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Dietary wariness influences the response of foraging birds to competitors

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Foraging animals must choose between familiar prey and novel prey of uncertain profitability and potential toxicity. Owing to a healthy aversion to potentially dangerous prey, foragers show an initial transient wariness of novel food (neophobia). In addition, some individuals display a much longer period of avoidance before incorporating the novel food into their diet (termed dietary conservatism). There are two stable foraging strategies found within forager populations: (1) adventurous consumers (AC) which rapidly accept novel foods and (2) foragers showing dietary conservatism (DC). The expression of these two strategies may also vary with environmental conditions. We measured the effect of competition on the plasticity of foraging strategies when domestic chicks, *Gallus gallus domesticus*, foraged for familiar and novel coloured crumbs with or without competitor chicks. In addition we investigated the effect of prey detectability on the response of foragers to a competitor, by making the familiar food cryptic or conspicuous. AC birds responded to competition by accepting the novel prey more quickly than when foraging alone, regardless of how hard familiar food was to find. In contrast, DC birds failed to reduce their wariness in response to competition when the competitor's food choice was obscured. The foraging strategies of the birds were thus found to be plastic in their expression, but this plasticity differed between inherently AC and DC individuals. The implications of these results are discussed in relation to the foraging strategies of wild and domestic birds.

Foragers must decide whether to spend their time and energy searching for known profitable prey, or whether to risk dietary expansion to include novel prey of unknown palatability and profitability. Most animals (Barnett, 1958; Brigham & Sibley, 1999) show some degree of 'dietary wariness', causing them to hesitate before approaching and consuming unfamiliar food. Dietary wariness comprises two distinct behavioural processes, neophobia and dietary conservatism (DC). These operate over different timescales and differ in important respects. The initial transient fear of novelty, termed neophobia, was first described in rats encountering new objects (Barnett, 1958). Neophobia has since been observed in many animal groups (including birds, fish, mammals; reviews in Brigham & Sibley, 1999; Kelly & Marples, 2004; Mappes, Marples, & Endler, 2005; Marples, Kelly, & Thomas, 2005), in response not only to objects, but also to novel foods. This hesitation in approach is typically brief, lasting only a few minutes in most animals (Marples & Kelly, 1999), and is followed by investigation of the novel food or object (Coppinger, 1969). DC is a secondary, more lasting refusal to accept novel food into their diets by some (but not all) members of a population (Marples, Roper, & Harper, 1998; Thomas, Bartlett, Marples, Kelly, & Cuthill, 2004; Thomas, Marples, Cuthill, Takahashi, & Gibson, 2003). It is thus the time between first contact with the novel food (the end of neophobia) and the consumption of the novel food whenever it is encountered. The combined durations of neophobia plus DC can together be described as dietary wariness, incorporating the entire process of novel food acceptance.

DC has been demonstrated both in birds (eight species; Marples et al., 2005) and in fish (five species; Thomas et al., 2010; Richards, Thomas, Marples, Snellgrove, & Cable, 2011; Richards et al. 2014). Marples and Kelly (1999) argued that neophobia and DC are two distinct processes, not only because of the large differences in duration of the avoidance, but also because neophobia is much easier to deactivate with experience of novel prey (Marples, Quinlan, Thomas, & Kelly, 2007). In addition, DC is a much more complex behaviour, comprising several steps (Marples & Kelly,

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1999), and is not correlated with neophobia (K. McMahon, unpublished data). All populations tested in either laboratory or field experiments have shown that only some individuals express DC (Marples et al., 1998), while other members of the same foraging population are quick to sample and incorporate new food items into their diets, and are known as adventurous consumers (AC; Marples et al., 2007; Thomas et al., 2010). This stable polymorphism of two foraging strategies within the population has been shown to be a genetically mediated trait in Japanese quail, *Coturnix coturnix japonicus* (see Marples & Brakefield, 1995).

Because neophobia lasts only a few minutes in domestic chicks, *Gallus gallus domesticus*, the behavioural strategy of each individual can be identified using a relatively brief DC test (Marples & Kelly, 1999). While all individuals initially exhibit neophobia, DC individuals refuse to eat novel prey even after they have approached and handled the item (i.e. overcome their neophobia) or observed conspecifics eating it. Rather than a fear of approaching or touching the novel prey, DC is expressed as a persistent unwillingness of these individuals to broaden their diets to include the novel prey (Marples et al., 1998). It is thus possible to measure the two aspects of dietary wariness separately, with neophobia being the length of time until an individual first touches or handles a novel prey item, and DC being the remaining time before the novel prey is eaten consistently (i.e. eaten each time it is encountered; Kelly & Marples, 2004). The expansion of an individual forager's diet therefore requires both its neophobia and its DC to be overcome (Marples et al., 2005, 2007).

The fact that DC has been documented in two very divergent taxa (birds and fish), suggests that it may be a widespread foraging strategy (Marples et al., 2005; Marples & Kelly, 1999; Thomas et al., 2010). For any species with a limited food supply, DC individuals in the population may be at a foraging disadvantage if they continue to avoid novel foods, but reducing their conservatism would also expose them to greater risks. A conservative approach to dietary sampling in individuals within a generalist species would help to minimize negative or unprofitable experiences, such as consumption of toxic prey (Lee, Marples, & Speed, 2009). Therefore, despite the reduction in potential food options, conservative feeders that foraged only on familiar prey of known value would avoid the risk of injury, illness or death through dietary indiscretion. These DC individuals might maintain their fitness levels alongside AC individuals, as the AC foragers may fall victim to prey defences at a greater rate, negating some of the fitness advantages conferred by a larger menu (Thomas et al., 2010). In addition, it is possible that DC foragers become more skilled at finding and handling their few favoured prey types, while AC foragers, with their wider diet, are likely to be less skilled at detection and handling of their many types of prey (Sherry & McDade, 1982). Investigating such choices in foraging strategies is crucial to understand the ecology and evolution both of foraging species and of their prey.

Despite the relevance of understanding the foraging strategies of individuals, limited attention has been given to the plasticity of expression of these strategies under differing foraging conditions. It might be expected that individual experience and ecological circumstances may modify the expression of the underlying genetic propensity of an individual to be AC or DC. Indeed, there is evidence that the expression of AC or DC in individuals can be modified by experience. For example, Marples et al. (2007) showed that the expression of DC can be reduced in domestic chicks through extensive experience with benign novel foods, although full reversion to DC will occur after only one experience with an unpalatable food. Further evidence (Barnett, 2007; Sherratt, 2002; Skelhorn & Rowe, 2006a, 2006b) suggests that increased hunger levels may temporarily decrease DC expression towards aposematic prey. To understand the degree of plasticity in DC expression, we aimed in this study to evaluate the effects of conspecific competition as an external factor affecting the costs and benefits of different foraging strategies.

Birds foraging in a flock are likely to compete with other flock members for food, through both interference and exploitation competition (Sih, 1993) which together reduce the amount of time that an individual can spend making foraging decisions. Optimal foraging theory would predict individuals experiencing high levels of competition would broaden their diets to include less valuable or possibly less familiar foods, so as to avoid starvation (Stephens & Krebs, 1986). Additionally, social learning may further encourage broadening of the diet to incorporate unfamiliar prey on which conspecifics are observed to feed (Fryday & Greig-Smith, 1994). The combination of competition and social learning may therefore favour a relaxation of DC expression, but it is also possible that birds may ignore conspecific foraging behaviours and remain inflexible in their level of DC (cf. Richards et al., 2011).

We used generalist foragers, domestic chicks, to test the hypothesis that DC expression is reduced when a forager is in competition with a conspecific that readily eats novel coloured food. A further experiment then evaluated DC expression in the same system, but in relation to the relative conspicuousness of novel and familiar foods. We hypothesized that when familiar food is relatively cryptic, increased search and attention costs will encourage foragers to reduce their expression of DC, and sample the more conspicuous novel prey (Jones, Krebs, & Whittingham, 2006). This study is the first to explore the degree of plasticity of AC and DC foraging strategies by birds in a complex foraging environment.

METHODS

Outline of Experiments

To classify individual chicks as DC or AC, before each experiment we first tested each chick for its baseline level of DC using a 'DC test'. We carried out three experiments to investigate: (1) the effects of testing for DC on the subsequent behaviour of the chicks; (2) the effects of a competitor on the expression of DC when the novel and familiar foods were equally conspicuous; and (3) the effects of a competitor on the expression of DC when the novel prey was more conspicuousness than the familiar prey.

Chick Husbandry

We carried out the three experiments using three separate batches of male 'Cobb 500' strain chicks, which were obtained at 1 day old from a commercial hatchery (Annyalla Chicks Ltd., Castlebury, Co. Monaghan, Ireland). The experiments were approved by the ethics committee of Trinity College Dublin, and the chicks were held under licence from the Department of Health and Children, Ireland number B100/2756 held by N. Marples. Batch 1 (used for experiment 1) contained 29 chicks, batch 2 (experiment 2) contained 55 chicks and batch 3 (experiment 3) contained 63 chicks. For each batch, individuals were housed together in a wooden holding pen (200 cm long × 60 cm wide) with wood shavings covering the floor. The chicks were maintained on a 12:12 h light:dark regime, under standard fluorescent lights in addition to natural lighting. Ambient temperature was 24 ± 4 °C, but chicks could find warmer areas by standing under two infrared heat lamps suspended above their holding pen. From their arrival at the laboratory, the chicks were fed chick starter crumbs (William Connolly & Sons, Red Mills, Goresbridge, Co. Kilkenny, Ireland), dyed green (O'Brien's liquid green 90; 1 ml dye: 30 ml water), which resulted in their subsequent treatment of this colour as familiar. Food and water were available ad libitum for the duration of the study, except