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Can starlings use a reliable cue of future food deprivation to adaptively modify foraging and fat reserves?

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Regulation of mass in small birds is based on simultaneously minimizing starvation and predation risk, but the mechanisms birds use to assess starvation risk are still debated. While we know that birds anticipate periods of unpredictable food availability/energy expenditure (e.g. the winter and night) by increasing their fat reserves, we do not know whether this anticipation involves learning. This study investigated whether birds could learn to use a light cue that predicted a period of food unavailability, to adaptively regulate their foraging and/or body weight. Sixteen captive starlings, *Sturnus vulgaris*, were subjected to 42 days of an irregular schedule of food deprivation that involved depriving them of food for 5 h on 20 pseudorandomly chosen days. Birds were randomly allocated to two treatment groups for which a 30 min period of reduced ambient light either provided perfect information (Predictable) or no information (Unpredictable) about upcoming food deprivation. Both groups of birds increased their dawn body mass over the period of the experiment, consistent with a response to unpredictable food deprivation. However, no differences in either foraging behaviour or dawn body mass emerged between the groups, suggesting that the Predictable birds were unable to learn to use the light cue to initiate anticipatory foraging ahead of food deprivation. Furthermore, both groups immediately decreased their foraging behaviour in response to the onset of the light cue, suggesting that starlings do not have an evolved anticipatory foraging response to low light levels. Further work is needed to test alternative cues and designs before any general conclusions can be drawn regarding the flexibility of anticipatory foraging.

For many animals, carrying body fat has costs and benefits: too little fat and they starve (Ketterson & King, 1977; Stuebe & Ketterson, 1982), too much fat and they increase their likelihood of predation (Blem, 1975; Brodin, 2001; Witter & Cuthill, 1993). Theoretical models show there is an optimum level of body fat that minimizes the combined risk of starvation and predation, and that this optimum will vary depending on environmental conditions (Lima, 1986; McNamara & Houston, 1990). A key prediction from these theoretical models is that if perceived starvation risk is lower, body masses will decline to reduce predation risk. Conversely, if perceived starvation risk is higher, body masses will increase to reduce starvation risk. Corroboration of these predictions comes from multiple field and laboratory studies on passerine birds (Cuthill, Maddocks, Weall, & Jones, 2000; Hudin et al., 2016; Witter, Swaddle, & Cuthill, 1995).

There is empirical evidence that passerine birds not only adjust body masses in response to current starvation risk, but that they also strategically regulate their body fat in anticipation of future starvation risk. Well-studied examples of anticipatory regulation include fat gain prior to winter and nightfall. In winter, food availability and energy expenditure are less predictable than in other seasons, and small birds increase foraging intensity and body fat levels in autumn (King & Mewaldt, 1981; McEwan & Whitehead, 1984; Pienkowski, Lloyd, & Minton, 1979) to buffer against upcoming periods of forced fasting and/or increased energy expenditure (Blem, 1976). Similarly, overnight starvation presents a significant survival risk for many small birds and they increase foraging intensity and body fat levels immediately before dusk to mitigate this risk (Houston, McNamara, & Hutchinson, 1993; Polo & Bautista, 2006; Witter & Cuthill, 1993). Despite their rapidity, short-term changes in fat within a day can be large and comparable to fat changes in winter (Meijer, Möhring, & Trillmich, 1994). For example, in European starlings, *Sturnus vulgaris*, the amount of

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weight gained prior to dusk may represent 6–14% of their total dawn body mass, which is similar to the amount of weight gained prior to winter corresponding to 11% of autumn body mass (Cuthill et al., 2000; Meijer et al., 1994).

While we know that anticipatory regulation of body fat occurs, the mechanisms that govern it are poorly understood (Kelly, Warnock, Page, & Weathers, 2002). We do not know whether anticipatory regulation is an inflexible evolved response to reliable natural cues, or whether birds can respond to novel cues by associative learning. There is evidence that the amount of body fat deposited in anticipation of winter reflects long-term average energy demands from past winters (Biebach, 1996; Evans, 1969). Yet even with the added buffer provided by winter fattening, the actual fat reserves for many small birds only allows for a very small period of disruption to foraging by unusually severe winter storms (Carey & Dawson, 1999). For example, in starlings, the amount of additional fat carried during winter can only buffer against a single 24 h period without food (Meijer et al., 1994). Consequently, it has been suggested that any mechanism involved in anticipatory winter fattening ought to be flexible, so that fat levels can be adjusted in response to short-term fluctuations in energy requirements or food availability (Blem & Shelor, 1986). Such a mechanism could use reliable cues of upcoming food unavailability (Lima, 1986), such as weather changes that signal approaching storms. Rapid, anticipatory adjustments of foraging behaviour and body fat could then occur, much in the same manner as the daily patterns of fat changes.

We have good reason to suspect that birds may be able to make flexible short-term, anticipatory adjustments in this way. In an opportunistic study, Middleton (1982) observed American goldfinches, *Spinus tristis*, flocking to bird feeders in the hour preceding a harsh snow storm. Inclement weather can severely reduce feeding opportunities (Graber & Graber, 1979) and may cause significant mortality to bird populations (Carey & Dawson, 1999). Middleton (1982) showed that the foraging effort of the goldfinches was much greater in the hour before the storm compared to similar time periods on days without storms and that the masses of birds captured during the storm were greater than on the days preceding it. He speculated that an increased mass and a full gut would help protect the birds from starvation and the low overnight temperature. Later work has provided some experimental support for the idea that birds undergo short-term increases in body fat in response to cues of upcoming storms, such as increased rainfall (Kelly et al., 2002), reduced ambient temperature (Krams et al., 2010) and reduced barometric pressure (Breuner, Sprague, Patterson, & Woods, 2013; Metcalfe, Schmidt, Bezner, Guglielmo, & MacDougall-Shackleton, 2013). However, except for barometric pressure, it could be that the increases in body fat observed were responses to the increased energy demands imposed by the meteorological changes themselves as opposed to adjustments in anticipation of increased starvation risk. Furthermore, these studies shed no light on whether birds have acquired knowledge of cues of storms by natural selection or by individual learning.

The aims of the current study were to test experimentally the hypothesis that birds can learn to use an environmental cue to anticipate and prepare for upcoming food deprivation. We used a laboratory experiment to eliminate confounds often present in natural environments. We studied European starlings, since there is strong evidence for body mass regulation in response to laboratory manipulations of food availability and energy expenditure in this species (Bednekoff & Krebs, 1995; Cuthill et al., 2000; Witter et al., 1995). Starlings were exposed to an environment in which food was occasionally (approximately every 2 days on average) unavailable for a period of 5 h. The birds were randomly allocated to two treatment groups. In the Predictable group an environmental cue perfectly predicted the periods of food unavailability and in the Unpredictable group the same cue was completely uninformative. By only manipulating the informativeness of the cue (via its correlation with subsequent food deprivation), we were able to keep constant the frequency, duration and sequence of food deprivation to ensure that the level of environmental harshness did not differ between treatment groups (cf. Cuthill et al., 2000). The cue that we used was an instant drop in the ambient light intensity that lasted 30 min. This cue was chosen to be an ecologically plausible predictor of storms, since it is possible that birds might be more prepared to learn ecologically relevant cues (Seligman, 1970). Furthermore, the cue was chosen so as not to change the energy expenditure of the birds themselves, to allow us to study true anticipatory fattening as opposed to a direct response to increased energy expenditure. Since the birds that we used were hand-reared in the laboratory (Nettle et al., 2017) and had never been housed outside, they had no exposure to storms, and hence no opportunity prior to the current experiment to learn an association between a sudden drop in ambient light and food unavailability.

If the birds learnt to respond adaptively to the light cue during our experiment, we predicted the following: (1) increased foraging activity following the onset of the cue for the Predictable group only; (2) increased food consumption following the onset of the cue for the Predictable group only; (3) lower dawn body masses for the Predictable group relative to the Unpredictable group, reflecting the fact that only the Predictable group could restrict their adaptive weight gain to the period immediately prior to the period of food unavailability. In addition, we predicted an emergence of differences between groups over time, reflecting the time needed to learn the association between cue and food unavailability. Alternatively, if starlings have an unlearnt response to a reduction in ambient light that has evolved because low light often precedes periods of food unavailability in natural environments, we predicted the following: (1) increased foraging activity following the onset of the cue for both groups; (2) increased food consumption following the onset of the cue for both groups; (3) no difference in dawn body masses between groups. In addition, we predicted an immediate difference in foraging behaviour and food consumption for both groups following the onset of the cue, reflecting the fact that the response to the cue was not learnt. Finally, independent of whether the birds showed any learnt or unlearnt response to the cue, we predicted that all birds should show a gradual increase in dawn body mass reflecting the initial unpredictable food deprivation present in both groups.

METHODS

Ethical Note

The study adhered to ASAB/ABS guidelines for the use of animals in research. Birds were taken from the wild under Natural England permit 20121066 and the research was completed under Home Office licence PPL 70/8089, with approval of the local ethical review committee at Newcastle University. After the completion of the current experiment the birds were retained in the laboratory for further studies. At the time of writing, the birds are alive at Newcastle University.

Husbandry and Housing

Subject historical information

Experimental animals were 16 starlings, eight males and eight females, that comprised four families of four siblings. At the time of the current experiment, the birds were 3 years of age. The birds were taken from nests on day 5 posthatching and hand reared to