



Population genetic structure and dispersal patterns of a cooperative breeding bird in variable environmental conditions

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Understanding the effects of environmental conditions in cooperatively breeding species helps reveal the nature of evolutionary forces leading to this type of social system. In particular, environmental variability may affect demographic processes such as mortality and dispersal which can ultimately define the fine-scale genetic structure of cooperatively breeding populations, including direct and indirect fitness opportunities for individuals. We investigated the population genetic structure and dispersal patterns of obligately cooperative white-winged choughs, *Corcorax melanorhamphos*, exploring within-group relatedness and genetic differentiation among groups sampled over several years of above average rainfall. We compared our results with data from a previous study in the surrounding area, conducted during a drought period. White-winged chough groups showed similar significant genetic differentiation among groups during both drought and nondrought periods. However, we found female-biased dispersal during abundant rainfall years, which contrasts with the previous study conducted during a drought. We also examined differences in genetic structure in the present study, between groups breeding in suburbs versus native woodlands, finding higher within-group relatedness in woodland birds. Dispersal was female biased in both suburban and woodland habitat but subadult females in suburban habitat were more likely to disperse than adult females. We suggest that higher mortality in chough populations (both during a drought and in suburban habitats) led to more breeding opportunities, resulting in higher dispersal, and reflecting lower group stability. Our study suggests ecological conditions are important drivers of social structure in a cooperatively breeding bird, which are likely to be impacted by environmental change, including climate and urbanization.

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Cooperative breeding is broadly defined as a social and mating system in which more than two individuals work together to rear offspring (Brown, 1978; Cockburn, 1998; Fry, 1977; Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2016). The motivation of some individuals, referred to as helpers, to delay their own reproduction and instead care for young that are not their own makes this social system particularly interesting from an evolutionary perspective (Cockburn, 2006; Hatchwell, 2009). If helping others is costly, this cooperative trait should only increase in frequency in the population if the benefits gained by helping outweigh the costs (Croft et al., 2015; Hamilton, 1964; Heinsohn & Legge, 1999). One important motive for helping is the indirect benefit of kin selection (Hamilton, 1964), which is the gain of inclusive fitness obtained by

assisting close relatives (Hatchwell & Komdeur, 2000; Hatchwell, 2009). Many species of cooperative breeders show fine-scale genetic structure, with higher relatedness within their social groups than among groups (Leedale et al., 2018; Painter et al., 2000; Temple et al., 2006; Woxvold et al., 2006), meaning that helpers are indeed aiding the production of close relatives. Helpers may also benefit directly from cooperating; for example, they can increase their own present and future mating opportunities, increase their probabilities of territory inheritance and learn skills that improve their survival (Cockburn, 1998; Riehl, 2013).

Understanding the evolution of helping requires identification of the environmental factors that encourage individuals to cooperate rather than disperse and breed as pairs (Arnold & Owens, 1998; Hatchwell & Komdeur, 2000). These factors have been viewed as ecological constraints that alter food and territory availability, predation rates and other elements, and thereby limit dispersal and independent breeding (Emlen, 1982). One

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manifestation of ecological constraints is that they may be associated with climatic variability and unpredictability, which can affect the availability of food and suitable territories (Jetz & Rubenstein, 2011; Rubenstein & Lovette, 2007). Breeding cooperatively in such environments gives individuals the opportunity to maximize fitness by cooperating under challenging environmental conditions, either by helping to raise close relatives or by obtaining direct benefits from group living (Clutton-Brock, 2002, 2009; Griffin & West, 2003; Hatchwell, 2009; Riehl, 2013).

We examined the genetic structure of an obligate cooperatively breeding bird, the white-winged chough, *Corcorax melanorhamphos*. This species must breed in groups to produce offspring, and reproductive success is highly dependent on food availability for the young, with bigger groups supporting and feeding more young than smaller groups (Heinsohn, 1991; Rowley, 1978). Parents and helpers also have to provide food to the young for many months after fledging (Heinsohn, 1991). Long-term studies have shown that the social stability of white-winged choughs is highly susceptible to environmental changes that limit food supply, such as the severe El Niño-driven droughts that occur in eastern Australia (Chiew et al., 1998; Heinsohn, 2009), or impose differing constraints such as when the birds live in highly altered urban habitats (Beck & Heinsohn, 2006). Droughts have been associated with a decline in the number of helpers, reduction in reproductive output, higher mortality and group disintegration in white-winged choughs and other species (Heinsohn et al., 2000; van de Pol et al., 2012), whereas white-winged choughs in urban environments experience higher fledgling mortality than those breeding in nonurban areas (Beck & Heinsohn, 2006). Urbanization has been a major cause of habitat alteration in recent decades and entails both habitat fragmentation and transformation to landscapes with entirely different ecological properties. Urbanized areas can be both advantageous for bird species by providing stable sources of food and water, or especially challenging due to increased hazards from vehicle traffic, noise and predation (Chiari et al., 2010; Halfwerk et al., 2011; Marzluff, 2001; Møller et al., 2011). Studies on the effects of urbanization on cooperatively breeding birds are scarce but are potentially important in terms of understanding the impact of increased urbanization on their behaviour and social systems, and for yielding important insights into the costs and benefits of sociality under variable ecological conditions.

This study examined the fine-scale genetic structure of white-winged chough populations using genotyping by sequencing methods (Jaccoud et al., 2001; Kilian et al., 2012). The aim was to investigate dispersal patterns and fine-scale genetic structure during above average rainfall conditions, which has not been done before. Then we aimed to compare these measures of genetic structure and dispersal patterns within the same population, which was studied previously during a period of severe drought (Beck et al., 2008). We calculate within-group relatedness, dispersal patterns and genetic differentiation among groups, and compared them to the results of the previous study. We predicted that within-group relatedness should be higher during non-drought periods than during droughts as groups suffer lower mortality and grow from within-group reproduction and recruitment in more stable conditions (Heinsohn et al., 2000; Rowley, 1978). The effects of habitat alteration were explored in the present study by comparing the same parameters between choughs living in natural woodland habitat with those in highly altered suburban habitat. We predicted that within-group relatedness should be higher in woodland habitat than suburban habitat based on higher mortality rates and faster turnover of group members in the latter.

METHODS

Study Species

White-winged choughs are large passerine birds (350–380 g) endemic to southeastern Australia. Choughs consume invertebrates found on the ground or by digging up to 10 cm beneath the surface. They live in stable groups of 3–20 individuals throughout the year, which typically consist of one breeding pair and many nonbreeding helpers which are usually offspring from previous years. Every group member contributes to nest building, incubating, feeding nestlings and fledglings and predator defence (Boland, 1998; Rowley, 1978). Group living in choughs is associated with the long time it requires for juveniles to learn how to forage without help. This means that the parents and helpers have to provide food to the young for many months after fledging, and that, even after independence, juveniles take until they are 4 years old to reach foraging proficiency and sexual maturity (Heinsohn et al., 1988; Rowley, 1978). A difficult foraging niche also means group members have to cooperate to raise nestlings (Heinsohn, 1991; Heinsohn et al., 1988; Rowley, 1978). Pairs have never been observed to reproduce successfully, and group size is positively correlated with the number of young fledged and their later survival (Heinsohn, 1992).

Study Population Background

We captured and banded 209 choughs from suburbs and woodland areas in northern Canberra, Australian Capital Territory, Australia, between August 2015 and March 2018 (Fig. 1). We caught choughs using baited walk-in cage traps. Each captured bird was marked with a standard metal band with number and a large white plastic band with a unique number that was easily visible through binoculars from up to 50 m away. We used eye colour to determine each individual's age up to 4 years following Rowley (1975). Birds were classified as '1' (first year, with a completely brown iris); '2' (second year, with a brown iris surrounded by an orange ring); '3' (third year, with an orange iris and a brown inner ring), '4' (fourth year, with an orange iris and yellow inner ring spotted in brown) and '5' (fifth year or older; with a red iris and orange inner ring). Birds were considered adults from age 4 years onwards, when they have reached sexual maturity (Rowley 1978). For genetic analyses, we took a small blood sample (ca. 50 µl) from the brachial vein from each banded bird. The sample was stored in 70% ethanol.

Sample Collection

For this study, we genotyped 172 individuals, including fledglings, from 27 groups studied in both 2016–2017 and 2017–2018 breeding seasons, 95 females and 77 males. The sex ratio (male/(male + female)) of all genotyped choughs was 0.447, with no significant difference from parity ($\chi^2 = 1.884$, $P = 0.170$). The individuals came from 27 group-years with group sizes ranging from four to 16 excluding fledglings (mean = 7.77), and from five to 23 (mean = 9.7) including fledglings (mean number of fledglings per group = 1.48; range 0–6; $N = 40$).

We aimed to have a high genetic representation of each sampled group of choughs, therefore we banded and took DNA samples from at least 67% of the members of each group.

Group membership of each individual was recorded during the breeding season, between August and January each year, as well as the geographical coordinates of 25 nests. Two groups were found with young fledglings, but as we did not find the nest we excluded them from the spatial autocorrelation analysis. A total of 13 choughs disappeared from the study. Choughs have short dispersal distances (usually <2 km) so these birds were assumed to have died

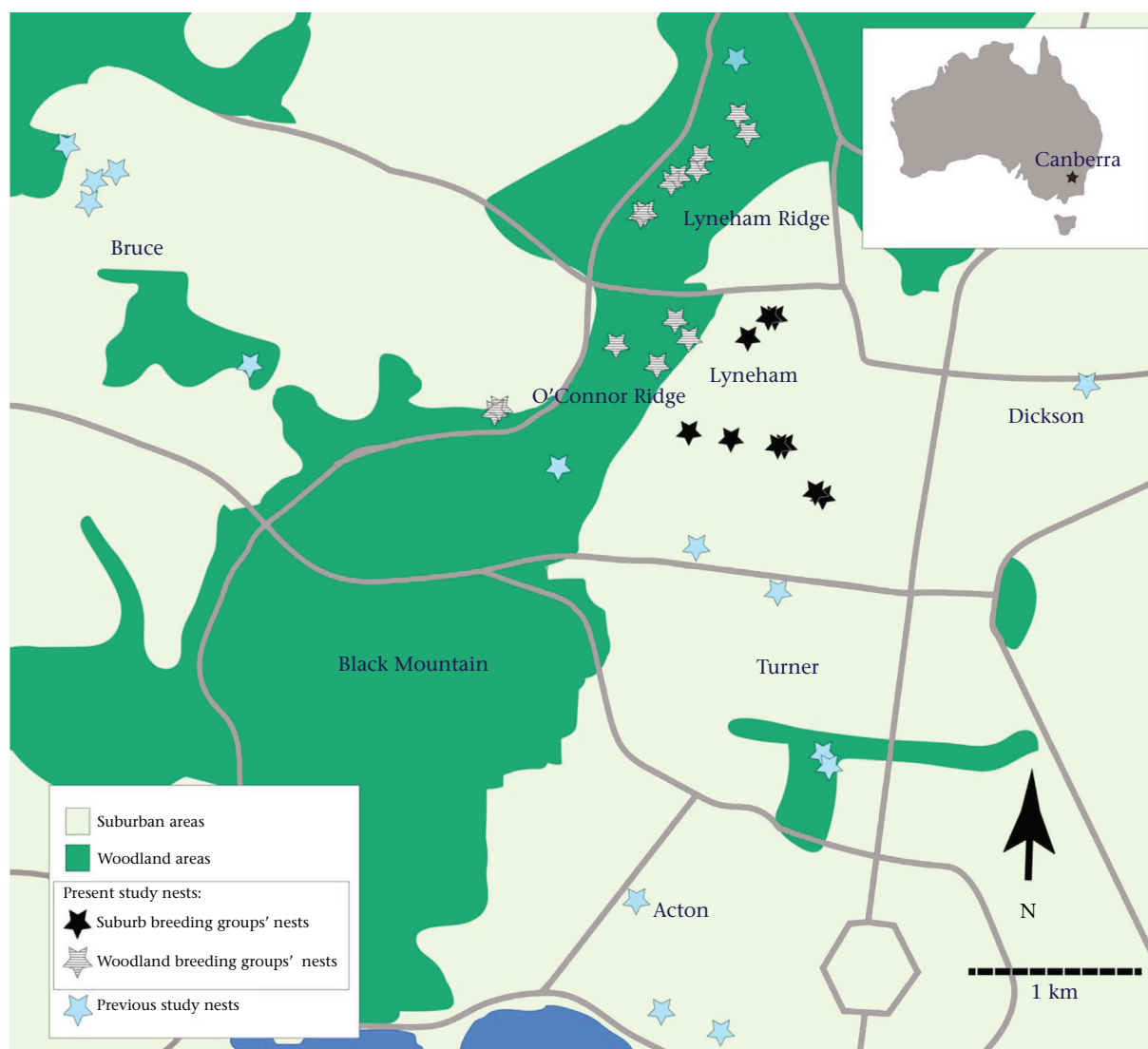


Figure 1. Map of Canberra inner north showing the present and previous study areas with nests of white-winged choughs in suburban (light yellow) and woodland habitat (green). In the right corner, a map of Australia showing the location of Canberra.

(Beck et al., 2008). In other cases, individuals dispersed to join different groups. Chough groups vary in composition between years through reproduction, mortality and changes in membership of older birds, which join or leave a group. Seven of the groups we included in this study varied in membership of older birds between 2016 and 2017, so we analysed them separately each year, since group numbers and/or identity of the breeding pair, and therefore the overall relatedness of the group, varied between breeding seasons.

Comparative Studies

We compared results from the present study with a subsample of a previous study conducted on the same population, during a severe drought, from March 2003 to March 2005 (Beck et al., 2008). The average annual rainfall was 575.77 mm between 2002 and 2004, with a severe drought registered during 2002, when the average annual rainfall was 525.5 mm. The average annual rainfall in Canberra is 615.6 mm, and during the present study (between 2015 and 2017), it was 708.9 mm (Bureau of Meteorology, 2020, <http://www.bom.gov.au/climate/current/annual/act/summary>.

[shtml](#)). To compare the genetic structure of white-winged chough populations in different climatic conditions, we used genetic data collected during the period of drought and conducted analyses on chough groups living in the same and surrounding areas of our present study (Fig. 1). We examined 83 individuals from 16 groups from the previous study. The sex ratio was 0.51, with 42 males and 41 females, and not significantly different from parity ($\chi^2 = 0.012$, $P = 0.913$).

Both studies used different molecular techniques. We used single nucleotide polymorphisms (SNPs) to estimate population genetic parameters, while the 2003–2005 study used microsatellite markers. Several studies comparing the performance of both types of molecular markers have found that estimates of genetic variation are highly correlated (Coates et al., 2009; Elbers et al., 2017), and therefore comparable. For instance, a study comparing SNPs and microsatellite markers in a cooperative breeding species of bird, for which kin relationships are implicated, found that they estimated kinship equally well (Weinman et al., 2015). Further, the methods we used to compare patterns of spatial genetic structure (F_{ST} and multilocus spatial autocorrelation) are standardized and therefore are, in principle, comparable among marker types. Since

microsatellites have high diversity, the same populations usually have higher F_{ST} for microsatellites than SNPs (Hedrick, 2005; Meirmans & Hedrick, 2011). Importantly, we did not compare the quantitative results between studies, but instead compared qualitative trends suggested by the genetic analyses, which we used to draw conclusions about general population structure patterns.

Genetic Methods

DARTSeq genotyping

Codominant SNP genotypes were obtained using a genotyping by sequencing method via the DARTSeq protocol from Diversity Arrays Technology (DART, Canberra, Australia; Jaccoud et al., 2001; Kilian et al., 2012). In total, 186 blood samples of ca. 2 μ l volume stored in 70% ethanol, including 172 different birds and 14 individuals genotyped twice as technical replicates, were genotyped. DART conducted the DNA extraction, sequencing and genotyping. The sequencing method is optimized for each organism, selecting the most appropriate complexity reduction method using specific restriction enzymes. DART used the genome of the American crow, *Corvus brachyrhynchos*, as reference. Quality control steps of the samples were conducted by DART as described in Melville et al. (2017). After initial SNP calling by DART a genotype matrix with 17 961 SNPs was obtained for 172 individuals with an average 10.3% missing data per SNP and average sequencing depth per SNP of 16.77, which indicates the average number of times an SNP locus has been sequenced and mapped (Schultz et al., 2017). More detail of the SNP genotyping methodology can be found in Wells and Dale (2018). We then filtered the data set further on criteria specific to our analyses.

Starting with 17 961 SNPs delivered by DART, we first filtered 63 sex-linked SNPs (see Sex determination section below for criteria details), leaving 17 936 SNPs. For the rest of the filtering steps, we used the R package DARTR (Gruber et al., 2018). Based on Shaw (2018), we followed filtering steps that optimized fine-scale population genetic analyses. First, we removed SNP loci that occurred in less than 95% of individuals (95% call rate filter in DARTR), with a reproducibility (based on technical replicates of 30% of samples) below 95% (12 886 SNPs left). We retained only a single SNP from each clustered sequence, filtering SNPs for which the reproducibility of the loci was below 95% (12 526 SNPs left), and removing duplicates from the same locus, choosing the SNPs with the highest average of polymorphic information content (PIC; 10 864 SNPs left). We then filtered SNPs with a minor allele frequency (MAF) lower than 0.05 (8445 SNPs left) and an average read depth of less than 10 across both alleles (1825 SNPs left). Finally, we filtered SNPs with an average PIC lower than 0.01, resulting in the final 1813 SNPs we used for genetic analyses. We do not expect enough genotypes to adhere to Hardy–Weinberg expectations due to the kinship-based social structure of their populations; therefore, we did not filter SNPs following this criterion since it might remove biological signal from the data.

Sex determination

Choughs are not sexually dimorphic (Rowley, 1978) so we initially determined the sex of a sample of 40 individuals using PCR. To do this, we carried out DNA extraction from blood using Qiagen DNeasy Blood and Tissue Kit (QIAGEN, Germantown, MD, U.S.A.). We used the method of avian molecular sexing based on the CHD gene (Fridolfsson & Ellegren, 1999), using primers P2/P8 to amplify sex chromosome-linked DNA fragments (Griffiths et al., 1998). Knowing the sex of these 40 choughs allowed us to determine the sex of the remaining 132 birds by identifying 63 sex-linked SNPs (25 W-linked and 38 Z-linked). Using the SNP Excel report from DARTSeq first, we identified W-linked SNPs looking for those that are always present in females (ZW) and not in males (ZZ). To find W-linked SNPs in the unidentified males, we applied a filter that

considered W-linked SNPs were those that were null in more than 0.8 (allowing for errors) of the already identified males, while they were present in all the identified females. We then looked for Z-linked SNPs which can show heterozygosity in males but not in females. We applied a filter to identify Z-linked SNPs that showed less than 0.05 heterozygosity in identified females, while males' heterozygosity for Z-linked SNPs ranged between 0.5 and 0.7.

Genetic diversity

Using GenAlex 6.5 (Peakall & Smouse, 2012) for the overall population we calculated mean observed heterozygosity (H_O), mean expected heterozygosity (H_S), total expected heterozygosity (H_T), inbreeding coefficient within individuals (F_{IS}) relative to groups, the group level fixation index (F_{ST}) relative to total and individual inbreeding coefficient (F_{IT}) relative to the rest of the population.

We conducted an analysis of molecular variance (AMOVA) using GenAlex 6.5, calculating group F_{ST} for males and females, for adults (4 years or older) and subadults (3 years or younger), and both sexes and life stages combined. For each analysis, we only included individuals from groups that contained two or more members of the same sex or age group. We also conducted this analysis on chough groups from the previous study, using a subset of the data, selecting those living in the same and surrounding areas of our study population.

To visualize genetic differences between individuals from different groups, we used the R package DARTR to perform principal coordinates analyses for each breeding season (2016–2017 and 2017–2018).

Fine-scale population structure

Using GenAlex 6.5 we calculated genetic distances between individuals using Smouse and Peakall (1999) genetic distance metric. We used the pairwise individual genetic distance matrix in a set of multilocus spatial autocorrelation analyses to investigate associations between genetic structure and spatial or social relationships among individuals. The genetic correlation coefficient r takes values between -1 and 1 , where zero indicates no genetic correlation. Random permutation (999 times) of the data set generated a null hypothesis of zero genetic autocorrelation, or relatedness, among individuals which allowed testing for significance. Within-group relatedness was estimated for all members in all groups in our sample ($N = 27$ groups) with a 95% confidence interval. We compared within-group relatedness for groups with more than one member of each sex (females = 27 groups, males = 24 groups), groups with more than one adult member of the same sex (female adults = 18, male adults = 17 groups), and groups with more than one subadult member of the same sex (female subadults = 15 groups, male subadults = 15 groups). We performed a two-tailed t test, using the function `t.test` in RStudio version 1.1.453 (RStudio Team, 2020), after testing for equal variances with an F test using the function `var.test` (all variances were not significantly different).

We generated geographical and genetic distance matrices separately for each breeding season, for males and females, for adults (4 years old or older) and subadults (3 years old or younger), and for male and female adults and subadults. We used the option 'Multiple Pops' in GenAlex 6.5 to allow the permutation within all these different categories in order to compare the results between them. The distance classes used for this analysis followed Beck et al. (2008) to allow a comparison of the studies. We also analysed data from the previous study including only groups that lived in the surrounding areas of our study (Fig. 1), matching the geographical ranges as much as possible. We used five distance classes for both this and the previous study (500 m, 1000 m, 2500 m and 3500 m),

since after 3500 m genetic correlation between groups is rarely positive (Beck et al., 2008). The differences in the geographical scale of both studies might affect the absolute r values, which would differ only due to sampling differences. These might also alter patterns of spatial autocorrelation in the data, but differences between the sexes within each study should not be affected.

Finally, we estimated the correlation between group size and multilocus genetic correlation among individuals within each group of the present study. For this analysis, we divided groups breeding in the suburbs (nests less than 50 m away from a residence), from groups breeding in areas of native eucalypt woodland adjacent to the suburbs (nests more than 200 m away from a residence). We used the R package *ggpubr* (function *ggscatter*; R Core Team, 2020; Kassambara, 2018), with the Spearman correlation method, to identify whether within-group genetic correlation and group size were correlated, to compare the result between groups living in the suburbs and those in native woodlands.

Ethical Note

All data collection and field methods were approved by The Australian National University Animal Ethics Committee (Animal Ethics protocol number: A2014/44, A2017/42), adhering to the ASAB/ABS Guidelines for the ethical treatment of animals. We obtained annual research permits issued by the ACT Government (#LT2015803) to trap and release white-winged choughs in our study areas. Each bird was handled for the shortest amount of time possible, under cool temperatures and released immediately after. No birds were harmed during our study.

RESULTS

SNP Filtering

From the initial 17 961 SNPs from 172 individuals (95 females and 77 males), we obtained 1813 SNPs (Appendix Fig. A1). Mean individual H_0 increased from 0.191 before filtering to 0.274 after filtering; mean H_T was 0.247 before filtering and 0.311 after filtering; mean MAF was 0.174 unfiltered and 0.22 filtered; mean F_{IT} was 0.246 before filtering and 0.121 filtered.

Genetic Diversity

Mean observed heterozygosity of subpopulations ($H_0 = 0.278 \pm 0.003$) was higher than mean subpopulation expected heterozygosity ($H_S = 0.251 \pm 0.003$), and lower than the total expected heterozygosity ($H_T = 0.314 \pm 0.003$). The individual inbreeding coefficient ($F_{IS} = -0.107 \pm 0.005$) was negative and close to zero, while the genetic differentiation between populations was positive ($F_{ST} = 0.2 \pm 0.002$).

Principal coordinates analysis for breeding seasons 2016–2017 and 2017–2018 (Appendix Fig. A2) showed that choughs that belong to the same group tended to cluster together and were genetically more similar. However, there were some exceptions where some individuals were closer to others from different groups, showing close relatedness among individuals belonging to different groups. The first principal coordinates analysis axis from breeding season 2016–2017 explained 8.8% of the variation, axis 2 7.6% and axis 3 4.9%; and from breeding season 2017–2018, axis 1 explained 8% of the variation, axis 2 6.2% and axis 3 5.5% (Appendix Fig. A2).

Comparison between studies

For the present study, the analysis of molecular variance showed significant genetic differentiation among groups. F_{ST} values for adult males, subadult males and subadult females were similar, but

the value for adult females was lower (Table 1). This compares with Beck et al.'s (2008) data, for which we also found genetic differentiation among groups. In the data set from the previous study, F_{ST} values for adult males were much higher than for subadult males, subadult females and adult females (Table 1).

We compared pairwise relatedness between group members of the same sex for choughs of the present study. We found no significant difference in relatedness when comparing all female members and all male members within groups (female mean = 0.215, SE = 0.003; male mean = 0.295, SE = 0.006; $t_{49} = -1.89$, $P = 0.064$). We also did not find significant differences in relatedness among female and male subadults within groups (female mean = 0.272, SE = 0.005; male mean = 0.304, SE = 0.008; $t_{28} = -0.549$, $P = 0.588$); however, adult females were significantly less related within groups than adult males (female mean = 0.183, SE = 0.007; male mean = 0.319, SE = 0.005; $t_{33} = -2.5138$, $P = 0.017$).

The spatial autocorrelation analysis detected significant and positive genetic structure within all groups (0 km distance; Fig. 2). It also showed positive and significant genetic structure between male adults in groups less than 0.5 km apart (Fig. 2d.) The r values between year, sex and age showed no significant differences between individuals within groups (0 km distance). However, when these were calculated for each sex combined to each age class, female adults showed significantly lower values of r within groups (Fig. 2f.). Spatial autocorrelation analysis of groups selected from the previous study (shown in Fig. 1) also revealed genetic structure within groups of choughs, and significantly lower r values in adult choughs than subadults at 0 km distance (Fig. 2a). There were no significant differences per sex or sex and age combined in genetic correlation between groups from the previous study in any of the distance classes (Fig. 2c, e).

Comparison between suburbs and native woodland

Estimates of genetic autocorrelation (r) within groups were higher than expected by chance (higher than zero and confidence intervals obtained by permutation) in 20 of the 27 sampled groups (74%; Fig. 3). These results were similar to those reported by Beck et al. (2008), where 19 of the 27 (70%) groups they studied were significantly more related within groups than expected by chance. Per year, in 2016 nine of 13 groups (69%) were more related within than between groups, while in 2017 it was 11 of 14 groups (79%). From the groups breeding in the suburbs six of nine (67%) were more related than expected by chance, while from groups breeding in the woodlands 14 of 16 (88%) were more related than expected by chance. Suburban breeding choughs presented a lower F_{ST} value than those breeding in the surrounding woodlands (Table 1).

Group size and relatedness were not significantly correlated overall ($R = 0.36$, $P = 0.076$) or when we separated groups according to whether they bred in the suburbs ($N = 9$) or woodland ($N = 16$; suburban groups: $R = 0.64$, $P = 0.066$; woodland groups: $R = 0.14$, $P = 0.59$). However, groups breeding in native woodland had significantly higher within-group genetic autocorrelation (mean = 0.290 ± 0.003 SE) than those breeding in the suburbs (mean = 0.135 ± 0.003 SE; $t_{23} = -3.7675$, $P < 0.001$). There was no significant difference in group size between groups breeding in the two habitats (woodland groups: mean = 8.375 ± 3.496 SE; suburban groups: mean = 6.778 ± 0.981 SE; Welch two-sample t test: $t_{22} = -1.4574$, $P = 0.159$).

Spatial autocorrelation categorized by breeding habitat showed that in chough groups in both the woodlands and suburbs there was significant positive spatial structure. However, woodland groups were significantly more spatially genetically structured than suburban groups in the 0 km category. Neighbouring groups in the

Table 1
Among-group differentiation using analysis of molecular variance (F_{ST}) between all groups (Total), between only males of each group and between only females of each group for both the present and previous studies

		Among group variation (%)	F_{ST}	F'_{ST}	df	P
AMOVA results present study	Total	15	0.148	0.207	26	0.01
	Female adults	10	0.103	0.146	17	0.01
	Male adults	17	0.184	0.249	16	0.01
	Female subadults	17	0.171	0.236	14	0.01
	Male subadults	18	0.181	0.247	14	0.01
	Woodland breeding choughs	17	0.185	0.25	15	0.01
AMOVA results previous study	Suburban breeding choughs	9	0.087	0.121	8	0.01
	Total	15	0.163	0.485	14	0.01
	Female adults	12	0.139	0.411	4	0.01
	Male adults	14	0.171	0.5	6	0.01
	Female subadults	13	0.146	0.444	5	0.01
	Male subadults	13	0.143	0.425	5	0.01

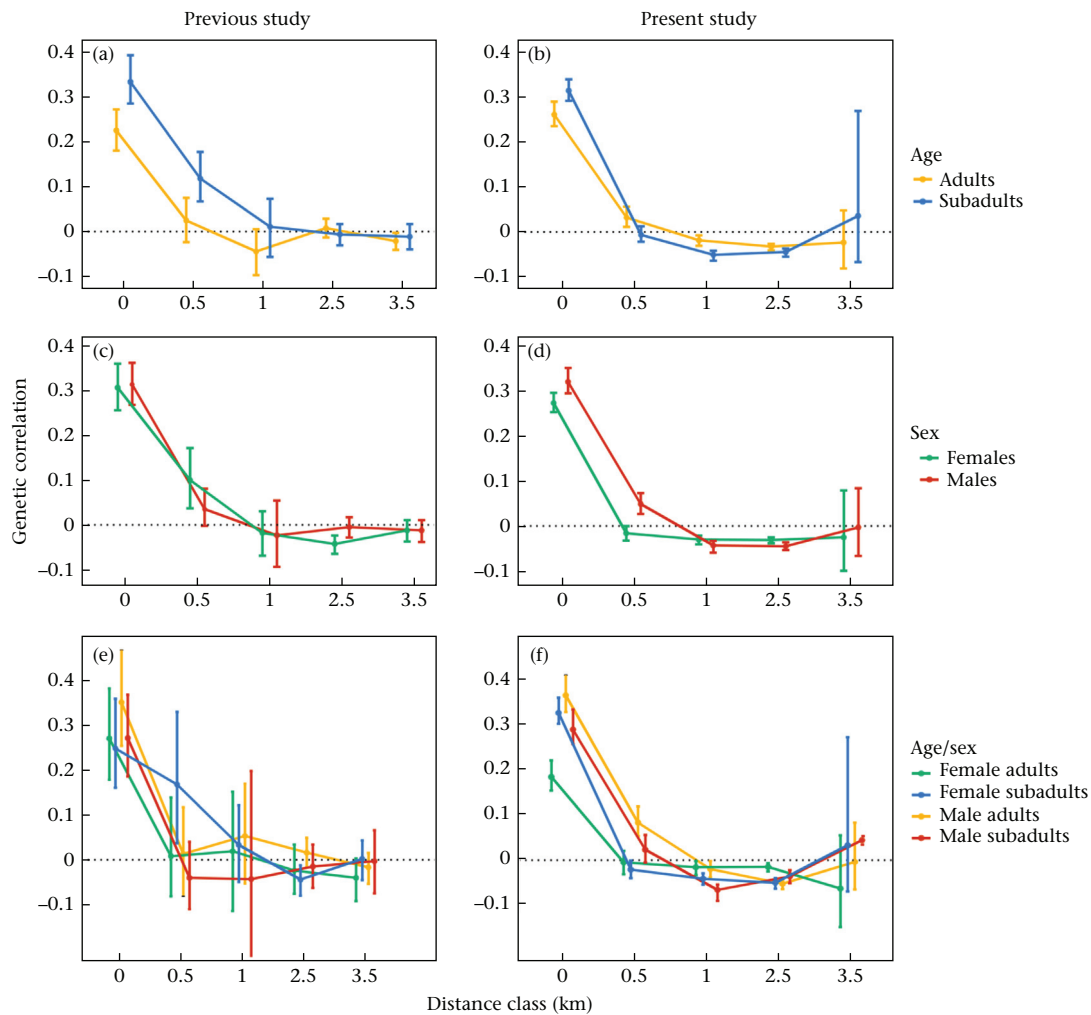


Figure 2. Plots of spatial genetic autocorrelation for individuals comparing (a, c, e) a previous study on white-winged choughs conducted during a drought to (b, d, f) the present study conducted during a nondrought period. Each graph shows the genetic correlation coefficient (r) as a function of distance (km), grouped by (a) previous study per age class, (b) present study per age class, (c) previous study per sex, (d) present study per sex, (e) previous study per age class and sex combined, (f) present study per age class and sex combined. Upper and lower bounds for the 95% confidence interval around the null hypothesis of no spatial structure ($r = 0$) calculated by bootstrap resampling are presented. The dotted line at zero bounds the 95% confidence interval of the null hypothesis of no genetic structure.

woodland category also showed higher genetic structure at the 0.5 km distance class. In woodland groups, adult females showed significantly lower genetic correlation than the other categories, while in suburban habitats female subadults had significantly lower values than the other categories (Fig. 4).

DISCUSSION

Our study of the genetic composition of white-winged chough groups furthers our understanding of the ecological drivers behind cooperative breeding (Brown, 1987; Emlen, 1982; Lott, 1991; Shen

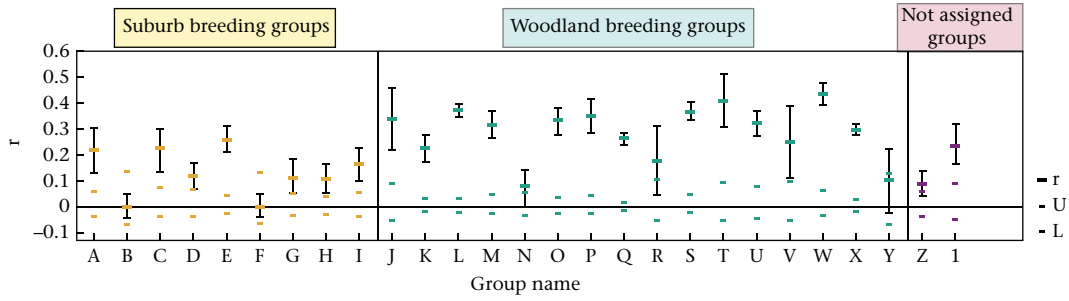


Figure 3. Within-group mean pairwise relatedness values (r) for 27 groups of choughs. Error bars indicate 95% confidence intervals as determined by bootstrap resampling. Thinner lines surrounding the line at zero show upper (U) and lower (L) 95% confidence limits for the null hypothesis of ‘no relatedness’ as determined by permutation.

et al., 2017; Stacey & Koenig, 1990). We compared the structure of social groups and likely inclusive fitness rewards to individuals under two main scenarios of variable environmental conditions, one pertaining to climate and the other to major habitat alteration. After conducting a genetic study during a prolonged nondrought period, we were interested in comparing our results with a previous study conducted in the same area during a severe drought

(Beck et al., 2008). Our results indicated that dispersal was female biased during a period of rainfall stability contrasting with the previous study during extreme drought that showed an absence of sex-biased dispersal (Beck et al., 2008), suggesting a major role for environmental factors in social organization. Further, the difference in within-group relatedness between chough groups breeding in different habitats suggests that both social organization and the

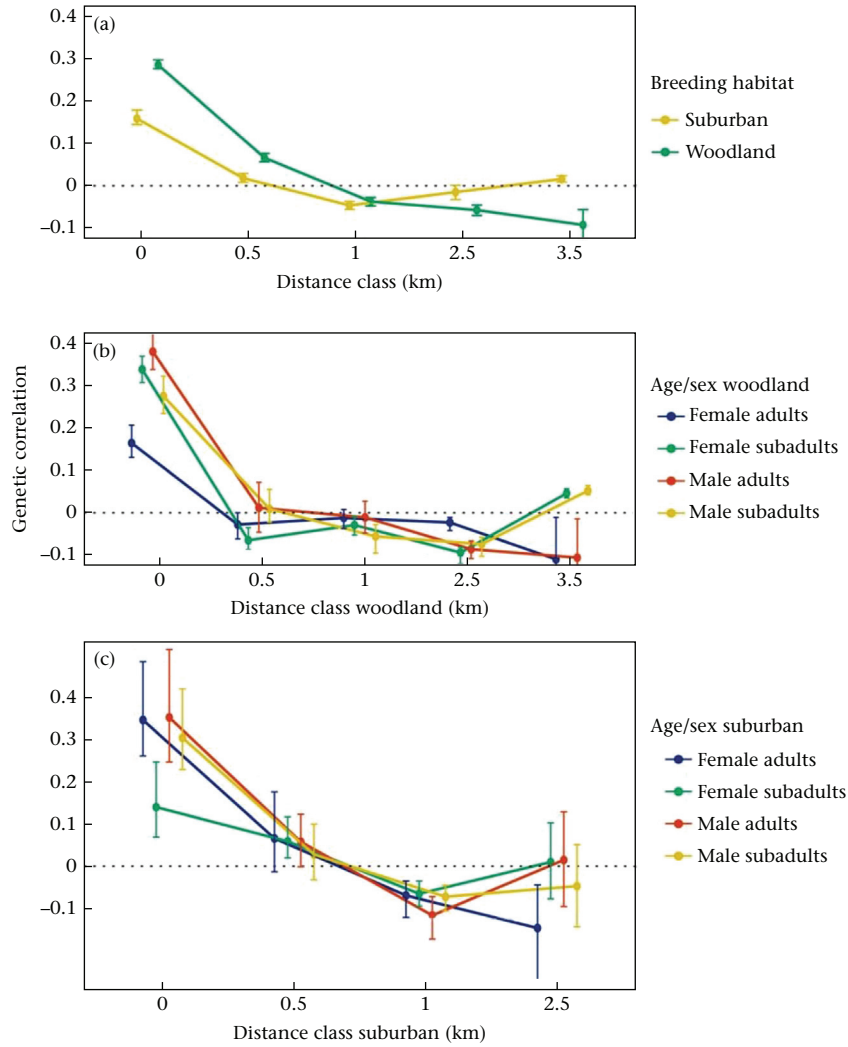


Figure 4. Plots of spatial genetic autocorrelation for individuals breeding in different habitats, showing the genetic correlation coefficient (r) as a function of distance, separated by (a) breeding habitats (suburbs and native woodland), (b) individuals breeding in the woodlands classified by age class and sex and (c) individuals breeding in the suburbs classified by age class and sex. Upper and lower bounds for the 95% confidence interval around the null hypothesis of no spatial structure ($r = 0$) calculated by bootstrap resampling are presented. The dotted line at zero bounds the 95% confidence interval of the null hypothesis of no genetic structure.

costs and benefits of cooperative breeding can change with anthropogenic habitat alteration.

Environmental Drivers

The search for environmental drivers such as climatic correlates of cooperative breeding has been carried out for several decades and continues to be a topic of high interest in evolutionary biology. While some studies have linked nonseasonal environments to the promotion of cooperative breeding (Ford et al., 1988; Gonzalez et al., 2013), others have found associations with high seasonality and interannual rainfall variability (Du Plessis et al., 1995; Jetz & Rubenstein, 2011; Rubenstein & Lovette, 2007). Nevertheless, cooperatively breeding birds inhabit ecologically and climatically diverse environments, and also show great diversity within this type of social and mating system (Cockburn & Russell, 2011; Russell, 2016).

As previous studies have observed disruption of the social structure of chough populations during severe droughts (Heinsohn et al., 2000; Beck et al., 2008; Heinsohn, 2009), and our present study was conducted during years of normal rainfall, we compared our genetic results to a previous genetic study conducted during a drought (Beck et al., 2008). We predicted that differences in environmental conditions would lead to different demographic outcomes within a cooperatively breeding species. The hypothesis was not supported by mean within-group relatedness but was supported by differences in sex-specific dispersal. Mean within-group relatedness was higher than expected by chance in 74% of the sampled groups from woodland habitat. This was similar to the proportion found by Beck et al. (2008), who carried out their study after a severe multiyear drought across eastern Australia. Thus, both studies showed that chough groups usually comprise close relatives. This result was supported by analysis of molecular variance, showing that both the chough populations in this study and that of Beck et al. (2008) were highly structured.

The most remarkable difference was that our study during nondrought weather conditions found evidence of adult female-biased dispersal whereas there was a lack of sex-biased dispersal during drought conditions (Beck et al., 2008). Most bird species have female-biased dispersal (Greenwood, 1980; Harrison et al., 2014) but white-winged choughs have been considered an exception (Beck et al., 2008). Local genetic structure between individuals in a population is expected to be higher when dispersal is infrequent, and relatedness between individuals is expected to decrease with growing geographical distances (Beck et al., 2008). From our study, the spatial autocorrelation analysis and the F_{ST} and F_{ST} estimates indicate that adult females disperse further than adult males. Subadult females and subadult males had higher F_{ST} and F_{ST} values, suggesting philopatry of younger birds, supporting observations from previous studies on this species (Heinsohn, 1992; Rowley, 1978). During the winter of 2017, we observed a group composed only of 14 adult birds, in which 10 were females, two were males and two were of unknown sex. In the following winter of 2018, not included in this study, a similar group of 20 adult birds was identified, with 14 females, two males and four unbanded individuals. In the 2018 group we could trace that 12 of the 20 birds came from groups studied in previous years, most of them from suburban groups. These groups were never observed to build a nest and were mostly composed of unrelated individuals (Leon & Heinsohn, 2018.). The formation of these groups supported our contention that adult females dispersed more during the present study.

The spatial autocorrelation analyses did not show a significant difference in genetic correlation between sexes by age in chough groups during the drought, supporting the finding of Beck et al.

(2008) of an absence of sex-biased dispersal. However, F_{ST} values were the lowest for female adults, which could be due to an actual decline in the adult female population, which was the case in suburban groups in the previous study (Beck et al., 2006). For instance, Heinsohn et al. (2000) found that group fragmentation was only observed when a severe drought occurred in 1994 after many years of group stability, which also matched an unusual increase in mortality throughout the whole population, especially of female breeders. During this drought, Heinsohn et al. (2000) observed the formation of an aggressive group composed only of males, suggesting male-biased dispersal during this period, at a time when the sex ratio of the population was also male biased. In previous studies, conducted under normal rainfall patterns and in woodland populations, white-winged chough dispersal was considered very rare (Heinsohn et al., 1992; Rowley 1978). In summary, white-winged chough dispersal patterns between groups might be strongly determined by environmental conditions, especially those that result in increased mortality. This suggests that the degree of sex bias in dispersal is a dynamic attribute of this species that depends on which demographic segments within the population are affected by environmental changes, such as rainfall patterns or other ecological factors, leading to breeding vacancies.

Habitat Alteration

When cooperative species persist in altered landscapes, examination of the changes to the social system and individual rewards may offer further opportunities for understanding both the drivers of cooperative breeding and the consequences of environmental change. We considered the impact of anthropogenic alteration of habitat, specifically urbanization, on chough social organization by comparing within-group relatedness between groups breeding in the suburbs and those in the surrounding woodland areas. Although this form of habitat change has been documented as a force changing the distribution and behaviour of species worldwide (La Sorte & Thompson, 2007; Marzluff, 2001; Meffert & Dziack, 2013) few studies have considered its impact on cooperatively breeding birds. In this study we compared groups breeding in the suburbs with those in the woodlands during a nondrought period. We found important differences in within-group relatedness between groups breeding in these two habitats, indicating the influence that changes in the landscape have in their kinship structure.

Beck et al. (2008) indicated that suburban breeding groups were slightly more related than woodland ones in their study conducted during a drought. In contrast, we found that individuals in suburban groups were less related to each other than individuals within woodland groups. Chough groups are mostly stable, and usually increase group size by adding offspring from previous years (Heinsohn, 1992). Thus, the result of this study could reflect higher mortality in groups breeding in the suburbs leading to higher dispersal of individuals from suburban groups and suggests greater instability of groups breeding in areas with higher human disturbance. Choughs living under stressful environmental conditions such as droughts form new groups composed of unrelated individuals (Beck et al., 2008; Heinsohn et al., 2000), which would account for the smaller difference in relatedness among groups from different habitats during a drought. This can also be the case for groups breeding under the stress of an urban environment, where bird mortality is higher due to predation, traffic and poisoning, among others (Baker et al., 2008; Beck & Heinsohn, 2006; Erritzoe et al., 2003; Reijnen & Foppen, 2006). In contrast, individuals in groups breeding in less disturbed areas are more closely related to each other since they most likely comprise a breeding pair and their offspring from previous years (Beck & Heinsohn, 2006; Heinsohn et al., 2000). One of the two groups

breeding in the woodlands with lower within-group relatedness was a new group that tried to breed with no success and was only together for one breeding season (Y group, Fig. 3). The second woodland group with low within-group relatedness was the only group that has been observed to move from the woodlands to the suburbs (Group N, Fig. 3).

The suburban groups in our investigation had lower F_{ST} values than woodland groups, probably resulting from more group disintegration and reestablishment with unrelated choughs, which has been common only during periods of high environmental stress like droughts (Heinsohn et al., 2000). This result again underlines the stress that suburban environments can impose on bird species, even though they can be a relief during drought periods by supplying food and water (Beck & Heinsohn, 2006). Finally, we found that subadult females in suburban nesting groups were significantly less related within their groups than the other group members. Suburban subadult females were also more related to groups with nests that were 500 m apart, reflecting higher rates of dispersal of younger female helpers to neighbouring groups than occurs among woodland breeding groups. Woodland groups instead showed adult male dispersal to neighbouring groups, and female adult dispersal from more distant groups (Fig. 4).

Reduced habitat quality can affect dispersal in cooperative breeders. Examples include red-cockaded woodpeckers, *Picoides borealis*, which need pine tree cavities for breeding (Walters et al., 1992) and superb fairy wrens, *Malurus cyaneus*, which depend on extensive vegetation patches (Parsons et al., 2009). However, little is known about the effects of urbanization on populations of cooperatively breeding species (Beck & Heinsohn, 2006). Canberra, often referred to as the 'bush capital', has many areas of parkland and reserves compared to other cities (Ignatieva et al., 2011), and these areas may even offer a refuge for choughs during drought conditions that affect the surrounding countryside (Beck et al., 2006). However, our study suggests that urbanization may present a major challenge for cooperatively breeding species, with isolation due to patchy habitats affecting not only dispersal events, but potentially also their population genetic structure. For instance, a noncooperative species, the house sparrow, *Passer domesticus*, showed increased relatedness among individuals that lived in close proximity in highly urbanized environments (Vangestel et al., 2011), and lower genetic variability and high genetic differentiation among isolated populations. Such trends have been observed in a variety of bird and other vertebrate species in urbanized areas (Delaney et al., 2010; Gil & Brumm, 2014; Unfried et al., 2013).

Rowley (1978), Heinsohn et al. (2000) and Beck et al. (2006) all pointed out that group disintegration and the formation of new groups is normally uncommon in white-winged choughs, but occurs more frequently when mortality is high, which is the case under severe drought conditions, and in suburban environments during nondrought periods. Therefore, low relatedness in some woodland breeding groups, which are probably affected by breeding close to suburban groups, suggests some instability even in nondrought conditions, reflected in the occurrence of dispersal events.

Author Contributions

C.L. and R.H. conceived the project; C.L. and N.B. collected the data; C.L. and S.B. analysed the data; C.L. and R.H. wrote the initial draft; and S.B. and N.B. contributed to improving the manuscript.

Data Availability

The data are available in Dryad at https://datadryad.org/stash/share/p7_SyoR4AvXaZRCeq9Bw6lJ5B3wMmf49t_rar_4f3w.

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APPENDIX

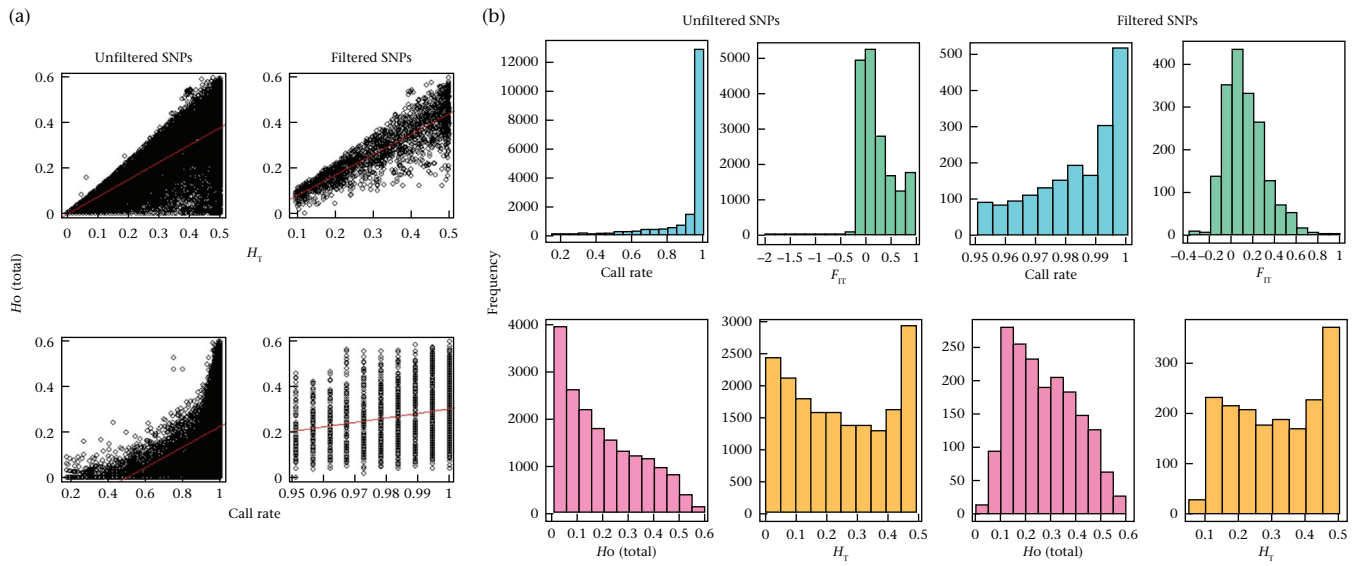


Figure A1. (a) Expected heterozygosity (H_T) versus observed heterozygosity (H_o) for unfiltered and filtered single nucleotide polymorphisms (SNPs) and H_o versus call rate for unfiltered and filtered SNPs; (b) frequency histograms of call rate, individual inbreeding coefficient (F_{IT}), observed heterozygosity (H_o) and expected heterozygosity (H_T) before and after filtering.

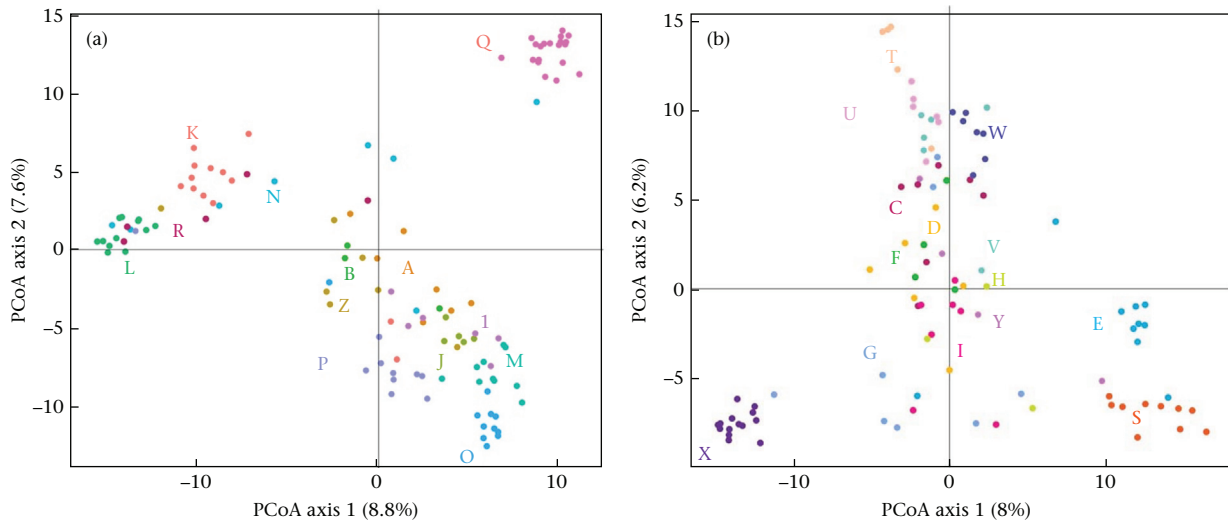


Figure A2. Principal coordinates analysis (PCoA) of white-winged chough populations during the (a) 2016–2017 and (b) 2017–2018 breeding seasons. Each point represents an individual chough, and each colour represents group membership. Proximity indicates genetic similarity between the individuals.