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Older and wiser? Age differences in foraging and learning by an endangered passerine

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ABSTRACT

Birds use cues when foraging to help relocate food resources, but natural environments provide many potential cues and choosing which to use may depend on previous experience. Young animals have less experience of their environment compared to adults, so may be slower to learn cues or may need to sample the environment more. Whether age influences cue use and learning has, however, received little experimental testing in wild animals. Here we investigate effects of age in a wild population of hihi (*Notiomystis cincta*), a threatened New Zealand passerine. We manipulated bird feeders using a novel colour cue to indicate a food reward; once hihi learned its location, we rotated the feeder to determine whether the birds followed the colour or returned to the previous location. Both age groups made fewer errors over trials and learned the location of the food reward, but juveniles continued to sample unrewarding locations more than adults. Following a second rotation, more adults preferred to forage from the hole indicated by the colour cue than juveniles, despite this no longer being rewarding. Overall, juveniles spent longer in the feeder arena to reach the same proportion of foraging time as adults. Combined, these results suggest that juveniles and adults may use an “explore and exploit” foraging strategy differently, and this affects how efficiently they forage. Further work is needed to understand how juveniles may compensate for their inexperience in learning and foraging strategies.

1. Introduction

It is well-established that animals can learn to associate cues with food resources (Boogert et al., 2010; Brodbeck, 1994; Hurly and Healy, 2002; Kamil and Roitblat, 1985), but natural environments provide many potential cues, and not all remain informative across time or space. Therefore, animals should use information from previous experiences to update foraging choices (Dall et al., 2005; Herborn et al., 2011; Thornton and Lukas, 2012). Younger individuals, however, have had fewer opportunities to gain experience (Galef and Laland, 2005). Consequently, this could affect how long it takes young animals to learn foraging behaviours compared to more experienced adults, and reduce their survival when there is competition for limited food resources (Sullivan, 1989; Whitfield et al., 2014). Impacts on juvenile survival may be especially critical in threatened species, where there are already a reduced number of juveniles contributing to population viability (Melbourne and Hastings, 2008). Despite the body of research exploring how juveniles learn (Benson-Amram and Holekamp, 2012; Vince, 1958; Weed et al., 2008), there are scant examples in species of conservation concern where understanding juvenile behaviour may inform conservation strategies (Buchholz, 2007; Sutherland, 1998).

Although juveniles can be more persistent at learning tasks compared to adults (Benson-Amram and Holekamp, 2012; Manrique and Call, 2015; Vince, 1958), and so more likely to innovate (Morand-Ferron et al., 2011; Reader and Laland, 2001), they are often less able to use the most appropriate learned cues across variable contexts (Thornton and Lukas, 2012; Weed et al., 2008; but see Bonté et al., 2014). This could lead to less efficient foraging; for example, if juveniles continue to sample more food sites to acquire information then they may return to non-rewarding sites more often (Naef-Daenzer, 2000; Wunderle and Lodge, 1988), rather than applying what they have already learned and forage optimally (Krebs et al., 1978). However, disentangling what drives differences in learning between adults and juveniles can be challenging if age classes also differ in body size or diet (Marchetti and Price, 1989). For example, juvenile meerkats were less likely to solve a puzzle box task than adults, but this was attributed to them lacking the physical capability of adults rather than a learning effect (Thornton and Samson, 2012). Passerine birds provide an opportunity to test age differences without these potential confounds as juveniles reach adult body size relatively quickly and by independence

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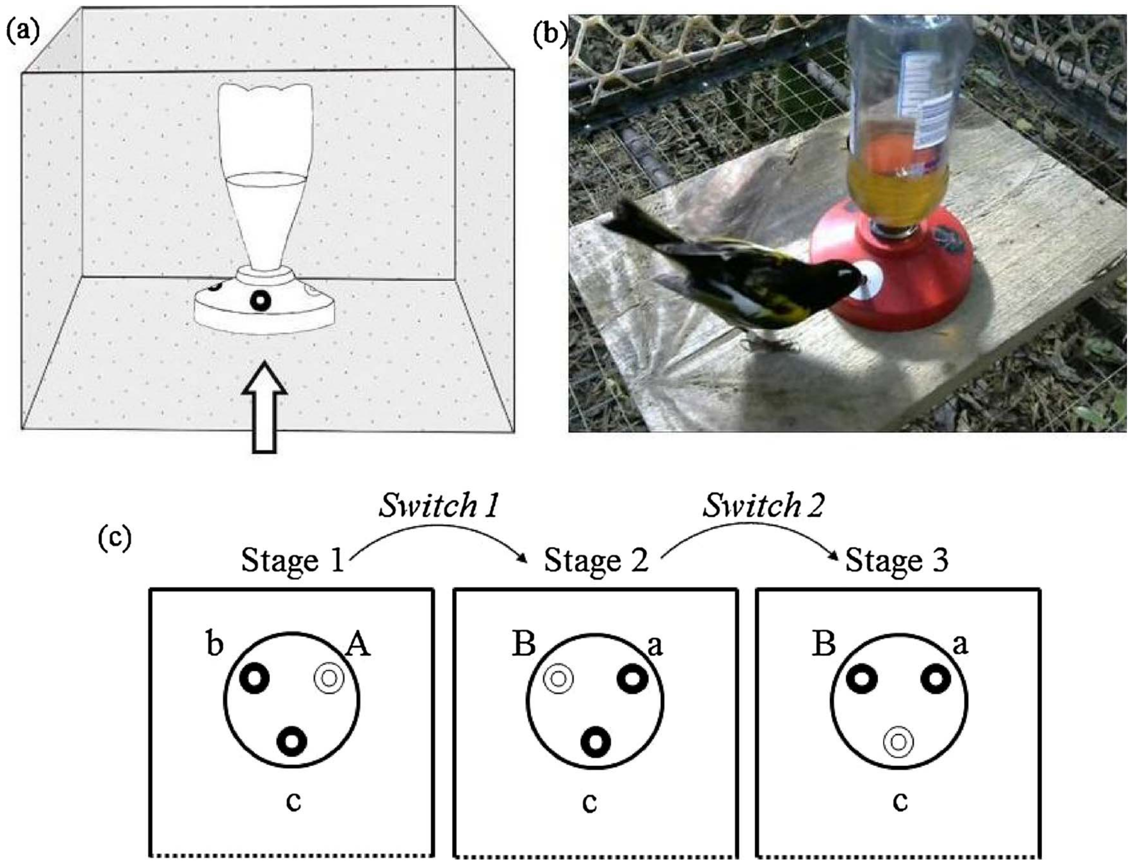

Fig. 1. The novel feeder bottle learning task. (a) Diagram of the feeder arena and feeder bottle (white arrows show the side through which hihi could enter); (b) the feeder arena in situ, with an adult male hihi feeding from the reward hole after entering from top left of picture; (c) the three stages of the experiment. Within the arena (square), the feeder bottle (large circle) shows colour markers (black, white), reward hole position (uppercase letter label), and non-rewarding holes (lowercase letter). Dashed line indicates side from which hihi could enter the arena.

from parents (Case, 1978).

Despite being similar to adults in body size, juveniles of many bird species do not forage as effectively as adults (Ashmole and Tovar, 1968; Gochfeld and Burger, 1984; Schuppli et al., 2012). In the wild these conclusions are largely based on field observations (Desrochers, 1992; Heinsohn, 1991; Marchetti and Price, 1989), and the few direct comparisons of adults' and juveniles' learning using experimental tests have found variable results across different species and tasks. For example, juvenile Australian magpies (*Cracticus tibicen dorsalis*) were less likely to solve a learning task than adults (Mirville et al., 2016), but in North Island robins (*Petroica australis*), there were no age differences in how long it took individuals to reach a learning criterion in two different tasks (Shaw, 2017). Therefore, more data is needed to assess differences in learning between juveniles and adults in a wild setting and to understand how birds apply information when environments change.

Here, we examined age differences in learning by a wild bird species of conservation concern. We presented a novel foraging task to wild adult and juvenile hihi (stitchbird, *Notiomystis cincta*), a nectarivorous passerine bird endemic to New Zealand, to investigate if juveniles learn differently from adults. We designed a food-cue learning task by manipulating hummingbird-style nectar feeders to track individual learning patterns. Birds learned the location of feeding holes that allowed access to sugar water, and holes were marked by a visual cue. We then moved the position and/or changed the cue to investigate how hihi learn to rely on cues to find food. Studying food-cue learning in hihi has particular relevance for this threatened species (listed as Vulnerable, Birdlife International, 2013), as conservation efforts rely on supplementary feeding (Chauvenet et al., 2012). Furthermore, seeding new populations of hihi involves translocation of juveniles to new sites (Thorogood et al., 2013), so understanding how they acquire information about food may be key for optimal design of feeding protocols. Learning about food, however, has not been investigated in hihi before.

We predicted that: (i) hihi would learn to find the rewarding hole and be more likely to visit it first as trials progressed. Over time, birds would also reduce the proportion of non-rewarding holes they visited but (ii) juveniles would be slower to learn and continue sampling for longer (shown by continuing to visit more holes). After cues changed, we also predicted that (iii) adults would be more likely to follow the visual cue than juveniles to relocate the reward hole more quickly.

2. Methods

2.1. Study population

We carried out this study in the population of hihi at Zealandia Ecosanctuary in Wellington, New Zealand (41°17′24.2″S, 174°45′13.2″E). Hihi were reintroduced here in 2005, with a breeding population of c.100 birds at the time of our study in May 2015. Juveniles were moulting into adult plumage during our study (male and female hihi are sexually dimorphic). As part of the management of hihi at Zealandia, each bird is identifiable by a unique combination of coloured leg rings, with one colour indicating its hatch year. We could thus track the learning of individual hihi and distinguish juveniles (from the 2014–2015 breeding season).

2.2. Experimental design

We conducted the experiment at one of the four permanent supplementary feeding sites that provide sugar water year-round. We chose