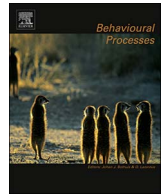




Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

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



Victoria R. Franks^{a,b,*}, Rose Thorogood^{a,c}

^a University of Cambridge, Cambridge CB2 3EJ, UK

^b Institute of Zoology, Zoological Society of London, London NW1 4RY, UK

^c Department of Biosciences, University of Helsinki, Helsinki 00014, Finland

ARTICLE INFO

Keywords:

Foraging
Cue use
Juvenile
Hihi
Learning
Cognition

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

* Corresponding author at: Department of Zoology, University of Cambridge, 20 Downing St, Cambridge CB2 3DT, UK.
E-mail address: vrf22@cam.ac.uk (V.R. Franks).

<https://doi.org/10.1016/j.beproc.2017.12.009>

Received 14 August 2017; Received in revised form 14 December 2017; Accepted 14 December 2017

Available online 19 December 2017

0376-6357/ © 2017 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

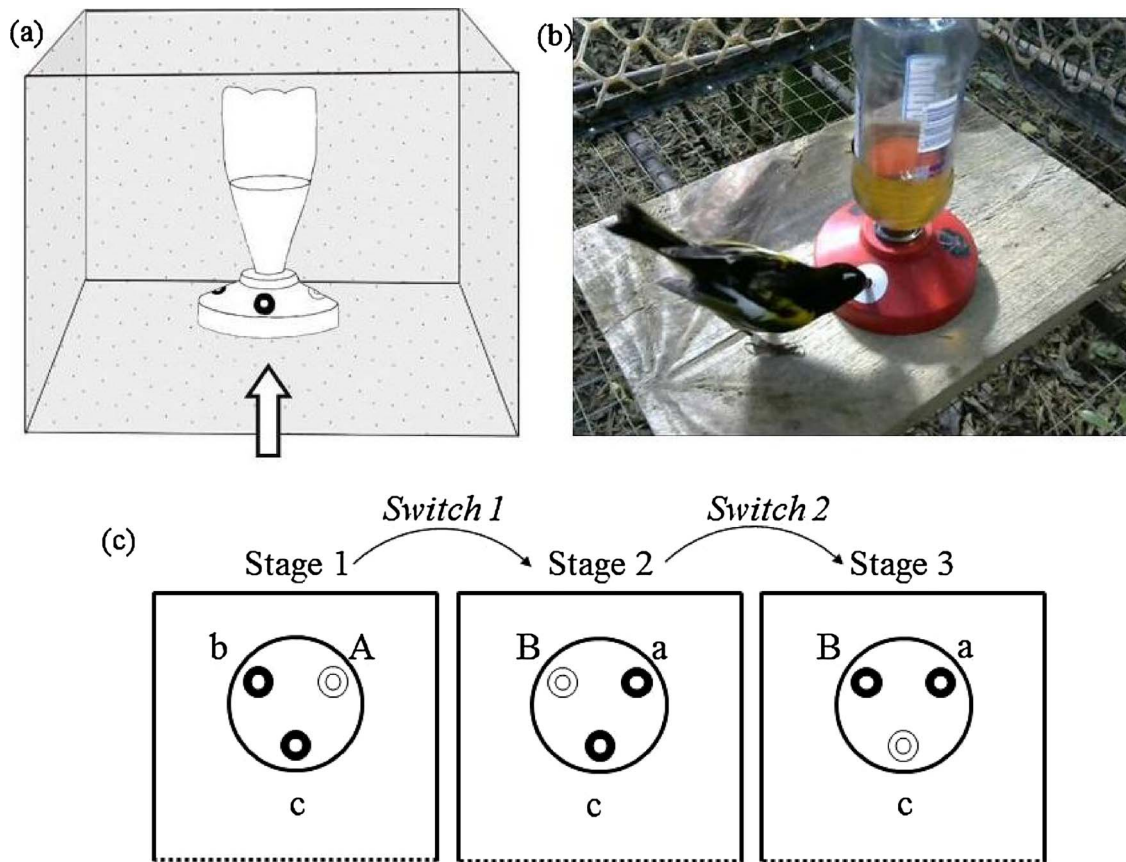


Fig. 1. The novel feeder bottle learning task. (a) Diagram of the feeder arena and feeder bottle (white arrows show the side through which hihi could enter); (b) the feeder arena in situ, with an adult male hihi feeding from the reward hole after entering from top left of picture; (c) the three stages 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

this site because it was used by the majority of the population ($N = 78$ birds). Food is normally provided in a square, steel-framed cage (0.5m^2) that allows entrance of hihi (and similarly sized bellbirds, *Anthornis melanura*), but not larger competitors. For our experiment, we modified the cage to make entry to the feeder arena possible through one side only. This prevented confusion over spatial cues as individuals always approached the feeder bottle from the same direction (Fig. 1). Every hihi that visited the feeder located and used this restricted entry point. Although the cage was not novel to the birds, the feeder bottle was. Sugar water is normally provided in a clear plastic covered dish with a feeding trough. Instead, we used a 400 ml clear plastic bottle attached to a Perky Pet® feeder base (213 Pop Bottle Hummingbird Feeder, c.15 cm base diameter and c.5 cm between holes) that normally allows access to sugar water from three feeding holes. For the purposes of the experiment, we blocked two of the holes with clear tape to prevent access to the sugar water in the reservoir below. During the experiment we observed hihi attempting to feed from these holes, showing they were a suitable deception. The third hole remained open and allowed access to the sugar water (“reward hole”).

We conducted our experiment in three stages where we changed either the position or marking of the rewarding hole (indicated in the text by a capital letter, Fig. 1c):

- (1) Hole A was rewarding and marked with a white circle. Holes b and c were non-rewarding and marked with black circles. We used black and white as they are achromatic and avoided any existing preferences or biases towards colours. Stage 1 continued until the number of completely new individuals arriving at the feeder arena per day declined below five (to include as much of the population as possible during the entire experiment), and the majority of birds attempted the reward hole first in each of three successive trials (learning criterion set *a priori*). This took five days.
- (2) Hole B was rewarding and marked with a white circle, while holes a and c were non-rewarding and marked with black circles. Thus, in this stage the colour cue indicated the rewarding hole as it did in Stage 1, but the hole was in a different location. This meant we could test if hihi had learned to associate the visual cue with the food reward, or continued to attempt the previously rewarded location. Stage 2 ended after five days so it was consistent with Stage 1.
- (3) Here we switched the colour cue but not the spatial location of the reward, so hole B was still rewarding (as in Stage 2), but it was now marked with a black circle. We marked a non-rewarding hole (hole c) with the white circle. If hihi associated the visual cue with a food reward, they should be more likely to follow the white circle and attempt the non-rewarding hole c. This was a control to exclude the possibility that hihi were simply detecting the open hole, rather than following the colour cue. We could also determine if hihi switched cue use between Stage 2 and Stage 3. This stage was run for 3 days because here we were interested in capturing the first return of previously recorded hihi, and not any further learning.

During all stages, we presented the feeder bottle for 3 h (1000–1300 h) per day. We collected data using field observations (by VF, from the same position c. 8 m from the feeder) and video recordings from a webcam (Logitech® C270 HD) situated in the upper right corner at the back of the cage. For each bird’s visit to the arena (“trial”), we recorded entry time (recorded when a bird had half of its body through the mesh on the entry side of the feeder), individual identity, age (adult or juvenile), sex, which holes the bird attempted to feed from, and time spent feeding at the reward hole. A feeding hole attempt was recorded if a hihi placed its beak at a hole entrance (Fig. 1b), or if a hihi paused next to a hole (approximately one second) and turned or cocked its head towards it. Feeding at the reward hole stopped when a bird moved away from the hole at least as far as its own body length.

The presence of conspecifics during the experiment was recorded to

account for social influences on hole choice (e.g. via local enhancement (Laland, 2004), or competition (Harper, 1982)). If no hihi was present in the feeder arena for at least 30 s before the focal bird, these trials were “alone” (based on Aplin et al., 2012, and personal observations of hihi by VF prior to this experiment). “Semi-social” trials were when other hihi were present in the feeder arena less than 30 s before the focal bird. Finally, “social” trials were where another hihi was present in the feeder arena at the same time as the focal bird. There was no bias in distribution of social category between the two age classes (Chi-square test: $\chi^2 = 2.81$, $P = 0.25$).

2.3. Data analysis

All data were analysed using R (version 3.3.1) (R Development Core Team, 2016).

2.3.1. Learning to locate the reward

From each trial we recorded (i) whether the reward hole was attempted first, (ii) the total number of holes attempted and (iii) the number of times an unrewarding hole was attempted. This allowed us to measure learning (if hihi became more likely to visit the rewarding hole first over trials), assess sampling behaviour (how many extra holes they visited over trials), and compare learning patterns before and after birds experienced a switch of reward location. For each bird we included the first 14 trials from Stage 1 and the first 8 trials from Stage 2 as fewer than three birds (per age group) came to the feeder arena more times than this (number of trials ranged from 1 to 44, no significant difference in number of trials made by adults and juveniles: Wilcoxon rank sum test, $W = 788$, $P = 0.78$).

Some individuals did not arrive during Stage 1 so their first opportunity to learn occurred during Stage 2 (Stage 1: $N = 59$; Stage 2: $N = 12$). Therefore, we labelled all trials within one stage as a learning sequence (LS) to account for changes in setup or environmental conditions. However, in both stages the reward hole was equidistant from the entry side, both times it was marked with a white circle, and overall there was no difference in which hole was first attempted in the first trial whether LS1 occurred during Stage 1 or 2 (Fisher’s exact test: adults: $N = 34$, $P = 0.67$; juveniles: $N = 23$, $P = 0.51$).

We used Generalised Linear Mixed Effects Models (GLMM), implemented with the lme4 package (Bates et al., 2015, version 1.1-7) and error distributions appropriate for the data. The probability of attempting the reward hole first (an indication of learning) was analysed as a binary response variable (“yes” = 1, “no” = 0) with a binomial error distribution. Sampling behaviour (an indication of accuracy) was analysed using a Poisson error distribution for the number of holes attempted, and a binomial error distribution to analyse the proportion of attempts that were to non-rewarding holes. All models were checked for over-dispersion but no correction was needed (Hector, 2015).

For all analyses we used a model selection approach (Symonds and Moussalli, 2011) using the AICcmodavg package (Mazerolle, 2016, version 2.0-3) where candidate models included all possible combinations of trial number as a linear term (to indicate learning), age (adult or juvenile), learning sequence (LS1, LS2), and social category (social, semi-social or alone). We included interactions between trial number and age, trial number and learning sequence, and learning sequence and age, to assess if learning rates differed between age groups and between stages after hihi had experienced a change in reward hole cues. When averaging across models, those including interactions were treated separately to avoid over-estimating their effect (Mazerolle, 2016). Trial number was included as a random slope and individual identity as a random intercept in all models to account for repeated measures of the same individuals, as birds could have multiple trials. This also accounted for differences in individual learning rate. Models were ranked according to their corrected Akaike Information Criterion (AICc) with the number of individuals used as the sample size. Effect sizes ($\pm 95\%$ confidence intervals) were averaged from all models

within 2 AICc units of the top-ranked model and used to assess the magnitude of each predictor variable's effect (Nakagawa and Cuthill, 2007; Symonds and Moussalli, 2011).

We also tested whether there was a pre-existing preference for black or white or for hole location, to understand how this may have affected foraging. We used a binomial sign test to compare the expected random probability of visiting a black hole (0.66, two out of three available holes was marked as black) with the observed hole visited by individuals during their first ever trial in the experiment. We then used a G-test for each age class to assess whether first holes attempted were randomly distributed to each of the three possible holes.

2.3.2. Foraging duration of adult and juvenile hihi

We analysed if differences in learning could have been affected by time spent in the feeder arena, and how the proportion of time spent feeding varied with age. We used GLMMs to analyse how three different variables changed between age groups. To understand foraging efficiency and learning opportunities, we analysed (i) the time spent in the feeder arena (with a Poisson error distribution) and (ii) the proportion of time spent feeding (with a binomial distribution). For both of these response variables we included age as a predictor variable. We then analysed (iii) the length of time between visits ("inter-trial interval") to explore if feeding behaviour changed after a longer interval (i.e. hihi became less likely to remember the feeder arrangement, or had higher feeding or sampling motivation). Here, we used two further sets of GLMMs. The first modelled if the first hole hihi attempted on their return was the reward hole (yes = 1, 0 = no, binomial error distribution). The second modelled the number of non-reward holes attempted as the response variable (with a Poisson error distribution), to measure how much non-rewarding behaviour hihi made on return to the feeder arena. Both models included age and inter-trial interval as predictor variables, separately and in interaction. In all of these analyses, we included a random intercept term for individual identity to account for repeated trials by individuals. Again, all models were ranked by AICc and effect sizes were calculated from all models within 2 AICc units of the top-ranked model.

2.3.3. Cue use

We determined if hihi associated cues to locate the reward hole after each switch by comparing the distributions of the first hole attempted by each bird post-switch, to an expected random distribution of 33% in adults and juveniles. We also determined how hole use changed in the trials before and after each switch by comparing the distribution of holes attempted post-switch to the distribution of the last hole attempted prior to the switch. For both of these analyses, we used G-tests following previous analyses of cue use by Herborn et al. (2011).

3. Results

A total of 78 hihi visited the feeder arena across the duration of the experiment; this included almost all known adult males ($N = 36$, 100%), juvenile males ($N = 24$, 92%) and juvenile females ($N = 16$, 84%) recorded during that year's population census (Anderson, 2016), but only 2 adult females (from 21 known birds, adult female hihi rarely use supplementary feeders during this time (Anderson, 2016)). As our main comparison of interest was age, we therefore focussed on male hihi behaviour. Adult males ranged from 1 – 6 years old (56% were first year adults, matching the population at large (Anderson, 2016)). Overall, our sample of birds captured the majority of the population, and included a range of adult ages.

3.1. Learning to locate the reward

Hihi showed evidence of learning as they became more likely to go to the rewarding hole first as trials progressed (trial number effect: 0.48 ± 0.11 , 95% CI = 0.27–0.70, Fig. 2a; models excluding trial

number had very little support: $\Delta\text{AICc} \geq 36.24$, Supplementary Table S1a) but juveniles always performed more poorly than adults (age effect: -0.70 ± 0.30 , 95% CI = $-1.30 - -0.11$). After the fourth trial, only three adults (8.3%) visited a non-rewarding hole first, while 14 juveniles (58.3%) continued to consistently make this error. However, looking only at the first hole attempted during each bird's first trial, adults showed a preference for the white hole (chance of choosing white hole higher than random, $N = 34$, $P = 0.005$), while juveniles showed no bias ($N = 23$, $p = 0.51$). There was no bias towards hole location in adults or juveniles (adults: $N = 34$, $G = 3.64$, $P = 0.16$; juveniles: $N = 21$, $P = 0.10$). To assess whether this influenced differences in learning, we modelled effects of the colour of the first hole attempted on our measures of learning but found little evidence that the learning task was not equivalent for age classes across the rest of the experiment (included for comparison in Supplementary Table S1, as "colour of first hole attempted").

We next focussed on the number of holes hihi attempted as a measure of continued sampling, as both a total number of holes and the proportion of holes visited that were non-rewarding (Fig. 2b,c; Supplementary Table S1). Hihi sampled fewer holes in total across trials, showing an increasing preference for visiting only the reward hole (trial number effect = -0.05 ± 0.01 , 95% CI = $-0.07-0.03$, Fig. 2b). Despite age being included in two of the top-ranked models, overall there was little difference in the number of holes adults and juveniles sampled (age effect = 0.13 ± 0.08 , 95% CI = $-0.03-0.29$; Fig. 2b). However, when sampling, juveniles were more likely to attempt non-rewarding holes compared to adults (age effect = 0.62 ± 0.21 , 95% CI = $0.21-1.04$, Fig. 2c). This difference was not because juveniles were less likely to locate the reward hole on their first attempt, as the total number of holes attempted did not differ between age classes (see above). Taken together, these results show that hihi learned to locate the reward, although juveniles remained poorer at this than adults (Fig. 2a). Hihi also became more likely to attempt only the rewarding hole over time, but juveniles continued to sample proportionally more non-rewarding holes (Fig. 2b, c).

We expected hihi that visited in both stages would become more familiar with the feeder arena. However there was negligible effect of learning sequence on any response variable (Supplementary Table S1). While it was not included in models with $\Delta\text{AICc} < 2$ for first hole visited (Supplementary Table S1a), learning sequence was included in the top model sets for total number of holes visited (Supplementary Table S1b), and proportion of non-rewarding holes (Supplementary Table S1c). Nevertheless, it showed no effect when models were averaged (total holes: age*learning sequence effect = -0.22 ± 0.17 , 95% CI = $-0.56-0.11$; learning sequence effect = -0.11 ± 0.08 , 95% CI = $-0.26-0.05$; proportion non-rewarding holes: trial number*learning sequence effect = -0.17 ± 0.1 , 95% CI = $-0.36-0.02$). Finally, social category had no effect (Supplementary Table S1).

3.2. Foraging duration of adult and juvenile hihi

Both juvenile and adult hihi spent the same proportion of time feeding at the reward hole while in the feeder arena: the null model analysing proportion of time spent feeding was ranked higher than one containing age as a parameter (effect of age on feeding proportion = -0.42 ± 0.36 , 95% CI = $-1.14-0.29$; Fig. 3a; Supplementary Table S2). However, juveniles spent longer in the feeding arena overall compared to adults (effect of age on time in feeding arena = 0.34 ± 0.14 , 95% CI = $0.06-0.62$, Fig. 3b; Supplementary Table S2). This suggested that, although juveniles had more opportunity to learn about the feeding task, they still had poorer foraging efficiency and needed to compensate by foraging for longer. Regardless of age, hihi were less likely to visit the reward hole first if they had been away for a longer inter-trial interval, and sampled more non-rewarding holes (effect of absence time on likelihood of visiting reward hole first = -0.36 ± 0.08 , 95% CI = $-0.51-0.20$, Supplementary Table S3a; effect of

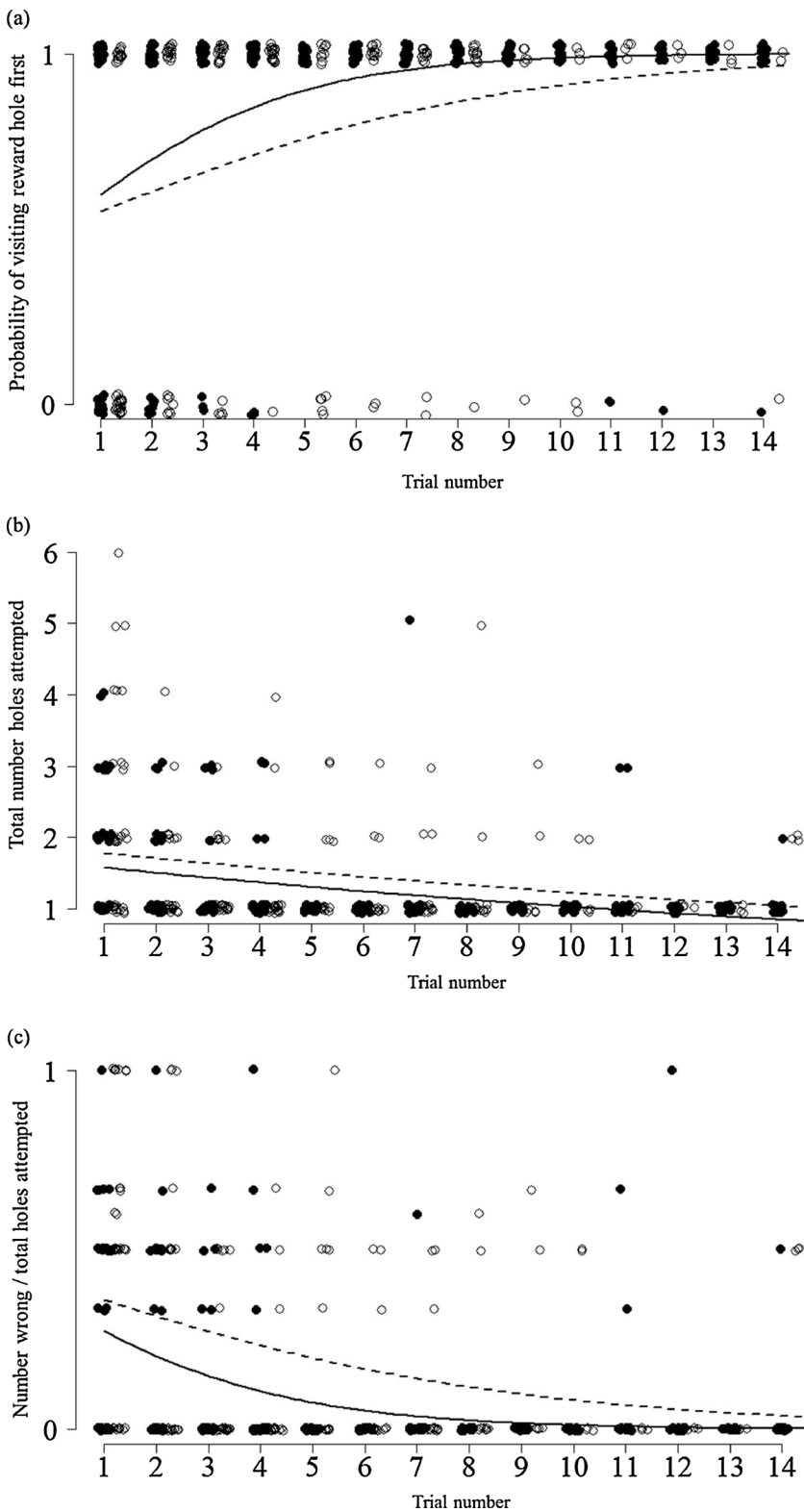


Fig. 2. Feeder holes attempted by adult (closed circles, solid line) and juvenile (open circles, dotted line) hihi over trials at the arena ($N = 60$ individuals). (a) Probability that the rewarding hole was chosen first, (b) total number of holes attempted during each trial, and (c) proportion of holes attempted that were non-rewarding. All points are jittered (by 0.3 on the x-axes, 0.1 on the y-axis) to improve visibility, and lines of best fit come from the relevant top-ranked models (see Supplementary Table S1).

absence time on number of non-rewarding holes = 0.39 ± 0.06 , 95% CI = 0.27–0.51, Supplementary Table S3b). Although juveniles spent longer away on average than adults (effect of age on inter-trial interval = 0.81 ± 0.36 , 95% CI = 0.10–0.52, Supplementary Table S3c), juveniles that were absent the longest actually sampled from fewer non-rewarding holes in total than adults (effect of inter-trial interval*age on number of wrong holes sampled: -0.26 ± 0.08 , 95% CI = $-0.41 - -0.11$, Fig. 3c, Supplementary Table S3b). Therefore,

these results suggest the differences in juvenile and adult learning preferences were not only an effect of juveniles having less opportunity to learn or more time to forget.

3.3. Cue use by adult and juvenile hihi

After moving the location (but not the colour cue) of the reward in Switch 1 (Fig. 1c), we found some evidence that adults and juveniles

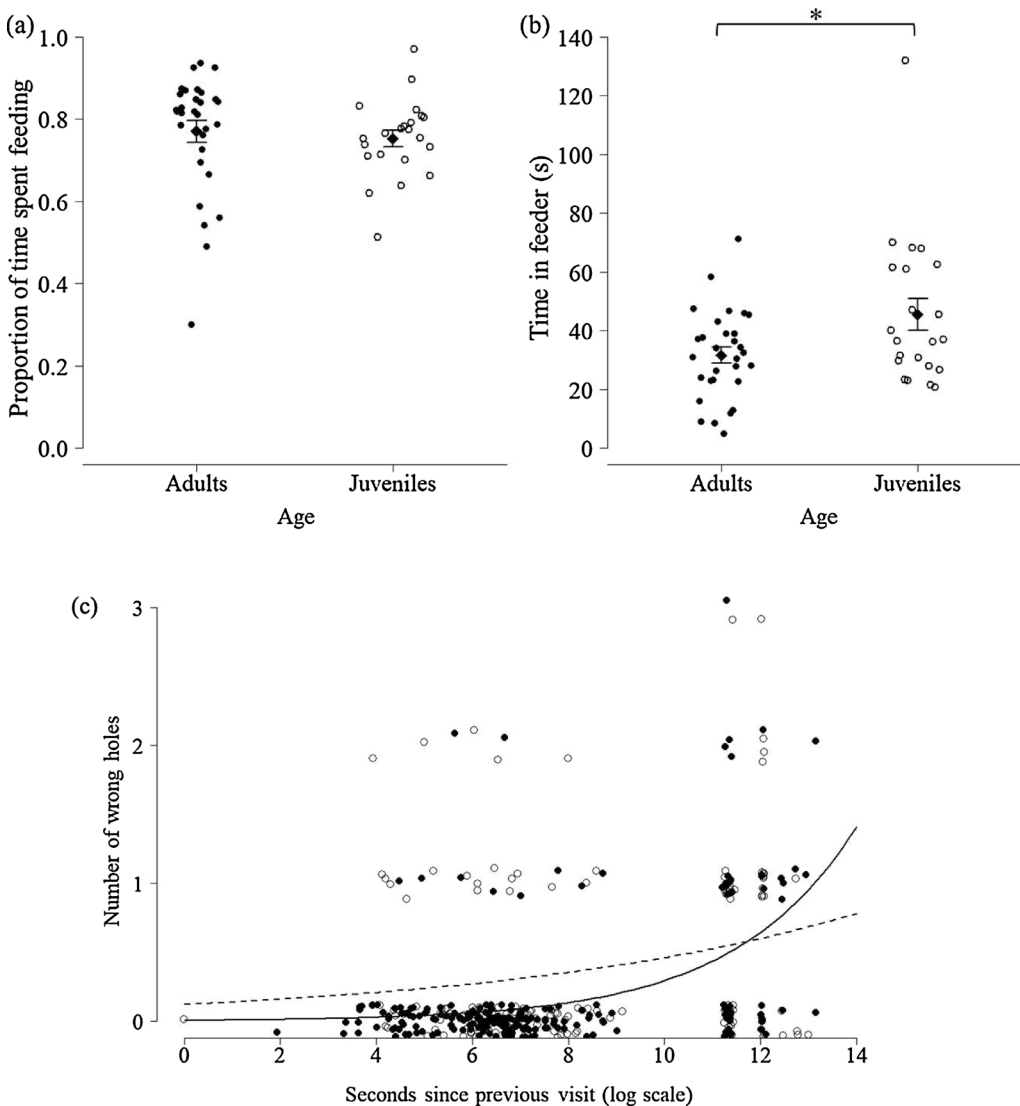


Fig. 3. Effects of time on aspects of feeding behaviour in adult and juvenile hihi ($N = 60$). (a) Proportion of time adult (closed circles) and juvenile (open circles) hihi spent feeding at the reward hole; (b) Length of time adult (closed circles) and juvenile (open circles) hihi spent in the feeder arena. Asterisk indicates that the time spent in the feeding arena was significantly different between adults and juveniles (see Results). For (a) and (b), mean and standard error indicated by closed diamonds and capped lines. Points jittered by 3 on the x-axis to improve visibility; (c) number of wrong holes attempted by adult (closed circles, solid line) and juvenile (open circles, dotted line) hihi on their return to the feeder arena, depending on the length of time since their previous visit (inter-trial interval). Points jittered by 0.2 on the y-axis to improve visibility, and lines of best fit come from the top-ranked model (Supplementary Table S3b). Please note time is plotted on a log-scale: as this experiment was conducted over days, hihi could have inter-trial intervals overnight (the gap at log-10 is due to this overnight period).

were using cues differently to locate food (Fig. 4a). Only a quarter of juveniles (5/17) followed the colour cue to feed from hole B, while the majority (10/17) continued to attempt the location that provided food in Stage 1 (pre- vs. post-switch 1 hole preference: $G = 4.48$, $P = 0.11$, Fig. 4a). Two chose hole c which had not been rewarding and was marked black. Adults, on the other hand, changed their behaviour (pre- vs. post-switch, $G = 9.77$, $P = 0.008$): while 8/18 birds continued to feed from hole a (now marked by a black circle), 7/18 followed the colour cue (3/18 chose hole c). As the proportions of adults and juveniles following the colour cue were small, however, there was no significant difference between the age classes in their cue preference post-switch ($G = 3.57$, $P = 0.17$).

The difference in cue use between adults and juveniles became more pronounced after Switch 2. Adults now clearly used the colour cue more than juveniles as post-switch preferences differed depending on age (post-switch juvenile vs post-switch adult: $G = 13.02$, $P = 0.002$, Fig. 4b). Most adults favoured the hole marked with the white circle (12/16 birds, $G = 13.02$, $P = 0.002$). Juveniles' hole preference, on the other hand, was random ($G = 3.60$, $P = 0.17$): 5/17 returned to the location that was rewarding in Stage 2, 9/17 attempted the hole marked with the white circle, and 3/17 attempted to feed from the alternative hole that had neither the white cue nor had been a previously-rewarded location. Separating the colour cue from the reward hole during Switch 2 also confirmed that hihi were learning cues and

not simply detecting which hole was open; the rewarding hole was not favoured by a majority of either adults or juveniles in Stage 3 (Fig. 4b). There was a trend for individuals that used the colour cue before the switch to be more likely to continue to follow this cue after the second switch than birds that first relied on location, although this was not statistically significant at $P = 0.05$ (before and after comparison of cues used, McNemar chi-squared test: $N = 33$, $X^2_1 = 3.5$, $P = 0.061$).

Regardless of which cue was used after either switch, most hihi subsequently adjusted their behaviour and relocated food by their third trial at the feeder arena (Switch 1: mean = after 1.72 ± 0.16 trials; Switch 2: after 1.93 ± 0.17 trials). There was no difference between adults and juveniles in the number of trials it took before they went straight to the rewarding hole (Wilcoxon rank sum test, Switch 1: $W = 95$, $P = 0.60$; Switch 2: $W = 98$, $P = 0.40$). Finally, the number of trials made during the stage prior to cues being switched did not predict which hole was chosen first following the switch (Switch 1: Kruskal-Wallis rank sum test, $X^2_{15} = 18.99$, $P = 0.21$; Switch 2: Kruskal-Wallis rank sum test, $X^2_{14} = 8.74$, $P = 0.85$). This shows that the differences in hole preferences we detected were unlikely to be a result of different levels of experience of the feeder arena.

4. Discussion

Associating cues with food rewards is well-known across the animal

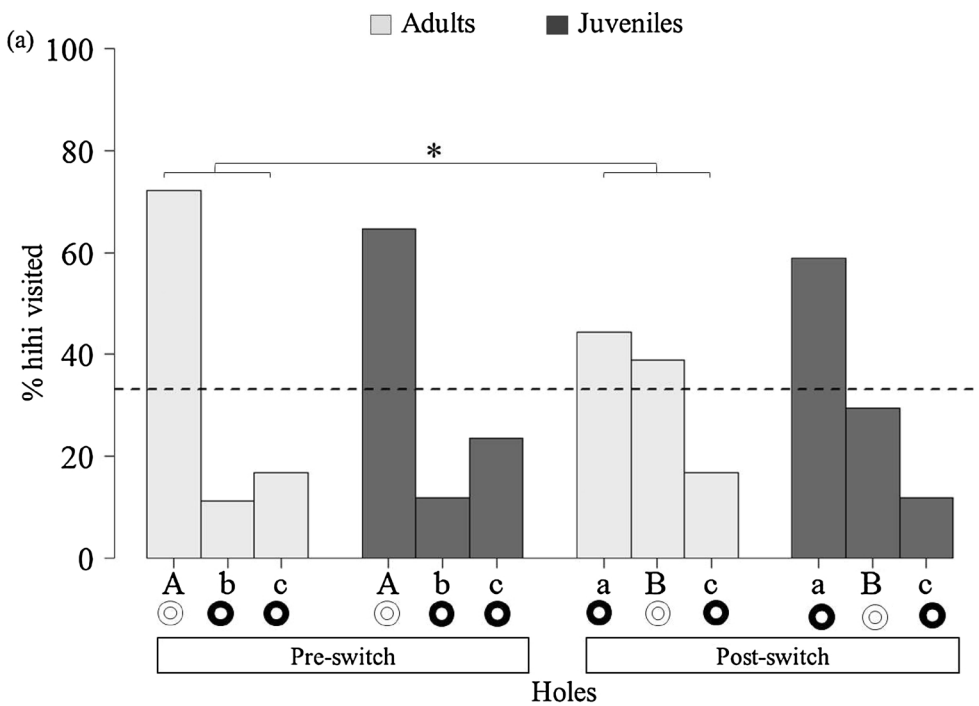
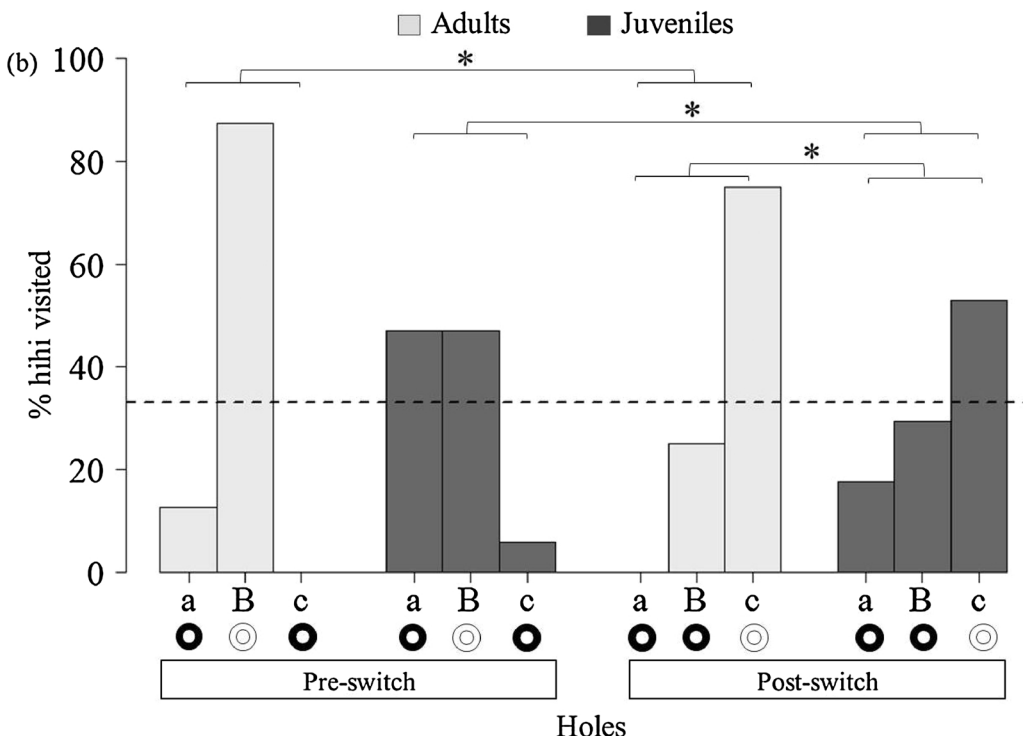


Fig. 4. First hole attempted by adult (light grey) and juvenile (dark grey) hihis during trials before and after a switch. (a) Holes attempted by adults ($N = 18$) and juveniles ($N = 17$) before and after Switch 1, and (b) before and after Switch 2 (adults: $N = 16$, juveniles: $N = 17$). Hole marking corresponds to Fig. 1c, where capitalised letters indicate rewarding holes and symbols indicate colour cue. Dashed line represents no preference (random distribution), and asterisks indicate significantly different distributions (using G-tests, see Results for details).



kingdom, but it remains less clear whether age affects cue use and learning in the wild. Our experiment shows that hihis, a generalist nectarivore, also learn to locate new food sources: both adult and juvenile hihis became more likely to attempt the reward location first over repeated trials. However, juveniles were less likely to attempt the reward first compared to adults. They also continued to sample non-rewarding holes more than adults, even after they had located the food reward; this may explain why juveniles spent longer feeding across trials. Although adults showed some pre-existing bias for the white hole, juveniles did not seem to compensate for initial differences during

learning: they remained more likely to sample non-rewarding holes even with experience, and as the reward moved during the experiment, adults appeared to follow the colour cue more than juveniles did (20% fewer juveniles followed the colour cue than adults after the final switch of the experiment). This suggests that more juveniles may have relied on location while adults favoured the colour cue, but juveniles also continued to sample the environment more than adults. Thus: why do learning patterns change with age, and what are the consequences?

There are two possible explanations: juveniles may learn more slowly than adults to use cues to find food (Thornton and Lukas, 2012),

or they may be using a different foraging strategy (Krebs and Inman, 1992; Krebs et al., 1978). If poorer learning is responsible for greater sampling by juveniles, this may be due to continuing musculoskeletal or neurological growth and maturation, and a lack of experience interacting with environmental stimuli (Healy and Hurly, 2004; Marchetti and Price, 1989). In macaques (*Macaca mulatta*), a lower performance at set-shifting tasks in juveniles compared to adults has been attributed to a less developed prefrontal cortex (Weed et al., 2008), and similarities with analogous regions of the avian brain (Olkowicz et al., 2016; Timmermans et al., 2000) could suggest that the development of these areas is also important for cognition in birds. Although our learning task was novel for both adults and juveniles, by virtue of their age adults are likely to have interacted with more cues in general. Adults' accumulated experience could make them better able to assess a range of cues, respond appropriately (Mery and Burns, 2010), and quickly select higher-gain patches than juveniles when foraging (Gass and Sutherland, 1985; Whitfield et al., 2014), even when they encounter novel environments. While juvenile foraging efficiency may improve with experience, acquiring this experience can be a slow process with many opportunities to make mistakes along the way.

On the other hand, flexible sampling by juveniles may help them keep an updated picture of their environment so they can forage optimally in the current conditions (Krebs and Inman, 1992; Krebs et al., 1978). In captive studies in baboons (*Papio papio*), behavioural flexibility helped juveniles reverse behaviour faster than adults (Bonté et al., 2014). In the wild, this may be adaptive because in many species (including hihi (Craig, 1985)), juveniles are subordinate to adults (Dingemans and De Goede, 2004; Verhulst et al., 2014). If juveniles have fewer opportunities to feed at high-quality food patches due to both contest and exploitation competition (Sol et al., 1998) having up-to-date knowledge from diverse foraging sites could help them make use of a variety of opportunities when displaced (Keynan et al., 2016). Sampling may also allow juveniles to compensate for using the wrong cue, and allow them to locate rewarding patches more quickly. This explore and exploit strategy (Krebs et al., 1978) could explain why we found no difference in the number of trials that it took adults and juveniles to re-locate the reward hole after it was moved, despite initial differences in their cue use. However, sampling also incurs costs when moving between patches (in both time budget allocation and energy expenditure) (Bryan et al., 1995; Stephens et al., 2007), and continuing to sample patches of no gain in case they later become rewarding may lead juveniles to waste energy. In our experiment, we found that juvenile hihi had to forage for longer than adults to reach the same level of reward intake, which may demonstrate how a sampling strategy may be costly to young hihi in terms of time budgeting, especially when they have lower chances of locating food to begin with. Therefore, determining if sampling by juveniles is actually adaptive requires further work, to understand if the costs of less efficient foraging are offset in other ways, or whether this gives one reason why juveniles, especially for birds, often have low survival (Naef-Daenzer and Gruebler, 2016).

How might our findings help hihi? The majority (six out of seven) of extant hihi populations have been established through translocations and are supplementary fed as a crucial part of their management (Chauvenet et al., 2012). Supplementary feeding is often used in conservation of vulnerable populations in other taxa, with conservation biologists calling for integration of nutritional and population ecology to provide the most effective management (Ewen et al., 2015). However, our findings suggest the cognitive ecology of the species being helped should also be considered to inform management practices. For example, the locations of feeding stations at managed hihi sites are sometimes changed, or even redesigned, for logistical reasons. Avoiding modifying feeder locations or establishing new feeding sites when juveniles are newly independent may give juveniles the best chances of learning appropriate cues and enable them to access food easily in the future. Cues may also need to be considered in other contexts, such as selecting nest sites (Seppänen et al., 2011). As nest boxes are also used

in some hihi populations, it would be interesting to test if we can manipulate cues to help hihi locate new nesting sites.

In summary, we found that both age classes learned to locate a food reward, but juveniles continued to sample foraging options more than adults and spent longer foraging overall. The range of cues used by each may have differed; adults were more likely to follow a colour cue whereas juveniles relied on location. Our study helps highlight that learning strategies change with age, and that young animals may be disadvantaged in several ways when compared to adults: they have had less opportunity to learn and generalise cues, and may not use the most efficient foraging strategies. Understanding how young animals use different sources of information to inform learning may help explain why some reach adulthood while others do not.

Acknowledgements

We thank Zealandia Ecosanctuary for permission to conduct this research. In particular, we thank Raewyn Empson, Neil Anderson, and Matu Booth of Zealandia Ecosanctuary for support and advice during the study. We thank John G. Ewen, N. Boogert, R. Shaw and our anonymous reviewers for helpful discussion and comments on previous versions of this manuscript. V.R.F. was supported by the University of Cambridge, Department of Zoology Balfour Studentship, R.T. was supported by an Independent Research Fellowship from NERC UK (NE/K00929X/1). There are no conflicts of interest with these funding bodies. Author contributions (following CRediT taxonomy): Conceptualisation, V.R.F., R.T.; Methodology, V.R.F., R.T.; Investigation, V.R.F.; Analysis, V.R.F., R.T.; Writing (original draft), V.R.F., R.T.; Writing (review & editing), V.R.F., R.T.; Supervision, R.T.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.beproc.2017.12.009>.

References

- Anderson, N., 2016. Hihi (*Notiomystis cincta*) report on 2015–16 breeding season Zealandia-Karori Sanctuary (unpublished report). Wellington.
- Aplin, L.M., Farine, D.R., Morand-Ferron, J., Sheldon, B.C., 2012. Social networks predict patch discovery in a wild population of songbirds. *Proc. R. Soc. B: Biol. Sci.* 279 (1745), 4199–4205. <http://dx.doi.org/10.1098/rspb.2012.1591>.
- Ashmole, N.P., Tovar, S.H., 1968. Prolonged parental care in royal terns and other birds. *The Auk* 85 (1), 90–100. <http://dx.doi.org/10.2307/4083627>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Package lme4. *J. Stat. Softw.* 67 (1), 1–91. <http://lme4.r-forge.r-project.org>.
- Benson-Amram, S., Holekamp, K.E., 2012. Innovative problem solving by wild spotted hyenas. *Proc. R. Soc. B: Biol. Sci.* 279 (1744), 4087–4095. <http://dx.doi.org/10.1098/rspb.2012.1450>.
- Birdlife International, 2013. *Notiomystis cincta*. (Retrieved August 23, 2016, from). www.iucnredlist.org.
- Bonté, E., Kemp, C., Fagot, J., 2014. Age effects on transfer index performance and executive control in baboons (*Papio papio*). *Front. Psychol.* 5 (March). <http://dx.doi.org/10.3389/fpsyg.2014.00188>.
- Boogert, N.J., Monceau, K., Lefebvre, L., 2010. A field test of behavioural flexibility in Zenaida doves (*Zenaida aurita*). *Behav. Process.* 85 (2), 135–141. <http://dx.doi.org/10.1016/j.beproc.2010.06.020>.
- Brodbeck, D.R., 1994. Memory for spatial and local cues: a comparison of a storing and a nonstoring species. *Anim. Learn. Behav.* 22, 119–133. <http://dx.doi.org/10.3758/BF03199912>.
- Bryan, A.L., Coulter, M.C., Pennycuik, C.J., 1995. Foraging strategies and energetic costs of foraging flights by breeding wood storks. *The Condor* 97 (1), 133–140. <http://dx.doi.org/10.2307/1368991>.
- Buchholz, R., 2007. Behavioural biology: an effective and relevant conservation tool. *Trends Ecol. Evol.* 22 (8), 401–407. <http://dx.doi.org/10.1016/j.tree.2007.06.002>.
- Case, T.J., 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Q. Rev. Biol.* 53 (3), 243–282.
- Chauvenet, A.L.M., Ewen, J.G., Armstrong, D.P., Coulson, T., Blackburn, T.M., Adams, L., Walker, L.K., Pettorelli, N., 2012. Does supplemental feeding affect the viability of translocated populations? The example of the hihi. *Anim. Conserv.* 15 (4), 337–350. <http://dx.doi.org/10.1111/j.1469-1795.2012.00522.x>.
- Craig, J.L., 1985. Status and foraging in New Zealand honeyeaters. *N. Z. J. Zool.* 12 (4), 589–597. <http://dx.doi.org/10.1080/03014223.1985.10428308>.
- Dall, S.R.X., Giraldeau, L.-A., Olsson, O., McNamara, J.M., Stephens, D.W., 2005.

- Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* 20 (4), 187–193. <http://dx.doi.org/10.1016/j.tree.2005.01.010>.
- Desrochers, A., 1992. Age and foraging success in European blackbirds: variation between and with individuals. *Anim. Behav.* 43 (6), 885–894. [http://dx.doi.org/10.1016/S0003-3472\(06\)80002-3](http://dx.doi.org/10.1016/S0003-3472(06)80002-3).
- Dingemanse, N.J., De Goede, P., 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behav. Ecol.* 15 (6), 1023–1030. <http://dx.doi.org/10.1093/beheco/arr115>.
- Ewen, J.G., Walker, L., Canessa, S., Groombridge, J.J., 2015. Improving supplementary feeding in species conservation. *Conserv. Biol.* 29 (2), 341–349. <http://dx.doi.org/10.1111/cobi.12410>.
- Galef, B.G., Laland, K.N., 2005. Social learning in animals: empirical studies and theoretical models. *Bioscience* 55 (6), 489. [http://dx.doi.org/10.1641/0006-3568\(2005\)055\[0489:SLIAES\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2).
- Gass, C.L., Sutherland, G.D., 1985. Specialization by territorial hummingbirds on experimentally enriched patches of flowers: energetic profitability and learning. *Can. J. Zool.* 63 (9), 2125–2133. <http://dx.doi.org/10.1139/z85-313>.
- Gochfeld, M., Burger, J., 1984. Age differences in foraging behavior of the American robin (*Turdus migratorius*). *Behaviour* 88 (3), 227–239. <http://dx.doi.org/10.1163/156853984x00335>.
- Harper, D.G.C., 1982. Competitive foraging in mallards: ideal free ducks. *Anim. Behav.* 30 (2), 575–584. [http://dx.doi.org/10.1016/S0003-3472\(82\)80071-7](http://dx.doi.org/10.1016/S0003-3472(82)80071-7).
- Healy, S.D., Hurly, T.A., 2004. Spatial learning and memory in birds. *Brain Behav. Evol.* 63 (4), 211–220. <http://dx.doi.org/10.1159/000076782>.
- Hector, A., 2015. *The New Statistics with R: An Introduction for Biologists*. Oxford University Press, Oxford.
- Heinsohn, R.G., 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *Am. Nat.* 137 (6), 864–881. <http://dx.doi.org/10.1086/285198>.
- Herborn, K., Alexander, L., Arnold, K.E., 2011. Colour cues or spatial cues? Context-dependent preferences in the European greenfinch (*Carduelis chloris*). *Anim. Cogn.* 14 (2), 269–277. <http://dx.doi.org/10.1007/s10071-010-0360-7>.
- Hurly, T.A., Healy, S., 2002. Cue learning by rufous hummingbirds (*Selasphorus rufus*). *J. Exp. Psychol. Anim. Behav. Process.* 28 (2), 209–223. <http://dx.doi.org/10.1037/0097-7403.28.2.209>.
- Kamil, A.C., Roitblat, H.L., 1985. The ecology of foraging behavior: implications for animal learning and memory. *Annu. Rev. Psychol.* 36, 141–169. <http://dx.doi.org/10.1146/annurev.psych.36.1.141>.
- Keynan, O., Ridley, A.R., Lotem, A., 2016. Task-dependent differences in learning by subordinate and dominant wild Arabian babblers. *Ethology* 122 (5), 399–410. <http://dx.doi.org/10.1111/eth.12488>.
- Krebs, J.R., Inman, A.J., 1992. Learning and foraging: individuals, groups, and populations. *Am. Nat.* 140 (S1), S63–S84. <http://dx.doi.org/10.1086/285397>.
- Krebs, J.R., Kacelnik, A., Taylor, P., 1978. Test of optimal sampling by foraging great tits. *Nature* 275 (5675), 27–31. <http://dx.doi.org/10.1038/275027a0>.
- Laland, K., 2004. Social learning strategies. *Anim. Learn. Behav.* 32 (1), 4–14. <http://dx.doi.org/10.3758/BF03196002>.
- Manrique, H.M., Call, J., 2015. Age-dependent cognitive inflexibility in great apes. *Anim. Behav.* 102, 1–6. <http://dx.doi.org/10.1016/j.anbehav.2015.01.002>.
- Marchetti, K., Price, T., 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biol. Rev.* 64 (1), 51–70. <http://dx.doi.org/10.1111/j.1469-185X.1989.tb00638.x>.
- Mazerolle, M.J., 2016. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R Package Version 1, 1–15.
- Melbourne, B.A., Hastings, A., 2008. Extinction risk depends strongly on factors contributing to stochasticity. *Nature* 454 (7200), 100–103. <http://dx.doi.org/10.1038/nature06922>.
- Mery, F., Burns, J.G., 2010. Behavioural plasticity: an interaction between evolution and experience. *Evol. Ecol.* 24 (3), 571–583. <http://dx.doi.org/10.1007/s10682-009-9336-y>.
- Mirville, M.O., Kelley, J.L., Ridley, A.R., 2016. Group size and associative learning in the Australian magpie (*Cracticus tibicen dorsalis*). *Behav. Ecol. Sociobiol.* 70 (3), 417–427. <http://dx.doi.org/10.1007/s00265-016-2062-x>.
- Morand-Ferron, J., Cole, E.F., Rawles, J.E.C., Quinn, J.L., 2011. Who are the innovators? A field experiment with 2 passerine species. *Behav. Ecol.* 22 (6), 1241–1248. <http://dx.doi.org/10.1093/beheco/arr120>.
- Naef-Daenzer, B., Grüebler, M.U., 2016. Post-fledging survival of altricial birds: ecological determinants and adaptation. *J. Field Ornithol.* 87 (3), 227–250. <http://dx.doi.org/10.1111/jof.12157>.
- Naef-Daenzer, B., 2000. Patch time allocation and patch sampling by foraging great and blue tits. *Anim. Behav.* 59 (5), 989–999. <http://dx.doi.org/10.1006/anbe.1999.1380>.
- Nakagawa, S., Cuthill, I.C., 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev.* <http://dx.doi.org/10.1111/j.1469-185X.2007.00027.x>.
- Olkowicz, S., Kocourek, M., Lučan, R.K., Porteš, M., Fitch, W.T., Herculano-Houzel, S., Némec, P., 2016. Birds have primate-like numbers of neurons in the forebrain. *Proc. Natl. Acad. Sci.* 113 (26), 7255–7260. <http://dx.doi.org/10.1073/pnas.1517131113>.
- R Development Core Team, 2016. *R Software R: A Language and Environment for Statistical Computing*. R Development Core Team, Vienna.
- Reader, S.M., Laland, K.N., 2001. Primate innovation: sex, age and social rank differences. *Int. J. Primatol.* 22 (5), 787–805. <http://dx.doi.org/10.1023/A:1012069500899>.
- Schuppli, C., Isler, K., van Schaik, C.P., 2012. How to explain the unusually late age at skill competence among humans. *J. Hum. Evol.* 63 (6), 843–850. <http://dx.doi.org/10.1016/j.jhevol.2012.08.009>.
- Seppänen, J.-T., Forsman, J.T., Mönkkönen, M., Krams, I., Salmi, T., 2011. New behavioural trait adopted or rejected by observing heterospecific tutor fitness. *Proc. R. Soc. B: Biol. Sci.* 278 (1712), 1736–1741. <http://dx.doi.org/10.1098/rspb.2010.1610>.
- Shaw, R.C., 2017. Testing cognition in the wild: factors affecting performance and individual consistency in two measures of avian cognition. *Behav. Process.* 134, 31–36. <http://dx.doi.org/10.1016/j.beproc.2016.06.004>.
- Sol, D., Santos, D.M., Garcia, J., Cuadrado, M., 1998. Competition for food in urban pigeons: the cost of being juvenile. *Condor* 100 (2), 298–304. <http://dx.doi.org/10.2307/1370270>.
- Stephens, D., Brown, J., Ydenberg, R. (Eds.), 2007. *Foraging: Behaviour and Ecology*. University of Chicago Press, Chicago.
- Sullivan, K.A., 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). *J. Anim. Ecol.* 58 (1), 275–286. <http://dx.doi.org/10.2307/5000>.
- Sutherland, W.J., 1998. The importance of behavioural studies in conservation biology. *Anim. Behav.* 56 (4), 801–809. <http://dx.doi.org/10.1006/anbe.1998.0896>.
- Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* 65 (1), 13–21. <http://dx.doi.org/10.1007/s00265-010-1037-6>.
- Thornton, A., Lukas, D., 2012. Individual variation in cognitive performance: developmental and evolutionary perspectives. *Phil. Trans. R. Soc. B: Biol. Sci.* 367 (1603), 2773–2783. <http://dx.doi.org/10.1098/rstb.2012.0214>.
- Thornton, A., Samson, J., 2012. Innovative problem solving in wild meerkats. *Anim. Behav.* 83 (6), 1459–1468. <http://dx.doi.org/10.1016/j.anbehav.2012.03.018>.
- Thorogood, R., Armstrong, D.P., Low, M., Brekke, P., Ewen, J.G., 2013. The value of long-term ecological research: integrating knowledge for conservation of hibi on Tiritiri Matangi Island. *N. Z. J. Zool.* 37 (3), 298–306.
- Timmermans, S., Lefebvre, L., Boire, D., Basu, P., 2000. Relative size of the hyperstriatum ventrale is the best predictor of feeding innovation rate in birds. *Brain Behav. Evol.* 56 (4), 196–203. <http://dx.doi.org/10.1159/000047204>.
- Verhulst, S., Geerdink, M., Salomons, H.M., Boonekamp, J.J., 2014. Social life histories: jackdaw dominance increases with age, terminally declines and shortens lifespan. *Proc. R. Soc. B: Biol. Sci.* 281 (1791), 20141045. <http://dx.doi.org/10.1098/rspb.2014.1045>.
- Vince, M.A., 1958. String-pulling in birds. (2) differences related to age in greenfinches, chaffinches and canaries. *Anim. Behav.* 6 (1–2), 53–54. [http://dx.doi.org/10.1016/0003-3472\(58\)90008-3](http://dx.doi.org/10.1016/0003-3472(58)90008-3).
- Weed, M.R., Bryant, R., Perry, S., 2008. Cognitive development in macaques: attentional set-shifting in juvenile and adult rhesus monkeys. *Neuroscience* 157 (1), 22–28. <http://dx.doi.org/10.1016/j.neuroscience.2008.08.047>.
- Whitfield, M., Kohler, A., Nicolson, S.W., 2014. Sunbirds increase foraging success by using color as a cue for nectar quality. *Behav. Ecol.* 25 (2), 328–334. <http://dx.doi.org/10.1093/beheco/art115>.
- Wunderlin, J.M., Lodge, D.J., 1988. The effect of age and visual cues on floral patch use by bananaquits (Aves: Emberizidae). *Anim. Behav.* 36 (1), 44–54. [http://dx.doi.org/10.1016/S0003-3472\(88\)80248-3](http://dx.doi.org/10.1016/S0003-3472(88)80248-3).