

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

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Abstract

Animal sociality arises from the cumulative effects of both individual social decisions and environmental factors. While juveniles' social interactions with parents prior to independence shape later-life sociality, in most bird and mammal species at least one sex undergoes an early-life dispersal before first-year reproduction. The social associations from this period could also have implications for later life, yet are rarely characterised. Here, we derive predictions from available examples of juvenile groups in the literature (mobile "flocks", spatially-stable "gangs", or adult-associated "creches") and then use three cohorts of juvenile hihi (*Notiomystis cincta*), a threatened New Zealand passerine, to demonstrate how multistate modelling and social network analysis approaches can be used to characterise group type based on residency, movement, relatedness, and social associations. At sites where hihi congregated, we found that juveniles were re-sighted at higher frequency than adults and associated predominantly with unrelated juveniles rather than siblings or parents. Movement among group sites occurred, but associations developed predominantly within the sites. We suggest therefore that juvenile hihi social structure is most similar to a "gang", a group structure in which juveniles congregate without adults at predictable sites. Such gangs have previously only been described in ravens. By combining spatial and social network analyses, our study demonstrates how social group structures can be described and therefore facilitate broader comparisons and discussion about the form and function of juvenile groups across taxa.

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

Introduction

Social groups form across the animal kingdom (Ward & Webster, 2016) when the benefits of sharing space and resources (e.g improved foraging: Brown, 1988; or improved vigilance against predators: Hass & Valenzuela, 2002; Molvar & Bowyer, 1994) outweigh the potential costs of competition (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

determine later social behaviour such as territory settlement choices (Firth & Sheldon, 2016), meaning that early-life social decisions might set up associations kept throughout life and have downstream consequences for later behaviour and fitness.

Three distinct types of social group which have been described for birds (Class Aves) may have particular importance for juveniles, as they illustrate how groups can represent very different social environments for this cohort. Mobile foraging units or “flocks” are groups of consistent individual identities but of mixed age and relatedness (and sometimes mixed-species e.g. Jullien and Thiollay, 1998) that move collectively between locations (Ekman, 1989; Morse, 1978; Saitou, 1978, 1979; Templeton et al., 2012). Other groups appear to be more juvenile-dominated (Dall & Wright, 2009; Hinde, 1952; Ward & Zahavi, 1973). Such juvenile aggregations, which have been termed “gangs” in species such as ravens (*Corvus corax*) (Dall & Wright, 2009; Marzluff et al., 1996), operate around stable sites (such as roosts) to access nearby patchy food resources (Dall & Wright, 2009) and are hypothesised to allow juveniles to out-compete more dominant adults (Dall & Wright, 2009; Wright et al., 2003) or learn to find food without parents (Ward & Zahavi, 1973). While there are few empirical examples of these gang-like groups, this may in part be because juvenile groups have not received substantial research attention. Thirdly, juveniles may form stable congregations as “crèches”. These groups contrast with gangs or flocks because crèches form before juveniles become fully independent and promote juvenile survival as parents actively care for their young with food provisioning and vigilance (Balda & Balda, 1978; Clayton & Emery, 2007; Marzluff & Balda, 1992). Although these groups show differences in broad structure, little is known in detail about juvenile behaviour within these groups, and few studies have investigated how group structure affects opportunities for associations between members (Templeton et al., 2012).

Here we quantify social structure in multiple cohorts of juvenile hihi (*Notiomystis cincta*), a threatened New Zealand passerine whose social behaviour remains poorly known. Juvenile hihi are anecdotally thought to be social during early life (Russell, 2000) as they have been recorded congregating during routine population monitoring censuses conducted at the end of the breeding season (in early Autumn).

Hihi are thought to become less social after this time, as juveniles then disperse during the winter before holding territories as monogamous adult pairs during the breeding season (Ranjard et al., 2017; Richardson, 2015). All male juveniles are not successful at attracting breeding partners, and extrapair paternity rates are high (Brekke et al., 2013; Ewen et al., 1999). Although the breeding biology of hihi has been studied intensively (Thorogood et al., 2013), little is known about social behaviour of either juveniles or adults outside of the breeding season. Nevertheless, hihi provide an excellent opportunity to study juvenile social behaviour: they are confiding and easy to observe because an absence of mammals across evolution means they do not fear of humans. In one study population in particular, the canopy height is low enough for birds to be viewable across all forest stories.

Our aim was to uncover juveniles' social environment by quantifying group membership, and associations in terms of age and location. We used complementary analysis methods that are, nevertheless, rarely combined, to quantify consistency in group structure in terms of presence/absence of members, capture movement and demographic structure, and then understand how associations were structured by age, relatedness, and location (Shizuka & Johnson, 2019; Spiegel & Pinter-Wollman, 2019). We then compared our data to examples described in the literature for other bird species (Table 1). Our hypothesis was that we could categorise hihi social structure according to pre-existing descriptions of group types already present in the literature. If hihi formed crèches, we predicted both adults (parents) and juveniles (siblings) would be consistently sighted together; if groups were more mobile flocks, then individuals would move collectively among locations, with no specific age or relatedness structure. However, if hihi formed "gangs" (Dall & Wright, 2009) we would expect juveniles to be present much more consistently than adults.

Methods

Study population

Our study was conducted over three years (2015 – 2017) on Tiritiri Matangi Island (Auckland, New Zealand, 36°36'00" S 174°53'21" E). Hihi in this study population typically breed between early September and the end of January, when parents hold a territory and raise altricial young in the nest-boxes we provide. After approximately two weeks of post-fledging dependency, young disperse from their natal territory. The study site is a 2.5 km² island characterised by a central longitudinal ridge (80m maximum altitude) with a series of latitudinal ridges and gullies on either side covered in a mixture of native flora (subtropical rainforest) and more open grassland. Supplementary sugar water feeders are provided year-round for hihi at six sites across the island. This is a closed population with no immigration or emigration except through birth and mortality, and all individuals are uniquely identifiable from coloured leg ring combinations. The population varied between 180 and 270 individuals over the three years, with similar proportions of juveniles and adults (second year or older) each year (McCready & Ewen, 2016, 2017; Smith & Ewen, 2015). All breeding attempts are monitored and identities of breeding pairs recorded. During this study, parentage was assigned by visually identifying the adult male and female hihi present throughout nest building, egg laying and chick care. Although there is variable extra-pair paternity in hihi (Brekke et al., 2013; Ewen et al., 1999), nest-mates were at least maternal-siblings and the male social mate cares for the offspring in his nest (Ewen & Armstrong, 2000). The first year of our study (2015) was a poorer breeding season than 2016 and 2017 (2015: 89 fledglings; 2016: 132 fledglings; 2017: 151 fledglings), so we specified which year data was from in any analyses using combined data. For reference, the adult population each year was at least 93 (2015), 88 (2016), and 120 (2017) (minimum counts recorded in February post-breeding surveys conducted as part of standard population management).

Ethical note

Ethical approval of this observation-based study design was issued through the Zoological Society of London Ethics Committee (UK). All yearly monitoring of breeding populations (including nestbox monitoring and colour-ring application) followed an established protocol conducted under a New Zealand Department of Conservation Research Permit (authorisation number: 44300-FAU).

Group site observations

Each year from mid-January to April, we observed hihi congregating in spatially-separated forested gullies (we define these as “group sites” from here, see Appendix). To record group-site membership of individual hihi, we conducted one-hour surveys at each group site. Each survey was divided into 30-second time blocks (one survey = 120 blocks), and in every 30 second block, we recorded the identity of all hihi perched within a 15-metre radius of the observer (observations were made from the same point in each group site for each survey). This timescale was used as the most detailed scale possible to capture changes in presence of small forest passerines, but was also long enough to allow for identification and recording of individuals. Any bird present across multiple blocks was re-recorded at the start of each block, so we could determine presence to the nearest 30 seconds. All observations were made with binoculars (Zeiss Conquest® HD 8x42) by one observer (VRF). In total we conducted 15 surveys per site in 2015, and 25 per site in 2016 and 2017; surveys were distributed evenly across the three months each year. In 2016 we verified that our survey method reliably captured group site use, by comparing the numbers of hihi recorded in each survey to the number of hihi present across the entire day (see Appendix).

Data analysis

Analysis of group site residency and movement between sites

To understand age-dependent presence within and movement between separate group sites by hihi, we used a multistate live recapture model in Program MARK (version 9.0) (White & Burnham, 1999). From repeated recordings of identifiable individuals across replicated surveys, this approach can quantify survival (S) of individuals, the likelihood that surviving individuals are detected (re-sighting, ρ) and the likelihood that individuals will move between different “states” (ψ) which can, for example, be used to represent spatially distinct locations (White et al., 2006). Previous studies in this population (Low & Pärt, 2009) and our own preliminary exploratory survival models indicated that both adult and juvenile hihi were extremely unlikely to die within our three-month study window each year (98-99% survival estimated for this period; we note survival conditions are likely optimal at this time of year), and we therefore fixed survival probability at 1. This meant we could interpret re-sighting probability (ρ) as the likelihood of residency within any of the groups we monitored each year (more frequent re-sighting across our replicated surveys would demonstrate higher residency, represented by larger values of ρ). To explore whether residency in sites differed between adults and juveniles, we included age (adult or juvenile) as a predictor for re-sighting (ρ). We also investigated whether residency patterns were consistent within each year of our study, by including survey number as a predictor for ρ (1-15 for 2015, and 1-25 for 2016 and 2017 analyses). We used ψ to explore the likelihood that individuals moved between the group sites (higher values of ψ would indicate greater movement). To explore if adults and juveniles moved between sites in different ways, we assessed whether movement rates (ψ) were predicted by age. We also explored whether movement rates depended on which sites birds moved between, as sites were not evenly separated and had variable topography between them which could have affected how likely hihi were to move from one location to another (Martin et al., 2006; Strandburg-Peshkin et al., 2017). Thus, to investigate residency and movement for each separate year, we constructed sets of models with all possible combinations of ρ and ψ parameters and ranked these by their corrected Quasi-Akaike Information Criterion (QAICc) values. All models were assessed for

goodness-of-fit (GOF) using median \hat{c} (variance inflation factor, a measure of overdispersion) (Burnham & Anderson, 2002; Gath, 2017; White & Burnham, 1999), revealing low levels of overdispersion in all years (median \hat{c} : 2015 = 1.51; 2016 = 1.39; 2017 = 1.72). We calculated QAICc weights based on change in QAICc from the top-ranked model (Burnham & Anderson, 2002). Models with QAICc weight > 0.005 were included in model-averaging to calculate effect sizes and 95% confidence intervals of parameters. Any averaged parameter with a confidence interval that did not span 0 was considered to have a significant effect.

All further analyses were conducted in R (version 3.5.0) (R Core Team, 2018). To investigate whether related individuals were present in group sites, we calculated the proportion of surveys in which each juvenile was observed in the same group site as either of its parents, and the proportion of surveys each juvenile was seen in the same group site as its maternal siblings from the same breeding season (hihi fledge 1-5 young per clutch; across our study years, we recorded a mean of 2.04 ± 0.08 siblings per nest in group site observations; numbers of nests with observed fledglings: 2015 = 20, 2016 = 36, 2017 = 42). We excluded any juveniles we only saw in one survey, as we could not calculate a proportion for these individuals (N : 2015 = 10; 2016 = 18; 2017 = 10). When calculating the proportions of surveys spent with maternal siblings, we also excluded juveniles with no recorded siblings, as either they were from single-fledgling nests or their siblings may have died after fledging (N : 2015 = 7; 2016 = 10; 2017 = 8). As these initial calculations showed many juveniles were never seen with siblings (See Results), we then analysed whether ever being seen with siblings (yes = 1, no = 0) was influenced by proximity between group sites and nests-of-origin (distance to nearest 50m from group site to nest-of-origin, measured using Google Maps 2018) using a binomial Generalised Linear Model (GLM). Nests were distributed across the 2.5 km² island, so how far hihi had to disperse from nests to reach group sites varied (median distance = 410 m; minimum distance = 50 m, maximum distance = 1400 m) and could have affected how likely siblings were to make it to the same area post-dispersal. We also included number of surveys each individual was seen in, and number of siblings each bird had to investigate if co-occurrence was predicted by random sampling chance. We constructed a set of candidate models including all combinations of predictors and ranked models by their AICc values. Including any model

< 2 AICc units larger than the top-ranked model, we calculated averaged effect sizes ($\pm 95\%$ confidence intervals) for predictors using the package AICcmodavg (version 2.1-1) (Mazerolle, 2017). Models were checked for over-dispersion, but correction was not needed (Hector, 2015). Based on the evidence of extremely infrequent co-occurrence of related individuals (see Results) from this initial exploration, we did not analyse effects of relatedness in any greater detail.

Quantifying association network structure

We determined whether juvenile hihi associated with others based on age or location characteristics using social network analysis. First, we constructed weighted social networks for each year, where associations between birds depended on spatiotemporal proximity of individuals (i.e. hihi observed in the same group site at similar times to one another). We used the gathering function “gmmevents” in the R package asnipe (version 1.1.9) (Farine, 2013), which assigns individuals to association events based on their temporal proximity (in our dataset, these times were to the nearest 30 seconds) (see Appendix). Before exploring patterns with age or group site, we checked that there was variation in associations strengths (i.e. networks were non-uniform) by calculating each network’s coefficient of variation (cv); this explains how much the strength of social ties between pairs (dyads) of birds differs (values over 0.6 are considered to represent strong, repeated connections) (Farine and Whitehead 2015). To show whether this differentiation was stronger than expected by random chance, we used pre-network data stream permutations to create 1000 randomised networks where we had reshuffled individuals between association events, then compared if our cv values were significantly higher than values from randomised networks (Farine, 2017; Farine & Whitehead, 2015). Significance of all further network analyses also used this same method of comparing to a null model, and all P -values generated using permutations are specified as P_{rand} . Finally, using our yearly networks we (1) analysed whether hihi in the same age class associated most strongly (adult and juvenile “assortment”), and (2) explored the strength of juvenile-juvenile associations between birds that frequented the same group site, versus those that did not (juveniles were categorised by the site they were seen in for >50% of their surveys). For each analysis we used the assortnet package (version 0.12) (Farine, 2014) to generate assortment

coefficients (r) for each network, a value from -1 (disassociation between individuals of the same age class or location) to +1 (strong association between individuals of the same age class or location). Again, we compared observed assortment to assortment in permuted networks to determine the significance of effects (Farine, 2014; Newman, 2002).

Results

Was grouping structured by age?

There were two group sites in 2015 and three group sites in each of 2016 and 2017 where the majority of juveniles were observed (juveniles N : 2015 = 37; 2016 = 79; 2017 = 91; adults N : 2015 = 45; 2016 = 62; 2017 = 68). For reference in terms of juvenile representation in groups, only 17 extra juveniles (16%, out of 108 total) were not seen in groups during 2017, when a full island search was conducted concurrently to group site observations as part of a complete population survey (see Franks et al., 2020). Our multistate analysis showed that while adults did visit group sites, they were more transient than juveniles; juveniles were re-sighted at least twice as frequently in successive survey occasions compared to adults in all three years (Table 2; Figure 1a, b, c; top-ranked models explaining re-sighting included age: Table A1). Re-sighting was constant in 2015 and 2017 but varied across survey occasions in 2016 for both adults and juveniles (Table A1), suggesting some variation in grouping behaviour across years. This meant that, on average, 70% ($\pm 2\%$ S.E.) of birds seen in group sites were juvenile (significant difference between counts of adults and juveniles present in each survey; Wilcoxon rank sum test: 2015: $W = 277$; $P = 0.002$; 2016: $W = 951.5$; $P < 0.001$; 2017: $W = 1290.5$; $P < 0.001$). This age composition was also reflected in social structure. All networks consisted of non-uniform associations (Table A2), which was partially due to strong positive assortment by age (Table 3): each year, the biggest proportion of associations occurred between juveniles only (2015: 38%; 2016: 57%; 2017: 56% of associations, Tables A3-5). Each year, individuals varied in their number of associates, (median number of associates recorded per individual: 2015 = 8, range = 0 – 36; 2016 = 11, range = 0 – 50; 2017 = 12, range = 0 – 69), so we note that not all juveniles were equally social while in group sites.

How much did hihi move between different sites?

Quantifying movement (Ψ) in our multistate analysis showed a low likelihood that hihi transitioned between group sites, although this did vary depending on the site birds were moving to and from (Table 2, Figure 1d, e, f; Table A1). Movement also depended on age: juveniles showed a small significant likelihood of transitioning from one group site to another between surveys, while our models did not show significant support for most adult movement likelihoods. Combined with their lower re-sighting probability, this suggests adults were only transitory visitors to group sites (Table 2; Figure 1d, e, f; Table A1). However, when juveniles did move it was as individuals (on average only two or three juveniles moved between each survey, mean: 2015 = 2; 2016 = 3; 2017 = 3), and the majority of juveniles were only ever seen at one site (proportion of juveniles that never moved group site: 2015 = 0.78; 2016 = 0.44; 2017 = 0.62; maximum number of moves by individuals: 2015 = 3; 2016 = 7; 2017 = 7). Furthermore, all juvenile-only networks in all three years were strongly positively assorted by primary group site, while associations among juveniles across different sites were much weaker (Table 3; Tables A6-8; Figure 1g, h, i). This meant juveniles were largely faithful to their group site, where they were likely to associate and interact with juveniles also commonly using the same site.

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

There were very few occasions when juveniles were seen in the same group site during the same survey occasion as their parents (mean \pm S.E. proportion of surveys: 2015 = 0.02 \pm 0.02; 2016 = 0.03 \pm 0.01; 2017 = 0.08 \pm 0.02; 86% of juveniles never seen with parents), or their maternal siblings (mean \pm S.E. proportion of surveys: 2015 = 0.22 \pm 0.08; 2016 = 0.25 \pm 0.04; 2017 = 0.28 \pm 0.04; 53% of juveniles never seen with siblings). Individuals that were seen in group sites closer to their nest-of-origin were not more likely to be seen with maternal-siblings each year (null model highest ranked; Table A9). Being recorded in more surveys did not affect co-occurrence with maternal siblings (Table A9).

Together, this low likelihood of juveniles being resident with parents or maternal siblings suggested that relatedness does not drive association in these groups.

Discussion

Here we combined multistate analysis and social network analysis to characterise age composition, relatedness, and the level of movement between spatially distinct sites in aggregations of birds, and then clarified how social structure related to opportunities for association in juveniles. Across three consecutive years of data collection in three different cohorts, we found that aggregations of juvenile hihi occurred consistently at the end of each breeding season, with limited movement between different group sites. Although some adults were observed, their presence was much more transient. Network associations reflected these differences in residency: rather than associating with adults, juveniles most strongly associated with other juveniles frequently present in the same group sites. Finally, juveniles were almost never seen with their parents (occurred in only 2-8% of surveys across the study) and were rarely sighted with their maternal siblings (22-28% of surveys). In relation to previously-described social structures (Table 1), our results suggest juvenile hihi groups resemble gangs, where juvenile birds aggregate around communal roosts (Wright et al., 2003) or other social meeting places (Ward & Zahavi, 1973) which are separate from adults (Dall & Wright, 2009). This is in contrast to flocks, where groups of individuals move together over large distances (Templeton et al., 2012) or crèches, where juveniles associate with related adults (Balda & Balda, 1978). Although modelling suggests gang-like groups may form across a range of foraging niches (Dall and Wright 2009), empirical detection of this group structure has received little attention with only two examples available in the literature (e.g. Common quelea *Quelea quelea*: Ward and Zahavi 2008; European raven: Dall and Wright 2009). Thus, by exploring factors structuring social aggregations, we are able to better understand the social environment that young birds encounter during their first few months of independence from parents.

Why might juvenile hihi form “gangs”? Dall & Wright (2009) hypothesised that gangs are most likely to occur when resources are patchily distributed, rapidly-depleting “bonanzas” that cannot be defended

alone. Individuals therefore maximise their grouping behaviour, given the probability of locating such a resource and ability to defend it. Although this model was developed to explain group formation in juvenile ravens and invoked large animal carcasses as the ephemeral resource, juvenile hihi may face a similar foraging challenge. During the late summer and autumn, juvenile hihi forage for fruits and nectar from a diversity of trees and shrubs that vary in availability, and they are often observed to consume fewer ripe fruits than either adults (C. Andrews, unpublished data), or the two other bird species that dominate their foraging guild (tūi *Prosthemadera novaeseelandiae*, and bellbird/korimako *Anthornis melanura*) (Craig, 1985; Craig et al., 1981). Water availability is also restricted on this island during this period. Overall, accessing these important resources alone may be unlikely for juvenile hihi, but foraging as a group could help provide them with an advantage.

Dall & Wright's model (2009) also predicted that gangs should be more likely to form when social groups are stable and there are opportunities for repeated interactions and formation of social reputations. We found that individuals formed stable associations within group sites, and observed them participating in both foraging activities and affiliative-type behaviours. For example, huddling (where 2-10 juveniles were seen lining up side-by-side on perches), following, and allopreening were observed throughout surveys (V. Franks, pers. obs.), which suggests that juvenile hihi interact in groups rather than simply co-occurring passively in the same place at the same time. However, the exact purposes of these behaviours are difficult to uncover, and unfortunately, we do not have data available on individual (or group) search efficiency or dominance over food to assess effects on outcomes such as social status. Furthermore, we only studied groups during the day; sociality at other times (for example, at night while roosting) may differ and influence diurnal foraging behaviour. Finally, individual-level variation may also be important to consider as our results showed some inter-individual variation in residency, social connections, and movement behaviour, which suggested there were gradients in how individual juveniles behaved within the group. Studying this variation further may help elucidate the extent to which individual juveniles employ alternative social strategies employed and should explore the consequences of such variation for later life. Nevertheless, demonstrating juvenile-dominated groups in hihi has provided rare empirical evidence that gangs occur beyond scavenging ravens and

granivorous queleas, and suggests that this type of sociality could be more common in juvenile birds than currently described. Future research could now experimentally test how these groups function, to further our understanding of whether gang-like sociality is particularly beneficial to naïve juveniles.

Ecological factors such as resource type and availability are also likely to drive *where* social groups (such as gangs) form, and encourage animals to coexist in the same place at the same time while they utilise localised resources (Gall & Manser, 2018; Mourier et al., 2012; Strandburg-Peshkin et al., 2017). For example, recent studies describing social structure for vulturine guineafowl (*Acryllium vulturinum*) and foxes (*Vulpes vulpes*) found that group composition and social behaviour changed between seasons, highlighting the influence of environmental conditions such as rainfall and temperature (Dorning & Harris, 2019; Papageorgiou et al., 2019). In our study, the aggregations of juvenile hihi that formed each year were structured by location as individuals consistently used particular sites, but across different breeding seasons there was variation in the location of group sites, amount of temporal consistency, and population productivity or size. Thus, socioecological factors may have an important influence on overall group dynamics. We did not quantify resources and vegetation for each site in the three years of our study, but anecdotally at least these sites tended to include water sources for bathing or drinking, which are otherwise limited at that time of year. Thus, it is likely that factors such as food or water availability may help explain the location of where juvenile aggregations form, and may be a subject for further experimental tests to help support the observational evidence linking environment and social aggregations that have been shown so far (e.g Dorning and Harris, 2019; Papageorgiou *et al.*, 2019).

Alternatively, structured groups can arise because of individual-level effects, such as phenotype (Croft et al., 2005; Firth & Sheldon, 2016; Fletcher, 2007). Individuals may group with others that are similar to themselves (positive assortment) (Jiang et al., 2013; Peuhkuri, 1999), but may avoid others if they occupy different niches due to characteristics including size and age (negative assortment) (Catterall et al., 1989; Marchetti & Price, 1989) or to avoid competition (Marchetti & Price, 1989; Sol et al., 1998). We found that hihi associated by age class in the group sites we studied, and few adults joined the

putative gangs. These adults were also neither parents nor maternal-siblings. Although we cannot yet explain why some adults were present at group sites while others were not, they may have been subordinate individuals, or otherwise unable to access resources without knowledge from the group (Dall & Wright 2009). Alternatively, they could have been paternal relatives (extra-pair paternity is high in hihi: Brekke et al., 2013), but unfortunately these data were not available at the time of our study. Even if associations arise only from co-occurrence in the same place at the same time, the composition of phenotypes may still have important consequences for finding food, and avoiding predators or disease (Aplin et al., 2012; Drewe, 2010; Krause et al., 2009; Krause & Ruxton, 2002; Schakner et al., 2017). This is because the individuals present will affect information sharing, likelihood of pathogen transmission, and the outcomes of competitive or affiliative interactions (Aplin et al., 2012; Danchin et al., 2004).

Exploring group structure should be an essential first step for research into social environment as it can generate discussion for later experiments manipulating group composition, or information availability, that test why animals form social groups. For example, a recent review highlighted that accounting for social structure has provided new biological knowledge or changed theoretical predications about the importance of factors such as relatedness and spatial influence on animal social organisation (Cantor et al., 2019). By combining spatial and social network analyses, here we have provided a putative example of a group form that has rarely been described in the literature, despite it being theoretically plausible (Dall & Wright, 2009). Nevertheless, more studies are required if we are to understand the similarities and differences in social structures across taxa and how they relate to species' ecology.

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

Y = Yes, N = No. References: ¹Saitou 1978; ²Saitou 1979; ³Marzluff et al., 1996; ⁴Marzluff & Balda 1992.

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

Estimates generated from multistate models in Table A1 with Δ QAIC weight > 0.005; significant estimates where confidence intervals (LCI, UCI) did not span 0.00 are highlighted in bold. For movement estimates, letters a-e correspond to group sites shown in Figure 1d, e, f to show likelihood of movement between each different group site.

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

Standard error and significance of assortment (P_{rand}) calculated in comparison to 1000 permuted networks. Significant values (at $P < 0.05$) are highlighted in bold.

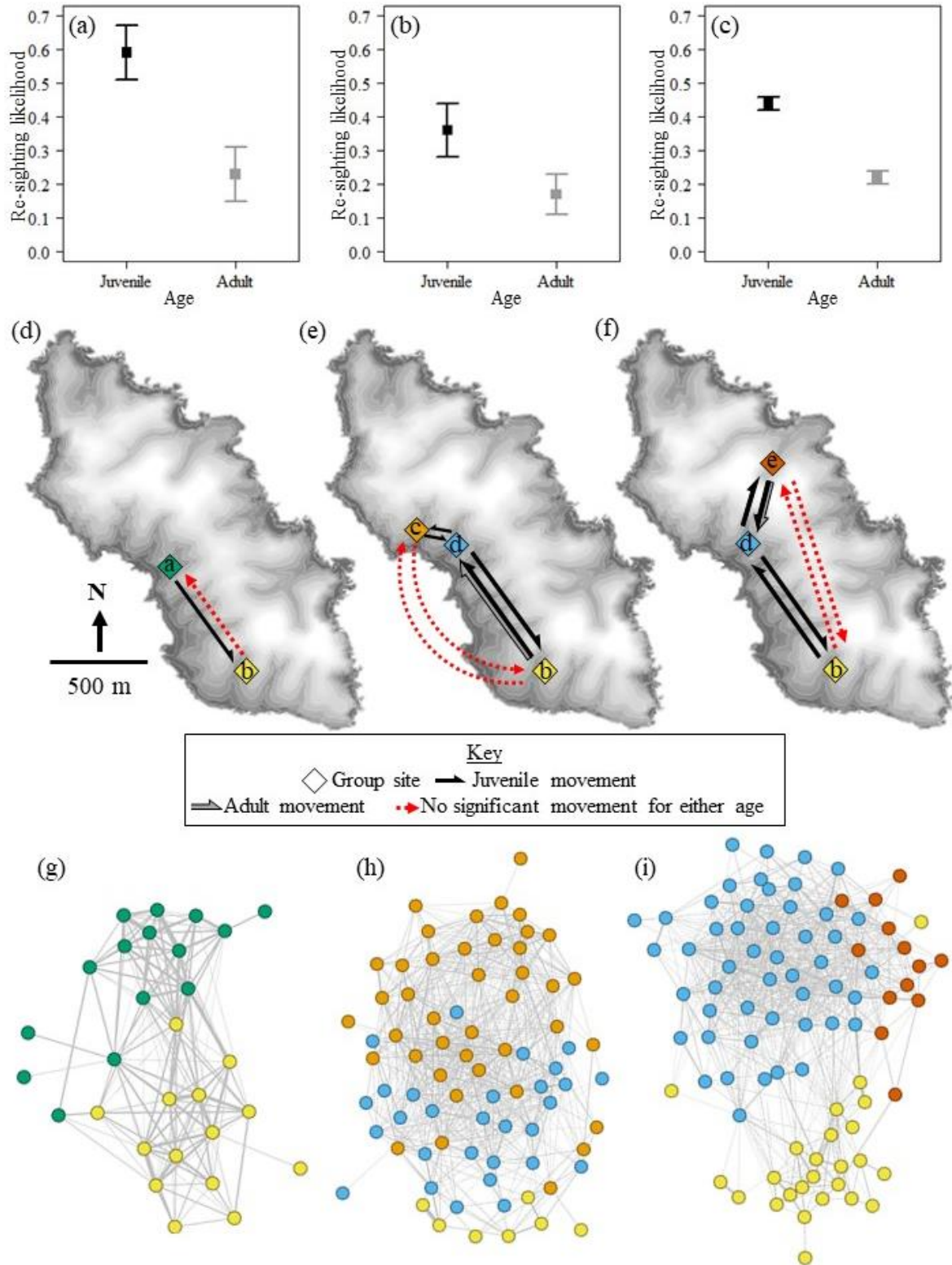


Figure 1. Re-sighting (a-c), movement (d-f) and associations (g-i) for 2015 (left), 2016 (middle) and 2017 (right)); (a-c) re-sighting probability estimates (\pm S.E.) for juveniles (black lines) and adults (grey lines); (d-f) movements between different group sites for juveniles (black arrows) and adults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

arrows). On map, shading corresponds to altitude, increasing in 10m steps from 0m (darkest) to approx. 80m (lightest). Lettered diamonds correspond to group sites in Table 2 and colours correspond to network figures in (g-i); (g-i) show social networks where nodes (circles) represent individual hihi and are coloured according to the site in (d-f) where they were observed in over 50% of their surveys (2015 network: N = 45 adults and 37 juveniles; 2016: N = 65 adults and 79 juveniles; 2017: N = 70 adults and 91 juveniles). Lines (edges) represent co-occurrence in group sites at similar times (N edges: 2015 = 435; 2016 = 1173; 2017 = 1439). Network visualisations were constructed in Gephi (version 0.9.2) (Bastian et al., 2009) with a force-atlas layout that clustered together more strongly associating nodes (individuals).

Appendix 1

Additional information on detecting groups for observations

Each year, we surveyed between five and nine sites from January to February to detect groups (in 2016 and 2017, we increased the search area to ensure no other groups were missed). All sites were forested gullies located on both the East and West sides of Tiritiri Matangi, and were the main patches of regenerating natural flora on the island. We recorded the numbers of unique juveniles for one hour in each gully location, and group sites were assigned after two weeks if we saw at least three juveniles in more than 8/10 surveys per location. We further confirmed that there were no other group sites during the annual February population survey, which is conducted every year by trained conservation staff who search the entire island over 40 hours. We then continued to survey group locations to collect grouping data from February to April.

Defining number of surveys for multistate analyses

Originally, during our group site observations we recorded a total of 15 hours per site in 2015, and 25 hours per site in 2016 and 2017 (surveys were distributed evenly across the three study months in each year). However, while multistate analyses require each site to be present at each replicated time point to quantify movement between sites, our different sites were not surveyed at the exact same time (due to one observer). Thus, we combined consecutive surveys from different sites so that each time point represented every group site. There was a maximum of two days between these combined surveys to limit movement between groups and prevent hihi from being recorded twice in the same survey occasion. Recording hihi in separate groups representing the same survey occasion happened very rarely (2015 = 1/656 re-sightings; 2016 = 9/1974 re-sightings; 2017 = 7/3180 re-sightings), but if it did, we treated the bird as a member of the group where it was seen last to acknowledge that a change of group had occurred. Different intervals between survey occasions were accounted for in analyses, so likelihoods were not confounded by time. Overall, there were 8 survey occasions in 2015, 14 in 2016, and 20 in 2017; an example re-sighting history for one individual in 2015 is “aa0aabbb”, where the bird was seen in group “a” in survey occasions 1, 2, 4 and 5, not seen in survey occasion 3, and seen in group “b” for the remainder of survey occasions.

Verifying survey method

In 2016, all hihi were fitted with Radio Frequency Identification (RFID) Passive Integrated Transponder (PIT) tags in plastic leg rings that replaced one colour ring in each bird’s combination (use of tags was approved by the Auckland Zoo Ethics Committee, New Zealand). We set up temporary supplementary sugar water feeders equipped with RFID loggers in the juvenile group sites (see Figure 2 for locations of group sites in 2016); these temporary feeders were additional to the main permanent supplementary sugar water feeders provided year-round for hihi. These RFID loggers remotely recorded visits of

individual hihi across a 15-hour period each day (encompassing sunrise to sunset) which allowed us to assess if the number of birds present in our hour-long surveys used to observe group sites captured an accurate representation of birds present over the entire day. We compared number of individuals collected from RFID logging at feeders and in each 1-hour survey on the same day over the period when feeders were present in group sites (7th Feb – 6th April 2016). There was strong correlation in numbers of hihi recorded by each of the two methods (Figure A1; $S = 22530$, $\rho = 0.69$, $P < 0.001$; PIT tag method recorded a median of 0.5 birds per day fewer compared to observations, range = -14 – +11 for PIT tag vs. observations). Overall, there was no significant difference in number of birds recorded by the two methods each day (paired Wilcoxon signed rank test: $V = 1278.5$, $P = 0.83$). Thus, busier days recorded more hihi using both methods, and suggested that collecting data on a coarser scale with 1-hour observations still accurately represented the number of birds present at a site that day.

Proximity network construction, checking, and analysis

We constructed weighted social networks for each year based on spatiotemporal proximity (hihi co-occurring in the same group site at the same time were associating) in the R package *asnipe* (version 1.1.9) (Farine, 2013). All networks were weighted, which incorporate both the number and strength of social connections (Farine, 2014). We used the “*gmmevents*” function in the R package *asnipe* (version 1.1.9) (Farine, 2013) to detect temporal clusters in our time-stamped (to within 30s) sightings data and build an association matrix (Farine, 2013; Psorakis et al., 2015). Using this approach avoided artificially restricted associations, which can occur using a more fixed time-window approach (Psorakis et al., 2015). Each year, we confirmed that hihi formed non-random associations by calculating the coefficient of variation (“*cv*”) of each network (values over 0.6 are considered to represent strong, repeated connections) (Farine and Whitehead 2015) (Table A2).

To ensure we accurately captured potential to associate based on length of “*gmmevents*” time windows, we compared the length of the time windows produced by the “*gmmevents*” function (“*event lengths*” in seconds), with the length of time hihi spent in the group sites based on repeated re-sightings in successive time blocks during surveys (seconds to the nearest 30s). The event lengths calculated by “*gmmevents*” were similar or shorter in length than re-sighting times (median length of event windows: 2015 = 119.37 s, 2016 = 90.44 s, 2017 = 90.52 s; median re-sighting from observation blocks: 2015 = 90 s, 2016 = 90 s, 2017 = 120 s; Wilcoxon rank sum test comparing length of event windows to re-sighting time, 2015: $W = 126700$, $P = 0.34$, 2016: $W = 541210$, $P = 0.54$; 2017: $W = 811840$, $P = 0.01$). This suggested the automated method reasonably defined the potential to associate over the same time, or a shorter time, than hihi were present in a group; we believe this is reasonable, as we would not expect birds to be associating for longer than they were observed, and it accounts for fluctuations in associations based on small scale individual movements in and out of our observation area.

For all hypothesis testing using networks, we compared observed networks to randomised networks as a null model (Croft et al., 2011; Farine, 2017; Farine & Whitehead, 2015). Randomised networks were generated using permutations of the data-stream in *asnipe*, which randomly swaps records of individuals while maintaining original data structure and controlling for sampling bias (Farine, 2013, 2014, 2017; Farine & Whitehead, 2015). Significance was calculated by comparing the size of the test statistic of the real network to test statistics of 1000 randomised networks (1000 = number of permutations).

Appendix 2

Table A1. Multistate models ranked by ΔQAICc values analysing re-sighting (ρ) and movement (Ψ) between groups of hihi for 2015, 2016, and 2017, depending on age of individuals, time (recapture event) and group sites.

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

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

Null model $S(.)\rho(.)\Psi(.)$ included for comparison. All models corrected by median \hat{c} following goodness-of-fit testing. AICc weight indicates relative likelihood of each model.

Table A2. Coefficient of variation (cv) values for each network used in analysis and significance of the differentiated associations they explain in comparison to permuted networks (P_{rand}).

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)

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

a_i^w = row sums, b_i^w = column sums; due to rounding, sum values may not be exact. Table is symmetrical so half the values are presented.

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

a_i^w = row sums, b_i^w = column sums; due to rounding, sum values may not be exact. Table is symmetrical so half the values are presented.

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

a_i^w = row sums, b_i^w = column sums; due to rounding, sum values may not be exact. Table is symmetrical so half the values are presented.

Table A6. Mixing matrix showing distribution of edge weights between juveniles depending on the group where they were most commonly located in 2015.

	Site a	Site b	a_i^w
Site a	0.499	-	0.588
Site b	0.009	0.322	0.412
b_i^w	0.588	0.412	1.000

Site lettering refers to group locations in Figure 6, a_i^w are the row sums, b_i^w are the column sums; due to rounding, sum values may not be exact. Table is symmetrical so half the values are presented.

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

Site lettering refers to group locations in Figure 6, a_i^w are the row sums, b_i^w are the column sums; due to rounding, sum values may not be exact. Table is symmetrical so half the values are presented.

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

Site lettering refers to group locations in Figure 6, a_i^w are the row sums, b_i^w are the column sums; due to rounding, sum values may not be exact. Table is symmetrical so half the values are presented.

Table A9. Ranking of generalised linear models analysing variation in the proportion of surveys where juveniles were seen with their nest siblings across all three years of the study.

	AICc	Δ AICc	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

Models are ranked by Δ AICc values, and weight indicates relative likelihood of each model. Null model (~1) included for comparison.

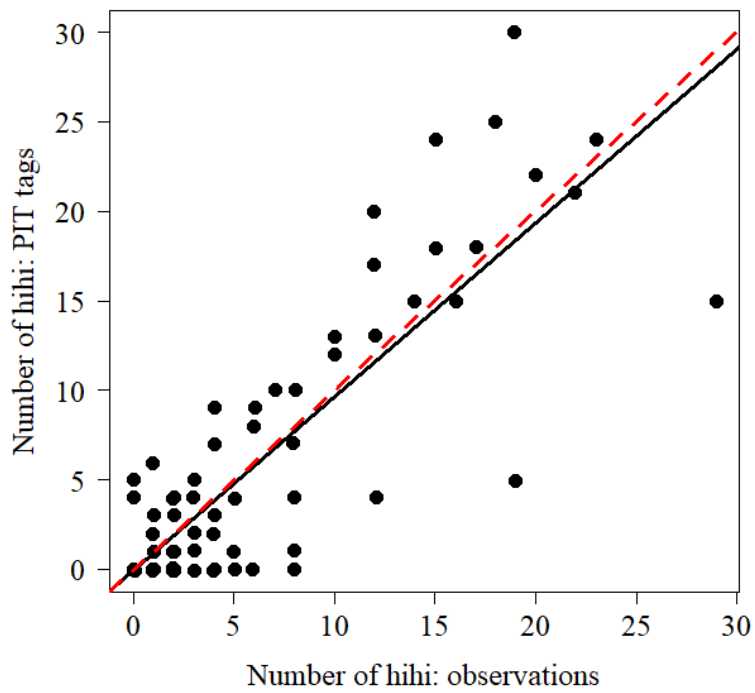


Figure A1. Correlation between the number of individual hihi recorded by 1-hour observations in group sites and from PIT-tag recorders at feeders across the entire length of the same day of survey. Red dashed line represents 1:1 correlation, and black line represents correlation from observed data, calculated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