

LETTER

Cooperative breeding and the emergence of multilevel societies in birds

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Abstract

Multilevel societies (MLSs), where social levels are hierarchically nested within each other, are considered one of the most complex forms of animal societies. Although thought to mainly occurs in mammals, it is suggested that MLSs could be under-detected in birds. Here, we propose that the emergence of MLSs could be common in cooperatively breeding birds, as both systems are favoured by similar ecological and social drivers. We first investigate this proposition by systematically comparing evidence for multilevel social structure in cooperative and non-cooperative birds in Australia and New Zealand, a global hotspot for cooperative breeding. We then analyse non-breeding social networks of cooperatively breeding superb fairy-wrens (*Malurus cyaneus*) to reveal their structured multilevel society, with three hierarchical social levels that are stable across years. Our results confirm recent predictions that MLSs are likely to be widespread in birds and suggest that these societies could be particularly common in cooperatively breeding birds.

KEYWORDS

cooperative breeding, *Malurus cyaneus*, multilevel society, social networks, social structure, sociality, superb fairy-wren

INTRODUCTION

Multilevel societies (MLSs) represent social structures that comprise two or more social levels nested within each other (e.g. family units or breeding pairs that form bands, and bands that form clans), and where units at each level (other than the upper-most) are socially cohesive (Grueter et al., 2020). MLSs were first described in Hamadryas baboons (*Papio hamadryas*) (Kummer, 1968) and subsequently in other primates (Kirkpatrick & Grueter, 2010; Snyder-Mackler, 2012), with a number

of two- and three-level societies also described in other mammals, such as African elephants (Wittemyer et al., 2005) and cetaceans (Tavares et al., 2016; Whitehead, 2012). The vast majority of human societies also show a multi-tiered structure to their social system, particularly hunter-gatherer societies consisting of families that form local bands, which in turn form higher-level tribes (Chapais, 2011; Grueter, 2017; Grueter et al., 2020; Migliano et al., 2017). The need for individuals to track and maintain highly differentiated relationships across each level—potentially spanning a large number of conspecifics—is thought to make multilevel societies one of the most complex forms of social structures in vertebrates (Swedell & Plummer, 2012). As a result, MLSs

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are of particular interest for understanding the evolution of sociality (Grueter et al., 2017). Nevertheless, we still have limited understanding of the drivers and functions of this type of social structure.

Multilevel societies are hypothesised to provide flexible social responses to environmental variability without compromising the integrity and composition of the social units (Kummer, 1968). Because MLSs allow groups to increase or decrease in size in response to unpredictable conditions, they provide members with a distinct advantage over species with fixed group sizes (Grueter, 2017). For example Hamadryas baboons, which usually live in one-male multi-female groups, can aggregate to form clans, then bands and troops (Schreier & Swedell, 2012), and in guinea baboons units form parties and gangs (Patzelt et al., 2014), coalescing at sleeping sites and water holes to collectively defend resources and reduce predation risk (Schreier & Swedell, 2009). By being able to split back into family units, baboons can avoid competition when the environment becomes more unpredictable, for example when resources are limited and/or dispersed (Schreier & Swedell, 2012). While a dynamic social structure allows animals to solve problems that fixed social units cannot (Grueter, 2017), it remains unclear why some species form several nested social units while others remain agonistic or strictly territorial (Grueter et al., 2020). There is a need to unravel the potential ecological, social and genetic drivers that underlie the evolution of sociality and cooperation between social units.

Although research initially focused predominately on primates, it is now clear that MLSs are more common than previously thought (Bigg, 1990; Papageorgiou & Farine, 2020; Rubenstein & Hack, 2004; Whitehead, 2012; Wittemyer et al., 2005). Recently, it has been shown that a bird (the vulturine guinea fowl *Acryllium vulturinum*) exhibits a multilevel social structure (Papageorgiou et al., 2019). A number of other nested societies are also known to exist in birds, but these have only recently started to be considered within the framework of MLSs (Papageorgiou & Farine, 2020). For example bell miners (*Manorina melanophrys*) (Clarke & Fitz-Gerald, 1994; Painter et al., 2000), white-fronted bee-eaters (*Merops bullockoides*) (Hegner et al., 1982) and buff-rumped thornbills (*Acanthiza reguloides*) (Bell & Ford, 1986) live in societies structured into breeding groups nested within clans. If these social levels are consistent and stable, their societies would meet the criteria of an MLS (Grueter et al. 2021). Most of these species also breed cooperatively, raising the possibility that cooperative breeding might facilitate, or be driven by similar factors to, the formation of MLSs.

A few arguments support the proposition that cooperative breeding might set the scene for MLSs. In mammals, MLSs are commonly found in kin-structured societies (Patzelt et al., 2014; Städele et al., 2015). Likewise, many cooperative breeding birds maintain family-units for consecutive seasons (Cockburn, 1998; Downing et al., 2020; Kingma et al., 2014; Koenig & Dickinson, 2016). While

the presence of family units in-and-of-itself might not predispose cooperative breeders to form MLSs (i.e. this represents the base level, which equally applies to pair-living species), cooperative breeding is often associated with local kin structure (Painter et al., 2000). As a result of limited dispersal distances, cooperative breeders generally show high social viscosity (Hamilton, 1964), a spatial pattern where more related individuals live in closer proximity (Wolf & Trillmich, 2008). Thus, when forming larger groups, social viscosity would allow individuals to group with relatives. Forming larger groups can be of particular benefit during harsh conditions, for example during the non-breeding season when many species are not territorial, and environmental conditions more challenging. At this time, increased sociality might provide information about food availability (Aplin et al., 2012), or better group vigilance and defence against predation (Kenward 1978). Environmental harshness is also thought to promote cooperative breeding (Jetz & Rubenstein, 2011), by allowing breeding groups to buffer poor reproductive conditions (Rubenstein & Lovette, 2007). Thus, the conditions hypothesised to favour the evolution of cooperative breeding align with those predicting the evolution of MLSs (Schreier & Swedell, 2009; Städele, 2016).

Here, we propose that cooperative breeding could facilitate the emergence of multilevel societies. In accordance with Grueter et al. (2020), we define MLSs as social structures exhibiting (i) consistency of membership in each level over time, and (ii) spatio-temporal cohesion of core and upper levels. To test our proposition, we first evaluate the evidence from the literature on social structure in cooperatively breeding versus non-cooperatively breeding birds. We focus our search on Australian and New Zealand avifauna because of the relatively high-quality information available on the social structure of these species, and the preponderance of cooperative breeding in this region (Griesser et al., 2017). Second, we formally test for the presence of a multilevel social structure in a cooperatively breeding species putatively identified as displaying an MLS.

MATERIALS AND METHODS

Comparative analysis of cooperatively breeding birds

We performed a systematic literature search for evidence suggestive of the existence of multilevel societies across the Australian and New Zealand bird families that are known to include at least one cooperative breeding species [$n = 17$ families; 43 cooperatively breeding species and 70 non-cooperative species (Cornwallis, 2017)]. Following Cockburn (2006) and Cornwallis et al. (2017), we define cooperative breeding as a breeding system in which at least 10% of young are retained on their natal territory and provide care to the offspring of a breeding pair.

We collected the information available on social structure from the detailed species accounts of Handbook of Australian, New Zealand and Antarctic birds (HANZAB) (Marchant et al., 2006). We then updated this information by searching for studies published after 2000. We conducted a step-wise structured search in Web of Science using the following search strings: 1) “common name of the species” AND (social* OR winter OR aggregation OR congregation); and 2) “scientific name of the species” AND (social* OR winter OR aggregation OR congregation). For the species for which no records or very few records were found, we repeated the search with 3) “common name of the species*” (including various spellings and * for the plural) and OR “scientific name of the species”. The title and abstract of each study were screened to determine if it met the inclusion criteria: information about sociality, social organisation, social structure or demography of the species. Studies that met at least one of these criteria ($n = 100$ out of 965 articles) were read in full, recording the information on the social organisation or social structure of the species during both breeding and non-breeding season.

Species for which any sources suggested they form at least one higher social unit than the breeding group/pair were classified as potential MLS. Our criteria included: repeated aggregations of breeding groups/family groups/breeding pairs; formation of stable foraging flocks, clans, bands; supergroups, which were reported to be stable but also were observed to separate periodically into the original breeding pairs/groups. Species reported to form large and loose flocks or aggregations, or to defend a territory year-round, were not considered to exhibit MLS.

To assess whether cooperative breeding predicts the presumed presence of multilevel societies, we used phylogenetic logistic regression with the function `phylglm` in the R package `phylolm` (Ho & Ane, 2014) with MLS as binary response, and cooperative or not as explanatory variable. The model also included the length of text (cm) devoted to the social organisation of the species in the HANZAB as a covariate to account for the possibility that species for which more information is available may be more likely to be considered to have MLS. Numerical covariate (length of text) was scaled to zero-mean and unit-variance. We incorporated phylogenetic uncertainty into the error estimates of each parameter by running the model across 100 phylogenies (obtained from www.birdtree.org), using the Hackett backbone (Jetz et al., 2012), and summarised parameters using Rubin's rules (Nakagawa & De Villemereuil, 2019). We computed relative efficiency for each model parameter to determine the efficacy of accounting for phylogenetic uncertainty. This parameter varies between 0 and 1, and quantifies the efficiency achieved with the number of phylogenies used relative to the theoretical (maximal) efficiency obtained by using an infinite number of phylogenies. Values exceeded

the recommended value of 0.99 (Nakagawa & De Villemereuil, 2019) for all parameters, which suggests that 100 phylogenies adequately capture phylogenetic uncertainty.

Field case study

Field study system

We studied the social behaviour and movement of a population of superb fairy-wrens *Malurus cyaneus*, a small (9–12 g) facultatively cooperatively breeding songbird. We observed the social structure of the population across two years, with a particular focus on the behaviour of individuals during the non-breeding season. During the breeding season, fairy-wrens form stable pairs or groups which actively defend their exclusive breeding territory from conspecific intruders (Cooney & Cockburn, 1995; Rowley, 1964). However, during the rest of the year individuals from multiple breeding territories can aggregate to form larger groups (Fallow & Magrath, 2009). We quantified this pattern at Lysterfield Park reserve, located near Melbourne, Australia ($-37^{\circ} 56' 56.40''\text{S}$, $145^{\circ} 17' 45.60''\text{E}$) on the traditional land of Bunurong Boon Wurrung and Wurundjeri Woi Wurrung peoples of the Eastern Kulin Nation. The study area is comprised of open woodland, including areas with dense shrubs and open grassland. Almost all (98%) individuals in the study ($n = 198$) were colour banded with a unique combination of two metal, and two plastic coloured rings. All birds were sexed based on morphological traits (males develop a black bill and male breeding plumage in their first Spring; females and juveniles are indistinguishable) with the exception of 13 individuals, which disappeared before exhibiting male characteristics. Of these, nine were sexed as females by PCR (following methods in Eastwood et al., 2018). For the other four, no blood sample was collected; these individuals were also presumed females.

Field observations

We observed all individuals throughout 2018, 2019 and 2020 as part of a long-term study. During the breeding seasons (September-January/February) we identified 19 territories based on the movement of birds, and calculated their total area, using GPS. Individuals in the breeding groups were recorded weekly, reproductive attempts were followed and offspring banded. Over both breeding seasons (2018–19 and 2019–20) eight of the 19 breeding groups had one or two helpers, and the average 2018–2019 breeding group size (excl. offspring of the same breeding season) was 2.7 individuals (3.2 incl. new offspring). During breeding season 2019–2020, the average breeding group size was 2.5 individuals (5.8 individuals incl. new offspring).

During the months before and after each breeding season (March–April and September), all individuals were sighted weekly by systematically searching all territories and the broader surrounding area. Throughout the non-breeding season (May–August), groups coalesce into larger roaming flocks, which we defined as temporary aggregations of individuals in the same place at the same time (following Shizuka et al., 2014). During these months, we systematically searched for flocks. Whenever a flock was encountered, we followed all individuals in the flock for a minimum of 30 min. As in previous studies on related species (e.g. Farine & Milburn, 2013), flock membership during observations was unambiguous, with flocks of individuals moving together and being separated from other flocks by a considerable distance. While following flocks, we recorded the movement of the flock at intervals of 5 min with a handheld GPS (for later determination of home range size). We assigned each flock a unique identifier code and recorded the identity of all individuals in the flock using their unique combination of colour rings, along with the time and GPS coordinates of the observation.

Constructing social networks and identifying social units

We used the *asnipe* package (Farine 2013) in R (R Core Team, 2020) to construct a group by individual matrix for each non-breeding season, with every individual in the population as a column and every unique flock as a row, with cell values 0 and 1 corresponding to whether the individual was absent or present in a given flock. From these matrices, we calculated a social network for the population using the Simple Ratio Index (Hoppitt & Farine, 2018). We omitted from the networks 85 colour banded individuals that were observed fewer than five times per season and which disappeared from the study area during the first month of the data collection, as these would have generated excessive uncertainty in the resulting network (Davis et al., 2018). These transient individuals appeared to be mostly dispersing juvenile females, as they were all in female/juvenile plumage and generally observed only once. We constructed two networks, representing the social structure of our study population during May–August in 2019 and 2020.

To identify social units across different levels, we first plotted a histogram of association strengths, and noted that this distribution was multimodal. We first defined non-breeding groups from the upper-most mode, comprising pairs of individuals that were observed together more than 75% of the time. Then, following Papageorgiou et al. (2019), we identified the upper-level communities in the networks, and their composition, by running the ‘fast-greedy’ statistical community-detection algorithm in the R package *igraph* (Csardi & Nepusz, 2006). We tested the robustness of the composition of the non-breeding groups and communities by running the algorithm described by

Shizuka and Farine (2016). When testing the robustness of the communities’ composition, this algorithm bootstraps the observed group by individual matrix, constructs a social network from each bootstrapped dataset, identifies the community with the fastgreedy algorithm mentioned above, and records the propensity for each pair of individuals to be allocated to the same community. To test the robustness of non-breeding groups, we replaced the community detection process with the same assignment pairs of individuals that were observed together more than 75% of the time to the same group, and recorded the propensity for each pair of individuals to be allocated to the same group as in the original dataset. We ran the robustness algorithm 1000 times for each network, and evaluated how structured the population was in each of the seasons using the test statistic r_{com} , representing the robustness of the assignment of individuals into the same community across all bootstrapped networks. An r_{com} value exceeding 0.5 suggests that the network is highly structured by communities and, therefore, that there are consistent preferences among individuals to associate (Shizuka & Farine, 2016).

To confirm that non-breeding groups and communities in the networks were more strongly connected than expected by chance, we compared the mean association strength within groups and within communities of the real networks with those from 1000 permuted networks, using established pre-network permutations that swap pairs of 1s and 0s in the group-by-individual matrix (Farine, 2017b; Farine & Carter, 2020). Visual observation of the p -values suggested that 1000 permutations were sufficient for them to stabilise.

Testing for community stability across years

We tested if the social composition of the communities was consistent across two consecutive non-breeding seasons. To do so, we first created a matrix of community co-membership for our two non-breeding season datasets. Given that the identity of the breeding groups was maintained throughout the study period (represented by high edge weights between individuals of the same breeding groups in network 2019: mean = 0.93, SD = 0.12 and network 2020: mean = 0.90, SD = 0.11, see results), and that these could easily drive a high between-year correlation, we collapsed the breeding units into one node for this analysis. Thus, we generated a network as a matrix in which the rows and columns represented breeding units, and cell values were given 0 and 1 depending on whether two breeding groups were part of the same non-breeding community or not. We used a Mantel test to compare the breeding unit association matrix of the 2019 network with the one developed for the 2020 dataset to determine their similarity. High correlation values suggest consistent preferences among social units to associate across years.

Effect of home range overlap and breeding territory proximity on network structure

To determine the role of home range overlap in driving community structure, we calculated the kernel density estimation for 95% of the home range of each group during the two years of study using the `hadehabitatHR` R package (Calenge, 2015). For each non-breeding season, we created a matrix representing home range overlap by measuring the home range overlap of each group with all the others using the software QGIS (3.12). We then performed Mantel tests to quantify the correlations between networks representing group home range overlap and individual social networks.

To test if spatial proximity between breeding territories could influence social preferences and spatial overlap between individuals during the following non-breeding season, we calculated the position of the centroid for each breeding territory using the software QGIS (3.12). We then measured the distances between the centroids of all the breeding territories for breeding seasons 2018–19 and 2019–20 using the R package `Raster` (Hijmans & van Etten, 2016), thus generating a matrix of spatial distances between breeding territories for each of the two breeding seasons. We ran Mantel tests to quantify the correlations between these spatial matrices of breeding territory centroids and those representing social connection between groups during the following non-breeding season.

RESULTS

Comparative analysis

We found sufficient data on the presence/absence of potential MLS and cooperative breeding for 74 species out of the 113 species included in our research (see Table S2), with 22 species having evidence for a potential MLS (17 of 35 cooperative breeders and 5 of 39 non-cooperative breeders). For the remaining 38 species, there was not

enough information available on social organisation to classify the potential presence or absence of MLS. The comparative analysis indicated that cooperative breeders were more likely to be described using terms suggesting that they have a propensity to exhibit a MLS compared to non-cooperative breeders (46.1%, C.I = 26–67.7% probability vs. 8.6%, C.I = 5.0–14.4% probability; $\beta_{\text{non-cooperative breeders}} = -2.21$, SE = 0.75, $p = 0.003$) (see Table S1). The amount of text devoted to the social organisation in the HANZAB did not significantly influence our classification of MLS ($\beta = 0.14$, SE = 0.27, $p = 0.607$). Full model output can be found in Table S1.

Field case study

Social networks and multi-tier social structure in the superb fairy-wren

Our dataset comprised 1632 social associations across two years, involving 113 individuals (60 males, 53 females) from 19 breeding groups. From the social networks, we identified three different stable social tiers. First, the upper-most mode of the distribution of association strengths suggested that this was comprised of individuals from the same breeding group/pair (units that are maintained during the breeding season) as well as some associations containing individuals from different breeding groups, which we called supergroups. We then found that these breeding- and super-groups were embedded within robust and stable communities (sets of breeding groups/pairs that associate preferentially during the non-breeding season).

Non-breeding groups are composed of breeding groups and supergroups

From the two non-breeding season social networks, we identified groups as distinct clusters of individuals

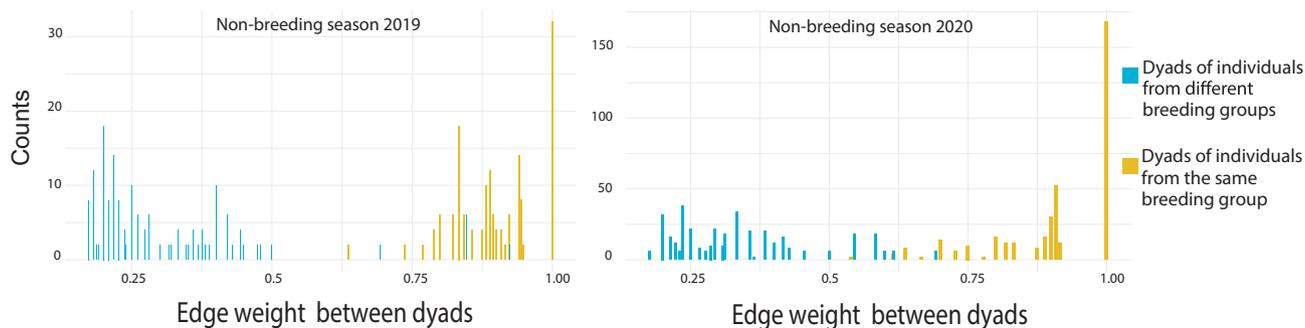


FIGURE 1 Base social tier of the MLS of superb fairy-wrens: individuals from the same breeding groups spend the non-breeding season together. Depicted is the strength of the social bond (edge weights) between dyads of individuals from 2019 and 2020 non-breeding season social network. Values above 0.75 show dyads forming part of the same non-breeding group, since they are consistently found together. Individuals that shared the same breeding groups the previous breeding season tend to maintain these social bonds during the non-breeding season by forming part of the same non-breeding group. Only edge weights higher than 0.17 are represented in the image

exhibiting very strong social bonds with each other (individuals found together more than 75% of the time) (see Figure 1). Robustness analysis of the co-membership of individuals in these groups confirmed that the study population had a clear group structure (non-breeding season 2019: $r_{\text{com}} = 1$; non-breeding season 2020 $r_{\text{com}} = 0.98$). Furthermore, our analysis on the structure of non-breeding groups in the social networks against 1000 permuted networks indicated that these were significantly more strongly connected than expected by chance ($p < 0.001$ for both years).

In 2019, 11 of 15 groups were composed solely of members of the previous season breeding group, but four were

formed by the members of two neighbouring breeding groups, forming supergroups (Figure 2). The same pattern was repeated in 2020, where 15 of the 17 clusters were composed of members of the previous season breeding group, while two formed supergroups (Figure 2). Moreover, the supergroups identified in 2020 were composed of the same breeding groups that had merged into supergroups in 2019, highlighting their stability across years. A post hoc analysis found that breeding group size was not related to supergroup formation ($\beta = 0.14$, $\text{SE} = 0.27$, $p = 0.607$). Rather, in at least three of the four supergroups, the dominant males of the two merging breeding groups had previously been part of the same breeding

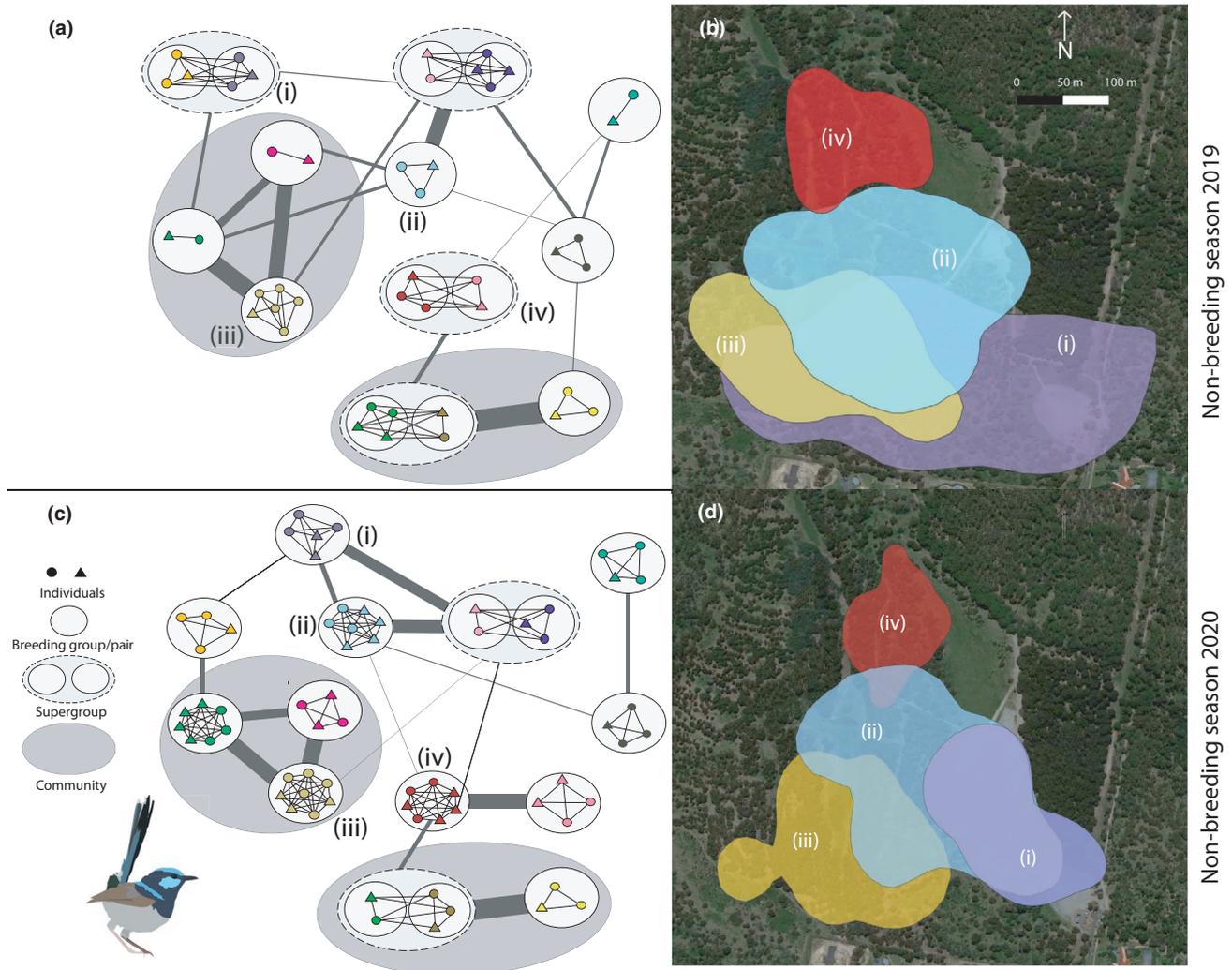


FIGURE 2 Overview of the multilevel structure of superb fairy-wren societies during the non-breeding season. Depicted is a portion of the network representing intergroup contacts in (a, b) 2019 and (c, d) 2020 non-breeding seasons. (a, c) At the lowest level of the society, colours refer to breeding group/pair membership with circles representing individual males and triangles representing individual females. Light grey ovals show non-breeding groups that are formed by breeding groups, while light blue ellipses with dashed line show non-breeding groups that correspond to supergroups. Dark grey ellipses represent examples of communities—sets of non-breeding groups that fission-fusion in and out of flocks, but have preferential associations with one-another. However, given the limited available space, only two communities per non-breeding season could be highlighted in the figure. Lines (in dark grey) connecting non-breeding groups represent whether they were observed together, with the thickness of the line showing the proportion of time each pair of non-breeding groups was in contact (highlighting that non-breeding flocks are not exclusive, but contain preferred associations). (b) The home range of four non-breeding groups represented by breeding groups (ii, iii) and two supergroups (i, iv) during the non-breeding season of 2019 and (d) the home range of the four non-breeding groups formed by breeding groups during 2020. The supergroups indicated by (i) and (iv) in 2019 split back into breeding groups during 2020 (d)

group (one the previous subordinate, the other the dominant). The converse was not always true: two dominant males that had previously been subordinates in the same breeding group did not join a supergroup. Unfortunately, we lack the data for the fourth supergroup since the dominant males were banded at the onset of the study in 2015, while they already occupied a dominant position.

Communities

In both non-breeding networks, the fast-greedy algorithm identified eight social communities in both the social networks. Analysis of the co-membership of individuals in these communities showed that the study population had a clear community structure (2019: $r_{\text{com}} = 0.79$, 2020: $r_{\text{com}} = 0.85$), confirming that preferential between-groups associations drive the highest social level in fairy-wren societies (Figure 2), while our analysis of the structure of communities in the social networks against 1000 permuted networks showed that these were significantly more strongly connected than expected by chance ($p < 0.001$ for both years). Furthermore, community social composition was correlated across the two years of study (Mantel test: $r = 0.53$, C.I. = 0.37–0.69, $p < 0.001$), confirming that communities represent long-term social preferences that are generally maintained across non-breeding seasons.

Effect of home range overlap and breeding territory proximity on network structure

Distance between breeding territories was significantly correlated with social structure during the non-breeding season. Mantel tests showed that breeding groups from more distant breeding territories had weaker social connections in non-breeding flocks [$r = -0.66$, C.I. = (-0.53, -0.79) for 2019 and $r = -0.6$, C.I. = (-0.45, -0.75), for 2020] and smaller home range overlap during the non-breeding season [$r = -0.42$, C.I. = (-0.25, -0.59) for 2019 and $r = -0.7$, C.I. = (-0.83, -0.57), for 2020], with all four correlations being statistically significant (at $p < 0.01$). The mean spatial distance (\pm SD) between breeding territories of individuals part of the same non-breeding community was 126 ± 53 m in 2020 and in 2019 mean = 122 ± 73 m. Breeding group home ranges during the non-breeding season were significantly larger than breeding territories [2019 median size breeding group home range during non-breeding season = 8.4 ha, IQR (Interquartile range, a measure equal to the difference between the 75th and 25th percentiles) = 5.6 ha; median breeding territory = 0.39 ha, IQR = 0.23; 2020 median non-breeding season home-range = 5.0 ha, IQR = 4.2 ha; median breeding territory = 0.76 ha, IQR = 0.39 ha]; breeding group size did not predict home-range size ($\beta = 1.16$, SE = 1.10, $t = 1.21$). Home-range size during the non-breeding

season varied between years (Wilcoxon test = 260, $p = 0.02$), as did the distance between breeding territory centroid and non-breeding home range centroid (2019 median = 84 m, IQR = 73 m, 2020 median = 48 m, IQR = 41 m). Many breeding groups showed large home range overlap during the non-breeding season, with an average (\pm SD) overlap between groups home range of $36 \pm 30\%$ during 2019 and $41 \pm 37\%$ during 2020.

DISCUSSION

Our comparative analysis of MLSs in cooperatively and non-cooperatively breeding birds shows that their emergence is likely facilitated by cooperative breeding and/or driven by similar factors to those driving cooperative breeding. Combining year-round detailed observations of individually marked fairy-wrens with social network analyses, we confirmed that one putative MLS species, superb fairy-wrens, live in a society that includes a multi-tiered structure outside of the breeding season, which is consistent between years. Together, these results support recent suggestions that MLSs are likely to be widespread in birds (Papageorgiou & Farine, 2020).

In superb fairy-wrens, three distinct social units emerge over the year, with the social units at each level having stable membership within and across years. When breeding, superb fairy-wrens live in territorial groups. However, the boundaries between territories collapse after the breeding season. During the non-breeding season, breeding groups interact with other breeding groups in a predictable way, sometimes forming supergroups (the intermediate social tier; Figure 2) that merge to form communities (the upper social tier; Figure 2). These communities are tightly connected clusters of individuals within the social networks of non-breeding flocks (Shizuka et al., 2014). During the following breeding season, communities and supergroups split back into breeding groups, reassembling again after the subsequent breeding season to re-form the same supergroups and communities.

The larger home ranges during non-breeding and variability in home ranges between years suggest that MLSs allow individuals to exploit larger areas during harsher periods. This is anecdotally supported by our data: groups exhibited larger non-breeding home ranges in 2019, which was preceded by four months (January–April) with dramatically less rainfall and higher maximum temperatures (harsher weather) relative to 2020 (see Supp. material 1). Additionally, an increase in predator pressure for adult individuals during the non-breeding season (unpubl. data) might increase the benefits of forming upper social units by providing safety when foraging is more challenging (Delm, 1990). Previous work in our population found that fairy-wrens spend less time being vigilant and more time foraging when in larger groups (McQueen et al., 2017). However, forming larger groups may also increase social conflict over future territories, breeding positions, or social partners. High

social viscosity, as in superb fairy-wrens, might mitigate inter-group aggression by allowing higher level groups to be formed among kin with established territories.

The importance of social viscosity

The potential role of relatedness and social viscosity is evident in the superb fairy-wren multilevel society. For

example in all known cases of the intermediate social level (supergroup), the dominant males involved were previously part of the same breeding group, meaning that they were most likely related. Furthermore, inter-territory proximity strongly explained the strength of the associations between breeding groups and, thus, the social composition of communities (upper social level). We cannot distinguish whether communities in the superb fairy-wren are driven exclusively by active

TABLE 1 Description of putative types of MLS across bird species from Australia and New Zealand

MLS society type	Description	Species	Cooperative?	References
Higher level social units during non-breeding	Individuals form large stable social units, called clans in some species, which typically disband into smaller breeding groups for breeding, and re-amalgamate after breeding	Chestnut-crowned Babbler	Yes	21
		White-browed Babbler	Yes	22
		Striated Thornbill	Yes	1
		Buff-rumped Thornbill	Yes	1;2
Higher level social units during breeding	94% of breeding groups were associated with at least one other group, <i>forming supergroups</i> . Males in a supergroup were related	Brown treecreeper	Yes	5;6
Colonial cooperative breeders	Colonies present discrete nested levels of social organisations. Within the colony, neighbouring males form coterries and within coterries, temporary coalitions between individuals from different nesting units can also arise	Bell miner	Yes	18;19
		Noisy miner	Yes	20
Higher level social unit during migration	Breeding groups congregate forming stable social units during the entire migration	Rainbow Bee-eater	Yes	23
Seasonal probabilistic fission-fusion MLS	Outside breeding season, breeding groups congregate preferentially with other breeding groups forming upper social units (i.e communities)	Black-faced Woodswallow	Yes	3;4
		Varied Sittella	Yes	7
		White-winged Fairy-wren	Yes	8–10
		Whitehead	Yes	11
		Apostlebird	Yes	12
		White-winged Chough	Yes	13
		Superb Fairy-wren	Yes	14
		Red-backed Fairy-wren	Yes	15;16
		Yellow-rumped Thornbill	Yes	17
		White-cheeked Honeyeater	No	24
Semi-colonial species	Species in which breeding pairs can show cohesion within well-defined groups of individuals within the colony, which cooperate to attack intruders or predators	Crimson Chat	No	25
		Orange Chat	No	26
		Yellow-plumed Honeyeater	No	27
		Fuscous Honeyeater	No	28

Note: We found support for a strong indication of multilevel society structure in 17 of 35 cooperatively breeding species, but only five of 39 non-cooperative species included in our search. For detailed species accounts and scientific names, see Supplemental dataset 1.

References: [1] HANZAB vol 6, pag 541. [2] HANZAB vol 6, pag 500. [3] HANZAB vol 7a, pag 445. [4] Rowley, 1999. Corella. [5] HANZAB vol 5, pag 232. [6] Doerr, E. and Doerr, V.A.J. (2006). *Anim Behav*. [7] HANZAB vol 6 pag 1007. [8] Rowley and Russel. (1995). *Emu*. [9] Rathburn, M.K. and Montgomerie R. (2003). *Emu*. [10] HANZAB Vol 5, pag 352. [11] HANZAB vol 6, pag 1027. [12] Griesser et al. (2009). *Ethology*. [13] Heinson, R.G. (1987). *Behav. Ecol. Sociobiol*. [14] Rowley, I. (1964). *Emu*. [15] Rowley I and Russell E. (1997). *Fairy-Wrens and Grasswrens*. Pag 183; [16] Macgillivray, W. (1914). *Emu*. [17] HANZAB vol 6, pag 510 [18] Bell, H.L. and Ford, H.A. (1986). *Behav. Ecol. Sociobiol*. [18] HANZAB vol 5, pag 615; [19] Painter et al. (2000). *Mol. Ecol*. [20] HANZAB vol 5, pag 631–632. [23] Garnett, S. (1985). *Emu*. [24] HANZAB vol 5, pag 1044–45. [25] HANZAB vol 5, pag 1212–1214. [26] HANZAB vol 5, pag 1203–1204. [27] HANZAB vol 5, pag 843–844. [28] HANZAB vol 5, pag 863.

social preference or involve ecologically driven mechanisms (Farine, 2017a; He et al., 2019), but we hypothesise that social viscosity leading to kin-neighbourhoods (Hatchwell, 2009) plays a fundamental role in driving the emergence of upper social units. Similarly,

in vulturine guineafowl, that have a similar social structure to superb fairy-wrens, preferred associations among groups appear to be linked to relatedness among males (D.R. Farine, *pers. obs.*) due to a strong female bias in dispersal (Klarevas-Irby et al., 2021).

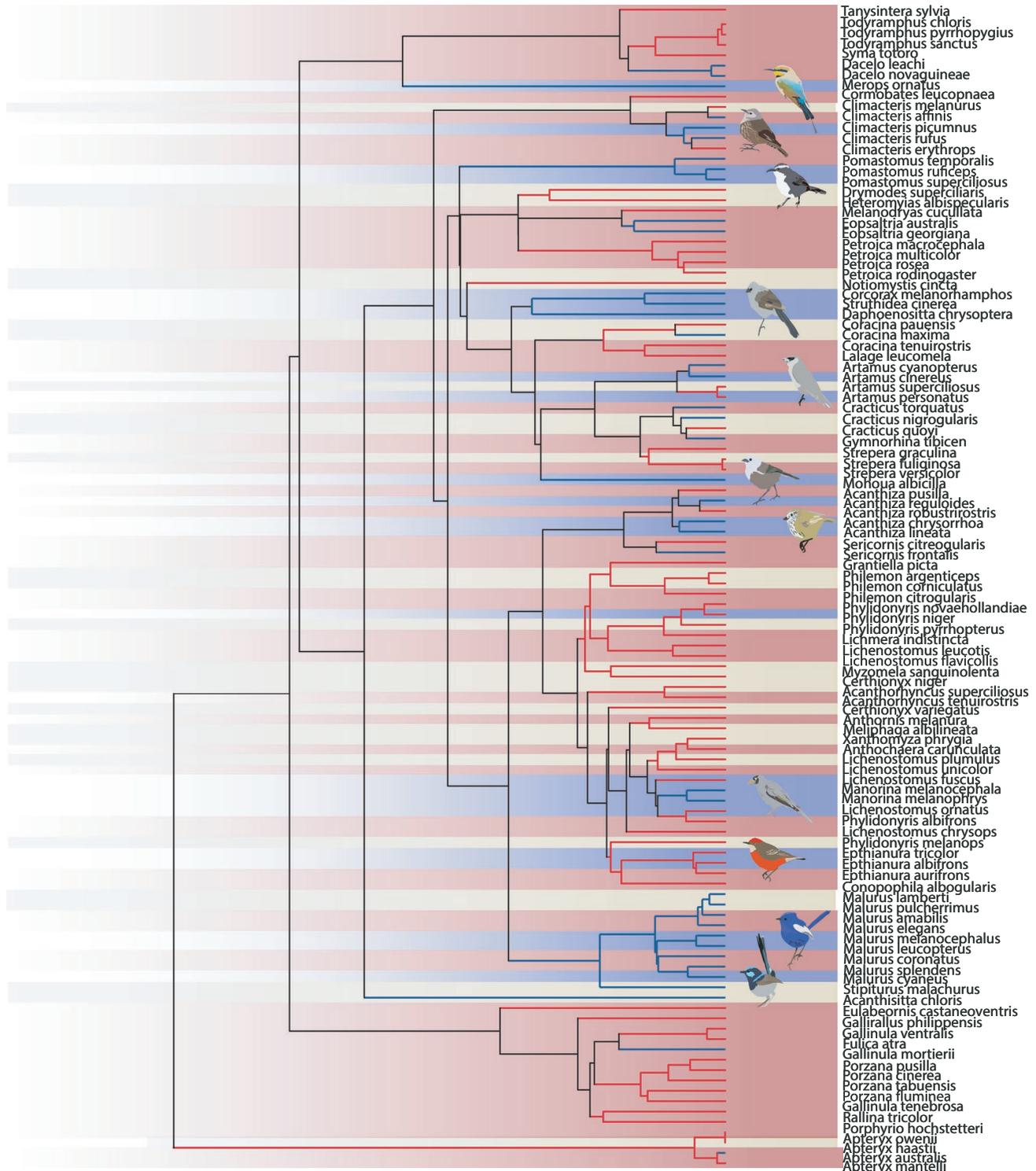


FIGURE 3 Overview of the phylogenetic relationships among Australian-New Zealand breeding birds. Colours of phylogenetic tree branches represent the presence (blue) or absence (red) of cooperative breeding. Blue background colour represents the probable existence of MLS, red represents the probable absence of MLS, while in yellow indicates the species for which we could not find enough evidence to suggest the presence or absence of MLS

Relatedness also appears to play an important role in mammalian MLSs. For example, as the level of association decreases and the strength of association increases (i.e. from community, to band, to team, to unit) in geladas (*Theropithecus gelada*) and guinea baboons, females are more likely to be genetically related (Patzelt et al., 2014; Tinsley Johnson, 2014). Yet, cooperative breeding is rare in mammals with MLSs (elephants being an exception; Lee, 1987). This raises the question whether different mechanisms 'set the scene' for the emergence of MLSs among birds and mammals, even if the drivers underlying the formation of MLSs (e.g. environmental harshness, the benefits of grouping and avoiding conflict with non-relatives) are similar.

Social viscosity is a key characteristic of cooperatively breeding birds, and our insights from superb fairy-wrens formally capture what literature suggests is a widespread social behaviour among cooperatively breeding birds. Our comparative analyses revealed that MLSs appear to be more commonly expressed by cooperatively breeding species. While we found evidence for possible MLSs in at least 17 Australian-New Zealand cooperatively breeding species, we found similar evidence in only five non-cooperative species (see Table 1 and Table S2). Among these, chats and white-cheeked honeyeater appear to form stable flocks (higher social unit) during the non-breeding season, which then split back into pairs of individuals defending breeding territories (see Table 1). Yellow-plumed and fuscous honeyeaters are semi-colonial species, that form well-defined clusters of individuals that associate to mob intruders (see Table 1); a potential MLS similar to miners. Furthermore, fairy-wrens (*Malurus spp*) and treecreepers (*Climacteris spp*) include cooperatively breeding species that have strict year-round territoriality which, inherently, cannot exhibit a multilevel social structure. Further studies are therefore necessary to explore the general importance of cooperative breeding and social viscosity in driving MLSs.

It seems unlikely that relatedness is a prerequisite for the formation of associations like those observed in the upper levels of MLSs. For example during the non-breeding season, superb fairy-wrens regularly form mixed species flocks with other passerine species, some of which are likely to also exhibit MLSs (striated thornbills; Bell, 1980). Similarly, cooperatively breeding yellow-rumped thornbills, which have no evidence of a MLS, also form mixed-species flocks with non-random membership, that include individuals from species likely exhibiting MLSs (such as buff-rumped thornbills; Farine & Milburn, 2013). This suggests not only that multilevel-like social structures could involve different species, but that the formation of upper levels could potentially take place among completely unrelated individuals. Comparisons of single- and multi-species avian societies could provide insights into the relative importance of social viscosity versus other factors in the emergence of MLSs.

CONCLUSION

One of the main open questions in the study of social evolution is what conditions and ecological pressures favour the emergence of MLSs (Grueter et al., 2020). The proximate mechanisms are presumed to vary widely (Grueter et al., 2020), and expanding the focus of research to other taxa can enhance the insight we can gain on the drivers of complex social structures (Papageorgiou & Farine, 2020). For example the social structure of cooperatively breeding superb fairy-wrens is strikingly similar to the phylogenetically distant vulturine guineafowl: in both societies, groups show a biased sex-ratio, centred around the philopatric sex, and significantly expand their home ranges during harsher seasons (Papageorgiou et al., 2021). More broadly, the weak phylogenetic signal of potential MLSs in cooperative breeding birds (see Table S1 and Figure 3) suggests it is a relatively fluid social trait that can emerge and disappear frequently. This highlights the opportunities that birds can offer for identifying the environmental drivers of MLSs (Papageorgiou & Farine, 2020). We encourage researchers who study social behaviour of cooperatively breeding species to investigate the social structure of their species during the non-breeding season, which will help to identify generalities and exceptions to the pattern we uncovered here. Another promising research avenue is the study of the non-breeding social behaviour of the non-cooperative species highlighted in our study as potentially displaying MLSs, which might further enhance our understanding of the ecological versus social drivers of MLSs. Explicitly including the often-neglected non-breeding period in studies of avian social behaviour could offer deeper insight into the social complexity of these species, and a better understanding of the drivers of MLSs across animals.

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AUTHORSHIP

KD performed phylogenetic analyses, EC collected data and performed network analysis, EC, SAK, DRF and AP wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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DATA AVAILABILITY STATEMENT

The datasets used in our analyses are available via the Figshare repository at https://figshare.com/articles/dataset/Cooperative_breeding_and_the_emergence_of_multilevel_societies_in_birds/17097038 (<https://doi.org/10.6084/m9.figshare.17097038>).

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REFERENCES

- Aplin, L.M., Farine, D.R., Morand-Ferron, J. & Sheldon, B.C. (2012) Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B*, 279, 4199–4205.
- Bell, H.L. (1980) Composition and seasonality of mixed-species feeding flocks of insectivorous birds in the Australian capital territory. *Emu*, 80, 227–232.
- Bell, H.L. & Ford, H.A. (1986) A comparison of the social organization of three syntopic species of Australian thornbill, *Acanthiza*. *Behavioral Ecology and Sociobiology*, 19, 381–392.
- Bigg, M.A., Olesiuk, P., Ellis, G.M. & Ford, J.K.B. (1990) Organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Report IWC*, 12, 384–485.
- Calenge, C. (2015) Package 'adehabitatHR'. R package version 1, 18.
- Chapais, B. (2011) The deep social structure of humankind. *Science*, 331, 1276–1277.
- Clarke, M.F. & Fitz-Gerald, G.F. (1994) Spatial organization of the cooperatively breeding bell miner *Manorina melanophrys*. *Emu*, 94, 96–105.
- Cockburn, A. (1998) Evolution of helping behaviour in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, 29, 141–177.
- Cockburn, A. (2006) Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B*, 273, 1375–1383.
- Cooney, R. & Cockburn, A. (1995) Territorial defence is the major function of female song in the superb fairy-wren, *Malurus cyaneus*. *Animal Behaviour*, 49, 1635–1647.
- Cornwallis, C.K., Botero, C.A., Rubenstein, D.R., Downing, P.A., West, S.A. & Griffin, A.S. (2017) Cooperation facilitates the colonization of harsh environments. *Nature Ecology & Evolution*, 1, 1–10.
- Csardi, G. & Nepusz, T. (2006) The igraph software package for complex network research. *InterJournal Complex Sy*, 1695. Available at: <http://igraph.org>
- Davis, G.H., Crofoot, M.C. & Farine, D.R. (2018) Estimating the robustness and uncertainty of animal social networks using different observational methods. *Animal Behavior*, 141, 29–44.
- Delm, M.M. (1990) Vigilance for predators: detection and dilution effects. *Behavioral Ecology and Sociobiology*, 26(5), 337–342.
- Doerr, E.D. & Doerr, V.A. (2006) Comparative demography of treecreepers: evaluating hypotheses for the evolution and maintenance of cooperative breeding. *Animal Behavior*, 72, 147–159.
- Downing, P.A., Griffin, A.S. & Cornwallis, C.K. (2020) Group formation and the evolutionary pathway to complex sociality in birds. *Nature Ecology & Evolution*, 4, 479–486.
- Eastwood, J.R., Mulder, E., Verhulst, S. & Peters, A. (2018) Increasing the accuracy and precision of relative telomere length estimates by RT-qPCR. *Molecular Ecology Resources*, 18, 68–78.
- Fallow, P. & Magrath, R.D. (2009) Eavesdropping on other species: mutual interspecific understanding of urgency information in avian alarm calls. *Animal Behavior*, 79, 411–417.
- Farine, D.R. (2017a) The dynamics of transmission and the dynamics of networks. *Journal of Animal Ecology*, 86, 415–418.
- Farine, D.R. (2017b) A guide to null models for animal social network analysis. *Methods in Ecology and Evolution*, 8(10), 1309–1320. <https://doi.org/10.1111/2041-210X.12772>
- Farine, D.R. & Carter, G.G. (2020). Permutation tests for hypothesis testing with animal social data: problems and potential solutions. *bioRxiv*.
- Farine, D.R. & Milburn, P. (2013) Social organisation of Thornbill-dominated mixed-species flocks using social network analysis. *Behavioral Ecology and Sociobiology*, 67, 321–330.
- Garnett, S. (1985) Mortality and group cohesion in migrating Rainbow Bee-eaters. *Emu*, 85, 267–268.
- Griesser, M., Barnaby, J., Schneider, N.A., Figenschau, N., Wright, J., Griffith, S.C. et al. (2009) Influence of winter ranging behaviour on the social organization of a cooperatively breeding bird species, the apostlebird. *Ethology*, 115, 888–896.
- Griesser, M., Drobnjak, S.M., Nakagawa, S. & Botero, C.A. (2017) Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLoS Biology*, 15, e2000483.
- Grueter, C.C., Qi, X., Li, B. & Li, M. (2017) Multilevel Societies. *Current Biology*, 27, 979–1001.
- Grueter, C.C., Qi, X., Zinner, D., Bergman, T., Li, M., Xiang, Z. et al. (2020) Multilevel organisation of animal sociality. *Trends in Ecology & Evolution*, 35(9), 1–14.
- Grueter, C.C., Qi, X., Zinner, D., Bergman, T., Li, M., Xiang, Z. et al. (2021) On multifaceted definitions of multilevel societies: response to Papageorgiou and Farine. *Trends in Ecology & Evolution*, 36(1), 17–19.
- Hamilton, W.D. (1964) The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7(1), 17–52.
- Hatchwell, B.J. (2009) The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Proceedings of the Royal Society B*, 364, 3217–3227.
- He, P., Maldonado-Chaparro, A.A. & Farine, D.R. (2019) The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. *Behavioral Ecology and Sociobiology*, 73, 1–14.
- Hegner, R.E., Emlen, S.T. & Demong, N.J. (1982) Spatial organization of the whited-fronted bee-eater. *Nature*, 298, 264–266.
- Heinsohn, R.G. (1987) Age-dependent vigilance in winter aggregations of cooperatively breeding white-winged choughs (*Corcorax melanorhamphos*). *Behavioral Ecology and Sociobiology*, 20, 303–306.

- Hijmans, R.J. & van Etten, J. (2016). raster: Geographic data analysis and modeling. R package version, 2(8).
- Ho, L. & Ané, C. (2014) A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology*, 63, 397–408.
- Hoppitt, W.J.E. & Farine, D.R. (2018) Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. *Animal Behaviour*, 136, 227–238.
- Jetz, W. & Rubenstein, D.R. (2011) Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology*, 21, 72–78.
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, 491, 444–448.
- Kingma, S.A., Santema, P., Taborsky, M. & Komdeur, J. (2014) Group augmentation and the evolution of cooperation. *Trends in Ecology & Evolution*, 29, 476–484.
- Kirkpatrick, R.C. & Grueter, C.C. (2010) Snub-nosed monkeys: multilevel societies across varied environments. *Evolutionary Anthropology*, 19, 98–113.
- Klarevas-Irby, J.A., Wikelski, M. & Farine, D.R. (2021) Efficient movement strategies mitigate the energetic cost of dispersal. *Ecology Letters*, 24(7), 1432–1442. <https://doi.org/10.1111/ele.13763>
- Koenig, W.D. & Dickinson, J.L. (2016) *Cooperative breeding in vertebrates*. Cambridge: Cambridge University Press.
- Kummer, H. (1968) *Social organization of Hamadryas baboon: a field study*. Chicago, IL: The University of Chicago Press.
- Lee, P.C. (1987) Allomothering among African elephants. *Animal Behaviour*, 35(1), 278–291.
- MacGillivray, W. (1914) Notes on some north Queensland birds. *Emu*, 13, 132–186.
- Marchant, S., Higgins, P.J., Ambrose, S.J. & Steele, W.K. (2006) *Handbook of Australian, New Zealand & Antarctic birds*: Oxford University Press, USA.
- McQueen, A., Naimo, A.C., Teunissen, N., Magrath, R.D., Delhey, K. & Peters, A. (2017) Bright birds are cautious: seasonally conspicuous plumage prompts risk avoidance by male superb fairy-wrens. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 284(1857), 20170446.
- Migliano, A.B., Page, A.E., Gómez-Gardeñes, J., Salali, G.D., Viguier, S., Dyble, M. et al. (2017) Characterization of hunter-gatherer networks and implications for cumulative culture. *Nature Human Behaviour*, 1, 00–43.
- Nakagawa, S. & De Villemereuil, P. (2019) A general method for simultaneously accounting for phylogenetic and species sampling uncertainty via Rubin's rules in comparative analysis. *Systematic Biology*, 68, 632–641.
- Painter, J.N., Crozier, R.H., Poiani, A., Robertson, R.J. & Clarke, M.F. (2000) Complex social organization reflects genetic structure and relatedness in the cooperatively breeding bell miner, *Manorina melanophrys*. *Molecular Ecology*, 9, 1339–1347.
- Papageorgiou, D., Christensen, C., Gall, G.E.C., Klarevas-Irby, J.A., Nyaguthii, B., Couzin, I.D. et al. (2019) The multilevel society of a small brained bird. *Current Biology*, 29, 1120–1121.
- Papageorgiou, D. & Farine, D.R. (2020) Multilevel societies in birds. *Trends in Ecology & Evolution*, 36, 15–17.
- Papageorgiou, D., Rozen-Rechels, D., Nyaguthii, B. & Farine, D.R. (2021) Seasonality impacts collective movements in a wild group-living bird. *Movement Ecology*, 9(1), 1–12.
- Patzelt, A., Kopp, G.H., Ndao, I., Kalbitzer, U., Zinner, D. & Fischer, J. (2014) Male tolerance and male-male bonds in a multilevel primate society. *Proceedings of the National Academy of Sciences*, 111, 14740–14745.
- Rathburn, M.K. & Montgomerie, R. (2003) Breeding biology and social structure of White-winged Fairy-wrens (*Malurus leucopterus*): comparison between island and mainland subspecies having different plumage phenotypes. *Emu*, 103, 295–306.
- Rowley, I. (1964) The life history of the superb blue wren. *Emu*, 64, 251–297.
- Rowley, I. (1999) Co-operative breeding by black-faced woodswallows *Artamus cinereus*. *Corella*, 23, 63–66.
- Rowley, I. & Russell, E. (1995) The breeding biology of the White-winged Fairy-wren *Malurus leucopterus leuconotus* in a Western Australian coastal heathland. *Emu*, 95, 175–184.
- Rowley, I. & Russell, E.M. (1997) *Fairy-wrens and grasswrens: Maluridae*. Oxford: Oxford University Press.
- Rubenstein, D.I. & Hack, M. (2004) Natural and sexual selection and the evolution of multi-level societies: insights from zebras with comparisons to primates. In: Kappeler, P.M. & van Schaik, C.P. (Eds.) *Sexual selection in primates: new and comparative perspectives*. Cambridge: Cambridge University Press, pp. 266–279.
- Rubenstein, D.R. & Lovette, I.J. (2007) Temporal environmental variability drives the evolution of cooperative breeding in birds. *Current Biology*, 17, 1414–1419.
- Schreier, A.L. & Swedell, L. (2009) The fourth level of social structure in a multi-level society: ecological and social functions of clans in hamadryas baboons. *American Journal of Primatology*, 71, 948–955.
- Schreier, A.L. & Swedell, L. (2012) Ecology and sociality in a multi-level society: ecological determinants of spatial cohesion.
- Shizuka, D., Chaine, A.S., Anderson, J., Johnson, O., Laursen, I.M. & Lyon, B.E. (2014) Across-year social stability shapes network structure in wintering migrant sparrows. *Ecology Letters*, 17(8), 998–1007.
- Shizuka, D. & Farine, D.R. (2016) Measuring the robustness of network community structure using assortativity. *Animal Behavior*, 112, 237–246.
- Snyder-Mackler, N., Beehner, J.C. & Bergman, T.J. (2012) Defining higher levels in a gelada multilevel society. *International Journal of Primatology*, 33, 1054–1068.
- Städele, V., Pines, V., Swedell, L. & Vigilant, L. (2016) The ties that bind: maternal kin bias in a multilevel society despite natal dispersal by both sexes. *American Journal of Primatology*, 78, 731–744.
- Städele, V., Van Doren, V., Pines, M., Swedell, L. & Vigilant, L. (2015) Fine-scale genetic assessment of sex-specific dispersal patterns in a multilevel primate society. *Journal of Human Evolution*, 78, 103–113.
- Swedell, L. & Plummer, T. (2012) A papionin multi-level society as a model for early hominin evolution. *International Journal of Primatology*, 33, 1165–1193.
- Tavares, S.B., Samarra, F.I.P. & Miller, P.J.O. (2016) A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. *Behavioral Ecology*, 28, 500–514.
- Tinsley Johnson, E., Snyder-Mackler, N., Beehner, J. & Bergman, T. (2014) Kinship and dominance rank influence the strength of social bonds in female geladas (*Theropithecus gelada*). *International Journal of Primatology*, 35(1), 288–304.
- Whitehead, H., Antunes, R., Gero, S., Wong, S.N.P., Engelhaupt, D. & Rendell, L. (2012) Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? *International Journal of Primatology*, 33, 1142–1164.
- Wittemyer, G., Douglas-Hamilton, I. & Getz, W.M. (2005) The socioecology of elephants: analysis of the processes creating multi-tiered social structures. *Animal Behavior*, 69, 1357–1371.
- Wolf, J.B. & Trillmich, F. (2008) Kin in space: social viscosity in a spatially and genetically substructured network. *Proceedings of the Royal Society B*, 275(1647), 2063–2069.

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