the food dish than rats trained under reward certainty, suggesting that the CS has acquired a higher motivational salience

(Robinson et al., 2014). Also, the brain structures and neurotransmitters controlling incentive motivation (in particular, dopamine in the nucleus accumbens) are recruited to a larger extent under reward uncertainty (e.g., Hart et al., 2015).

Second, birds and mammals are sensitive to the delay between a response and reward. A reward obtained following a short time interval has a higher subjective value – is more attractive – than the same reward obtained after a longer time interval (e.g., Bateson and Kacelnik, 1995; Estle et al., 2006; Mazur, 1987). This property reflects the fact that, in nature, competition for resources makes delayed rewards less likely. For this reason, animals typically prefer an unpredictable (variable) delay, which may allow a quicker delivery of food, to a predictable (fixed) delay equivalent to its mean (Kacelnik and Bateson, 1996). Bateson and Kacelnik (1997) manipulated reward distribution and showed that the propensity of food-deprived starlings (*Sturnus vulgaris*) to choose a variable-delay option as opposed to a fixed-delay option is higher when variability is unpredictable (3-3-18-3-18-18-… s) than when variability is predictable (3-18-3-18-3-… s). This result confirms the "sooner is better" hypothesis. In the unpredictably variable option, the reward could potentially come after the short delay on any trial. In contrast, if a reward was obtained after the short delay on a trial in the predictably variable option, the starlings were 100% sure that the next trial would involve a longer delay. Consequently, they preferred unpredictable variability – especially when hungry. Simultaneous encounters ("should I eat this or that") are unlikely to occur very often in nature; animals are mainly exposed to sequential encounters ("should I eat this now or wait and look for a better alternative"; Shapiro et al., 2008; Stephens, 2008). But short delays during sequential encounters are associated with higher dopamine release (Kobayashi and Schultz, 2008; Day et al., 2010), suggesting that short delays are motivationally attractive.

There is evidence that the propensity of rats to approach and interact with (press, nibble) a lever CS in a Skinner box, a behavior called sign-tracking, is related to foraging. Sign-tracking is positively correlated with novelty place preference in rats and mice (Beckmann et al., 2011; Dickson et al., 2015), and midbrain dopamine is involved in this process (Flagel et al., 2010). Birds, like other animals, use various CSs in their environment to predict the presence of food – e.g., the holes of earthworms, the odor of fruits, the sounds of flying insects, etc. (Feenders and Smulders, 2011; Heppner, 1965; Wenzel, 1968). However, often enough, CSs are only imperfect predictors of food because they may persist long after a potential prey is gone (e.g., earthworms' holes) or because they are associated with unpalatable or dangerous prey (e.g., the sound of a flying hornet), causing repeated failures in the attempts to get a prey. The uncertain predictive value of CSs may lead animals to inspect them more often and more avidly when they are detected (e.g., Robinson et al., 2015). With respect to delays, a distribution of scarce food resources has the effect of increasing the mean delays before an edible item can be found. This may cause of risk of starvation. Under these circumstances, the uncertainty associated with the opportunity to obtain food following a short delay is important and may boost seeking behavior.

How are behavioral invigoration and short-delay attraction under uncertainty possible? It is not sufficient to say that uncertainty increases motivation, because the modern theory of incentive motivation (also called "wanting"; Berridge and Robinson, 1998) does not predict anything about this effect. We therefore need a mechanism compatible with the incentive motivation theory that succeeds in capturing the effects of reward uncertainty. Wanting uncertain rewards is the very definition of the concept of hope; it is hypothesized that uncertain rewards generate *incentive hope*, which adds some motivational salience to "wanted" rewards (Anselme, 2015, 2016). Of course, we are not postulating that animals hope in the full (human) sense of the term: incentive hope means that the motivational effects of that psychological state are comparable to those of conscious hope, just as "wanting" has motivational effects comparable to those of conscious desires – and

might therefore be the core processes underpinning such complex products of the brain (Anselme and Robinson, 2016). The concept of incentive hope initially aimed to explain the excitatory effects of probabilistic uncertainty in Pavlovian conditioning (Anselme, 2015, 2016). It is not sure whether this psychological state can develop in laboratory animals exposed to a free choice between a variable and a constant delay because variability does not represent real uncertainty here – why to hope for reward when all trials are rewarded, irrespective of the option selected. They just choose the option associated with quicker food, a behavior also observed in the absence of variability (e.g., Lea, 1979). In contrast, in an environment with scarce food items, hoping for food following short delays is more likely because the long delays associated with low-food density may imperil survival. The unpredictability of short delays is assumed to recruit incentive hope in this context. In summary, we defend the hypothesis that birds exposed to food uncertainty may become fatter because uncertainty (in probability and in delay) increases their motivation to forage through incentive hope. It is argued that incentive hope can motivationally modulate food seeking in a way that is functionally adaptive. First, the absence of incentive hope in safe (or "predictable") environments restrains seeking behavior and consumption, minimizing the risk of predation. In contrast, the occurrence of incentive hope in unpredictable environments magnifies seeking behavior and consumption, minimizing the risk of starvation. (In this article, a safe density of food denotes an environment in which there is no risk of starvation. Under a safe density of food, animals do not eat more to stay alive, they eat less to minimize the risk of predation. The reverse situation represents what an unpredictable or unsafe environment is.)

4. The mechanism of incentive hope

Learning-based theories (Rescorla and Wagner, 1972; Glimcher, 2011) predict a decrease in responding under reward uncertainty, while the incentive motivation theory does not make any prediction (Berridge and Robinson, 1998). We argue that incentive hope has the potential of increasing the motivation to respond under unavoidable uncertainty – whether it occurs in autoshaping or in a natural context. Two mechanisms operate here. The first one is counterconditioning, which means that unreliable CSs can come to be approached rather than avoided when they are occasionally associated with food delivery. Counterconditioning is believed to be strong and stronger – or conditioned inhibition weaker and weaker – with training (Laude et al., 2014). Counterconditioning does not mean that nonrewards become attractive, but simply that the CS becomes less aversive. Given that animals are sensitive to the cues in their environment (e.g., Feenders and Smulders, 2011; Heppner, 1965; Wenzel, 1968), we can suspect that counterconditioning plays a role in controlling the approach of unreliable CSs during a foraging bout – even if its effects are difficult to measure in the wild. In short, counterconditioning can explain why reliable and unreliable CSs are *similarly* approached, but another mechanism is necessary to explain that unreliable CSs and low-food densities may stimulate seeking behavior *more* than reliable CSs and high-food densities.

This second mechanism is that underpinning incentive hope itself. Uncertainty is a recognized stressor, and animals seeking food in unpredictable environments often have higher glucocorticoid levels – as a hormonal stress response – than those exposed to safe environments (Fokidis et al., 2012; Marasco et al., 2015; Pravosudov, 2003). The important point here is that chronic mild stress may increase foraging motivation (Breuner, 1998; Martins et al., 2007; Pravosudov, 2003; Reneerkens et al., 2002; Sandi et al., 1996), because the release of glucocorticoids boosts the production of dopamine from the ventral tegmental area (Barrot et al., 2000; Piazza et al., 1996; Rougé-Pont et al., 1998). A number of studies demonstrate that this midbrain region is strongly involved in incentive motivational processes (for a review, see Berridge, 2007), and stress-induced glucocorticoids might enhance

motivation through its stimulation (Sinha and Jastreboff, 2013). Glu-cocorticoid-induced dopamine release is the ground on which incentive hope can develop. Unreliable CSs and low-food densities are assumed to generate incentive hope because of the uncertainty-induced stress response associated with unreliable CSs (nonrewards remain stressful, despite counterconditioning) and the occurrence of short delays for food, respectively.

5. Method

We used an agent-based model to study the role of motivation in foraging. This bottom-up approach tries to decompose a system (environment, population, etc.) in its different parts (individuals, abiotic factors, etc.), and to see how the interactions between those parts can result in emergent, global properties at the system level (e.g., DeAngelis and Grimm, 2014; Esposito et al., 2010; Grimm and Railsback, 2005; Sibly et al., 2013). Agent-based models are relevant to the study of energy management problems, whose resolution implies that realistic algorithmic rules govern the interconnections of many variables, including randomness related to food distribution in the environment.

5.1. Computer model

The model may be considered to represent a single small bird traveling a fixed distance in lawns or in clearings in the search of bugs. The 2D environment in which the agent foraged was homogenous and contained only CSs and UCSs (food items) – 0.25 million possible locations. Most locations were empty, while others could contain a food UCS and its predictive CS (CS+) or a predictive CS without food UCS (CS−). Their distribution was pseudorandom, generated by the Mersenne Twister algorithm of MATLAB (The Mathworks, Natick, MA). All food items had the same energy value, and a food UCS was consumed if the agent (or forager) took up the same coordinates in the environment. After consumption, the food UCS and its predictive CS disappeared and a new CS+ occurred elsewhere in the environment. All CSs− were maintained (did not appear or disappear) during a simulation bout. These latter two conditions were used to hold the predictive value of CSs and food density constant over time.

The forager started in the middle of the environment and moved from one location to the next (=one step) at a constant speed while following a pseudorandom trajectory. At start and at each directional change, the forager could choose between four directions with an equal probability (25%). Once a direction was selected, the probability to maintain that direction depended on the forager's motivational strength, and it decreased after each new step. This strategy allowed the agent to explore larger portions of the environment when motivated to seek food – a constraint in line with the evidence that birds explore unpredictable environments more extensively (Daunt et al., 2006; Hiraldo and Donázar, 1990; Lahti et al., 1998; Lovette and Holmes, 1995). The probability decreased after each new step in order that the forager has a chance to explore other areas and therefore to adopt an effective foraging strategy. However, approaching a border increased the probability to move in the opposite direction, and detecting a CS increased to probability to move in its direction. Fig. 1A and B shows that a forager typically explored larger portions of an unpredictable environment in comparison with a safe environment. Fig. 2 represents the general architecture of the model, described below in more details.

5.1.1. Energy batteries

When a food item was consumed, its energy value was initially stored in a short-term storage system (STS, size: [0,1], representing "stomach and gut"), and then it was transferred at a fixed rate to a longer-term storage system (LTS, size: [0,10], representing "fat reserves"). So, the energy level in the LTS increased because of food consumption. We recognize that fat regulation may also depend on other parameters (Cornelius et al., 2017; Cuthill et al., 2000; Fokidis
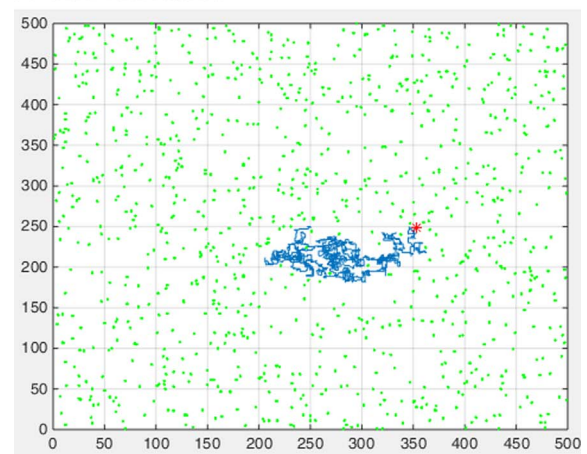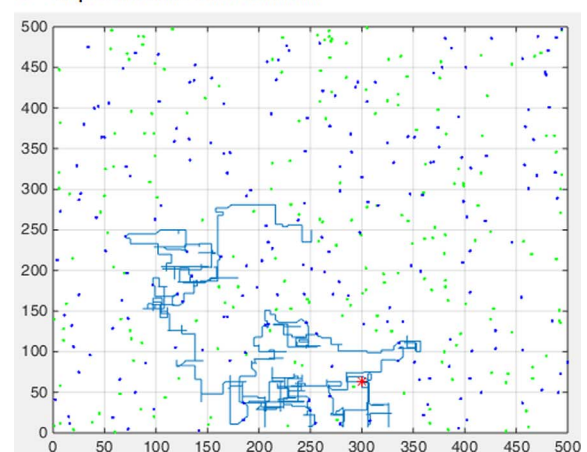

Fig. 1. Environmental arena (500 × 500) in which a single agent or forager (*) freely moved. This environment contained CSs associated with a food UCS (green spots), and also possibly CSs without associated food UCS (blue spots). The forager started in the middle of the environment and its pseudorandom trajectory is indicated by a blue line. (A) Typical trajectory of a forager traveling in a safe environment. (B) Typical trajectory of a forager traveling in an unpredictable environment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2012), but we specifically focused on increased consumption of food that may result from improved seeking behavior here (Bauer et al., 2011; Dolnik, 1967; Haftorn, 1976; King and Farner, 1965; Pravosudov and Grubb, 1997; van Balen, 1980). The energy level in the LTS also decreased continuously because of the energy costs associated with the forager's movements, the rest periods, the handling of prey, and the inspection of CSs without UCS. The absence of energy reserves in the LTS meant starvation, and the forager died. The resulting energy level E, in the LTS, determined incentive motivation or "wanting" for food, w ($\in [0,1]$), according to the non-linear equation:

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

5.1.2. Memory buffers

A first memory buffer allowed the forager to store the last 30 rewarded (CS+) and nonrewarded (CS−) trials – or attempts to catch a prey item. The sequence of trials (CS− = 0 and CS+ = 1) was arithmetically averaged after each new trial in a cumulative way. On this basis, a "subjective" probability of reward could be calculated. A second memory buffer allowed the forager to store the last 30 distances (measured as a number of steps) traveled between two CSs+. On this
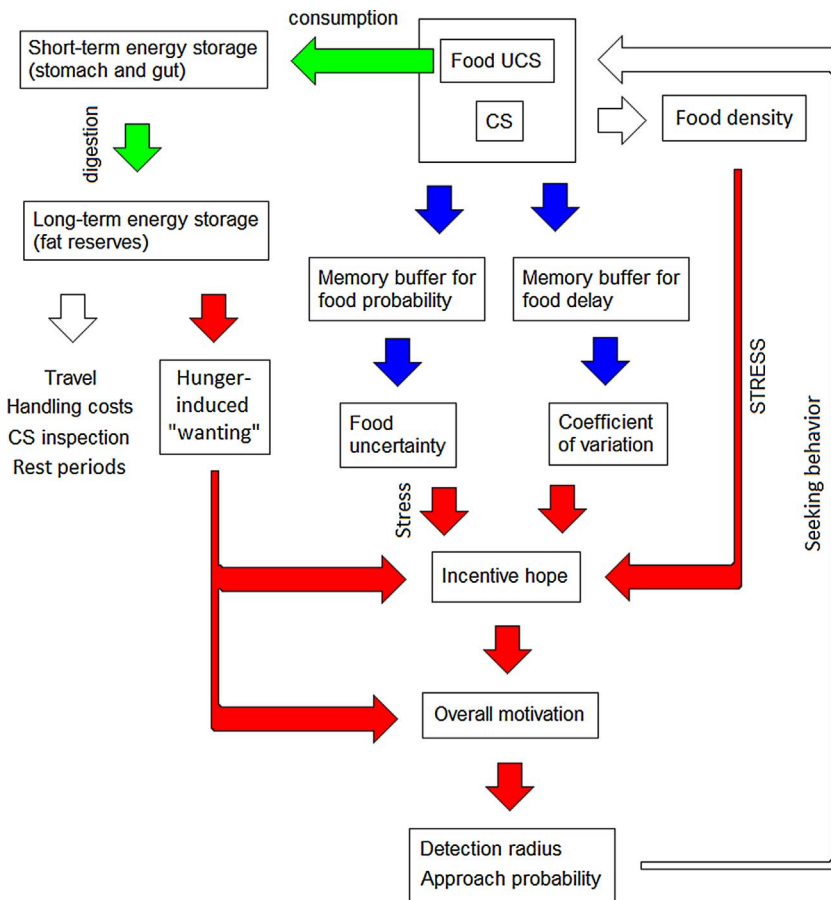
Fig. 2. Computational architecture of the forager. Green arrows link together the modules related to energy storage; blue arrows link together the modules related to memory processing, and red arrows link together the modules related to motivation. For clarity, predation risk and the probability of taking refuge are not indicated. More details in the text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

basis, variability in the number of steps was calculated as a coefficient of variation (standard deviation in the number of steps traveled between the CS+ that were found, divided by the mean number of steps traveled for those CS+). Energy expenditure depended on the number of steps traveled. The forager had not any form of spatial memory. Although animals may sometimes use their spatial memory to optimize food search (e.g. cache retrieval), they must do this activity on a random basis when they ignore where the food items are located (e.g., Bartumeus, 2007; Humphries et al., 2012).

5.1.3. Foraging motivation

In addition to "wanting" rewards, the forager could also "hope" to find them when food access was unpredictable (in probability and/or in delay). The overall motivation to forage (γ, in which incentive hope was added to "wanting") was expressed as follows:

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

Where c is counterconditioning (and was set at its maximal value throughout, $c = 1$), p_i the probability of a CS+ on trial i (here, with $i \in$ [1,30]), $p_i(1 - p_i)$ uncertainty-induced stress, d the coefficient of variation in the number of steps traveled between two CS+, and the expression $(\frac{\pi}{\alpha} - 1)$ the stress induced by the detection/expectation of food scarcity in the environment. In this expression, α represents the actual density of food and π an arbitrary threshold of safe density of food. Stress intensity equals zero when there is no detection/expectation of food scarcity ($\alpha = \pi$), so that variability in steps traveled (factor d) is ignored – the opportunity to obtain quicker food is unimportant. However, stress intensity increases with the detection/expectation of food scarcity ($\alpha < \pi$). In this case, variability in the number of steps

traveled matters – obtaining quicker food becomes crucial for survival. The question whether the ability to detect/expect food density is learned by individuals over the years or is a result of evolutionary adaptations over many generations is not investigated here. We presuppose that birds can estimate the π/α ratio and that this estimate remains stable over a short period of time – not supposed to be longer than one day in the model.

5.1.4. Detection radius and approach probability

A higher strength of foraging motivation (γ) increased the detection radius, R_D, of CSs around the forager and increased the probability of approaching a detected CS, P_A:

$$R_D = 12/(1 + e^{-3\gamma + 4}) \tag{3}$$

$$P_A = (\gamma/1.5)^* P_{A(max)} \tag{4}$$

5.1.5. Handling costs

Inspecting a CS and handling a prey may require some time and energy (Stephens and Krebs, 1986). Our model could not distinguish between space, time, and energy; all of them were counted as a function of a number of steps traveled. So, each time a food item or a CS were found, the forager became insensitive to any new stimulus for a fixed number of steps and lost the amount of energy associated with those steps. Therefore, the time/space/energy available to seek food over a simulation bout was reduced.

5.1.6. Predation risk

Two forms of predation risk were taken into account. First, predation risk that depends on habitat structure was a fixed number that represented environmental risk ($R_{env} \in [0,1]$) for the forager. Second, predation risk that depends on body mass ($R_{mass} \in [0,1]$) increased

exponentially as the energy level in the LTS, E, went beyond a fixed body mass threshold, Θ. The distinction between these two forms of predation risk in the model meant that predation risk could continue to exist ($R_{env} > 0$), even when $E < \Theta$ ($R_{mass} = 0$). The equation controlling mass-dependent predation risk was:

$$R_{mass} = 10^{-\Theta * E^{\Theta}} \qquad (5)$$

5.1.7. Rest periods

An increase in predation risk increased the probability, P_R, that the forager will take refuge after a fixed number of steps. Also, the actual food density (α, relative to the safety threshold π) contributed to increase $P(R)$ – note, however, that 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 available. The equation governing P_R was:

$$P_R = \left(1 - \left(1 - R_{env}\right)*\left(1 - R_{mass}\right) + \frac{\pi}{\alpha}\right)/2 \qquad (6)$$

5.2. Pre-testing of the model

The model was pre-tested in order to find the optimal values used here. For example, a decrease in approach probability ($P_A = 1, 0.90, 0.75, 0.50$) and detection radius ($R_D = 12, 10, 8, 6$) had the effects of significantly reducing the number of food items consumed and, consequently, the ability to put on fat reserves. Also, $R_D > 12$ often caused an unrealistic behavior that consisted of repeated round trips from one location to another, leading the forager to lose its energy without additional gains. For the calculation of the detection radius (Eq. (3)), a sigmoid function was used to reflect the great magnitude differences that may exist in the ability to detect (pay attention to) stimuli depending on whether motivation (γ) is high or low. The exponent determines the slope of the sigmoid function; it was adjusted to reflect significant motivational changes relative to hunger-induced "wanting" (w). With respect to the probability of approaching a detected CS (Eq. (4)), we used constant $k = 1.5$ in order to keep that probability within realistic boundaries, especially in the absence of incentive hope – in a safe environment, animals reject opportunities to feed ($P_A < 1$), although they do not starve to death ($P_A > 0$; e.g., Brodin, 2007). The forager's motivational strength modulated the P_A value relative maximal P_A defined in advance. Mass-dependent predation risk (Eq. (5)) denotes the detrimental effect of fat reserves in determining the agility and rapidity of birds, although moderate increases in fat reserves have no effects (Brodin, 2001; Witter et al., 1994). So, we used a fixed threshold (Θ) at which body mass came to influence predation risk. Below, the changes in the values of some parameters (π, R_{mass}, R_{env}, etc.) aim to show that the model can work in a number of situations, although it is also shown that some of those situations do not lead to an upregulation of fat reserves when access to food is unpredictable.

5.3. Procedure

A simulation bout consisted of a single forager that moved in an environment (500×500) containing food UCSs and predictive CSs. The program stopped and data were recorded after traveling 5000 steps, or in case E (in the LTS) = 0. All program runs were kept for analysis. The safe environment (denoted S-800 thereafter) was composed of 800 CS+ and 0 CS− ($p = 1.0$), for a π value of 800 ($\alpha = \pi$). The unpredictable environment (denoted U-200 thereafter) was composed of 200 CS+ and 200 CS− ($p = 0.5$), for a π value of 800 as well ($\alpha < \pi$). Thus, compared to S-800, U-200 had four times fewer CS+ and led foragers to lose time and energy to reach CS−. Most of the simulations below were based on those characterizations.

Each condition was treated as an empirical issue, whose testing

(simulation) included several groups and 10 foragers per group – a number of individuals compatible with that used in traditional experimental procedures. By and large, foragers seeking food in a S-800 and an U-200 environment were compared with respect to the number of food items consumed and the long-term energy (fat) reserves stored. Specifically, we studied how handling costs, foraging motivation, rest periods, food quality, initial fat reserves, and predation risk can influence food consumption and the acquisition of fat. Data were analyzed using t-tests for unrelated samples and one-way ANOVAs (Statistica 12). Planned comparisons were used to compare data from two groups. Also, a calculation of the effect size (partial eta-squared) allowed us to determine the magnitude of the measured differences (Statistica 12). The values of the parameters used for the simulations are presented in Appendix A. When changes in some of those values were required, this is indicated in the text. The model was implemented using MATLAB software, whose main two files are provided as Supplementary material.

6. Results

6.1. Handling costs

Animals spend some time and energy handling (which includes attack, preparation, and consumption) their prey, and also perhaps inspecting their predictive CSs. A number of factors may influence handling, such as prey size (Schluter, 1982; Kaspari, 1990), the presence of competitors (Johnson et al., 2001), and the carrying of prey to protective cover (Lima, 1985). In our model, handling a prey or inspecting a CS meant that any new item (prey or CS) was ignored for a predefined number steps. This reduced the overall number of steps available to find food (all foragers were limited to traveling 5000 steps) and consumed some energy (0.001 unit energy per step ignored).

Three conditions were compared. Low handling costs denoted a loss of three foraging steps for a food item and of one foraging step for a CS. Middle handling costs represented a loss of 12 steps for a food item and of 4 steps for a CS. Finally, high handling costs meant a loss of 21 steps for a food item and of 7 steps for a CS. Those categories have no meaning in themselves; they must be compared to the energy provided by a food item (0.30 unit energy). For lawn foragers, we can expect that the costs of handling a prey (earthworms, spiders, woodlice, etc.) or of inspecting a CS are low relative to the energy provided by those items (about 23 J/mg on average; see Török and Ludvig, 1988). Predation risk was not considered here in order to determine the effects of handling costs in themselves – which were included in the next simulations.

Fig. 3A indicates that handling costs had no significant effects on the number of food items consumed, whether handling occurred in a safe or in an unpredictable environment ($F(1,54)$'s ≤ 2.472, p's ≥ 0.122; $\eta_p^2 \leq 0.12$), although there was a trend for a reduction in consumption between conditions Low and High in the unpredictable environment ($F(1,54) = 3.982$, p = 0.051) – with an effect size of medium value ($\eta_p^2 = 0.18$). So, food consumption is likely to be affected by costly prey handling, relative to the net energy gain of the prey (e.g., birds of prey having to catch and dismember small prey items), especially in unfavorable environments. But this problem might be insignificant for lawn foragers. Importantly for our purpose, in each condition, food consumption was higher in the unpredictable environment compared to the safe environment ($F(1,54)$'s ≥ 12.302, p's ≤ 0.0009), although the effect size gradually decreased − while remaining large – in proportion to handling costs (Low: $\eta_p^2 = 0.64$; Middle: $\eta_p^2 = 0.43$; High: $\eta_p^2 = 0.37$).

With respect to energy or fat reserves (Fig. 3B), there were no significant effects of handling constraints in the safe environment ($F(1,54)$'s ≤ 1.109, p's ≥ 0.297; $\eta_p^2 \leq 0.09$). A reduction in energy reserves was obtained in the unpredictable environment between the conditions Low-Middle and between the conditions Low-High (F
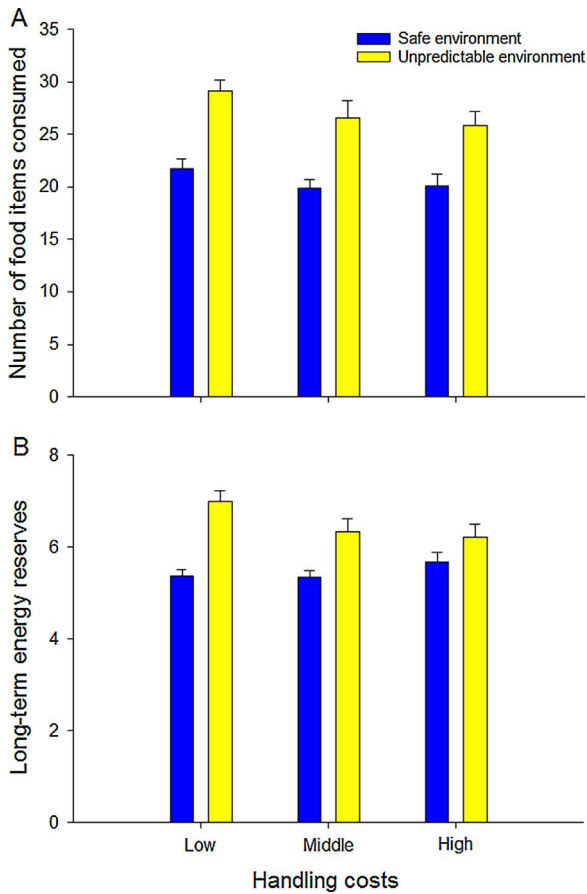
Fig. 3. Effects of handling costs. (A) They did not alter the number of food items consumed, although stronger costs tended to decrease consumption in the unpredictable environment. (B) They did not alter the ability to store fat reserves in the safe environment, but stronger costs decreased fattening in the unpredictable environment.

(1,54)'s ≥ 4.546, p's ≤ 0.037) – with a medium effect size between the conditions Low and the High ($\eta_p^2 = 0.20$). This result suggests that seeking prey items with high-cost handling constraints in an unpredictable, but not in a safe, environment increased the risk of starvation. Energy reserves were more elevated in the unpredictable environment compared to the safe environment for conditions Low and Middle (F(1,54)'s ≥ 10.633, p's ≤ 0.002; $\eta_p^2 \geq 0.39$), but not for condition High (F(1,54)'s = 3.381, p = 0.071; $\eta_p^2 = 0.13$). The evidence captured here that high handling costs under unpredictability failed to increase energy reserves yet in foragers that consumed significantly more items (see above) is a computational indication that consuming more food when scarcely distributed may act against starvation.

6.2. Rest periods and the role of foraging motivation

Predation risk influences the propensity of small birds to hide under cover (e.g., Mónus and Barta, 2011). Here, the foragers were exposed to an environmental predation risk in each environment ($R_{env} = 0.5$) and no mass-dependent predation risk at start ($E = 5$ and $\Theta = 6$, hence $R_{mass} = 0$). The probability to take refuge was checked every 200 steps, and handling costs were considered negligible (see Section 5.1, Low condition). Food items had an energy value of 0.33.

The model's outputs are reported in Table 1: Compared to foragers exposed to a S-800 environment, foragers in U-200 were significantly different for each variable considered. They consumed more food items, had higher fat reserves, had higher hopes for food (but were less hungry), and hence showed increased approach probability and detection radius. They also took refuge less often than foragers in S-800.

Table 1
Outputs of the model for agents foraging in a safe (S-800) and an unpredictable (U-200) environment. Values represent the means and standard errors (in brackets) for the 5000 steps traveled. The bold values indicate significant increase or decrease (p < 0.05). More details in the text. * Effects size calculated as partial eta-squared (η_p^2).

Variables	S-800	U-200	Effect size*
Items consumed	16.700 (1.116)	**25.200 (0.904)**	0.66
Fat reserves (E)	4.822 (0.182)	**6.911 (0.264)**	0.70
Hunger (w)	0.937 (0.009)	**0.716 (0.033)**	0.69
Total motivation (γ)	0.937 (0.009)	**4.895 (0.290)**	0.91
Approach probability (P_A)	0.562 (0.006)	**0.880 (0.010)**	0.97
Detection radius (R_D)	2.885 (0.057)	**11.084 (0.358)**	0.96
Periods rested	17.900 (0.674)	**9.500 (0.703)**	0.80
Predation risk ($R_{env} + R_{mass}$)	0.500 (8*10^{-6})	**0.509 (0.007)**	0.30

Finally, foragers in U-200 were exposed to a higher predation risk. For all measures, the effect size was large – although in the case of predation risk, the mean difference between the two environments was objectively small.

As the foragers in U-200 took refuge less often than foragers in S-800, it was possible that their higher food intake was a direct consequence of their extended foraging time. So, we compared group S-800 to group U-200 in the absence of rest periods and of predation risk. The foragers in U-200 continued to put on significantly more energy reserves than the foragers in S-800 (U-200: 7.11 ± 0.16 versus S-800: 5.65 ± 0.15; t(18) = −6.586, p = 0.000). The suppression of rest periods did not alter the patterns of fat storage, suggesting that the available time for foraging is not per se a cause of downregulation of fat (Fransson and Weber, 1997; Lilliendahl, 1998; Pravosudov and Grubb, 1998; MacLeod et al., 2007).

We also tested the effects that incentive hope may have on fat reserves by comparing the U-200 foragers above (p = 0.5 and α < π) to U-200* foragers without incentive hope (p = 1 and α = π). The "wanting" factor w was unaffected. The absence of incentive hope had a strong detrimental effect on the ability of foragers to store fat reserves (U-200*: 3.247 ± 0.185 vs. U-200: 6.911 ± 0.264; F(1,18) = 128.986, p = 0.000; $\eta_p^2 = 0.88$). As depicted in Fig. 4, fat reserves gradually decreased over the 5000 steps traveled in group U-200*, whereas it gradually increased in group U-200. In fact, incentive hope allowed foragers to find more food items in U-200 (25.2 ± 0.904), despite the presence of 200 unrewarded CS−, compared to foragers exposed to U-200* without CS− (6.3 ± 1.033; F(1,18) = 189.445, p = 0.000; $\eta_p^2 = 0.91$). In the model, food probability influences incentive hope to a lesser extent than food density – a realistic assumption
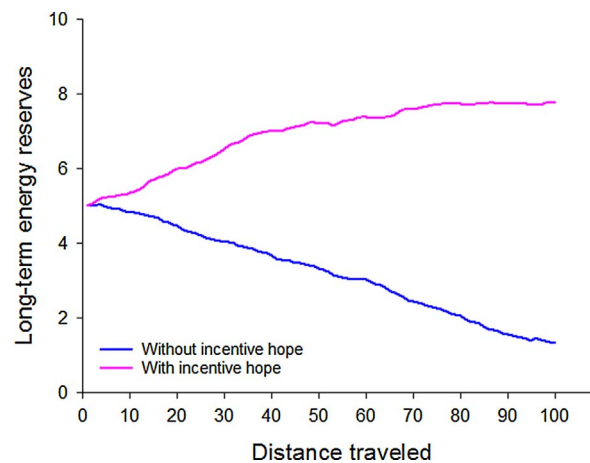

Fig. 4. Effects of incentive hope on the accumulation of long-term energy (fat) reserves. The foragers gradually gained reserves when searching for food under the influence of incentive hope (U-200). In contrast, they gradually lost their reserves when searching for food in the absence of incentive hope (U-200*).
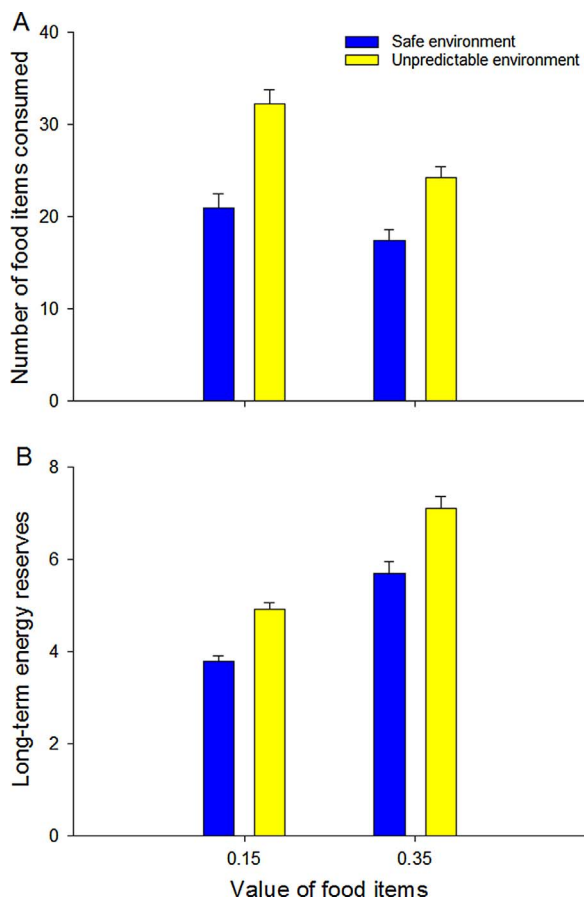
Fig. 5. Effects of the energy value of food items. (A) More food items were consumed in an unpredictable environment compared to a safe environment, irrespective of their energy value. The number of food items consumed was independent of their energy value in the safe environment, while it was lower for high-energy value items in the unpredictable environment. (B) Long-term energy reserves were higher with high-energy food items in both environments.

in the sense that a low-food density with reliable CSs is likely to imperil survival more than a high-food density with unreliable CSs. This result shows that a decrease in food probability and density does not prevent foragers from eating more food and storing more fat, provided that environmental poverty is compensated for by a motivational mechanism that boosts food seeking.

6.3. Food quality

Fat reserves may sometimes be higher in birds foraging in safe environments compared to birds foraging in unpredictable environments, especially when dominants put subdominants away from high-quality feeding sites (e.g., Ficken et al., 1990; Piper and Wiley, 1990; Polo and Bautista, 2002; Wiedenmann and Rabenold, 1987). Here, we tested the effect of food quality on fat regulation without predation risk, in order to determine whether significant changes in the energy value of food had an impact on the ability to store fat.

Foragers were tested with two energy values for food: 0.15 (poor) and 0.35 (rich) unit energy per item. Fig. 5A shows the impact of food quality on the number of items consumed. For each energy value, more food items were consumed in the unpredictable environment than in the safe environment (F(1,36)'s ≥ 13.633, p's ≤ 0.0007; η_p^2 ≥ 0.49). The energy value of food did not significantly alter the number of items consumed in the safe environment (F(1,36) = 3.711, p = 0.062; η_p^2 = 0.17), but richer items strongly reduced it in the unpredictable environment (F(1,36) = 18.326, p = 0.0001; η_p^2 = 0.51). It is noticeable that, on average, almost twice as many food items were consumed

in U-200-0.15 (32.3 items) as in S-800-0.35 (17.4 items), and this difference was strongly significant (F(1,36) = 63.573, p = 0.000; η_p^2 = 0.78). In contrast, a similar amount of food items was consumed in U-200-0.35 and S-800-0.15 (F(1,36) = 3.118, p = 0.086; η_p^2 = 0.15).

The reason why food consumption was similar in U-200-0.35 and S-800-0.15 is that the foragers were less hungry under rich-food unpredictability (Fig. 5B). But more fat was stored in U-200 compared to S-800, irrespective of food quality (F(1,36)'s ≥ 15.460, p's ≤ 0.0004; η_p^2 ≥ 0.46). Interestingly, long-term energy reserves were significantly higher in S-800-0.35 compared to U-200-0.15 (F(1,36) = 7.476, p = 0.010; η_p^2 ≥ 0.29), despite the fact that they consumed much fewer food items. Thus, the model predicts that birds may become fatter in an environment in which food is both in safe amounts and rich in terms of energy content. This result is in line with current evidence that obesity in humans (and domestic animals) is partly due to the presence of easy-to-access foods with high caloric value within modern Western societies (e.g., Bodor et al., 2010; Nettle et al., in press). In contrast, less energy reserves were stored in S-800-0.15 than in U-200-0.35 (F(1,36) = 134.743, p = 0.000; η_p^2 = 0.88), although the two groups consumed an equivalent amount of food.

6.4. Effect of the initial level of fat reserves

Ekman and Hake (1990) showed that greenfinches (*Carduelis chloris*) exposed to unpredictable food conditions, increased their fat reserves to a greater extent when they were initially lean than when they were initially fatter (see also Thomas, 2000). Also, Pravosudov and Grubb (1997) found that initially lean tufted titmice (*Parus bicolor*) put on more fat, while initially fatter individuals tended to cache more food items and to fly less. Some changes in fat accumulation could be observed within a one-day period.

We used a U-200 environment (with π = 800) for the foragers of all groups, which were characterized by a specific initial fat level: E = 2, E = 6, and E = 8. Predation risk was set to zero in order that initial energy reserves are the only factor influencing weight gains – but given that predation risk increases with body mass and increases the number of rest periods (Eqs. (5) and (6)), we can predict that the effects on weight gains shown below would be magnified.

The number of food items consumed increased in inverse proportion to the initial long-term energy reserves (Fig. 6A). All comparisons were significant (F(1,27)'s ≥ 5.908, p's ≤ 0.022; η_p^2 ≥ 0.26), except between the conditions E = 2 and E = 6 (F(1,27) = 1.804, p = 0.190; η_p^2 = 0.09). Nevertheless, the average number of food consumed was higher for E = 2 (33.9) than for E = 6 (29.7). It is important to note that, for real birds, high fat reserves are both costly to acquire and to maintain, so that fat optimal reserves are sometimes reached over many days or even weeks. This means that a large difference in daily foraging time/rate between lean and fatter birds may not always exist; the sum of small daily differences in foraging time/rate becomes only visible in the long-term (W. Cresswell, pers. com.). Because fatter birds should be less motivated to find food than leaner animals, we used w = 0.1 ("wanting"), ℏ = 0 (incentive hope), and R_D = 3 (detection radius) as initial values in the conditions E = 6 and E = 8, while we used w = 1, ℏ = 10, and R_D = 12 as initial values in the condition E = 2. The values were quickly readjusted during the simulations, and the results indicate that this manipulation had no influence on the number of food items consumed – which depended only on the initial level of energy reserves. Fig. 6B depicts the change in long-term energy reserves for a traveled distance of 5000 steps in each condition. The strongest average increase occurred for E = 2 (0.91 unit energy, range: 2–3.36), a lower increase was observed for E = 6 (0.21 unit energy, range: 6–6.49), and there was a strong decrease for E = 8 (−0.97 unit energy, range: 8–6.51).
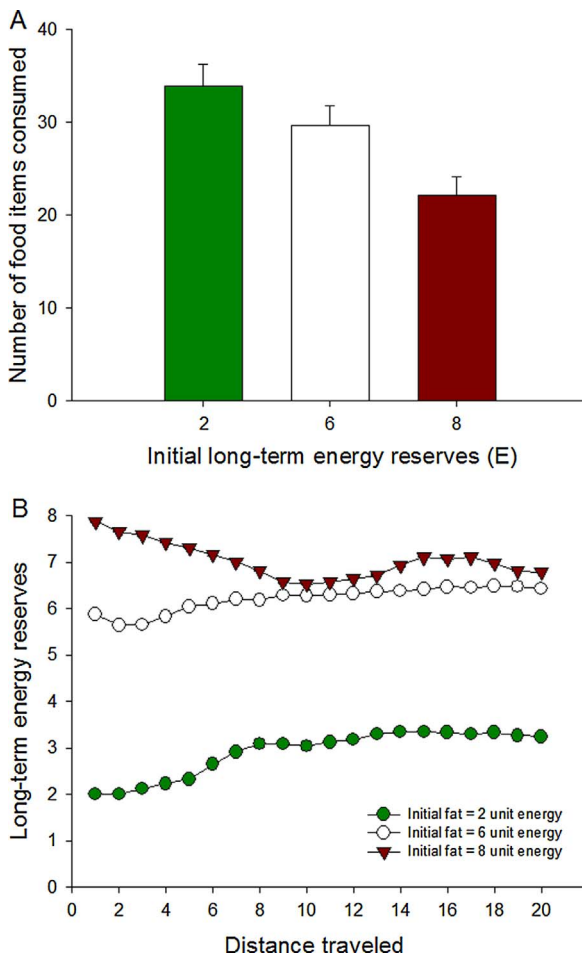
Fig. 6. Effects of initial long-term energy reserves. (A) A larger number of food items were consumed when the initial level of energy reserves was low, at least on average. A non-significant difference (here, $E = 2$ vs. $E = 6$ conditions, p = 0.190) may simply mean that a longer period of time is necessary for the foragers to put on enough fat. (B) Fat reserves increased when their initial level was low ($E = 2$), remained relatively stable with moderate initial level ($E = 6$), and decreased when initial level was high ($E = 8$). Each data point represents an average value for 250 steps.

6.5. Predation risk may decrease or increase body mass

As discussed earlier, predation risk does not systematically decrease body mass, but rather may contribute to increase it if the environmental conditions are good enough to compensate for predator-induced interruptions in foraging (Fransson and Weber, 1997; Lilliendahl, 1998; Pravosudov and Grubb, 1998; MacLeod et al., 2007).

We defined three conditions of predation risk in two environmental contexts (S-1000 and U-200). In one condition (200-NR), the probability of taking refuge was checked every 200 steps and there was no predation risk ($R_{env} = 0$, $R_{mass} = 0$). In a second condition (200-R), the probability of taking refuge was also checked every 200 steps but predation risk was present ($R_{env} = 0.7$, $E = 5$ and $\Theta = 3$). In a third condition (50-R), the probability of taking refuge was checked every 50 steps and the risk parameters were set with the same values as with group 200-R, so that the additional constraint of checking the probability more often could potentially lead the foragers in 50-R to reduce their foraging time and to lose more energy.

Our model produced outcomes that are partly compatible with the bimodal effect of predation risk. Fig. 7A shows the number of food items consumed in each condition and in each environmental context. Consumption was similar between conditions 200-NR and 200-R in the safe environment (F(1,54) = 0.147, p = 0.703; $\eta_p^2 = 0.03$) and strongly decreased under 200-R in the unpredictable environment (F
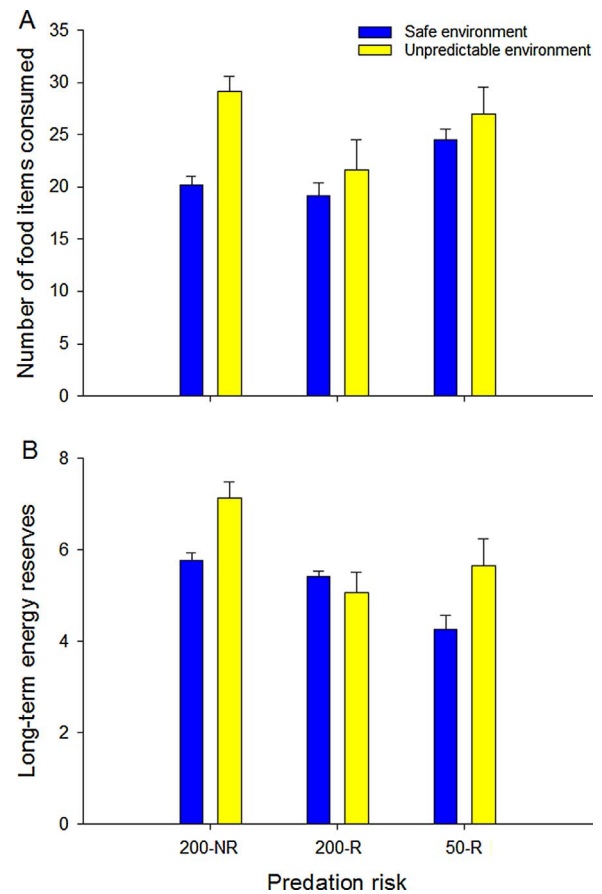

Fig. 7. Effects of predation risk. (A) Compared to a situation without predation risk (200-NR), the number of food items consumed remained stable (200-R) or increased (50-R) in the safe environment, while it decreased or remained stable in the unpredictable environment. (B) Long-term energy reserves remained stable or decreased in the safe environment but they only decreased in the unpredictable environment.

(1,54) = 8.505, p = 0.005; $\eta_p^2 = 0.23$). In 200-R, a larger number of foraging interruptions occurred in the safe environment (range: 20–24) compared to the unpredictable one (range: 4–15). When predation risk was higher (50-R), the mean number of food items consumed was increased in the safe environment (from 20.2 to 24.5) and decreased in the unpredictable environment (from 29.2 to 27), although these changes were not significant (F(1,54)'s ≤ 2.722, p's ≥ 0.105). However, although the effect size was small for the unpredictable environment ($\eta_p^2 = 0.09$), it was large for the safe environment ($\eta_p^2 = 0.38$), suggesting that predation risk tended to enhance food intake in a rich environment. Here also, the individuals took refuge more often in the safe environment (range: 81–88) than in the unpredictable one (range: 41–52). Overall, the propensity of foragers under a high predation risk (50-R) to increase food consumption in a safe environment and to decrease it in an unpredictable one (relative to 200NR) was compatible with the way predation risk is known to modulate foraging (e.g., MacLeod et al., 2007).

An examination of long-term energy reserves in the different groups indicates that it was here not possible to highlight this bimodal effect of predation risk (Fig. 7B): in one or the other environment, energy reserves decreased between the 200-NR and the 50-R conditions (F (1,54)'s ≥ 8.252, p's ≤ 0.006; $\eta_p^2 ≥ 0.21$). However, energy reserves remained stable between condition 200-NR and condition 200-R in the safe environment (F(1,54) = 0.517, p = 0.475; $\eta_p^2 = 0.16$), while it decreased in the unpredictable environment (F(1,54) = 16.076, p = 0.000; $\eta_p^2 ≥ 0.43$). In other words, foragers in the safe environment were able to maintain their reserves despite predation risk and a larger number of foraging interruptions (200-NR: 3–13; 200-R: 20–24),

but this was not the case of foragers in the unpredictable environment (200-NR: 1–5; 200-R: 4–15). Overall, our model tends to suggest that predation risk increases food consumption in a safe environment and decreases it in an unpredictable one, although the expected effects on fat reserves are not fully visible in the safe environment – in which fat should increase rather than stabilize (200-R) or decrease (50-R).

7. Discussion

The present model is an attempt to explain and to predict the accumulation of fat reserves in small birds exposed to unpredictable food access, by means of a mechanistic rather than a functional theory. We show that a psychological mechanism is capable of upregulating fat reserves under harsh environmental conditions – although unexplored mechanisms could also play a role (Cornelius et al., 2017; Cuthill et al., 2000; Fokidis et al., 2012). This psychological mechanism may therefore contribute to explain how foraging works at the individual level. In the model, unpredictability has the effect of increasing the detectability of distal CSs as well as that of increasing the probability of approaching them once detected, leading the forager to travel longer distances and to consume larger amounts of food. Those effects can be viewed as an improvement of attentional focus resulting from a surge of motivation (incentive hope). The idea that unpredictability arouses attention is compatible with Pearce's findings that an orienting attentional response occurs when the predictive accuracy of a CS decreases (e.g., Collins et al., 1983; Pearce et al., 1985), although these works did not try to explain the origin of attentional arousal. Here, we propose an original motivational mechanism that bridges the gap between unpredictability and attention.

The excitatory property of food uncertainty has been demonstrated in birds and mammals tested in the laboratory. Is it possible that they exhibit this pattern of responses because they are hungrier than animals tested under food certainty? This hypothesis is disconfirmed by studies showing that such an effect is obtained despite access to an equivalent amount of food per session, as well as between the sessions (e.g., Anselme et al., 2013). However, common sense suggests that, in nature, birds foraging on unpredictable food sources might be hungrier than birds whose access to food is easier. Our simulations reveal that this intuition is correct when the environment is highly constraining – i.e., when handling costs are strong, when motivation is low, when food quality is low, and when predation risk is elevated. But, it is not correct in other circumstances, even under predation risk. We showed that hunger-induced "wanting" (w in the model) may be lower in an unpredictable environment than in a safe one, because enhanced seeking and consumption resulting from incentive hope can compensate for the difficulty to get food. In the absence of such a compensatory mechanism, starvation is reached more often because individuals (especially leaner ones) are less effective in their ability to seek food. This compensatory mechanism is an evolutionary requirement (Anselme, 2013) and may explain why death by predation is more frequent than death by starvation in small wintering birds (Jansson et al., 1981; Brodin, 2007). As a result, we can reasonably reject the hypothesis that the excitatory property of food uncertainty in the laboratory is a schedule-induced behavior. Schedule-induced behaviors, such as polydipsia, are modulated by motivational factors (for a review, see Roper, 1983). But schedule induction increases the frequency of occurrence of an *unreinforced* behavior (Wallace and Singer, 1976), while reward uncertainty increases that of a *reinforced* behavior. Thus, it is likely that autoshaping is revealing something about foraging rather than inducing an adjunctive behavior related to experimental design constraints.

We suggested that our model can describe the behavior of lawn foragers. We used only one energy value for all the items that could be found within a simulation bout. However, many different prey items may co-exist in a lawn, and their energy value may vary (Greenwood and Harvey, 1978; Török and Ludvig, 1988). Although considering prey with distinct energy values is likely to improve the ecological accuracy

of the model, we think that this would not alter the conclusions we can draw from its current version: Incentive hope will also enhance food-seeking – and energy reserves – in an environment with distinct food types. The effect of unpredictability might even be more pronounced, as suggested by autoshaping results (Anselme et al., 2013; for a mathematical formulation of this effect, see Anselme, 2015). In addition, birds may almost exclusively forage on specific items for a while. For example, blackbirds mainly eat earthworms in April and May, when frequent rain falls moisten the soil, allowing prey to reach the surface and to become accessible (Török and Ludvig, 1988).

One possible limit of the model is that foragers moved at constant speed, as opposed to real animals. This was due to the model's insensitivity to time – in fact, time, space, and energy were together measured in terms of step counts. We considered that 5000 steps represented a distance traveled instead of a time period. In this case, a forager's travel and the number of items consumed by this forager become independent of its speed. But then, we do not have real measures of handling *time* – only a measure of the loss of energy and of traveling opportunities caused by the need to handle prey; handling time is the same for each prey. We think that this limitation would be problematic if we aimed to account for food seeking in bird species where the individuals have to handle large prey and to dismember them before they can be consumed – e.g. birds of prey. But the time required to collect bugs at the surface of a lawn is short and relatively similar from prey to prey, so that we can reasonably presuppose that handling time has no significant effect on foraging behavior in small passerines. A related potential limit of the model is that foragers were unable to seek food while handling a prey item. But if the handing time of lawn foragers is short, it is unlikely that it can strongly influence their ability to find new prey. Finally, the influence of some parameters such as handling costs and food quality were assessed in isolation, independently of predation risk. It was important to determine how these parameters can alter responding to food. They were then included or varied in the next simulations in order to test the robustness of the model. The model appeared to be robust in the sense that the changes across many different situations often maintained the ability to store fat under food unpredictability.

Only a few studies refer to motivational processes as a factor that may control foraging. Cresswell (2003) suggested that blackbirds with a low foraging rate (poor foragers) are not less motivated to find food than individuals with a higher foraging rate (good foragers) because there is no correlation between the absolute feeding rate and the decrease in feeding rate when competitors enter a patch. Pravosudov and Clayton (2001) found that mountain chickadees (*Poecile gambeli*) maintained on a limited and unpredictable food supply retrieve caches with more accuracy than individuals maintained on an ad libitum food access. They suggested that birds in the former group were perhaps more motivated to search for food, although they noted no significant group difference in caching intensity. One possible explanation for the absence of effect is that the criterion (foraging intensity) used to measure motivation in these two studies is not appropriate. In our model, for example, all foragers forage with the same intensity (travel speed is constant). They only differ in their ability to reach distal CSs. Interestingly, Pravosudov and Clayton (2001) noted that the motivation to cache food and hunger level are not directly related, as birds continue to cache food during periods of food surplus (see also Clayton and Dickinson, 1999). Although we did not aim to account for food hoarding and cache retrieval behaviors in this study, it is interesting to note that incentive hope is relatively independent of hunger. It is reasonable to think that, like food seeking, hoarding and cache retrieval somehow depend on incentive hope since birds are uncertain whether the "wanted" food items will be found or retrieved.

Overall, it is argued that incentive hope is a mechanism shaped by natural selection, allowing an adaptive regulation of fat reserves as a function of the availability of food in the environment. When food is easy to access (predictable), the low motivation to forage can be seen as

an adaptation to remain fast and agile to escape from predatory attacks. By contrast, when food is harder to access (unpredictable), the higher motivation to forage consists of an adaptation to stay alive in unfavorable environmental conditions. The objective predation risk (R_{mass} and R_{env} in the model) can be interpreted as a modulator of an innate propensity to modulate motivation depending on food availability, in the absence of predators (Verdolin, 2006) or even when predators do not exist anymore (Nettle et al., in press). In nature, hunger-induced "wanting" (w in the model) enables animals to approach a detected food, but it is unlikely to be a strong determinant of food seeking because a hungry animal may be weakened – and hence is subject to a high risk of starving to death. But incentive hope is different, and only partly related to hunger: this process is unnecessary to approach a detected food, but is very effective in motivating food seeking – when food has not been detected yet. Thus, it is reasonable to suggest that incentive hope was shaped by evolution because its functional consequences improve the chance of survival in any context – i.e., it plays no role in safe environments to minimize predation risk and exerts a strong influence in unpredictable environments to minimize starvation risk.

The model presented here suggests that motivational processes may play a determining role in the management of fat reserves in response to unpredictable food supplies. We successfully replicated some results from the literature, and also identified boundary conditions beyond which food unpredictability cannot increase fat reserves in small birds. These predictions, among others, could be empirically tested and perhaps help refine the current version of the model.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2017.08.013.

Appendix A

This section contains the definitions and values of the variables used for the simulations. If the values were different in the safe (S) and in the unpredictable (U) environment, this is indicated. Some values may have changed (*) depending on the simulations carried out. The changed values are indicated in the appropriate sections.

Number of steps traveled: 5000.
Size of the 2D environment: 500 rows and 500 columns.
Number of food items (α): 800* (P) or 200 (U).
Number of CSs: 0 (P) or 200 (U).
Safety threshold (π) relative to food density: 800*.
Maximal probability (P_A) to move toward a detected CS: 0.9.
Maximal radius of the detection field (R_D): 12.
LTS-threshold (Θ) to compute mass-dependent predation risk: 6*.
Number of steps before checking the probability (P_R) of taking refuge: 200*.
Decrease in energy when taking refuge: 0.05.
Prey-handling costs per CS+: 3*.
Handling costs per CS−: 1*.
Last memory entries used to compute UCS probability: 30.
Last memory entries used to compute the mean number of steps between two UCSs: 30.
Energy decrease per step traveled: 0.001.
Energy increase per food item consumed: 0.33*.
Energy transferred from the STS to the LTS after each step: 0.004.
Decrease in the probability to change direction after each step: 0.0005.

Initial energy level in the STS: 0.
Initial energy level in the LTS (E): 5*.
Initial value for hunger-induced "wanting" (w): 0.5
Initial value for incentive hope: 0 (P) or 5 (U).
Constant value for predation risk associated with habitat structure (R_{env}): 0.5*.
Initial value for predation risk associated with body mass (R_{mass}): 0*.
Initial value for the detection radius (R_D): 3 (P) or 10 (U).

References

Ahearn, W., Hineline, P.N., 1992. Relative preferences for various bivalued ratio schedules. Anim. Learn. Behav. 20, 407–415.

Amsel, A., 1958. The role of frustrative nonreward in noncontinuous reward situations. Psychol. Bull. 55, 102–119.

Anselme, P., Robinson, M.J.F., 2016. Wanting, liking, and their relation to consciousness. J. Exp. Psychol. Anim. Learn. Cogn. 42, 123–140.

Anselme, P., Robinson, M.J.F., Berridge, K.C., 2013. Reward uncertainty enhances incentive salience attribution as sign-tracking. Behav. Brain Res. 238, 53–61.

Anselme, P., 2013. Dopamine, motivation, and the evolutionary significance of gambling-like behaviour. Behav. Brain Res. 256, 1–4.

Anselme, P., 2015. Incentive salience attribution under reward uncertainty: a Pavlovian model. Behav. Process. 111, 6–18.

Anselme, P., 2016. Motivational control of sign-tracking behaviour: a theoretical framework. Neurosci. Biobehav. Rev. 65, 1–20.

Barrot, M., Marinelli, M., Abrous, D.N., Rougé-Pont, F., Le Moal, M., Piazza, P.V., 2000. The dopaminergic hyper-responsiveness of the shell of the nucleus accumbens is hormone-dependent. Eur. J. Neurosci. 12, 973–979.

Bartness, T.J., Keen-Rhinehart, E., Dailey, M.J., Teubner, B.J., 2011. Neural and hormonal control of food hoarding. Am. J. Physiol. Regul. Integr. Comp. Physiol. 301, R641–R655.

Bartumeus, F., 2007. Lévy processes in animal movement: an evolutionary hypothesis. Fractals 15, 1–12.

Bateson, M., Kacelnik, A., 1995. Preferences for fixed and variable food sources: variability in amount and delay. J. Exp. Anal. Behav. 63, 313–329.

Bateson, M., Kacelnik, A., 1997. Starlings' preference for predictable and unpredictable delays to food. Anim. Behav. 53, 1129–1142.

Bauer, C.M., Glassman, L.W., Cyr, N.E., Romero, L.M., 2011. Effects of predictable and unpredictable food restriction on the stress response in molting and non-molting European starlings (*Sturnus vulgaris*). Comp. Biochem. Physiol. A 160, 390–399.

Beckmann, J.S., Marusish, J.A., Gipson, C.D., Bardo, M.T., 2011. Novelty seeking, incentive salience and acquisition of cocaine administration in the rat. Behav. Brain Res. 216, 159–165.

Berridge, K.C., Robinson, T.E., 1998. What is the role of dopamine in reward: hedonic impact, reward learning, or incentive salience? Brain Res. Rev. 28, 309–369.

Berridge, K.C., 2007. The debate over dopamine's role in reward: the case for incentive salience. Psychopharmacology (Berl.) 191, 391–431.

Boakes, R.A., 1977. Performance on learning to associate a stimulus with positive reinforcement. In: Davis, H., Hurvitz, H.M.B. (Eds.), Operant Pavlovian Interactions. Erlbaum Associates, Hillsdale, NJ, pp. 67–97.

Bodor, J.N., Rice, J.C., Farley, T.A., Swalm, C.M., Rose, D., 2010. The association between obesity and urban food environments. J. Urban Health 87, 771–781.

Breuner, C.W., 1998. The Avian Stress Response: Corticosterone and Behaviour in a Wild, Seasonal Vertebrate. Ph.D. Thesis. University of Washington.

Brodin, A., 2001. Mass-dependent predation and metabolic expenditure in wintering birds: is there a trade-off between different forms of predation? Anim. Behav. 62, 993–999.

Brodin, A., 2007. Theoretical models of adaptive energy management in small wintering birds. Phil. Trans. R. Soc. B 362, 1857–1871.

Cabanac, M., Swiergiel, A.H., 1989. Rats eating and hoarding as a function of body weight and cost of foraging. Am. J. Physiol. Regul. Integr. Comp. Physiol. 26, R952–R957.

Cabanac, M., 1992. Pleasure: the common currency. J. Theor. Biol. 155, 173–200.

Cicerone, R.A., 1976. Preference for mixed versus constant delay of reinforcement. J. Exp. Anal. Behav. 25, 257–261.

Clayton, N.S., Dickinson, A., 1999. Motivational control of food storing in the scrub jay *Aphelocoma coerulescens*. Anim. Behav. 57, 435–444.

Collins, L., Young, D.B., Davies, K., Pearce, J.M., 1983. The influence of partial reinforcement on serial autoshaping with pigeons. Q. J. Exp. Psychol. 35B, 275–290.

Cornelius, E.A., Vezina, F., Regimbald, L., Hallot, F., Petit, M., Love, O.P., Karasov, W.H., 2017. Chickadees faced with unpredictable food increase fat reserves but certain components of their immune function decline. Physiol. Biochem. Zool. 90, 190–200.

Cresswell, W., 1998. Diurnal and seasonal mass variation in blackbirds *Turdus merula*: consequences for mass-dependent predation risk. J. Anim. Ecol. 67, 78–90.

Cresswell, W., 2003. Testing the mass-dependent predation hypothesis: in European blackbirds poor foragers have higher overwinter body reserves. Anim. Behav. 65, 1035–1044.

Cuthill, I.C., Hunt, S., Cleary, C., Clark, C., 1997. Colour bands, dominance, and body mass regulation in male zebra finches (*Taeniopygia guttata*). Proc. R. Soc. Lond. B 264, 1093–1099.

Cuthill, I.C., Maddocks, S.A., Weall, C.V., Jones, E.K.M., 2000. Body mass regulation in response to changes in feeding predictability and overnight energy expenditure.

Behav. Ecol. 11, 189–195.

Daunt, F., Afanasyev, V., Silk, J.R.D., Wanless, S., 2006. Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. Behav. Ecol. Sociobiol. 59, 381–388.

Day, J.J., Jones, J.L., Wigthman, R.M., Carelli, R.M., 2010. Phasic nucleus accumbens dopamine release encodes effort- and delay-related costs. Biol. Psychiatry 68, 306–309.

DeAngelis, D.L., Grimm, V., 2014. Individual-based models in ecology after four decades. F1000 Prime Rep. 6, 39.

Dickson, P.E., McNaughton, K.A., Hou, L., Anderson, L.C., Long, K.H., Chesler, E.J., 2015. Sex and strain influence attribution to incentive salience to reward cues in mice. Behav. Brain Res. 292, 305–315.

Dolnik, W.R., 1967. Bioenergetische anpassungen der vogel an die uberwinterung in verschledenen Breiten. Der Falke 14, 305–306.

Ekman, J.B., Hake, M.K., 1990. Monitoring starvation risk: adjustments of body reserves in greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. Behav. Ecol. 1, 62–67.

Esposito, S., Incerti, G., Giannino, F., Russo, D., Mazzoleni, S., 2010. Integrated modelling of foraging behaviour, energy budget and memory properties. Ecol. Model. 221, 1283–1291.

Estle, S.J., Green, L., Myerson, J., Holt, D.D., 2006. Differential effects of amounts on temporal and probability discounting of gains and losses. Mem. Cogn. 34, 914–928.

Feenders, G., Smulders, T.V., 2011. Magpies can use local cues to retrieve their food caches. Anim. Cogn. 14, 235–243.

Ferrari, M.C.O., Sih, A., Chivers, D.P., 2009. The paradox of risk allocation: a review and prospectus. Anim. Behav. 78, 579–585.

Ficken, M., Weise, C., Popp, J., 1990. Dominance rank and resource access in winter flocks of black-capped chickadees. Wilson Bull. 102, 623–633.

Flagel, S.B., Robinson, T.E., Clark, J.J., Clinton, S.M., Watson, S.J., Seeman, P., Phillips, P.E.M., Akil, H., 2010. An animal model of genetic vulnerability to behavioral disinhibition and responsiveness to reward-related cues: implications for addiction. Neuropsychopharmacology 35, 388–400.

Fokidis, H.B., Burin des Roziers, M., Sparr, R., Rogowski, C., Sweazea, K., Deviche, P., 2012. Unpredictable food availability induces metabolic and hormonal changes independent of food intake in a sedentary songbird. J. Exp. Biol. 215, 2920–2930.

Fransson, T., Weber, T.P., 1997. Migratory fuelling in blackcaps (*Sylvia atricapilla*) under perceived risk of predation. Behav. Ecol. Sociobiol. 41, 75–80.

Gibbon, J., Church, R.M., Fairhurst, S., Kacelnik, A., 1988. Scalar expectancy theory and choice between delayed rewards. Psychol. Rev. 95, 102–114.

Glimcher, P.W., 2011. Understanding dopamine and reinforcement learning: the dopamine reward prediction error hypothesis. Proc. Natl. Acad. Sci. 108, 15647–15654.

Gosler, A.G., Greenwood, J.J.D., Perrins, C., 1995. Predation risk and the cost of being fat. Nature 377, 621–623.

Gosler, A.G., 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major*. J. Anim. Ecol. 65, 1–17.

Gottlieb, D.A., 2004. Acquisition with partial and continuous reinforcement in pigeon autoshaping. Learn. Behav. 32, 321–334.

Greenwood, P.J., Harvey, P.H., 1978. Foraging and territory utilization of blackbirds (*Turdus merula*) and song thrushes (*Turdus philomelos*). Anim. Behav. 26, 1222–1236.

Grimm, V., Railsback, S.F., 2005. Individual-Based Modeling and Ecology. Princeton University Press, Princeton, NJ.

Ha, J.C., Lehner, P.N., Farley, S.D., 1990. Risk-prone foraging behaviour in captive grey jays, *Perisoreus canadensis*. Anim. Behav. 39, 91–96.

Haftorn, S., 1976. Variation in body weight, wing length and tail length in the great tit *Parus major*. Norw. J. Zool. 4, 241–271.

Hart, A.S., Clark, J.J., Phillips, P.E.M., 2015. Dynamic shaping of dopamine signals during probabilistic Pavlovian conditioning. Neurobiol. Learn. Mem. 117, 84–92.

Heppner, F., 1965. Sensory mechanisms and environmental clues used by the American robin in locating earthworms. Condor 67, 247–256.

Higginson, A.D., Fawcett, T.W., Trimmer, P.C., McNamara, J.M., Houston, A.I., 2012. Generalized optimal risk allocation: foraging and antipredator behavior in a fluctuating environment. Am. Nat. 180, 589–603.

Hiraldo, F., Donázar, J.A., 1990. Foraging time in the Cinereous vulture *Aegypius monachus*: seasonal and local variations and influence of weather. Bird Study 37, 128–132.

Homberger, B., Jenni, L., Duplain, J., Lanz, M., Schaub, M., 2014. Food unpredictability in early life increases survival of captive grey partridges (*Perdix perdix*) after release into the wild. Biol. Conserv. 177, 134–141.

Houston, A.I., McNamara, J.M., Hutchinson, J.M.C., 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philos. Trans. R. Soc. B 341, 375–397.

Humphries, N.E., Weimerskirch, H., Queiroz, N., Southall, E.J., Sims, D.W., 2012. Foraging success of biological Lévy flights recorded in situ. Proc. Natl. Acad. Sci. 109, 7169–7174.

Hurly, T.A., 1992. Energetic reserves of marsh tits (*Parus palustris*): food and fat storage in response to variable food supply. Behav. Ecol. 3, 181–188.

Jansson, C., Ekman, J., von Brömssen, A., 1981. Winter mortality and food supply in tits *Parus* spp. Oikos 37, 313–322.

Johnson, C.A., Giraldeau, L.-A., Grant, J.W.A., 2001. The effect of handling time on interference among house sparrows foraging at different seed densities. Behaviour 138, 597–614.

Kacelnik, A., Bateson, M., 1996. Risky theories: the effects of variance on foraging decisions. Am. Zool. 36, 402–434.

Kamil, A.C., 1983. Optimal foraging theory and the psychology of learning. Am. Zool. 23, 291–302.

Kaspari, M., 1990. Prey preparation and the determinants of handling time. Anim. Behav.

40, 118–126.

King, J.R., Farner, D.S., 1965. Studies of fat deposition in migratory birds. Ann. N. Y. Acad. Sci. 131, 422–440.

Kobayashi, S., Schultz, W., 2008. Influence of reward delays on responses of dopamine neurons. J. Neurosci. 28, 7837–7846.

Krams, I., 2000. Length of feeding day and body weight of great tits in a single- and two-predator environment. Behav. Ecol. Sociobiol. 48, 147–153.

Lahti, K., Orell, M., Rytkönen, S., Koivula, K., 1998. Time and food dependence in willow tit winter survival. Ecology 79, 2904–2916.

Laude, J.R., Stagner, J.P., Zentall, T.R., 2014. Suboptimal choice by pigeons may result from the diminishing effect of nonreinforcement. J. Exp. Psychol. Anim. Learn. Cogn. 40, 12–21.

Lea, S.E.G., 1979. Foraging and reinforcement schedules in the pigeon: optimal and non-optimal aspects of choice. Anim. Behav. 27, 875–886.

Lilliendahl, K., 1998. Yellowhammers get fatter in the presence of a predator. Anim. Behav. 55, 1335–1340.

Lima, S.L., Bednekoff, P.A., 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. Am. Nat. 153, 649–659.

Lima, S.L., 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. Oecologia 66, 60–67.

Lima, S.L., 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. Ecology 67, 377–385.

Lovette, I.J., Holmes, R.T., 1995. Foraging behavior of American redstarts in breeding and wintering habitats: implications for relative food availability. Condor 97, 782–791.

Lucas, J.R., 1994. Regulation of cache stores and body mass in Carolina chickadees (*Parus carolinensis*). Behav. Ecol. 5, 171–181.

Lundberg, P., 1985. Dominance behaviour, body weight and fat variations: and partial migration in European blackbirds *Turdus merula*. Behav. Ecol. Sociobiol. 17, 185–189.

Mónus, F., Barta, Z., 2011. Degree of synchronization of tree sparrows in flocks under different predation risk. Behaviour 148, 733–744.

MacLeod, R., Lind, J., Clark, J., Cresswell, W., 2007. Mass regulation in response to predation risk can indicate population declines. Ecol. Lett. 10, 945–955.

MacLeod, R., Clark, J., Cresswell, W., 2008. The starvation-predation risk trade-off, body mass and population status in the common starling *Sturnus vulgaris*. Ibis 150, 199–208.

Marasco, V., Boner, W., Heidinger, B., Griffiths, K., Monaghan, P., 2015. Repeated exposure to stressful conditions can have beneficial effects on survival. Exp. Gerontol. 69, 170–175.

Martins, T.L.F., Roberts, M.L., Giblin, I., Huxham, R., Evans, M.R., 2007. Speed of exploration and risk-taking behavior are linked to corticosterone titres in zebra finches. Horm. Behav. 52, 445–453.

Mazur, J.E., 1987. An adjusting procedure for studying delayed reinforcement. In: Commons, M.L., Mazur, J.E., Nevin, J.A., Rachlin, H. (Eds.), Quantitative Analyses of Behavior: V. The Effect of Delay and of Intervening Events on Reinforcement Value. Lawrence Erlbaum, New Jersey, pp. 55–73.

McNamara, J.M., Houston, A.I., 1985. Optimal foraging and learning. J. Theor. Biol. 117, 231–249.

McNamara, J.M., Houston, A.I., 1990. The value of fat reserves and the tradeoff between starvation and predation. Acta Biotheor. 38, 37–61.

McNamara, J.M., Houston, A.I., 2009. Integrating function and mechanism. Trends Ecol. Evol. 24, 670–675.

Nettle, D., Andrews, C., Bateson, M., in press. Food insecurity as a driver of obesity in humans: the insurance hypothesis. Behav. Brain Sci.

Ollason, J.G., 1980. Learning to forage–optimally? Theor. Popul. Biol. 18, 44–56.

Pearce, J.M., Hall, G., 1980. A model for Pavlovian learning: variations in the effectiveness of conditioned but not of unconditioned stimuli. Psychol. Rev. 87, 532–552.

Pearce, J.M., Kaye, H., Collins, L., 1985. A comparison of the effects of partial reinforcement schedules using a within-subject serial autoshaping procedure. Q. J. Exp. Psychol. B 37, 379–396.

Piazza, P.V., Rouge-Pont, F., Deroche, V., Maccari, S., Simon, H., Le Moal, M., 1996. Glucocorticoids have state-dependent effects on the mesencephalic dopamine transmission. Proc. Natl. Acad. Sci. 93, 8716–8720.

Piper, W.H., Wiley, R.H., 1990. The relationship between social dominance subcutaneous fat, and annual survival in wintering white-throated sparrows *(Zonotridua albicolis)*. Behav. Ecol. Sociobiol. 26, 201–208.

Polo, V., Bautista, L.M., 2002. Daily body mass regulation in dominance-structured coal tit (*Parus ater*) flocks in response to variable food access: a laboratory study. Behav. Ecol. 13, 696–704.

Polo, V., Bautista, L.M., 2006. Daily routines of body mass gain in birds: 2. An experiment with reduced food availability. Anim. Behav. 72, 517–522.

Pravosudov, V.V., Clayton, N.S., 2001. Effect of demanding foraging conditions on cache retrieval accuracy in food-caching mountain cheekadees (*Poecile gambeli*). Proc. R. Soc. Lond. B 268, 363–368.

Pravosudov, V.V., Grubb, T.C., 1997. Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. Behav. Ecol. 8, 332–339.

Pravosudov, V.V., Grubb, T.C., 1998. Management of fat reserves in tufted titmice *Baelophus bicolor* in relation to risk of predation. Anim. Behav. 56, 49–54.

Pravosudov, V.V., Lucas, J.R., 2001. A dynamic model of short-term energy management in small food caching and non-caching birds. Behav. Ecol. 12, 207–218.

Pravosudov, V.V., Smulders, T.V., 2010. Integrating ecology, psychology and neurobiology within a food-hoarding paradigm. Philos. Trans. R. Soc. B 365, 859–867.

Pravosudov, V.V., 2003. Long-term moderate elevation of corticosterone facilitates avian food-caching behavior and enhances spatial memory. Proc. R. Soc. Lond. B 270, 2599–2604.

Pravosudov, V.V., 2007. Stress hormones and the predation-starvation trade-off. In:

Stephens, D.W., Brown, J.S., Ydenberg, R.C. (Eds.), Foraging: Behavior and Ecology. University of Chicago Press, London, pp. 439–442.

Ratikainen, I.I., Wright, J., 2013. Adaptive management of body mass by Siberian Jays. Anim. Behav. 85, 427–434.

Reneerkens, J., Piersma, T., Ramenofsky, M., 2002. An experimental test of the relationship between temporal variability of feeding opportunities and baseline levels of corticosterone in a shorebird. J. Exp. Zool. 293, 81–88.

Rescorla, R.A., Wagner, A.R., 1972. A theory of Pavlovian conditioning: variations in the effectiveness of reinforcement and nonreinforcement. In: Black, A.H., Prokasy, W.F. (Eds.), Classical Conditioning II: Current Theory and Research. Appleton-Century-Crofts, New-York, pp. 64–99.

Robinson, M.J.F., Anselme, P., Fischer, A.M., Berridge, K.C., 2014. Initial uncertainty in Pavlovian reward prediction persistently elevates incentive salience and extends sign-tracking to normally unattractive cues. Behav. Brain Res. 266, 119–130.

Robinson, M.J.F., Anselme, P., Suchomel, K., Berridge, K.C., 2015. Amphetamine-induced sensitization and reward uncertainty similarly enhance the incentive salience of conditioned cues. Behav. Neurosci. 129, 502–511.

Rogers, C.M., 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? Ecology 68, 1051–1061.

Roper, T.J., 1983. Schedule-induced behavior. In: Mellgren, R.L. (Ed.), Animal Cognition and Behavior. North-Holland Publishing Company, Amsterdam, pp. 127–163.

Rougé-Pont, F., Deroche, V., Le Moal, M., Piazza, P.V., 1998. Individual differences in stress-induced dopamine release in the nucleus accumbens are influenced by corticosterone. Eur. J. Neurosci. 10, 3903–3907.

Sandi, C., Venero, C., Gauza, C., 1996. Novelty-related rapid locomotor effects of corticosterone in rats. Eur. J. Neurosci. 84, 794–800.

Schluter, D., 1982. Seed and patch selection by galapagos ground finches – relation to foraging efficiency and food-supply. Ecology 63, 1106–1120.

Shapiro, M.S., Siller, S., Kacelnik, A., 2008. Simultaneous and sequential choice as a function of reward delay and magnitude: normative, descriptive and process-based models tested in the European starling (*Sturnus vulgaris*). J. Exp. Psychol. Anim. Behav. Process. 34, 75–93.

Sherry, D.F., Mitchell, J.B., 2007. Neuroethology of foraging. In: Stephens, D.W., Brown, J.S., Ydenberg, R.C. (Eds.), Foraging: Behavior and Ecology. University of Chicago Press, London, pp. 61–102.

Shettleworth, S.J., Hampton, R.R., Westwood, R.P., 1995. Effects of season and photoperiod on food storing by black-capped chickadees, Parus atricapillus. Anim. Behav. 49, 989–998.

Sibly, R.M., Grimm, V., Martin, B.T., Johnston, A.S.J., Kulakowska, K., Topping, C.J., Calow, P., Nabe-Nielsen, J., Thorbek, P., DeAngelis, D.L., 2013. Representing the acquisition and use of energy by individuals in agent-based models of animal populations. Methods Ecol. Evol. 4, 151–161.

Sinha, R., Jastreboff, A.N., 2013. Stress as a common risk factor for obesity and addiction. Biol. Psychiatry 73, 827–835.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press, New Jersey.

Stephens, D.W., 2008. Decision ecology: foraging and the ecology of decision making. Cogn. Affect. Behav. Neurosci. 8, 475–484.

Török, J., Ludvig, E., 1988. Seasonal changes in foraging strategies of nestling blackbirds (*Turdus merula* L.). Behav. Ecol. Sociobiol. 22, 329–333.

Thomas, R.J., 2000. Strategic diel regulation of body mass in European robins. Anim. Behav. 59, 787–791.

van Balen, J.H., 1980. Population fluctuations of the great tit and feeding conditions in winter. Ardea 68, 143–164.

Verdolin, J.L., 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behav. Ecol. Sociobiol. 60, 457–464.

Wallace, M., Singer, G., 1976. Schedule induced behavior: a review of its generality, determinants and pharmacological data. Pharmacol. Biochem. Behav. 5, 483–490.

Wenzel, B.M., 1968. Olfactory prowess of the kiwi. Nature 220, 1133–1134.

Wiedenmann, R.N., Rabenold, K.N., 1987. The effects of social dominance between two subspecies of dark-eyed juncos, *Junco hyemalis*. Anim. Behav. 35, 856–864.

Wingfield, J.C., Breuner, C., Jacobs, J., 1997. Corticosterone and behavioral responses to unpredictable events. In: Harvey, S., Etches, R.J. (Eds.), Perspectives in Avian Endocrinology. J. Endocrinol. Ltd, Bristol, pp. 267–278.

Witter, M.S., Swaddle, J.P., 1995. Dominance, competition, and energetic reserves in the European starling, *Sturnus vulgaris*. Behav. Ecol. 6, 343–348.

Witter, M.S., Cuthill, I.C., Bonser, R.H.C., 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. Anim. Behav. 48, 201–222.