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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