Analysing age structure, residency and relatedness uncovers social network structure in aggregations of young birds

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30   Abstract

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32   Animal sociality arises from the cumulative effects of both individual social decisions and

33   environmental factors. While juveniles' social interactions with parents prior to independence shape

34   later-life sociality, in most bird and mammal species at least one sex undergoes an early-life dispersal

35   before first-year reproduction. The social associations from this period could also have implications for

36   later life, yet are rarely characterised. Here, we derive predictions from available examples of juvenile

37   groups in the literature (mobile "flocks", spatially-stable "gangs", or adult-associated "creches") and

38   then use three cohorts of juvenile hihi (*Notiomystis cincta*), a threatened New Zealand passerine, to

39   demonstrate how multistate modelling and social network analysis approaches can be used to

40   characterise group type based on residency, movement, relatedness, and social associations. At sites

41   where hihi congregated, we found that juveniles were re-sighted at higher frequency than adults and

42   associated predominantly with unrelated juveniles rather than siblings or parents. Movement among

43   group sites occurred, but associations developed predominantly within the sites. We suggest therefore

44   that juvenile hihi social structure is most similar to a "gang", a group structure in which juveniles

45   congregate without adults at predictable sites. Such gangs have previously only been described in

46   ravens. By combining spatial and social network analyses, our study demonstrates how social group

47   structures can be described and therefore facilitate broader comparisons and discussion about the form

48   and function of juvenile groups across taxa.

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50   Keywords: gang; juvenile; passerine; social groups; social networks

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52   Introduction

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54   Social groups form across the animal kingdom (Ward & Webster, 2016) when the benefits of sharing

55   space and resources (e.g improved foraging: Brown, 1988; or improved vigilance against predators:

56   Hass & Valenzuela, 2002; Molvar & Bowyer, 1994) outweigh the potential costs of competition

57   (Krause & Ruxton, 2002; Rubenstein, 1978). However, the ecological and social factors that determine

what type of social structure forms are more poorly understood. Recent studies have begun to provide insights into how animal sociality forms and functions (Armansin et al., 2016; see Farine et al., 2015; He et al., 2019; Morrison et al., 2019; Papageorgiou et al., 2019 for examples) and have highlighted surprising similarities across animal taxa. For example, multilevel societal structure (where sub-groups associate at different hierarchical levels, similar to human societies) has recently been described for both non-human primates (Morrison et al., 2019) and birds (Papageorgiou et al., 2019), indicating it may have evolved earlier than previously thought. Ecological factors such as food availability have also been found to play a key role in determining group structure across taxa, from fish (Mourier et al., 2012), to mammals (Dorning & Harris, 2019), and birds (Wright et al., 2003). Nevertheless, many studies occur during limited time windows (e.g. the breeding season) and only provide snap-shots of groups and subsequently our understanding of how social groups form at particular key life-stages remains poor.

Juvenile independence is an important transition in ontogeny with important consequences for later life and population stability (Donovan & Thompson, 2001). However, little is known for many species about the period between dispersal from natal sites and recruitment to the first breeding season. In particular, there are few studies that directly examine juvenile sociality (but see Templeton et al., 2012). In part, this is because young animals in many species are challenging to observe. Nevertheless, understanding sociality in young animals is pertinent considering that juveniles are naïve and may be especially reliant on socially-provided information (Galef & Laland, 2005) to find food, avoid predation, and navigate their environment (Franks & Thorogood, 2018; Lind & Welsh, 1994; Sullivan, 1989). If different classes of individuals are represented in a group, this will in turn determine the social conditions that juveniles experience, and affect life-history decisions of others. For example, if parents remain and interact with juveniles in social groups, this may represent continued parental investment that is otherwise ignored if parent-offspring interactions are only considered within the natal territory (Matthysen et al., 2010). Alternatively, the presence of a broad range of unrelated individuals with different personal experience could provide increased opportunities for gathering social information about foraging or predators, for example (Ramakers et al., 2016). Finally, prior social experiences can

86 determine later social behaviour such as territory settlement choices (Firth & Sheldon, 2016), meaning

87 that early-life social decisions might set up associations kept throughout life and have downstream

88 consequences for later behaviour and fitness.

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90 Three distinct types of social group which have been described for birds (Class Aves) may have

91 particular importance for juveniles, as they illustrate how groups can represent very different social

92 environments for this cohort. Mobile foraging units or "flocks" are groups of consistent individual

93 identities but of mixed age and relatedness (and sometimes mixed-species e.g. Jullien and Thiollay,

94 1998) that move collectively between locations (Ekman, 1989; Morse, 1978; Saitou, 1978, 1979;

95 Templeton et al., 2012). Other groups appear to be more juvenile-dominated (Dall & Wright, 2009;

96 Hinde, 1952; Ward & Zahavi, 1973). Such juvenile aggregations, which have been termed "gangs" in

97 species such as ravens (*Corvus corax*) (Dall & Wright, 2009; Marzluff et al., 1996), operate around

98 stable sites (such as roosts) to access nearby patchy food resources (Dall & Wright, 2009) and are

99 hypothesised to allow juveniles to out-compete more dominant adults (Dall & Wright, 2009; Wright et

100 al., 2003) or learn to find food without parents (Ward & Zahavi, 1973). While there are few empirical

101 examples of these gang-like groups, this may in part be because juvenile groups have not received

102 substantial research attention. Thirdly, juveniles may form stable congregations as "crèches". These

103 groups contrast with gangs or flocks because crèches form before juveniles become fully independent

104 and promote juvenile survival as parents actively care for their young with food provisioning and

105 vigilance (Balda & Balda, 1978; Clayton & Emery, 2007; Marzluff & Balda, 1992). Although these

106 groups show differences in broad structure, little is known in detail about juvenile behaviour within

107 these groups, and few studies have investigated how group structure affects opportunities for

108 associations between members (Templeton et al., 2012).

109

110 Here we quantify social structure in multiple cohorts of juvenile hihi (*Notiomystis cincta*), a threatened

111 New Zealand passerine whose social behaviour remains poorly known. Juvenile hihi are anecdotally

112 thought to be social during early life (Russell, 2000) as they have been recorded congregating during

113 routine population monitoring censuses conducted at the end of the breeding season (in early Autumn).

114 Hihi are thought to become less social after this time, as juveniles then disperse during the winter before

115 holding territories as monogamous adult pairs during the breeding season (Ranjard et al., 2017;

116 Richardson, 2015). All male juveniles are not successful at attracting breeding partners, and extrapair

117 paternity rates are high (Brekke et al., 2013; Ewen et al., 1999). Although the breeding biology of hihi

118 has been studied intensively (Thorogood et al., 2013), little is known about social behaviour of either

119 juveniles or adults outside of the breeding season. Nevertheless, hihi provide an excellent opportunity

120 to study juvenile social behaviour: they are confiding and easy to observe because an absence of

121 mammals across evolution means they do not fear of humans. In one study population in particular, the

122 canopy height is low enough for birds to be viewable across all forest stories.

123

124 Our aim was to uncover juveniles' social environment by quantifying group membership, and

125 associations in terms of age and location. We used complementary analysis methods that are,

126 nevertheless, rarely combined, to quantify consistency in group structure in terms of presence/absence

127 of members, capture movement and demographic structure, and then understand how associations were

128 structured by age, relatedness, and location (Shizuka & Johnson, 2019; Spiegel & Pinter-Wollman,

129 2019). We then compared our data to examples described in the literature for other bird species (Table

130 1). Our hypothesis was that we could categorise hihi social structure according to pre-existing

131 descriptions of group types already present in the literature. If hihi formed crèches, we predicted both

132 adults (parents) and juveniles (siblings) would be consistently sighted together; if groups were more

133 mobile flocks, then individuals would move collectively among locations, with no specific age or

134 relatedness structure. However, if hihi formed "gangs" (Dall & Wright, 2009) we would expect

135 juveniles to be present much more consistently than adults.

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141 Methods

143 Study population

145 Our study was conducted over three years (2015 – 2017) on Tiritiri Matangi Island (Auckland, New

146 Zealand, 36°36'00" S 174°53'21" E). Hihi in this study population typically breed between early

147 September and the end of January, when parents hold a territory and raise altricial young in the nest-

148 boxes we provide. After approximately two weeks of post-fledging dependency, young disperse from

149 their natal territory. The study site is a 2.5 km^2 island characterised by a central longitudinal ridge (80m

150 maximum altitude) with a series of latitudinal ridges and gullies on either side covered in a mixture of

151 native flora (subtropical rainforest) and more open grassland. Supplementary sugar water feeders are

152 provided year-round for hihi at six sites across the island. This is a closed population with no

153 immigration or emigration except through birth and mortality, and all individuals are uniquely

154 identifiable from coloured leg ring combinations. The population varied between 180 and 270

155 individuals over the three years, with similar proportions of juveniles and adults (second year or older)

156 each year (McCready & Ewen, 2016, 2017; Smith & Ewen, 2015). All breeding attempts are monitored

157 and identities of breeding pairs recorded. During this study, parentage was assigned by visually

158 identifying the adult male and female hihi present throughout nest building, egg laying and chick care.

159 Although there is variable extra-pair paternity in hihi (Brekke et al., 2013; Ewen et al., 1999), nest-

160 mates were at least maternal-siblings and the male social mate cares for the offspring in his nest (Ewen

161 & Armstrong, 2000). The first year of our study (2015) was a poorer breeding season than 2016 and

162 2017 (2015: 89 fledglings; 2016: 132 fledglings; 2017: 151 fledglings), so we specified which year data

163 was from in any analyses using combined data. For reference, the adult population each year was at

164 least 93 (2015), 88 (2016), and 120 (2017) (minimum counts recorded in February post-breeding

165 surveys conducted as part of standard population management).

169 Ethical note

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171 Ethical approval of this observation-based study design was issued through the Zoological Society of

172 London Ethics Committee (UK). All yearly monitoring of breeding populations (including nestbox

173 monitoring and colour-ring application) followed an established protocol conducted under a New

174 Zealand Department of Conservation Research Permit (authorisation number: 44300-FAU).

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176 Group site observations

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178 Each year from mid-January to April, we observed hihi congregating in spatially-separated forested

179 gullies (we define these as "group sites" from here, see Appendix). To record group-site membership

180 of individual hihi, we conducted one-hour surveys at each group site. Each survey was divided into 30-

181 second time blocks (one survey = 120 blocks), and in every 30 second block, we recorded the identity

182 of all hihi perched within a 15-metre radius of the observer (observations were made from the same

183 point in each group site for each survey). This timescale was used as the most detailed scale possible to

184 capture changes in presence of small forest passerines, but was also long enough to allow for

185 identification and recording of individuals. Any bird present across multiple blocks was re-recorded at

186 the start of each block, so we could determine presence to the nearest 30 seconds. All observations were

187 made with binoculars (Zeiss Conquest® HD 8x42) by one observer (VRF). In total we conducted 15

188 surveys per site in 2015, and 25 per site in 2016 and 2017; surveys were distributed evenly across the

189 three months each year. In 2016 we verified that our survey method reliably captured group site use, by

190 comparing the numbers of hihi recorded in each survey to the number of hihi present across the entire

191 day (see Appendix).

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197   Data analysis

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199   Analysis of group site residency and movement between sites

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201   To understand age-dependent presence within and movement between separate group sites by hihi, we

202   used a multistate live recapture model in Program MARK (version 9.0) (White & Burnham, 1999).

203   From repeated recordings of identifiable individuals across replicated surveys, this approach can

204   quantify survival (S) of individuals, the likelihood that surviving individuals are detected (re-sighting,

205   ρ) and the likelihood that individuals will move between different "states" (ψ) which can, for example,

206   be used to represent spatially distinct locations (White et al., 2006). Previous studies in this population

207   (Low & Pärt, 2009) and our own preliminary exploratory survival models indicated that both adult and

208   juvenile hihi were extremely unlikely to die within our three-month study window each year (98-99%

209   survival estimated for this period; we note survival conditions are likely optimal at this time of year),

210   and we therefore fixed survival probability at 1. This meant we could interpret re-sighting probability

211   (ρ) as the likelihood of residency within any of the groups we monitored each year (more frequent re-

212   sighting across our replicated surveys would demonstrate higher residency, represented by larger values

213   of ρ). To explore whether residency in sites differed between adults and juveniles, we included age

214   (adult or juvenile) as a predictor for re-sighting (ρ). We also investigated whether residency patterns

215   were consistent within each year of our study, by including survey number as a predictor for ρ (1-15 for

216   2015, and 1-25 for 2016 and 2017 analyses). We used ψ to explore the likelihood that individuals moved

217   between the group sites (higher values of ψ would indicate greater movement). To explore if adults and

218   juveniles moved between sites in different ways, we assessed whether movement rates (ψ) were

219   predicted by age. We also explored whether movement rates depended on which sites birds moved

220   between, as sites were not evenly separated and had variable topography between them which could

221   have affected how likely hihi were to move from one location to another (Martin et al., 2006;

222   Strandburg-Peshkin et al., 2017). Thus, to investigate residency and movement for each separate year,

223   we constructed sets of models with all possible combinations of ρ and ψ parameters and ranked these

224   by their corrected Quasi-Akaike Information Criterion (QAICc) values. All models were assessed for

225 goodness-of-fit (GOF) using median ĉ (variance inflation factor, a measure of overdispersion)

226 (Burnham & Anderson, 2002; Gath, 2017; White & Burnham, 1999), revealing low levels of

227 overdispersion in all years (median ĉ: 2015 = 1.51; 2016 = 1.39; 2017 = 1.72). We calculated QAICc

228 weights based on change in QAICc from the top-ranked model (Burnham & Anderson, 2002). Models

229 with QAICc weight > 0.005 were included in model-averaging to calculate effect sizes and 95%

230 confidence intervals of parameters. Any averaged parameter with a confidence interval that did not span

231 0 was considered to have a significant effect.

232

233 All further analyses were conducted in R (version 3.5.0) (R Core Team, 2018). To investigate whether

234 related individuals were present in group sites, we calculated the proportion of surveys in which each

235 juvenile was observed in the same group site as either of its parents, and the proportion of surveys each

236 juvenile was seen in the same group site as its maternal siblings from the same breeding season (hihi

237 fledge 1-5 young per clutch; across our study years, we recorded a mean of 2.04 ± 0.08 siblings per nest

238 in group site observations; numbers of nests with observed fledglings: 2015 = 20, 2016 = 36, 2017 =

239 42). We excluded any juveniles we only saw in one survey, as we could not calculate a proportion for

240 these individuals (N: 2015 = 10; 2016 = 18; 2017 = 10). When calculating the proportions of surveys

241 spent with maternal siblings, we also excluded juveniles with no recorded siblings, as either they were

242 from single-fledgling nests or their siblings may have died after fledging (N: 2015 = 7; 2016 = 10; 2017

243 = 8). As these initial calculations showed many juveniles were never seen with siblings (See Results),

244 we then analysed whether ever being seen with siblings (yes = 1, no = 0) was influenced by proximity

245 between group sites and nests-of-origin (distance to nearest 50m from group site to nest-of-origin,

246 measured using Google Maps 2018) using a binomial Generalised Linear Model (GLM). Nests were

247 distributed across the 2.5 km^2 island, so how far hihi had to disperse from nests to reach group sites

248 varied (median distance = 410 m; minimum distance = 50 m, maximum distance = 1400 m) and could

249 have affected how likely siblings were to make it to the same area post-dispersal. We also included

250 number of surveys each individual was seen in, and number of siblings each bird had to investigate if

251 co-occurrence was predicted by random sampling chance. We constructed a set of candidate models

252 including all combinations of predictors and ranked models by their AICc values. Including any model

9

253   < 2 AICc units larger than the top-ranked model, we calculated averaged effect sizes (±95% confidence

254   intervals) for predictors using the package AICcmodavg (version 2.1-1) (Mazerolle, 2017). Models

255   were checked for over-dispersion, but correction was not needed (Hector, 2015). Based on the evidence

256   of extremely infrequent co-occurrence of related individuals (see Results) from this initial exploration,

257   we did not analyse effects of relatedness in any greater detail.

258

259   Quantifying association network structure

260

261   We determined whether juvenile hihi associated with others based on age or location characteristics

262   using social network analysis. First, we constructed weighted social networks for each year, where

263   associations between birds depended on spatiotemporal proximity of individuals (i.e. hihi observed in

264   the same group site at similar times to one another). We used the gathering function "gmmevents" in

265   the R package asnipe (version 1.1.9) (Farine, 2013), which assigns individuals to association events

266   based on their temporal proximity (in our dataset, these times were to the nearest 30 seconds) (see

267   Appendix). Before exploring patterns with age or group site, we checked that there was variation in

268   associations strengths (i.e. networks were non-uniform) by calculating each network's coefficient of

269   variation (cv); this explains how much the strength of social ties between pairs (dyads) of birds differs

270   (values over 0.6 are considered to represent strong, repeated connections) (Farine and Whitehead 2015).

271   To show whether this differentiation was stronger than expected by random chance, we used pre-

272   network data stream permutations to create 1000 randomised networks where we had reshuffled

273   individuals between association events, then compared if our cv values were significantly higher than

274   values from randomised networks (Farine, 2017; Farine & Whitehead, 2015). Significance of all further

275   network analyses also used this same method of comparing to a null model, and all P-values generated

276   using permutations are specified as P_{rand}. Finally, using our yearly networks we (1) analysed whether

277   hihi in the same age class associated most strongly (adult and juvenile "assortment"), and (2) explored

278   the strength of juvenile-juvenile associations between birds that frequented the same group site, versus

279   those that did not (juveniles were categorised by the site they were seen in for >50% of their surveys).

280   For each analysis we used the assortnet package (version 0.12) (Farine, 2014) to generate assortment

281   coefficients (*r*) for each network, a value from -1 (disassociation between individuals of the same age

282   class or location) to +1 (strong association between individuals of the same age class or location). Again,

283   we compared observed assortment to assortment in permuted networks to determine the significance of

284   effects (Farine, 2014; Newman, 2002).

285

286   Results

287

288   Was grouping structured by age?

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290   There were two group sites in 2015 and three group sites in each of 2016 and 2017 where the majority

291   of juveniles were observed (juveniles *N*: 2015 = 37; 2016 = 79; 2017 = 91; adults *N*: 2015 = 45; 2016

292   = 62; 2017 = 68). For reference in terms of juvenile representation in groups, only 17 extra juveniles

293   (16%, out of 108 total) were not seen in groups during 2017, when a full island search was conducted

294   concurrently to group site observations as part of a complete population survey (see Franks et al., 2020).

295   Our multistate analysis showed that while adults did visit group sites, they were more transient than

296   juveniles; juveniles were re-sighted at least twice as frequently in successive survey occasions

297   compared to adults in all three years (Table 2; Figure 1a, b, c; top-ranked models explaining re-sighting

298   included age: Table A1). Re-sighting was constant in 2015 and 2017 but varied across survey occasions

299   in 2016 for both adults and juveniles (Table A1), suggesting some variation in grouping behaviour

300   across years. This meant that, on average, 70% (±2% S.E.) of birds seen in group sites were juvenile

301   (significant difference between counts of adults and juveniles present in each survey; Wilcoxon rank

302   sum test: 2015: W = 277; P = 0.002; 2016: W = 951.5; P < 0.001; 2017: W = 1290.5; P < 0.001). This

303   age composition was also reflected in social structure. All networks consisted of non-uniform

304   associations (Table A2), which was partially due to strong positive assortment by age (Table 3): each

305   year, the biggest proportion of associations occurred between juveniles only (2015: 38%; 2016: 57%;

306   2017: 56% of associations, Tables A3-5). Each year, individuals varied in their number of associates,

307   (median number of associates recorded per individual: 2015 = 8, range = 0 – 36; 2016 =11, range = 0 –

308   50; 2017 = 12, range = 0 – 69), so we note that not all juveniles were equally social while in group sites.

309

310   How much did hihi move between different sites?

311

312   Quantifying movement (Ψ) in our multistate analysis showed a low likelihood that hihi transitioned

313   between group sites, although this did vary depending on the site birds were moving to and from (Table

314   2, Figure 1d, e, f; Table A1). Movement also depended on age: juveniles showed a small significant

315   likelihood of transitioning from one group site to another between surveys, while our models did not

316   show significant support for most adult movement likelihoods. Combined with their lower re-sighting

317   probability, this suggests adults were only transitory visitors to group sites (Table 2; Figure 1d, e, f;

318   Table A1). However, when juveniles did move it was as individuals (on average only two or three

319   juveniles moved between each survey, mean: 2015 = 2; 2016 = 3; 2017 = 3), and the majority of

320   juveniles were only ever seen at one site (proportion of juveniles that never moved group site: 2015 =

321   0.78; 2016 = 0.44; 2017 = 0.62; maximum number of moves by individuals: 2015 = 3; 2016 = 7; 2017

322   = 7). Furthermore, all juvenile-only networks in all three years were strongly positively assorted by

323   primary group site, while associations among juveniles across different sites were much weaker (Table

324   3; Tables A6-8; Figure 1g, h, i). This meant juveniles were largely faithful to their group site, where

325   they were likely to associate and interact with juveniles also commonly using the same site.

326

327   Were juveniles related to other hihi present in the same group sites?

328

329   There were very few occasions when juveniles were seen in the same group site during the same survey

330   occasion as their parents (mean ± S.E. proportion of surveys: 2015 = 0.02 ± 0.02; 2016 = 0.03 ± 0.01;

331   2017 = 0.08 ± 0.02; 86% of juveniles never seen with parents), or their maternal siblings (mean ± S.E.

332   proportion of surveys: 2015 = 0.22 ± 0.08; 2016 = 0.25 ± 0.04; 2017 = 0.28 ± 0.04; 53% of juveniles

333   never seen with siblings). Individuals that were seen in group sites closer to their nest-of-origin were

334   not more likely to be seen with maternal-siblings each year (null model highest ranked; Table A9).

335   Being recorded in more surveys did not affect co-occurrence with maternal siblings (Table A9).

336   Together, this low likelihood of juveniles being resident with parents or maternal siblings suggested

337   that relatedness does not drive association in these groups.

338

339   Discussion

340

341   Here we combined multistate analysis and social network analysis to characterise age composition,

342   relatedness, and the level of movement between spatially distinct sites in aggregations of birds, and then

343   clarified how social structure related to opportunities for association in juveniles. Across three

344   consecutive years of data collection in three different cohorts, we found that aggregations of juvenile

345   hihi occurred consistently at the end of each breeding season, with limited movement between different

346   group sites. Although some adults were observed, their presence was much more transient. Network

347   associations reflected these differences in residency: rather than associating with adults, juveniles most

348   strongly associated with other juveniles frequently present in the same group sites. Finally, juveniles

349   were almost never seen with their parents (occurred in only 2-8% of surveys across the study) and were

350   rarely sighted with their maternal siblings (22-28% of surveys). In relation to previously-described

351   social structures (Table 1), our results suggest juvenile hihi groups resemble gangs, where juvenile birds

352   aggregate around communal roosts (Wright et al., 2003) or other social meeting places (Ward & Zahavi,

353   1973) which are separate from adults (Dall & Wright, 2009). This is in contrast to flocks, where groups

354   of individuals move together over large distances (Templeton et al., 2012) or crèches, where juveniles

355   associate with related adults (Balda & Balda, 1978). Although modelling suggests gang-like groups

356   may form across a range of foraging niches (Dall and Wright 2009), empirical detection of this group

357   structure has received little attention with only two examples available in the literature (e.g. Common

358   quelea *Quelea quelea*: Ward and Zahavi 2008; European raven: Dall and Wright 2009). Thus, by

359   exploring factors structuring social aggregations, we are able to better understand the social

360   environment that young birds encounter during their first few months of independence from parents.

361

362   Why might juvenile hihi form "gangs"? Dall & Wright (2009) hypothesised that gangs are most likely

363   to occur when resources are patchily distributed, rapidly-depleting "bonanzas" that cannot be defended

364   alone. Individuals therefore maximise their grouping behaviour, given the probability of locating such

365   a resource and ability to defend it. Although this model was developed to explain group formation in

366   juvenile ravens and invoked large animal carcasses as the ephemeral resource, juvenile hihi may face a

367   similar foraging challenge. During the late summer and autumn, juvenile hihi forage for fruits and nectar

368   from a diversity of trees and shrubs that vary in availability, and they are often observed to consume

369   fewer ripe fruits than either adults (C. Andrews, unpublished data), or the two other bird species that

370   dominate their foraging guild (tūī *Prosthemadera novaeseelandiae*, and bellbird/korimako *Anthornis*

371   *melanura*) (Craig, 1985; Craig et al., 1981). Water availability is also restricted on this island during

372   this period. Overall, accessing these important resources alone may be unlikely for juvenile hihi, but

373   foraging as a group could help provide them with an advantage.

374

375   Dall & Wright's model (2009) also predicted that gangs should be more likely to form when social

376   groups are stable and there are opportunities for repeated interactions and formation of social

377   reputations. We found that individuals formed stable associations within group sites, and observed them

378   participating in both foraging activities and affiliative-type behaviours. For example, huddling (where

379   2-10 juveniles were seen lining up side-by-side on perches), following, and allopreening were observed

380   throughout surveys (V. Franks, pers. obs.), which suggests that juvenile hihi interact in groups rather

381   than simply co-occurring passively in the same place at the same time. However, the exact purposes of

382   these behaviours are difficult to uncover, and unfortunately, we do not have data available on individual

383   (or group) search efficiency or dominance over food to assess effects on outcomes such as social status.

384   Furthermore, we only studied groups during the day; sociality at other times (for example, at night while

385   roosting) may differ and influence diurnal foraging behaviour. Finally, individual-level variation may

386   also be important to consider as our results showed some inter-individual variation in residency, social

387   connections, and movement behaviour, which suggested there were gradients in how individual

388   juveniles behaved within the group. Studying this variation further may help elucidate the extent to

389   which individual juveniles employ alternative social strategies employed and should explore the

390   consequences of such variation for later life. Nevertheless, demonstrating juvenile-dominated groups

391   in hihi has provided rare empirical evidence that gangs occur beyond scavenging ravens and

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392 granivorous queleas, and suggests that this type of sociality could be more common in juvenile birds

393 than currently described. Future research could now experimentally test how these groups function, to

394 further our understanding of whether gang-like sociality is particularly beneficial to naïve juveniles.

395

396 Ecological factors such as resource type and availability are also likely to drive *where* social groups

397 (such as gangs) form, and encourage animals to coexist in the same place at the same time while they

398 utilise localised resources (Gall & Manser, 2018; Mourier et al., 2012; Strandburg-Peshkin et al., 2017).

399 For example, recent studies describing social structure for vulturine guineafowl (*Acryllium vulturinum*)

400 and foxes (*Vulpes vulpes*) found that group composition and social behaviour changed between seasons,

401 highlighting the influence of environmental conditions such as rainfall and temperature (Dorning &

402 Harris, 2019; Papageorgiou et al., 2019). In our study, the aggregations of juvenile hihi that formed

403 each year were structured by location as individuals consistently used particular sites, but across

404 different breeding seasons there was variation in the location of group sites, amount of temporal

405 consistency, and population productivity or size. Thus, socioecological factors may have an important

406 influence on overall group dynamics. We did not quantify resources and vegetation for each site in the

407 three years of our study, but anecdotally at least these sites tended to include water sources for bathing

408 or drinking, which are otherwise limited at that time of year. Thus, it is likely that factors such as food

409 or water availability may help explain the location of where juvenile aggregations form, and may be a

410 subject for further experimental tests to help support the observational evidence linking environment

411 and social aggregations that have been shown so far (e.g Dorning and Harris, 2019; Papageorgiou *et*

412 *al.*, 2019).

413

414 Alternatively, structured groups can arise because of individual-level effects, such as phenotype (Croft

415 et al., 2005; Firth & Sheldon, 2016; Fletcher, 2007). Individuals may group with others that are similar

416 to themselves (positive assortment) (Jiang et al., 2013; Peuhkuri, 1999), but may avoid others if they

417 occupy different niches due to characteristics including size and age (negative assortment) (Catterall et

418 al., 1989; Marchetti & Price, 1989) or to avoid competition (Marchetti & Price, 1989; Sol et al., 1998).

419 We found that hihi associated by age class in the group sites we studied, and few adults joined the

420 putative gangs. These adults were also neither parents nor maternal-siblings. Although we cannot yet

421 explain why some adults were present at group sites while others were not, they may have been

422 subordinate individuals, or otherwise unable to access resources without knowledge from the group

423 (Dall & Wright 2009). Alternatively, they could have been paternal relatives (extra-pair paternity is

424 high in hihi: Brekke et al., 2013), but unfortunately these data were not available at the time of our

425 study. Even if associations arise only from co-occurrence in the same place at the same time, the

426 composition of phenotypes may still have important consequences for finding food, and avoiding

427 predators or disease (Aplin et al., 2012; Drewe, 2010; Krause et al., 2009; Krause & Ruxton, 2002;

428 Schakner et al., 2017). This is because the individuals present will affect information sharing, likelihood

429 of pathogen transmission, and the outcomes of competitive or affiliative interactions (Aplin et al., 2012;

430 Danchin et al., 2004).

431

432 Exploring group structure should be an essential first step for research into social environment as it can

433 generate discussion for later experiments manipulating group composition, or information availability,

434 that test why animals form social groups. For example, a recent review highlighted that accounting for

435 social structure has provided new biological knowledge or changed theoretical predications about the

436 importance of factors such as relatedness and spatial influence on animal social organisation (Cantor et

437 al., 2019). By combining spatial and social network analyses, here we have provided a putative example

438 of a group form that has rarely been described in the literature, despite it being theoretically plausible

439 (Dall & Wright, 2009). Nevertheless, more studies are required if we are to understand the similarities

440 and differences in social structures across taxa and how they relate to species' ecology.

441

453

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686   **Table 1.** Predictions for group structure and social associations for juvenile hihi, with reference to

687   previously-described groups of birds.

	Group type		
	Flock e.g. Parid tits[1,2]	Gang e.g Ravens[3]	Crèche e.g. Pinyon jays[4]
Consistent group members with preferred associations	Y	Y	Y
Structured by age: juveniles present more frequently than adults, associations strongest between juveniles	N	Y	N
Structured by spatial location: low movement between separate locations; associations characterised by location	N	Y	Y
Structured by relatedness: both parents and offspring consistently present; associations strongest between parents and offspring, and siblings	N	N	Y

688   Y = Yes, N = No. References: [1]Saitou 1978; [2]Saitou 1979; [3]Marzluff et al., 1996; [4]Marzluff & Balda

689   1992.

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702 **Table 2.** Model-averaged estimates of re-sighting (ρ) and movement (Ψ) for adult and juvenile hihi in

703 2015, 2016, and 2017.

Parameter	Estimates (LCI – UCI)		
	2015	2016	2017
ρ Adult	**0.23 (0.12 – 0.41)**	**0.17 (0.09 – 0.31)**	**0.22 (0.17 – 0.28)**
ρ Juvenile	**0.59 (0.42 – 0.73)**	**0.36 (0.22 – 0.53)**	**0.44 (0.40 – 0.49)**
Ψ a to b Adult	0.01 (0.00 – 0.02)	**-**	**-**
Ψ a to b Juvenile	**0.09 (0.01 – 0.47)**	-	-
Ψ b to a Adult	0.00 (-0.01 – 0.02)	-	-
Ψ b to a Juvenile	0.02 (0.00 – 0.15)	-	-
Ψ b to c Adult	-	0.00 (0.00 – 0.00)	-
Ψ b to c Juvenile	-	0.00 (-0.02 – 0.02)	-
Ψ b to d Adult	-	**0.04 (0.01 – 0.23)**	0.01 (0.00 – 0.02)
Ψ b to d Juvenile	-	**0.15 (0.09 – 0.31)**	**0.05 (0.03 – 0.11)**
Ψ b to e Adult	-	-	0.00 (0.00 – 0.01)
Ψ b to e Juvenile	-	-	0.01 (0.00 – 0.09)
Ψ c to b Adult	-	0.00 (-0.01 – 0.02)	-
Ψ c to b Juvenile	-	0.02 (0.00 – 0.11)	-
Ψ c to d Adult	-	0.02 (0.00 – 0.11)	-
Ψ c to d Juvenile	-	**0.09 (0.04 – 0.19)**	-
Ψ d to b Adult	-	0.01 (-0.01 – 0.03)	0.00 (0.00 – 0.01)
Ψ d to b Juvenile	-	**0.04 (0.01 – 0.23)**	**0.02 (0.01 – 0.04)**

Ψ d to c Adult	-	0.01 (0.00 – 0.07)	-
Ψ d to c Juvenile	-	**0.04 (0.02 – 0.10)**	-
Ψ d to e Adult	-	-	0.01 (0.00 – 0.02)
Ψ d to e Juvenile	-	-	**0.04 (0.02 – 0.08)**
Ψ e to b Adult	-	-	0.00 (0.00 – 0.01)
Ψ e to b Juvenile	-	-	0.01 (0.00 – 0.02)
Ψ e to d Adult	-	-	**0.04 (0.01 – 0.13)**
Ψ e to d Juvenile	-	-	**0.20 (0.11 – 0.33)**

704 Estimates generated from multistate models in Table A1 with ΔQAIC weight > 0.005; significant

705 estimates where confidence intervals (LCI, UCI) did not span 0.00 are highlighted in bold. For

706 movement estimates, letters a-e correspond to group sites shown in Figure 1d, e, f to show likelihood

707 of movement between each different group site.

708 **Table 3.** Assortment strengths in networks (r) between ages (adult/juvenile), juveniles depending on

709 their residency in different group sites.

Year	r	S.E.	P_{rand}
Age assortment (adult/juvenile network)			
2015	0.26	0.002	**<0.001**
2016	0.29	0.002	**<0.001**
2017	0.21	0.001	**0.028**
Group site assortment (juvenile-only network)			
2015	0.63	0.005	**0.001**
2016	0.32	0.003	**<0.001**
2017	0.58	0.004	**0.001**

710 Standard error and significance of assortment (P_{rand}) calculated in comparison to 1000 permuted

711 networks. Significant values (at $P < 0.05$) are highlighted in bold.

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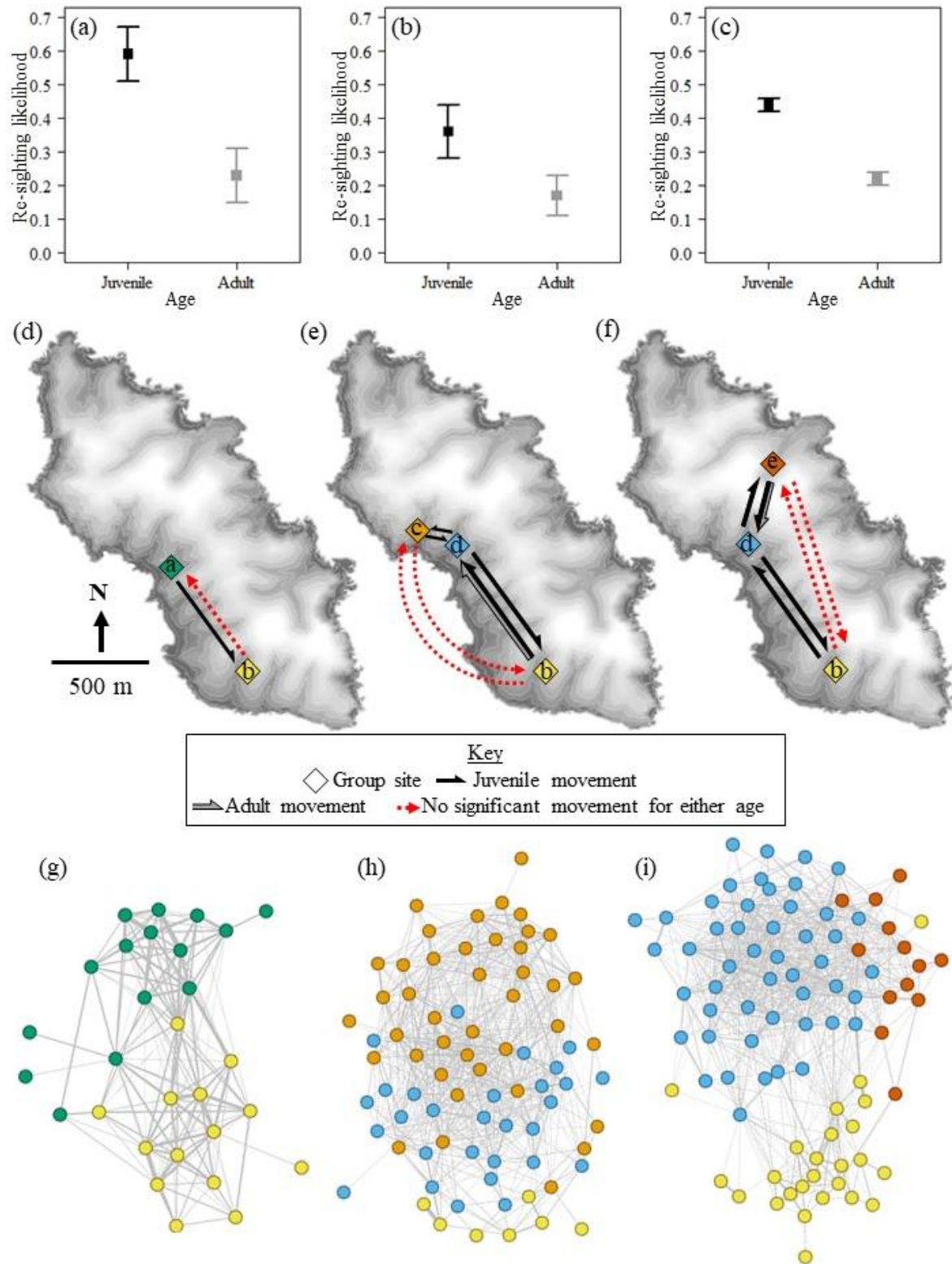**Figure 1.** Re-sighting (a-c), movement (d-f) and associations (g-i) for 2015 (left), 2016 (middle) and 2017 (right)); (a-c) re-sighting probability estimates ($\pm$ S.E.) for juveniles (black lines) and adults (grey lines); (d-f) movements between different group sites for juveniles (black arrows) and adults (grey arrows) (movements that were not significantly likely to occur as shown in Table 2 are dashed red

732   arrows). On map, shading corresponds to altitude, increasing in 10m steps from 0m (darkest) to approx.

733   80m (lightest). Lettered diamonds correspond to group sites in Table 2 and colours correspond to

734   network figures in (g-i); (g-i) show social networks where nodes (circles) represent individual hihi and

735   are coloured according to the site in (d-f) where they were observed in over 50% of their surveys (2015

736   network: N = 45 adults and 37 juveniles; 2016: N = 65 adults and 79 juveniles; 2017: N = 70 adults and

737   91 juveniles). Lines (edges) represent co-occurrence in group sites at similar times (N edges: 2015 =

738   435; 2016 = 1173; 2017 = 1439). Network visualisations were constructed in Gephi (version 0.9.2)

739   (Bastian et al., 2009) with a force-atlas layout that clustered together more strongly associating nodes

740   (individuals).

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Appendix 1

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767 **Additional information on detecting groups for observations**

768 Each year, we surveyed between five and nine sites from January to February to detect groups (in 2016

769 and 2017, we increased the search area to ensure no other groups were missed). All sites were forested

770 gullies located on both the East and West sides of Tiritiri Matangi, and were the main patches of

771 regenerating natural flora on the island. We recorded the numbers of unique juveniles for one hour in

772 each gully location, and group sites were assigned after two weeks if we saw at least three juveniles in

773 more than 8/10 surveys per location. We further confirmed that there were no other group sites during

774 the annual February population survey, which is conducted every year by trained conservation staff

775 who search the entire island over 40 hours. We then continued to survey group locations to collect

776 grouping data from February to April.

777

778 **Defining number of surveys for multistate analyses**

779 Originally, during our group site observations we recorded a total of 15 hours per site in 2015, and 25

780 hours per site in 2016 and 2017 (surveys were distributed evenly across the three study months in each

781 year). However, while multistate analyses require each site to be present at each replicated time point

782 to quantify movement between sites, our different sites were not surveyed at the exact same time (due

783 to one observer). Thus, we combined consecutive surveys from different sites so that each time point

784 represented every group site. There was a maximum of two days between these combined surveys to

785 limit movement between groups and prevent hihi from being recorded twice in the same survey

786 occasion. Recording hihi in separate groups representing the same survey occasion happened very rarely

787 (2015 = 1/656 re-sightings; 2016 = 9/1974 re-sightings; 2017 = 7/3180 re-sightings), but if it did, we

788 treated the bird as a member of the group where it was seen last to acknowledge that a change of group

789 had occurred. Different intervals between survey occasions were accounted for in analyses, so

790 likelihoods were not confounded by time. Overall, there were 8 survey occasions in 2015, 14 in 2016,

791 and 20 in 2017; an example re-sighting history for one individual in 2015 is "aa0aabbb", where the bird

792 was seen in group "a" in survey occasions 1, 2, 4 and 5, not seen in survey occasion 3, and seen in group

793 "b" for the remainder of survey occasions.

794

795 **Verifying survey method**

796 In 2016, all hihi were fitted with Radio Frequency Identification (RFID) Passive Integrated Transponder

797 (PIT) tags in plastic leg rings that replaced one colour ring in each bird's combination (use of tags was

798 approved by the Auckland Zoo Ethics Committee, New Zealand). We set up temporary supplementary

799 sugar water feeders equipped with RFID loggers in the juvenile group sites (see Figure 2 for locations

800 of group sites in 2016); these temporary feeders were additional to the main permanent supplementary

801 sugar water feeders provided year-round for hihi. These RFID loggers remotely recorded visits of

802   individual hihi across a 15-hour period each day (encompassing sunrise to sunset) which allowed us to

803   assess if the number of birds present in our hour-long surveys used to observe group sites captured an

804   accurate representation of birds present over the entire day. We compared number of individuals

805   collected from RFID logging at feeders and in each 1-hour survey on the same day over the period when

806   feeders were present in group sites (7th Feb – 6th April 2016). There was strong correlation in numbers

807   of hihi recorded by each of the two methods (Figure A1; $S = 22530$, *rho* $= 0.69$, $P < 0.001$; PIT tag

808   method recorded a median of 0.5 birds per day fewer compared to observations, range $= -14 – +11$ for

809   PIT tag vs. observations). Overall, there was no significant difference in number of birds recorded by

810   the two methods each day (paired Wilcoxon signed rank test: $V = 1278.5$, $P = 0.83$). Thus, busier days

811   recorded more hihi using both methods, and suggested that collecting data on a coarser scale with 1-

812   hour observations still accurately represented the number of birds present at a site that day.

813

814   **Proximity network construction, checking, and analysis**

815   We constructed weighted social networks for each year based on spatiotemporal proximity (hihi co-

816   occurring in the same group site at the same time were associating) in the R package asnipe (version

817   1.1.9) (Farine, 2013). All networks were weighted, which incorporate both the number and strength of

818   social connections (Farine, 2014). We used the "gmmevents" function in the R package asnipe (version

819   1.1.9) (Farine, 2013) to detect temporal clusters in our time-stamped (to within 30s) sightings data and

820   build an association matrix (Farine, 2013; Psorakis et al., 2015). Using this approach avoided artificially

821   restricted associations, which can occur using a more fixed time-window approach (Psorakis et al.,

822   2015). Each year, we confirmed that hihi formed non-random associations by calculating the coefficient

823   of variation ("cv") of each network (values over 0.6 are considered to represent strong, repeated

824   connections) (Farine and Whitehead 2015) (Table A2).

825

826   To ensure we accurately captured potential to associate based on length of "gmmevents" time windows,

827   we compared the length of the time windows produced by the "gmmevents" function ("event lengths"

828   in seconds), with the length of time hihi spent in the group sites based on repeated re-sightings in

829   successive time blocks during surveys (seconds to the nearest 30s). The event lengths calculated by

830   "gmmevents" were similar or shorter in length than re-sighting times (median length of event windows:

831   2015 = 119.37 s, 2016 = 90.44 s, 2017 = 90.52 s; median re-sighting from observation blocks: 2015 =

832   90 s, 2016 = 90 s, 2017 = 120 s; Wilcoxon rank sum test comparing length of event windows to re-

833   sighting time, 2015: $W = 126700$, $P = 0.34$, 2016: $W = 541210$, $P = 0.54$; 2017: $W = 811840$, $P = 0.01$).

834   This suggested the automated method reasonably defined the potential to associate over the same time,

835   or a shorter time, than hihi were present in a group; we believe this is reasonable, as we would not

836   expect birds to be associating for longer than they were observed, and it accounts for fluctuations in

837   associations based on small scale individual movements in and out of our observation area.

838

839   For all hypothesis testing using networks, we compared observed networks to randomised networks as

840   a null model (Croft et al., 2011; Farine, 2017; Farine & Whitehead, 2015). Randomised networks were

841   generated using permutations of the data-stream in asnipe, which randomly swaps records of individuals

842   while maintaining original data structure and controlling for sampling bias (Farine, 2013, 2014, 2017;

843   Farine & Whitehead, 2015). Significance was calculated by comparing the size of the test statistic of

844   the real network to test statistics of 1000 randomised networks (1000 = number of permutations).

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870   **Table A1.** Multistate models ranked by ΔQAICc values analysing re-sighting (ρ) and movement (Ψ)

871   between groups of hihi for 2015, 2016, and 2017, depending on age of individuals, time (recapture

872   event) and group sites.

Model	QAICc	ΔQAICc	AICc Weights	Number of parameters
2015 group sites				
S(.)ρ(age)ψ(age+site)	232.40	0.00	0.35	5
S(.)ρ(age)ψ(age)	232.70	0.29	0.30	4
S(.)ρ(age)ψ(.)	234.08	1.68	0.15	4
S(.)ρ(age)ψ(site)	234.20	1.79	0.14	5
S(.)ρ(age+time)ψ(age+site)	238.55	6.15	0.02	11
S(.)ρ(age+time)ψ(age)	238.62	6.22	0.02	10
S(.)ρ(age+time)ψ(.)	240.01	7.61	0.01	10
S(.)ρ(age+time)ψ(site)	240.35	7.94	0.01	11
S(.)ρ(.)ψ(age+site)	240.73	8.32	0.01	4
S(.)ρ(.)ψ(.)	242.44	10.04	0.00	3
S(.)ρ(time)ψ(site+age)	247.01	14.61	0.00	10
S(.)ρ(time)ψ(age)	247.12	14.72	0.00	9
S(.)ρ(age*time)ψ(age)	247.33	14.92	0.00	16
S(.)ρ(age*time)ψ(age+sites)	247.52	15.11	0.00	17
S(.)ρ(time)ψ(.)	248.51	16.10	0.00	9
S(.)ρ(age*time)ψ(.)	248.71	16.31	0.00	16
S(.)ρ(time)ψ(site)	248.81	16.40	0.00	10
S(.)ρ(age*time)ψ(sites)	249.31	16.91	0.00	17
2016 group sites				
S(.)ρ(age+time)ψ(age+sites)	869.66	0.00	0.88	21
S(.)ρ(age+time)ψ(sites)	874.32	4.66	0.09	20
S(.)ρ(age+time)ψ(age)	876.37	6.71	0.03	17
S(.)ρ(age+time)ψ(.)	881.03	11.37	0.00	16
S(.)ρ(time)ψ(age+sites)	884.84	15.19	0.00	20
S(.)ρ(time)ψ(sites)	889.52	19.86	0.00	19
S(.)ρ(age*time)ψ(age+sites)	890.28	20.62	0.00	33
S(.)ρ(age)ψ(age+sites)	891.09	21.43	0.00	9
S(.)ρ(time)ψ(age)	891.62	21.96	0.00	16

S(.)ρ(age*time)ψ(sites)	894.74	25.08	0.00	32
S(.)ρ(age)ψ(sites)	895.93	26.27	0.00	8
S(.)ρ(age*time)ψ(age)	896.19	26.53	0.00	29
S(.)ρ(time)ψ(.)	896.29	26.63	0.00	15
S(.)ρ(age)ψ(age)	898.51	28.85	0.00	5
S(.)ρ(.)ψ(age+sites)	903.28	33.62	0.00	8
S(.)ρ(age)ψ(.)	903.34	33.68	0.00	4
S(.)ρ(.)ψ(.)	915.60	45.95	0.00	3
2017 group sites				
S(.)ρ(age)ψ(age+sites)	1434.21	0.00	0.99	10
S(.)ρ(age)ψ(sites)	1443.48	9.26	0.01	9
S(.)ρ(age+time)ψ(age+sites)	1447.63	13.41	0.00	28
S(.)ρ(age)ψ(age)	1456.37	22.16	0.00	5
S(.)ρ(age+time)ψ(sites)	1456.76	22.55	0.00	27
S(.)ρ(age)ψ(.)	1463.00	28.79	0.00	4
S(.)ρ(.)ψ(age+sites)	1463.69	29.48	0.00	9
S(.)ρ(age+time)ψ(age)	1469.17	34.96	0.00	23
S(.)ρ(age*time)ψ(age+sites)	1472.60	38.38	0.00	46
S(.)ρ(age+time)ψ(.)	1475.68	41.47	0.00	22
S(.)ρ(time)ψ(age+sites)	1477.41	43.20	0.00	27
S(.)ρ(age*time)ψ(sites)	1481.60	47.39	0.00	45
S(.)ρ(time)ψ(sites)	1486.56	52.35	0.00	26
S(.)ρ(.)ψ(.)	1492.52	58.30	0.00	3
S(.)ρ(age*time)ψ(age)	1493.47	59.26	0.00	41
S(.)ρ(time)ψ(age)	1498.99	64.78	0.00	22
S(.)ρ(age*time)ψ(.)	1499.85	65.64	0.00	40
S(.)ρ(time)ψ(.)	1505.51	71.30	0.00	21

873 Null model $S(.)$ $\rho(.)$ $\Psi(.)$ included for comparison. All models corrected by median ĉ following

874 goodness-of-fit testing. AICc weight indicates relative likelihood of each model.

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880   Table A2. Coefficient of variation (cv) values for each network used in analysis and significance of the

881   differentiated associations they explain in comparison to permuted networks (P_{rand}).

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Year	Network type	cv value	P_{rand}
2015	Juvenile and adult	4.27	0.004
2015	Juvenile-only	3.26	0.006 (within-location)
2015	Juvenile-only	3.26	0.002 (across-location)
2016	Juvenile and adult	4.18	0.008
2016	Juvenile-only	2.39	<0.001 (within-location)
2016	Juvenile-only	2.39	<0.001 (across-location)
2017	Juvenile and adult	4.20	<0.001
2017	Juvenile-only	2.60	0.013 (within-location)
2017	Juvenile-only	2.60	<0.001 (across-location)

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897   Table A3. Mixing matrix showing distribution of edge weights between adults ("A") and juvenile ("J")

898   hihi in 2015.

	A	J	a_i^w
A	0.239	-	0.428
J	0.188	0.384	0.572
b_i^w	0.428	0.572	1.000

899   a_i^w = row sums, b_i^w = column sums; due to rounding, sum values may not be exact. Table is symmetrical

900   so half the values are presented.

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921   Table A4. Mixing matrix showing distribution of edge weights between adults ("A") and juvenile ("J")

922   hihi in 2016.

	A	J	a_i^w
A	0.118	-	0.273
J	0.155	0.572	0.727
b_i^w	0.273	0.727	1.000

924   a_i^w = row sums, b_i^w = column sums; due to rounding, sum values may not be exact. Table is symmetrical

925   so half the values are presented.

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946   Table A5. Mixing matrix showing distribution of edge weights between adults ("A") and juvenile ("J")

947   hihi in 2017.

	A	J	a_i^w
A	0.122	-	0.281
J	0.159	0.559	0.719
b_i^w	0.281	0.719	1.000

948   a_i^w = row sums, b_i^w = column sums; due to rounding, sum values may not be exact. Table is symmetrical

949   so half the values are presented.

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970   Table A6. Mixing matrix showing distribution of edge weights between juveniles depending on the

971   group where they were most commonly located in 2015.

	Site a	Site b	a_i^w
Site a	0.499	-	0.588
Site b	0.0.09	0.322	0.412
b_i^w	0.588	0.412	1.000

972   Site lettering refers to group locations in Figure 6, a_i^w are the row sums, b_i^w are the column sums; due

973   to rounding, sum values may not be exact. Table is symmetrical so half the values are presented.

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994　Table A7. Mixing matrix showing distribution of edge weights between juveniles depending on the

995　group where they were most commonly located in 2016.

	Site c	Site d	Site b	a_i^w
Site c	0.507	-	-	0.657
Site d	0.142	0.137	-	0.293
Site b	0.009	0.014	0.027	0.050
b_i^w	0.657	0.293	0.050	1.000

996　Site lettering refers to group locations in Figure 6, a_i^w are the row sums, b_i^w are the column sums; due

997　to rounding, sum values may not be exact. Table is symmetrical so half the values are presented.

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1017 Table A8. Mixing matrix showing distribution of edge weights between juveniles depending on the

1018 group where they were most commonly located in 2017.

	Site d	Site b	Site e	a_i^w
Site d	0.583	-	-	0.678
Site b	0.027	0.154	-	0.189
Site e	0.068	0.008	0.058	0.133
b_i^w	0.678	0.189	0.133	1.000

1019 Site lettering refers to group locations in Figure 6, a_i^w are the row sums, b_i^w are the column sums; due

1020 to rounding, sum values may not be exact. Table is symmetrical so half the values are presented.

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1040 Table A9. Ranking of generalised linear models analysing variation in the proportion of surveys where

1041 juveniles were seen with their nest siblings across all three years of the study.

	AICc	ΔAICc	AICc Weight
~1	138.55	0.00	0.36
~ proximity to nest	139.90	1.35	0.18
~ number of surveys	140.58	2.03	0.13
~ year	140.74	2.19	0.12
~ proximity to nest + number of surveys	141.94	3.39	0.07
~ proximity to nest + year	141.98	3.43	0.07
~ number of surveys + year	142.78	4.23	0.04
~ proximity to nest + number of surveys + year	144.07	5.52	0.02

1042 Models are ranked by ΔAICc values, and weight indicates relative likelihood of each model. Null

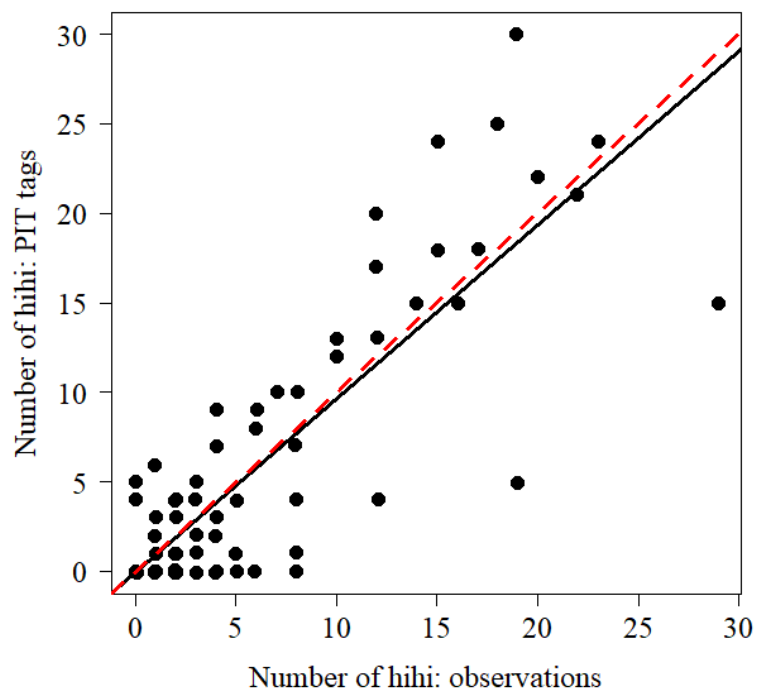1043 model (~1) included for comparison.

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Figure A1. Correlation between the number of individual hihi recorded by 1-hour observations in group sites and from PIT-tag recorders at feeders across the entire length of the same day of survey. Red dashed line represents 1:1 correlation, and black line represents correlation from observed data, calculated using Spearman's rank analysis.