

REPORT FROM A BOU-FUNDED PROJECT

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Importance of social connections for winter survival of juvenile Hihi *Notiomystis cincta* in New Zealand

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INTRODUCTION

Surviving the first winter is challenging for young birds (Cox, Thompson, Cox, & Faaborg, 2014; Naef-Daenzer & Gruebler, 2016). If they are to reach their first breeding season, locating resources while avoiding predation is critical. As young animals have limited experience with stochastic food availability, they are predicted to acquire information from a wide range of sources to update their foraging behaviour. Information can come from personal experience or social interactions (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005); because young animals have little personal experience, social information is thought to be of great importance (Webster & Laland, 2008). However, how social behaviour in early life influences success over winter remains unclear.

We tested if early life social characteristics predict food discovery and overwinter survival in the Hihi (*Notiomystis cincta*), a threatened New Zealand passerine. In our main study population on Tiritiri Matangi Island (Tiri, 36°36'0" S, 174°53'24" E), juvenile Hihi form social flocks shortly after fledging which persist in reliable locations for approximately 2 months. Despite 20 years of monitoring, it remains unknown if these groups (and their social bonds) aid foraging and survival. This knowledge may help conservation efforts; current practice involves translocating juveniles to seed new populations (Ewen, 2017) but these have had variable outcomes so far (Thorogood, Armstrong, Low, Brekke, & Ewen, 2013).

We tested four hypotheses: (1) juveniles would be poorer at finding novel feeding sites than adults; (2) more sociable birds would find these sites faster; (3) juvenile Hihi with stronger social bonds from early life would find feeding sites at similar times; (4) juvenile Hihi that found more feeding sites would be more likely to survive winter.

METHODS

Experimental set-up

We set up temporary supplementary sugar water feeder stations in three discrete forest areas on Tiri between April-May 2016, and monitored their discovery by Hihi. Hihi were fitted with an RFID (radio frequency identification) PIT (passive integrated transponder) tag in a plastic leg ring, which meant that every visit to a feeder was recorded by an RFID data logger. In each area, we selected two random locations to set up feeders. We refilled feeders daily until the number of new discoveries declined to the point where most feeders had no new birds recorded on 3 successive days. This took 2 weeks. We then moved feeders twice (to locations at least 10m from the previous sites), and used the same feeder discovery protocol each time. Thus, we collected 6 feeder replicates per area (18 replicates total).

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A social network was established prior to the start of the experiment. This used PIT tag-recorded visits to pre-established feeders in juvenile group sites, and associations were defined based on similarities in timing of visits over 2 months (Farine, 2013). Finally, to determine survival we used data collected from biannual population surveys, carried out each year in September (pre-breeding) and February (post-breeding) as part of the long-term monitoring. Sightings of individual Hihi (based on their unique colour-ring combination) in September 2016 and February 2017 were used to determine survival over the 2016 winter.

Data analysis

From the records of feeder visits, we collected: the timing of every feeder discovery (the first visit to a feeder for each Hihi), the identity of the discoverer, its age (juvenile, the 2015-2016 cohort, or adult, any older bird), and sex. We also calculated each Hihi's "weighted degree" (degree from here on), and "tie strength" to the preceding bird, from the social network. Weighted degree was the number of social connections to other individuals proportional to the number of records for that bird. Tie strength was the number of times the discoverer bird and the preceding bird had associated in the network (relative to total number of recordings for the focal bird). From the population census data we extracted if a bird was seen (1) or not seen (0) in September 2016 and February 2017. If a Hihi was not seen in either survey it was assumed to have not survived the 2016 winter.

Where analyses used Generalised Linear Mixed Effect models (GLMMs) or Generalised Linear Models (GLMs), we created sets of candidate models, ranked these by their corrected Akaike Information Criterion (AICc), and then used all models within $\Delta AICc < 2$ of the top-ranked models to calculate effect sizes (\pm 95% confidence intervals) for predictor variables (Symonds & Moussalli, 2011).

MAIN FINDINGS

36 adult and 40 juvenile Hihi discovered at least one feeder across the experiment (Supplementary Table 1). 220 discovery events were recorded at 17 feeders (no data were collected from one feeder due to problems with the RFID data logger). Hihi continued to discover feeders throughout each repeat of the experiment (discovery times: average = 5 days, minimum = 22 minutes, maximum = 14 days).

Age and social effects on feeder discoveries

Hihi with more social connections discovered feeders faster, irrespective of their age or sex. The only supported model ($\Delta AICc < 2$) contained degree as the sole predictor variable (Supplementary Table 2; Figure 1; effect of degree on discovery rank = -0.63 ± 0.25 , 95% CI = $-1.11 - -0.15$). However, greater social connections did not mean that birds found more feeders during the course of the experiment: although degree was included in the top-ranked models for analysis of number of feeders discovered (Supplementary Table 3), it had a small effect (effect of degree = 0.13 ± 0.1 , 95% CI = $-0.08 - 0.33$). Instead, contrary to our prediction, juveniles discovered more feeders compared to adults (effect of being juvenile = 0.63 ± 0.24 , 95% CI = $0.16 - 1.11$; Figure 2). Sex was included in models with $\Delta AICc < 2$, but overall there was little difference in the number of feeders males and females discovered (effect of being male = -0.15 ± 0.18 , 95% CI = $-0.5 - 0.2$). The effect of age was not due to adults being more resident in one area than juveniles, because there was no difference in the average number of days adults and juveniles were recorded at a feeder (Wilcoxon rank sum test, $W = 668$, $P = 0.91$).

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Finally, we analysed how closely a juvenile Hihi discovering a feeder followed another Hihi. Models including tie strength and weighted degree were higher-ranked than the null model (Supplementary Table 5), but overall Hihi with stronger ties did not find food at similar times (effect of tie strength on lapse between visits = -1.79 ± 5.69 , 95% CI = $-12.94 - 9.35$), and more sociable Hihi did not follow another bird more closely (effect of discoverer's degree on lapse since previous Hihi's visit = -0 ± 0.32 , 95% CI = $-0.63 - 0.63$). Taken together, these results suggest that more sociable Hihi may be more likely to pay attention to the behaviour of other individuals to help inform their own behaviour, but they do not need to directly copy the behaviour of others (suggesting more general "local enhancement" social learning (Laland, 2004)), and do not rely on familiar peers from early-life.

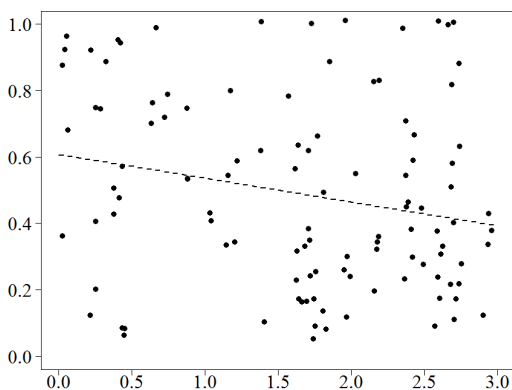


Figure 1. Discovery rank of patch discovery feeders for Hihi (adults and juveniles, N = 76), depending on their number of social ties (weighted degree) from a social network collected in the months preceding the experiment.

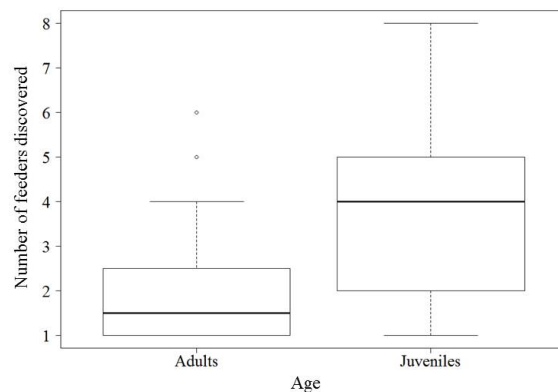


Figure 2. The number of feeders discovered by adults (N = 36) and juveniles (N = 40) across the patch discovery experiment. Bold lines show the median number of feeders discovered, boxes show lower and upper quartiles, and thin lines show the maximum and minimum numbers.

Survival and foraging ability

Survival rates were higher during the year of study than in previous years. For example, 41% (54/132) of juveniles survived the winter compared to 28% (43/154) in 2014 and 34% (30/89) in 2015. However, Hihi that survived the winter discovered fewer feeders on average than those that did not survive (effect = -0.58 ± 0.28 , 95% CI = $-1.12 - -0.04$). There was no difference in survival based on a bird's sociability (effect of degree on survival = 0.37 ± 0.68 , 95% CI = $-0.95 - 1.69$), however both of these analyses are limited because the number of juveniles recorded during our experiment that did not survive the winter was small (7/40, 18%). Why birds that did not survive were those that discovered more feeders is unclear, but it could be linked to energetic costs from extensive sampling between patches (Eliassen, Jørgensen, Mangel, & Giske, 2007). For Hihi, sampling tendency may link to dispersal in new sites, which is an important consideration for survival and establishment of populations in Hihi translocations (Richardson, 2015).

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ACKNOWLEDGEMENTS

We are grateful to the BOU for awarding a research grant of £1765 in 2015, which made this project possible. V.F. was also supported by a Balfour Studentship at the University of Cambridge. R.T. was supported by a NERC research grant and J.E. was supported by funding from the Zoological Society of London. We thank Mhairi McCready for conducting the 2016 and 2017 Hihi population censuses and banding and monitoring all Hihi with PIT tags, and we thank the Department of Conservation and Supporters of Tiritiri Matangi for their assistance during this project.

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Supplementary material below (pages 5–7)

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SUPPLEMENTARY MATERIAL

Supplementary Table 1

Summary of the number of Hihi (total, adults, and juveniles) that discovered each feeder across the experiment, and the total number of visits made to each feeder. Feeder abbreviation corresponds to “area.location” (e.g. feeder 1.1 was in area 1 and location 1). Due to problems with RFID data logger no data were collected at feeder 3.2 (excluded from table).

Feeder	Total number of Hihi	Number of adults	Number of juveniles	Total number of visits
1.1	12	2	10	394
1.2	12	2	10	290
1.3	10	4	6	112
1.4	8	3	5	151
1.5	10	2	8	379
1.6	9	3	6	228
2.1	8	1	7	257
2.2	9	2	7	61
2.3	2	0	2	54
2.4	4	1	3	7
2.5	24	13	11	584
2.6	11	3	8	212
3.1	19	4	15	522
3.3	35	14	21	2055
3.4	17	5	12	137
3.5	11	5	6	116
3.6	18	4	14	1931

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Supplementary Table 2

Ranking of all generalised linear mixed effects models used to analyse variation in discovery rank at patch discovery feeders. Predictors include weighted degree, age (adult or juvenile), and sex. Models are ranked according to $\Delta AICc$ values, and the weight indicates the relative likelihood of the respective model. All models contained a random effect term to account for repeated discoveries by the same individuals across the experiment (1 | ID). Null model presented for comparison.

Model	AICc	$\Delta AICc$	AICc Weight
~ degree	148.67	0.00	0.52
~ age + degree	150.63	1.96	0.19
~ sex + degree	150.75	2.08	0.18
~ age + sex + degree	152.85	4.18	0.06
~ age*degree + sex	154.84	6.17	0.02
~ age + degree*sex	155.08	6.41	0.02
~ 1	195.24	46.57	0.00
~ sex	196.49	47.82	0.00
~ age	197.35	48.68	0.00
~ age + sex	198.82	50.15	0.00

Supplementary Table 3

Ranking of all generalised linear models analysing variation in number of feeders each Hihi discovered. Predictors include weighted degree, age (adult or juvenile), and sex. Models are ranked according to $\Delta AICc$ values, and the weight indicates the relative likelihood of the respective model. Null model presented for comparison.

Model	AICc	$\Delta AICc$	AICc Weight
~ age+ degree	203.62	0.00	0.65
~ age + sex+ degree	205.25	1.63	0.29
~ degree	209.04	5.41	0.04
~ sex + degree	210.07	6.45	0.03
~ age	282.31	78.68	0.00
~ age + sex	282.93	79.30	0.00
~ sex	296.32	92.70	0.00
~ 1	302.10	98.47	0.00

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Supplementary Table 4

Ranking of all generalised linear mixed effects models used to analyse variation in how closely a Hihi discovering a feeder followed another Hihi. Predictors include weighted degree of the discovering bird as a measure of its sociability ("discoverer degree"), and the strength of its social bond to the preceding bird ("tie strength"). Models are ranked according to $\Delta AICc$ values, and the weight indicates the relative likelihood of the respective model. All models contained a random effect term to account for repeated discoveries by the same individuals across the experiment (1 | ID). Null model presented for comparison.

Model	AICc	$\Delta AICc$	AICc Weight
~ tie strength + discoverer degree	2145.36	0.00	0.78
~ tie strength*discoverer degree	2147.87	2.51	0.22
~ tie	2209.17	63.81	0.00
~ discoverer degree	2345.51	200.15	0.00
~ 1	2409.32	263.96	0.00

Supplementary Table 5

Ranking of all generalised linear models analysing variation in overwinter survival (1 or 0, as a binomial term). Predictors include weighted degree, and number of feeders discovered during the patch discovery experiment. Models are ranked according to $\Delta AICc$ values, and the weight indicates the relative likelihood of the respective model. Null model presented for comparison.

Model	AICc	$\Delta AICc$	AICc Weight
~ number of feeders discovered	35.79	0.00	0.61
~ number of feeders discovered + degree	37.77	1.98	0.23
~ 1	39.22	3.42	0.11
~ degree	40.68	4.89	0.05