The absence of sex-biased dispersal in the cooperatively breeding grey-crowned babbler

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Summary

1. Cooperatively breeding birds are thought to be especially vulnerable to habitat fragmentation, in part because dispersal is typically restricted for one sex, increasing the likelihood of inbreeding. Knowledge of dispersal is essential to conservation efforts, but is often hampered by our inability to measure its frequency and distance when dispersal is infrequent and difficult to observe.

2. Disrupted dispersal is a purported cause of decline in the Australian grey-crowned babbler (*Pomatostomus temporalis*). Both sexes of offspring delay dispersal for up to several years to help parents raise subsequent broods, yet little else is known about the dispersal of this cooperatively breeding woodland bird.

3. As both sexes appear to help, but only male helpers boost fledgling production, we hypothesized that males would be the more philopatric sex in this species, and that female grey-crowned babblers would disperse over greater distances.

4. To ensure reliable determination of sex and minimize bias towards detecting short-distance dispersal events, we combined molecular-based sexing and analyses of population genetic structure using polymorphic microsatellite loci with observational data obtained over multiple field seasons.

5. Observations of banded birds showed only infrequent fission of groups or short-distance dispersal (mean = 854 m), but no apparent sex-bias in these patterns.

6. There was significant genetic differentiation between social groups, but not between the sexes. Spatial genetic autocorrelation analysis of breeders revealed a random distribution of genotypes across the study area for both sexes. Thus, contrary to expectations, we found no genetic evidence for restricted dispersal or for sex-biased dispersal over the 85-km scale of this study, indicating that effective dispersal occurs over greater distances and more frequently than recoveries of banded birds indicated.

7. We conclude that while constraints on independent breeding encourage high rates of philopatry, incest avoidance nonetheless drives high rates of dispersal by both sexes. In fragmented habitat, the dispersal dynamics of this cooperatively breeding species are unlikely to render them particularly vulnerable to genetic consequences such as inbreeding, but may lead to increased group dissolution.

Key-words: spatial genetic structure, inbreeding, dispersal behaviour, cooperative breeding, habitat fragmentation

Introduction

Habitat fragmentation and other forms of landscape modification are well-acknowledged drivers of species extinction. Together with the interacting threats of habitat loss, degradation and isolation, and altered interactions with other species, populations may decline as a result of changes in biology and behaviour (Allee 1938; Sæther, Ringsby & Røskaft 1996;

Reed 1999; Haila 2002). In general, species with complex social or breeding systems may be more prone to having their biological processes disrupted than species with simpler biological systems (Fischer & Lindenmayer 2007). One likely example of behavioural change because of habitat fragmentation is reduced post-natal dispersal, which may lead to detrimental demographic and genetic consequences, including the loss of adaptive genetic variation, fixation of deleterious mutations and inbreeding depression (Franklin 1980; Soulé 1980; Lande 1998).

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The complex social behaviours of cooperatively breeding birds are thought to render them especially sensitive to habitat fragmentation. Permanent territoriality may increase vulnerability to habitat loss, and behavioural mechanisms for inbreeding avoidance may be disrupted (Walters *et al.* 2004). In almost all cooperative bird species, offspring of typically one sex but occasionally both sexes remain on the natal territory to help raise subsequent broods. Social groups are likely to be comprised of a breeding pair and their offspring, and may rely heavily on immigrants to fill breeding vacancies. In small isolated populations, the availability of unrelated mates (Walters *et al.* 2004) or the availability of one particular sex when dispersal is sex-biased (Dale 2001) may be limited. High levels of philopatry may be expected to result in a high incidence of incestuous matings (Koenig & Haydock 2004), exacerbating the risk of inbreeding should fragmentation disrupt immigration.

The ramifications of complex sociality may be a contributing factor to the decline of some Australian passerines that inhabit fragmented woodland (Brooker & Brooker 2002; Cooper & Walters 2002). For example, much of the habitat of the Australian grey-crowned babbler, *Pomatostomus temporalis*, has been extensively fragmented by human activity. Disrupted dispersal as a consequence of this fragmentation is purported to be a cause of decline in this species (Garnett & Crowley 2000). However, little is known about its dispersal behaviour. Among cooperative breeders, it is commonplace for one sex to disperse earlier, more frequently or further than the other. For example, in white-browed babblers (*Pomatostomus superciliosus*), sons are generally philopatric and, if they do disperse, travel no further than approximately one kilometre, whereas daughters disperse more frequently and travel greater distances (Cale 1999, 2002). Grey-crowned babblers, however, show no obvious sex differences in dispersal: offspring of both sexes may remain on the natal territory for several years and there are no sex differences in the age structure of helpers (Blackmore & Heinsohn 2008).

Despite high levels of philopatry by both sexes of grey-crowned babbler, an allozyme study by Johnson & Brown (1980) found no genetic evidence for inbreeding across the 9-km range of their study. More recent studies using microsatellite markers confirm a lack of relatedness between breeders, and a disproportionate number of helpers that are unrelated to the breeder of the opposite sex in otherwise closely related social groups (Blackmore & Heinsohn 2008), suggesting that outbreeding in this species is maintained by dispersal between groups.

Dispersal patterns can be difficult to study, especially in cooperative breeders where dispersal may be intermittent. In general, observational studies based on resighting or recapture data are biased towards detecting short-distance and regular dispersal events (Koenig, Van Vuren & Hooge 1996). Direct observations of dispersal in grey-crowned babblers are hampered because the birds must be followed through their extended period of delayed breeding (generally at least 3 years; Blackmore & Heinsohn 2008), and because it is not possible to reliably sex non-breeders morphologically (King

1980). As expected, most recoveries of marked individuals show movements over only short distances (Higgins & Peter 2002).

Combining demographic data with DNA-based analyses can offer insights into animal behaviour that are not evident from demography alone and is especially useful where species are rare or difficult to observe (Walters 2000; Berg *et al.* 2009). For example, genetic methods can be used to sex individuals reliably (e.g. Griffiths *et al.* 1998), and spatial genetic analysis can reveal the extent of effective dispersal. In general, spatial genetic analysis can be conducted at one of two scales: at the broad scale among groups and populations of individuals (a scale of kilometres to hundreds of kilometres) and at the fine scale among individuals within populations (a scale of metres to several kilometres). Investigation into the fine-scale distribution of genotypes in space can reveal information about extant processes such as restricted dispersal, sex-biased dispersal and current social structures (Peakall, Ruibal & Lindenmayer 2003; Smouse *et al.* 2008). For example, in some cooperatively breeding birds, recent analysis of fine-scale genetic patterns has detected positive local genetic structure indicating clusters of proximate individuals with above-average relatedness. The non-random distribution of genotypes in these species is likely a consequence of the philopatric sex remaining on the natal territory or dispersing only short distances (Double *et al.* 2005; Temple, Hoffman & Amos 2006; Beck, Peakall & Heinsohn 2008).

Here, we studied dispersal in a mostly natural population of grey-crowned babblers to identify any form of dispersal restriction that fragmentation might exacerbate. Population genetic analysis was combined with demographic data obtained by observation over multiple field seasons to improve our understanding of dispersal and recruitment. While both sexes of babbler appear to contribute to all aspects of raising young and territory defence, only male helpers have a positive effect on reproductive success, increasing the production of fledglings (Blackmore & Heinsohn 2007). Consequently, we hypothesized that male grey-crowned babblers would be the more philopatric sex. It was expected that males would leave the natal group less often, that dispersing males but not females would be recovered close to their natal territories and thus that males would exhibit greater positive fine-scale genetic structure than females.

Materials and methods

STUDY SPECIES

The grey-crowned babbler is a group-living woodland bird weighing about 80 g. It is multibrooded and generally breeds from July to March (Blackmore & Heinsohn 2007). Social rank corresponds to age (King 1980), and breeding birds are usually at least 3 years old, although younger birds do sometimes breed (Counsilman 1979; Blackmore & Heinsohn 2008). Babblers can breed successfully as pairs, but socially monogamous, dominant pairs are usually assisted by up to eleven subordinate helpers (Brown *et al.* 1978; King 1980; Blackmore & Heinsohn 2007).

Helpers may be of either sex, and 95% ($n = 95$) are the philopatric offspring of the breeding pair. Consequently, group members are generally closely related, with the exception of dominant pairs (Blackmore & Heinsohn 2008). About ten per cent of helpers ($n = 59$) are unrelated to the offspring they help raise because they are immigrants or the product of extra-pair mating, joint-nesting or intraspecific brood parasitism. Helpers rarely reproduce. They usually inherit breeding vacancies if they are unrelated to the surviving dominant, but immigrants typically fill breeding vacancies when helpers are related to the remaining breeder (Blackmore & Heinsohn 2008).

FIELD METHODS

Between June 2003 and October 2005, 254 of 306 grey-crowned babblers (subsp. *P. t. temporalis*) living in 46 social groups were colour-banded in the Pilliga Nature Reserve (PNR; 149° 30′ E, 30° 53′ S) and surrounding district near Coonabarabran in northern NSW, Australia. Individuals were captured in mistnets or as 9- to 14-day-old nestlings and banded with a numbered Australian Bird and Bat Banding Scheme (ABBBS) stainless steel band and three colour bands for individual identification. Blood samples (20–70 μL) were taken from the brachial vein of 252 banded birds. These 252 individuals are included in population genetic analyses. Adults and juveniles (first-year birds) were aged by plumage and iris colour. Until 3 months after fledging, juveniles are dependent on group members for food and protection and can be distinguished by pale grey ear coverts (Counsilman & King 1977). Irides are dark brown in juveniles and lighten to yellow by about 3 years of age (Counsilman & King 1977; King 1980; Brown *et al.* 1983). The maximum age assigned at first capture was '3 +' years.

Because of logistic constraints, a subset of 28 of the 46 sampled social groups were closely monitored for demographic composition, breeding success and dispersal. There were 179 individuals present in or recruited to the 28 groups monitored for dispersal: 33 dominant males (27 banded), 29 dominant females (24 banded), 78 independent male helpers (77 banded) and 39 independent female helpers (all banded). Groups in this subset were censused at least weekly between 1 July and 31 March in both 2003 and 2004, and on at least one occasion between July and October 2005. Twenty-one groups lived contiguously in the PNR, and seven groups inhabited fragmented farming land. Because monitoring was limited outside of the breeding season, birds that disappeared between March and June are reported as last observed in March, including one female and five males last observed in May 2003. Birds that disappeared from their groups prior to reaching independence were assumed to have died.

Observed dispersal distances were calculated in metres using Global Positioning System (GPS) coordinates from the site where each individual was banded to where it was first resighted with a new group. The average distance between adjacent social groups was 1·1 km (± 0.14 SE; $n = 15$), calculated from nest locations.

MOLECULAR METHODS

Sex was determined using the method of Griffiths *et al.* (1998) to test for a sex-linked CHD (chromo-helicase-DNA-binding) gene. Samples were genotyped using universal dye labelling (Schuelke 2000), and fragment sizes were scored in GENEMAPPER software (Applied Biosystems, Foster City, CA, USA). Genotyping procedures and microsatellite loci are described in full in Blackmore *et al.* (2006). All samples were genotyped at seven polymorphic, unlinked microsatellite loci (Pte 17, Pte 24, Pte 28, Pte 42, Pte 47, Pte48 and Pte50). Males

were also genotyped at the sex-linked locus Pte06. Among a subset of 19 randomly selected male babblers genotyped at Pte06 and 26 to 28 babblers of both sexes genotyped at other loci, allelic frequencies averaged four alleles (range = 2–7 alleles), and the mean observed heterozygosity was 64% (range = 44–88%); the combined exclusion probability of these loci was 0·99 with one parent known. All loci met Hardy–Weinberg expectations when tested with GENEPOP version 3·4 (Raymond & Rousset 1995; Blackmore *et al.* 2006).

GENETIC ANALYSES

The GENALEX 6 software program (Peakall & Smouse 2006) was used to conduct broad-scale population genetic structure analyses, an assignment test for sex-bias, and fine-scale spatial autocorrelation analyses, as described later in the text. The total sampled population ($n = 252$) was geographically structured as follows: 169 birds lived in 29 adjacent social groups along a riparian zone in the PNR (0·5–12·6 km between groups); 21 birds in four groups lived along the southern edge of the PNR (0·8–20·4 km from the PNR population); and 62 birds in 13 groups inhabited fragments 36·6–72·7 km south-east of the PNR population. Pairwise group-by-group and individual-by-individual geographic distance matrices were computed as the Euclidean geographic distance from the GPS coordinates at which the individuals from a group were first sampled i.e. all members of a group had the same geographic coordinates.

Population genetic structure

The Analysis of Molecular Variance (AMOVA) framework within GENALEX was used to estimate Wright's F-statistics (Wright 1931) following the methods of Excoffier, Smouse & Quattro (1992) and Peakall, Smouse & Huff (1995), and to partition genetic variation within and between social groups following Beck, Peakall & Heinsohn (2008). The sex-linked Pte06 was excluded. To compare genetic variation within and between social groups, all individuals were included in a single AMOVA with social groups included as 'populations', or subsets. For this analysis, only groups from which two or more birds were sampled were included, with group size ranging from two to 16 birds and averaged six (mean = 5·9, median = 5·0 individuals, 42 groups).

We tested for isolation-by-distance using Mantel tests (Smouse, Long & Sokal 1986; Smouse & Long 1992) at both the individual and group levels, excluding Pte06. At the group level, the input matrices consisted of a pairwise geographic distance matrix and a matrix of pairwise F_{ST} values among groups. At the individual level, a pairwise genotypic distance among individuals was computed following Smouse & Peakall (1999) and compared against a geographic distance matrix. We performed analysis both across all individuals and for only the dominant individuals. Statistical significance was tested by random permutation (1000 permutations) against a null hypothesis of no relationship between genetic and geographic distance.

Spatial autocorrelation analysis

GENALEX 6 provides a multivariate, multilocus approach to spatial autocorrelation to enable the detection of fine-scale spatial genetic structure (Smouse & Peakall 1999; Peakall, Ruibal & Lindenmayer 2003; Smouse *et al.* 2008). As described by Peakall, Ruibal & Lindenmayer (2003), two matrices are required as inputs for this analysis: a pairwise individual-by-individual genotypic distance matrix based on the multiallele, multilocus genotype data and computed following Smouse & Peakall (1999); and a pairwise individual-by-individual

geographic distance matrix computed as the Euclidean geographic distance from the GPS coordinates at which the individuals were sampled. Based on these matrices and user-specified distance classes, an autocorrelation coefficient, *r*, (ranging −1 to 1) is computed. Correlograms were produced with *r* varying as a function of distance, with 1000 random permutations used to generate 95% confidence intervals around a null hypothesis of no spatial genetic structure. Values of *r* above the upper 95% confidence interval indicate positive genetic structure, and the first distance class where *r* is no longer significant estimates the extent of detectable structure (Peakall, Ruibal & Lindenmayer 2003). Note that because this spatial autocorrelation method is a generic distance-based procedure that can be applied to both genetic and ecological data (e.g. Andrew *et al.* 2007; Smouse *et al.* 2008), the autocorrelation coefficient *r* is not necessarily synonymous with genetic relatedness. However, in practice, when this method is applied to genetic data, as in the present study, *r* is closely correlated with other frequency-based relatedness estimators (see Double *et al.* 2005; Smouse *et al.* 2008; Gonzales *et al.* 2010).

As territory width averages *c.* 1 km, 500-m distance classes were chosen to separate within- and among-territory classes. We conducted spatial autocorrelation analyses on all samples and on dominants only.

Sex-bias tests

Separate AMOVA analyses were performed for each sex on its own, and for the combined male and female data set to determine whether the amount of within- and between-group genetic variation was similar for males and females. Only groups with two or more sampled individuals of the relevant sex were included (134 males in 32 groups, 91 females in 28 groups). We also performed a hierarchical AMOVA analysis with males and females included in the one data set, with males and females grouped separately and each further partitioned into same sex groups each containing more than two samples per group (in this analysis, males and females are called 'regions' in the terminology of the software package with social groups of the respective relevant sex again included as 'populations'). This hierarchical analysis enabled a simultaneous estimate of the differentiation among sexes and groups. Random permutation (1000 permutations) was used to test for significant departure from the null hypothesis of no genetic differentiation among the sexes and among the groups. Under strong sex-biased dispersal, where the dispersing sex is drawn from genetically differentiated neighbouring populations, significant differentiation among the sexes may be expected. We also compared fine-scale genetic spatial structure between the sexes by conducting separate spatial autocorrelation analyses on males and females.

As a further test to detect sex-biased dispersal, we applied an assignment test-based procedure following the methods of Favre *et al.* (1997) and Mossman & Waser (1999). The probability that a genotype occurs by chance given allelic frequencies in that population was calculated for each individual following Paetkau *et al.* (1995) and log transformed to give an individual assignment index (*AI*). An assignment index correction (*AIc*) was then computed by subtracting population means from *AI*. *AIc* values will average to zero across the population, while individuals with negative values have a higher-than-average probability of being immigrants. A significant difference in the frequency distribution of *AIc* values between males and females (assessed with a nonparametric statistical test) indicates sex-biased dispersal. Only birds in the PNR were included in this analysis to avoid any bias arising from including geographically distinct subpopulations. The tests were conducted across all sampled individuals in PNR groups, and separately for dominant individuals only, and excluded the sex-linked locus Pte06.

Results

OBSERVATIONS OF DISPERSAL AND RECRUITMENT

Nine banded helpers (six male, three female) were recovered after dispersal, and their movements are reported in Table 1. Both male and female helpers established new territories through fission, or 'budding', and dispersed to help in other groups (Table 1). Some individuals appeared to form dispersal coalitions: two brothers (YMO and WWG) dispersed together to become breeder and helper respectively to the same female; female RYA fissioned a new territory with a same-age female from an unknown group and together they defended the territory for 136 days before attracting an immigrant male. Most (8/9) banded recoveries had moved to an adjacent territory. Dispersal movements from the natal territory ranged from zero territories, where a helper nested with an immigrant female on his natal territory, while the natal group moved, to four territories. The median observed dispersal distance was 739 m (mean = 854 m). Dispersers were aged from 215 days (WWG) to 3 years old (Table 1). With one exception (RYA), 2- and 3-year-olds became breeders, while first-year birds and 1-year-olds dispersed to helping positions.

Including the banded recoveries in Table 1, 40% of males (31/78; 25 banded) and 54% of females (21/39; 18 banded) disappeared from their groups during the study period. It is possible but unlikely that we failed to detect further disappearances if unbanded helpers were replaced immediately by unbanded immigrants, as recruitment of immigrant helpers is rare (Blackmore & Heinsohn 2008). We were unable to disentangle dispersal from mortality unless helpers were recovered, but could compare the sex and age structure of birds that disappeared to detect sex differences. Most babblers disappeared from their groups as 1-year-olds (male mean age = 1·39 years ± 0·17 SE; *n* = 31; female mean age = 1·24 (±0·26 SE; *n* = 21; Fig. 1). More females (29%)

Table 1. The sex, age and dispersal distances of recovered colour-banded dispersing helpers (*n* = 9)

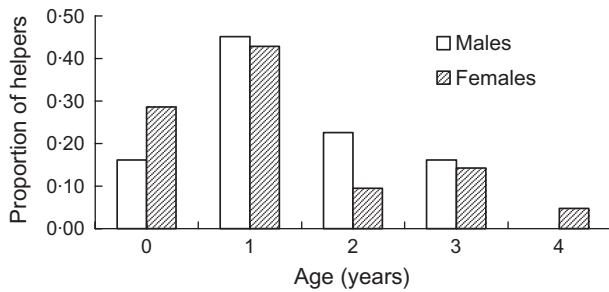| Helper	Sex	Age (years)	Distance (m)	Distance (territories)
Budded off new territory				
RYA	F	1	739	1
YRY	F	3	1123	1
RGB	M	2	0	1
OMY	M	2	582	1
Became breeder on established territory				
WRM	M	3	505	1
YMO	M	2	799	1
Became helper on established territory				
YAR	M	1	2707	4
WWG	M	0	799	1
ROY	F	1	429	1

Fig. 1. The proportion of male ($n = 31$) and female ($n = 21$) helpers that disappeared from their groups as 1-, 2- 3- or 4-year olds.

than males (16%) disappeared in their first year, and fewer females (10%) than males (23%) disappeared as 2-year-olds (Fig. 1), but these sex differences were not significant (contingency table analysis: $\chi^2_4 = 4.09$, $P = 0.40$).

During this study, 24 breeding vacancies arose – 19 in existing groups (15 male, four female) and five (three male, two female) when new groups were established. Of these, thirteen vacancies (11 males, two females) arose where there was a helper within the group available to inherit the vacancy, but only six male and both female vacancies were inherited. Two male vacancies were not filled, and the remaining three male vacancies (23%) were filled by immigrants. In four of the five cases where male helpers did not inherit, all helpers disappeared at the same time as the dominant or before an immigrant was recruited (one female helper (ROY) was recovered as a helper on a neighbouring territory; Table 1). In two groups, the dominant females failed to re-pair, remaining alone on their territories until disappearing when overrun by neighbouring groups.

Overall, immigrants filled 58% (14/24) of all breeding vacancies. Despite evidence from banded recoveries that babblers generally only dispersed to neighbouring territories, only two of the 14 immigrants recruited to breeding positions were from adjacent territories.

POPULATION GENETIC STRUCTURE

Genetic differentiation between social groups of babblers was significant (Table 2). Mantel tests did not reveal any evidence for isolation-by-distance at the group level ($Rxy = 0.110$, $n = 42$, $P = 0.111$). At the individual level, there was significant isolation-by-distance when all individuals were included ($Rxy = 0.230$, $n = 248$, $P = 0.001$), but not when only dominant birds were tested ($Rxy = 0.059$, $n = 71$, $P = 0.125$).

Table 2. Genetic differentiation (F_{ST}) between social groups of grey-crowned babblers (with sample size of $n > 1$ per group), using AMOVA to partition variation between social groups and test for significance

Samples	N groups	Between-group variation (%)	F_{ST}	df	P
Males only	32	15	0.172	31	0.001
Females only	28	16	0.185	27	0.001
Males and females	42	13	0.155	41	0.001

The outcomes of spatial autocorrelation analysis confirmed and extended the individual-level genetic patterns revealed by the Mantel tests. When all individuals were included in the analysis, significant positive local spatial genetic structure was detected up to a distance of 1·5 km (Fig. 2a). However, there was no significant positive spatial structure when helpers were removed from the analysis (Fig. 2b, c).

These results indicate that within groups, individuals are more related than average; however, breeders that live near each other are no more related than would be expected by chance. The local positive genetic structure in the population thus results from the presence of relatives within groups and not from restricted gene flow among breeders.

ABSENCE OF SEX-BIASED DISPERSAL

Between-group genetic differentiation was similarly high when group males ($F_{ST} = 0.172$) and group females ($F_{ST} = 0.185$) were considered independently (Table 2). When males and females were considered as regions within a single hierarchical AMOVA, no genetic differentiation was found between the sexes ($F_{RT} = -0.007$, df = 1, $P = 1.000$), despite significant differentiation among same sex groups ($F_{SR} = -0.177$, $P = 0.001$). Collectively, the AMOVA analyses failed to detect evidence of differences in the extent of genetic differentiation among the sexes, consistent with a lack of sex-biased dispersal. Neither dominant females (Fig. 2b) nor dominant males (Fig. 2c) displayed the positive fine-scale spatial genetic structure expected as evidence of restricted dispersal. There were no significant differences in the frequency distributions of corrected assignment indices (AIc) between all males (mean $AIc = 0.09 \pm 0.09$; $n = 100$) and all females (mean $AIc = -0.124 \pm 0.162$; $n = 69$), or between dominant males (mean $AIc = -0.15 \pm 0.16$ SE) compared with dominant females (mean $AIc = 0.184 \pm 0.22$ SE; all individuals: $P = 0.963$, Mann-Witney U-test, Fig. 2; dominants only: $P = 0.73$, Mann-Witney U-test). This indicates that rates of immigration and philopatry were similar for both sexes in both the breeding and total populations. Birds with the lowest assignment indices were always female (Fig. 3), but this weak trend was not significant.

Discussion

Combining molecular and observational data in this study provided new insight into the dispersal behaviour of a declining cooperatively breeding species, the grey-crowned babbler. Contrary to our expectations that males would be the more philopatric sex and exhibit comparatively restricted dispersal, genetic evidence supported our observations of similar dispersal traits in both sexes. Among cooperatively breeding birds, the absence of sex-biased dispersal is extremely rare. Grey-crowned babblers of both sexes fissioned territories or moved to help or breed on a neighbouring territory, but the genetic evidence indicated that they also
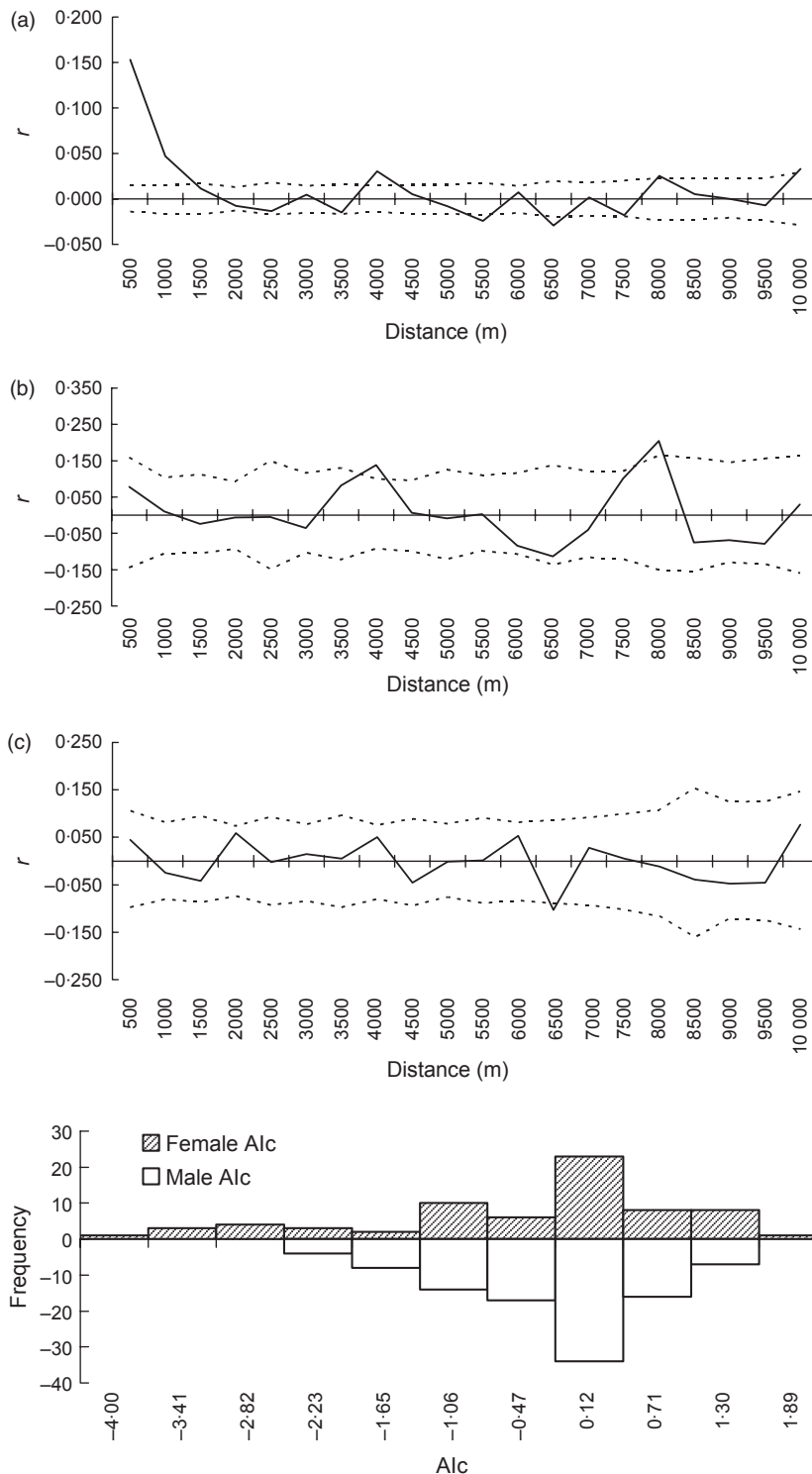
(a)

(b)

(c)

Fig. 2. Correlogram plots showing the outcome of spatial genetic autocorrelation analysis between (a) all sampled individuals ($n = 252$); (b) dominant females ($n = 36$); and (c) dominant males ($n = 45$). The correlograms show the genetic autocorrelation coefficient r as a function of distance (solid line) compared with the permuted 95% confidence interval (dotted lines) about the null hypothesis of no spatial genetic structure (i.e. a random distribution of genotypes in space).

Fig. 3. The distribution of corrected assignment indices (*AIc*) among males and females in the main study population of grey-crowned babblers ($n = 169$). Positive values indicate individuals probably born near where they were sampled; negative values indicate individuals with a higher likelihood of being immigrants.

dispersed more frequently and over longer distances than observations indicated. Consequently, the population genetic structure detected was driven by the retention of philopatric offspring on their natal territories and did not arise because subsequent dispersal was limited. This suggests that the complex social and breeding behaviours of grey-crowned babblers do not make them especially prone to disrupted dispersal or inbreeding in fragmented habitat. Nonetheless, the species does exhibit clear inbreeding avoidance behaviour

that fragmentation may act on to increase group dissolution and loss of range.

POPULATION GENETIC STRUCTURE AND ABSENCE OF INBREEDING

Grey-crowned babblers exhibited high among-group differentiation and low within-group genetic variation. Similarly, high differentiation has been found in white-winged choughs

(Beck, Peakall and Heinsohn 2008) and apostlebirds (*Struthidea cinerea*; Woxvold 2005), two other Australian species that exhibit stable groups, mostly monogamous mating restricted to a small proportion of the population, and uncommonly for birds, philopatry by both sexes (Rowley 1978; Heinsohn *et al.* 2000; Woxvold 2004, 2005). However, as neither sex of breeder exhibited the positive fine-scale spatial genetic structure expected under restricted dispersal, high differentiation in grey-crowned babblers appears to result from the presence of philopatric offspring on territories, and not because subsequent dispersal is limited for one or both sexes.

Unlike other fine-scale autocorrelational genetic studies of cooperative birds (e.g. superb fairy-wrens *Malurus cyaneus*, Double *et al.* 2005; white-winged choughs *Corcorax melanorhamphos*, Beck, Peakall and Heinsohn 2008), positive spatial structure did not extend beyond the home territory. Moreover, grey-crowned babbler loci are generally in Hardy–Weinberg equilibrium in the study population (Blackmore *et al.* 2006), suggesting minimal inbreeding despite the extreme philopatry, high within-group relatedness and occasional incestuous matings observed (Blackmore & Heinsohn 2008). Our results suggest dispersal in grey-crowned babblers is not locally restricted, consistent with Johnson & Brown's (1980) conclusion from their allozyme study. We could not ascertain how far long-distance dispersers travel, but as Edwards (1993) found mitochondrial evidence for rare but ongoing gene flow between Melville Island and mainland populations separated by 150 km, we can conclude that dispersal distances are likely to be far in excess of observed events. While philopatry by both sexes could be expected to increase the risk of inbreeding (Koenig & Haydock 2004) and render grey-crowned babblers especially vulnerable to inbreeding depression in fragmented habitat, genetic variability appears to be maintained by dispersal by both sexes from the natal area. Consequently, this cooperatively breeding species is unlikely to be particularly vulnerable to negative genetic consequences of habitat fragmentation such as inbreeding.

ABSENCE OF SEX-BIAS

We found no evidence of significant sex-biased dispersal from demographic or genetic data. Helpers of both sexes inherited breeding positions, formed new territories through fission, and were usually observed to disperse to an adjacent territory. The age distribution of helpers that left their territories was similar for both sexes. (It is likely that at least some 'disappearances' represent dispersal events (Waser, Creel & Lucas 1994), although dispersal cannot be disentangled from mortality.) Genetic differentiation was similar for males and females, population assignment indicated equivalent rates of immigration and philopatry, and neither sex of breeder showed positive fine-scale spatial genetic structure.

The absence of detectable sex-biased dispersal is extremely unusual among well-known cooperative breeders. Among cooperative species where offspring typically delay dispersal

to help parents raise subsequent broods, the absence of sex-bias has only recently been detected in one other species, the white-winged chough (Beck, Peakall & Heinsohn 2008). Green woodhoopoes also exhibit a general lack of sex-bias, usually remaining on the natal territory or moving to an adjacent territory, but females may occasionally undertake long-distance (*c.* 13 territories) emigration, and can therefore be considered the more dispersive sex (Lignon & Lignon 1990). Our finding is particularly surprising given that grey-crowned babblers otherwise demonstrate sex differences typical of many cooperative breeders with female-biased dispersal e.g. only male helpers increase the number of fledglings produced from nests (Blackmore & Heinsohn 2007), and brood and population sex-ratios are skewed towards the 'helpful' sex (Blackmore 2006).

It is difficult to explain the absence of sex-biased dispersal in grey-crowned babblers when the phenomenon is so widespread among otherwise similar cooperatively breeding birds. The forces driving sex-biased dispersal in cooperative birds and mammals are poorly understood (Berg *et al.* 2009). Greenwood (1980) suggested that, in avian species, female-biased dispersal is linked to male resource defence, while in mammals, male-biased dispersal arises through competition and defence of mates. This theory has been criticized for failing to explain rare cases of female-biased dispersal (Berg *et al.* 2009) or the absence of sex-bias (Beck, Peakall & Heinsohn 2008) in cooperatively breeding birds. Yaber & Rabenold (2002) extended Greenwood's theory to formulate the 'breeding diversity' hypothesis, in which sex-biased dispersal reflects the comparative diversity of opportunities for breeding in natal and non-natal groups. Under this hypothesis, the philopatric sex faces greater constraints from local resource defence or social status, and if natal and non-natal breeding opportunities were equivalent for the sexes, sex-bias in either, or neither, direction could occur. Unlike most cooperative breeders, both sexes of babbler adopt a range of dispersal strategies that afford both natal and non-natal breeding opportunities, including occasional joint-nesting and sharing of reproduction among groups males on the natal territory (Blackmore & Heinsohn 2008), behaviour also exhibited by white-winged choughs (Beck 2006). However, it is unclear whether such opportunities are a cause or consequence of dispersal (Berg *et al.* 2009).

Both sexes of babbler are subject to similar severe constraints on independent breeding, irrespective of the relative indirect fitness benefits that accrue to male and female helpers. Breeders are likely to be long-lived (Higgins & Peter 2002), and breeding pairs commonly endure for at least three or 4 years (Counsilman 1977). Here, we found that male breeding vacancies arose more frequently than female vacancies, but as males are more numerous in the population, (Blackmore 2006) competition is potentially equivalent for both sexes. When new groups are formed by fission, population subdivision is increased, especially if groups are kin-structured (Whitlock & McCauley 1999). Thus, the high genetic differentiation between social groups of grey-crowned babblers supports observations that new group

formation is infrequent and always by fission. Fission is the process of new group formation in many cooperatively breeding species (Woolfenden & Fitzpatrick 1978, 1990; Strahl & Schmitz 1990; Walters 1990; Legge & Cockburn 2000; Komdeur & Edelaar 2001b) and indicates that opportunities for independent breeding are rare (Komdeur & Edelaar 2001b). By remaining on the natal territory, helpers expand group size, and larger groups are better able to extend the natal territory to create opportunity for fission (Emlen 1991). This process has been shown to operate independently of helpers providing alloparental care (Komdeur & Edelaar 2001a), and, as both male and female babblers fission territories, it may partially explain why both sexes of babbler remain on the natal territory despite only male helpers gaining indirect fitness benefits by increasing non-descendent kin (Blackmore & Heinsohn 2007).

Further, while new territories were formed by fission, breeding vacancies were frequently filled by immigrants. If the costs associated with dispersing to search for a vacancy were similarly high for males and females, some individuals of both sexes would benefit from increased survival by remaining on the natal territory to await a vacancy nearby (Ekman, Bylin & Tegelström 2000). This could encourage philopatry irrespective of sex differences in indirect fitness benefits and even when dispersers had greater opportunity to secure a breeding vacancy (Kokko & Ekman 2002). Unfortunately, given the difficulties associated with observing dispersal in this species, we were unable to study sex differences in the survival and success of long-distance dispersers.

INBREEDING AVOIDANCE MECHANISMS

As social animals can reduce inbreeding through either sex-biased dispersal or behaviours that avoid incestuous matings (Pusey 1987; Clutton-Brock 1989; Pusey & Wolf 1996; Koenig & Haydock 2004), selective pressure for sex-biased dispersal in grey-crowned babblers may be low because alternative inbreeding avoidance mechanisms exist. Elsewhere, we have shown that females paired to a close relative avoid incestuous matings by obtaining extra-pair fertilizations (Blackmore & Heinsohn 2008).

Further incest avoidance mechanisms appear to be entrenched in the dispersal behaviour of this species. Like acorn woodpeckers (*Melanerpes formicivorus*, Koenig, Haydock & Stanback 1998) and Seychelles warblers (*Acrochepalus sechellensis*, Komdeur & Edelaar 2001a), recruitment is socially constrained. Not all grey-crowned babbler helpers stand to inherit the breeding position; helpers usually inherit the territory only if they are unrelated to the dominant of the opposite sex (Blackmore & Heinsohn 2008). Our observations that related helpers usually disperse following the death of a breeder suggest that incest avoidance may trigger dispersal. While this could arise if replacement breeders drive out potentially competitive same sex helpers (Woolfenden & Fitzpatrick 1980; Goldstein, Woolfenden & Hailman 1998), we found here that helpers left their groups before a replacement arrived. Group disintegration following a breeder death also occurs in acorn woodpeckers (Hannon *et al.* 1985), common marmosets (*Callithrix jacchus*, Lazaro-Perea *et al.* 2000) and white-winged choughs (Rowley 1978; Heinsohn *et al.* 2000; Beck 2006). In these species, disintegration probably occurs because incest avoidance and reproductive conflict prevent either inheritance or acceptance of an immigrant (Koenig & Haydock 2004; Beck 2006), but this is unlikely to explain the disintegration of the two babbler groups where the breeding female failed to re-pair, as dissolution was gradual and both sexes of helper dispersed. While failure to re-pair and subsequent group dissolution occurred relatively infrequently in this study, the social forces driving such dispersal warrant further investigation as they are likely to have a profound impact on this declining species. A failure of pairing success is the variable most associated with forest fragmentation (Lampila, Mönkkönen & Desrochers 2005), and large numbers of unpaired individuals are linked to declining populations in other territorial cooperative species (Dale 2001). In small or isolated populations of grey-crowned babbler where the chances of re-pairing are reduced, dispersal following the death of a breeder could result in rapid local population extinction. Further research into dispersal and recruitment near the edge of the species range may help to clarify the impact of heavy habitat fragmentation on this unusual social system.

Conclusions

This study demonstrates the value of combining observations with genetic analysis to gain a more comprehensive understanding of dispersal behaviour. Observations of grey-crowned babblers from this and earlier studies indicated that dispersal is restricted in frequency and distance, leading to the hypothesis that fragmentation-induced disruption on already restricted dispersal patterns are a likely cause of decline. However, genetic analyses failed to detect any evidence for restricted dispersal in either sex, and we conclude that the complex social system of this species is unlikely to make it more vulnerable than species with simpler social systems to the negative effects of habitat fragmentation on genetic variability. However, combining methodologies revealed that while ecological and biological constraints on independent breeding appear to be severe and to encourage philopatry, incest avoidance may sometimes enforce dispersal by both sexes, such as after the death of a breeder. Consequently, while genetic variability is likely to be maintained, lowered re-pairing success in fragmented habitat could result in more frequent disintegration of social groups and subsequent local extinctions.

Acknowledgements

field; the NSW National Parks and Wildlife Service and the Brookhouse, Graham, Lang, Drysdale, Jerry and Middleton families for access to their properties; and the ABBBS, NSW Department of Environment, Climate Change and Water and ANU Animal Experimentation Ethics Committee for licensing and approval.

References

Allee, W.C. (1931) *Animal Aggregations: A Study in General Sociology*. University of Chicago Press, Chicago.

Andrew, R.L., Peakall, R., Wallis, I.R. & Foley, W.J. (2007) Spatial distribution of defense chemicals and markers and the maintenance of chemical variation. *Ecology*, **88**, 716–728.

Beck, N. (2006) Causes and consequences of dispersal in an obligate cooperative breeder, the white-winged chough (*Corcorax melanorhamphos*). PhD thesis, Australian National University, Canberra.

Beck, N.R., Peakall, R. & Heinsohn, R. (2008) Social constraint and an absence of sex-biased dispersal drive fine-scale genetic structure in white-winged choughs. *Molecular Ecology*, **17**, 4346–4358.

Berg, E.C., Eadie, J.M., Langen, T.A. & Russell, A.F. (2009) Reverse sex-biased philopatry in a cooperative bird: genetic consequences and a social cause. *Molecular Ecology*, **18**, 3486–3499.

Blackmore, C.J. (2006) Breeding biology and behaviour of the grey-crowned babbler. PhD thesis, Australian National University, Canberra.

Blackmore, C.J. & Heinsohn, R. (2007) Reproductive success and helper effects in the cooperatively breeding grey-crowned babbler *Pomatostomus temporalis*. *Journal of Zoology*, **273**, 326–332.

Blackmore, C.J. & Heinsohn, R. (2008) Variable mating strategies and incest avoidance in cooperatively breeding grey-crowned babblers. *Animal Behaviour*, **75**, 63–70.

Blackmore, C.J., Adcock, G.J., Ebert, D. & Heinsohn, R. (2006) Microsatellite loci for population and behavioural studies of grey-crowned babblers (*Pomatostomus temporalis*: Aves). *Molecular Ecology Notes*, **6**, 412–414.

Brooker, L. & Brooker, M. (2002) Dispersal and population dynamics of the blue-breasted fairy-wren, *Malurus pulcherrimus*, in fragmented habitat in the Western Australian wheatbelt. *Wildlife Research*, **29**, 225–233.

Brown, J.L., Dow, D.D., Brown, E.R. & Brown, S.D. (1978) Effects of helpers on feeding of nestlings in the grey-crowned babbler (*Pomatostomus temporalis*). *Behavioral Ecology and Sociobiology*, **4**, 43–59.

Brown, J.L., Dow, D.D., Brown, E.R. & Brown, S.D. (1983) Socio-ecology of the Grey-crowned Babbler: population structure, unit size and vegetation correlates. *Behavioural Ecology and Sociobiology*, **13**, 115–124.

Cale, P.G. (1999) The spatial dynamics of the white-browed babbler in a fragmented agricultural landscape. PhD thesis, University of New England, Armidale.

Cale, P.G. (2002) The influence of social behaviour, dispersal and landscape fragmentation on population structure in a sedentary bird. *Biological Conservation*, **109**, 237–248.

Clutton-Brock, T. (1989) Female transfer and inbreeding avoidance in social mammals. *Nature*, **337**, 70–72.

Cooper, C.B. & Walters, J.R. (2002) Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology*, **16**, 471–478.

Counsilman, J.J. (1977) A comparison of two populations of the grey-crowned babbler (Part 1). *Bird Behaviour*, **1**, 43–82.

Counsilman, J.J. (1979) Notes on the breeding biology of the grey-crowned babbler. *Bird Behaviour*, **1**, 114–124.

Counsilman, J.J. & King, B. (1977) Ageing and sexing the grey-crowned babbler (*Pomatostomus temporalis*). *The Babbler*, **1**, 23–41.

Dale, S. (2001) Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos*, **92**, 344–356.

Double, M.C., Peakall, R., Beck, N. & Cockburn, A. (2005) Dispersal, philopatry, and infidelity: dissecting local genetic structure in superb fairy-wrens (*Malurus cyaneus*). *Evolution*, **59**, 625–635.

Edwards, S.V. (1993) Mitochondrial gene genealogy and gene flow among island and mainland populations of a sedentary songbird, the grey-crowned babbler (*Pomatostomus temporalis*). *Evolution*, **47**, 1118–1137.

Ekman, J., Bylin, A. & Tegelström, H. (2000) Parental nepotism enhances survival of retained offspring in the Siberian jay. *Behavioral Ecology*, **11**, 416–420.

Emlen, S.T. (1991) Evolution of cooperative breeding in birds and mammals. *Behavioural Ecology: An Evolutionary Approach* (eds J.R. Krebs & N.B. Davies). pp. 301–337, Blackwell Scientific, Oxford.

Excoffier, L., Smouse, P.E. & Quattro, J.M. (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics*, **131**, 479–491.

Favre, L., Balloux, F., Goudet, J. & Perrin, N. (1997) Female-biased dispersal in the monogamous mammal *Crocidura russula*: evidence from field data and microsatellite patterns. *Proceedings of the Royal Society of London Series B Biological Sciences*, **264**, 127–132.

Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265–280.

Franklin, I.R. (1980) Evolutionary change in small populations. *Conservation Biology, an Evolutionary-ecological Perspective* (eds M.E. Soulé & B.A. Wilcox). pp. 135–150, Sinauer, Sunderland.

Garnett, S.T. & Crowley, G.M. (2000) *The Action Plan for Australian Birds 2000*. Environment Australia, Canberra.

Goldstein, J.M., Woolfenden, G.E. & Hailman, J.P. (1998) A same-sex stepparent shortens a prebreeder's duration on the natal territory: tests of two hypotheses in Florida scrub-jays. *Behavioral Ecology and Sociobiology*, **44**, 15–22.

Gonzales, E., Hamrick, J.L, Smouse, P.E., Trapnell, D.W. & Peakall, R. (2010) The impact of landscape disturbance on spatial genetic structure in the Guanacaste tree, *Enterolobium cyclocarpum* (Fabaceae). *Journal of Heredity*, **101**, 133–143.

Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.

Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998) A simple DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.

Haila, Y. (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications*, **12**, 321–334.

Hannon, S.J., Mumme, R.L., Koenig, W.D. & Pitelka, F.A. (1985) Replacement of breeders and within-group conflict in the cooperatively breeding acorn woodpecker. *Behavioral Ecology and Sociobiology*, **17**, 303–312.

Heinsohn, R., Dunn, P., Legge, S. & Double, M. (2000) Coalitions of relatives and reproductive skew in cooperatively breeding white-winged choughs. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 243–249.

Higgins, P.J. & Peter, J.M. (2002) *Handbook of Australian, New Zealand and Antarctic Birds. Volume 6. Pardalotes to Spangled Drongo*. Oxford University Press, Melbourne.

Johnson, M.S. & Brown, J.L. (1980) Genetic variation among trait groups and apparent absence of close inbreeding in grey-crowned babblers. *Behavioural Ecology and Sociobiology*, **7**, 93–98.

King, B.R. (1980) Social organization and behaviour of the grey-crowned babbler *Pomatostomus temporalis*. *Emu*, **80**, 59–76.

Koenig, W.D. & Haydock, J. (2004) Incest and incest avoidance. *Ecology and Evolution of Cooperative Breeding in Birds* (eds W. D. Koenig & J. Dickinson). pp. 142–156, Cambridge University Press, Cambridge.

Koenig, W.D., Haydock, J. & Stanback, M.T. (1998) Reproductive roles in the cooperatively breeding acorn woodpecker: incest avoidance versus reproductive competition. *American Naturalist*, **151**, 243–255.

Koenig, W.D., Van Vuren, D. & Hooge, P.N. (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology & Evolution*, **11**, 514–517.

Kokko, H. & Ekman, J. (2002) Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. *American Naturalist*, **160**, 468–484.

Komdeur, J. & Edelaar, P. (2001a) Evidence that helping at the nest does not result in territory inheritance in the Seychelles warbler. *Proceedings of the Royal Society of London Series B Biological Sciences*, **268**, 2007–2012.

Komdeur, J. & Edelaar, P. (2001b) Male Seychelles warblers use territory budding to maximize lifetime fitness in a saturated environment. *Behavioral Ecology*, **12**, 706–715.

Lampila, P., Mönkkönen, M. & Desrochers, A. (2005) Demographic Responses by Birds to Forest Fragmentation. *Conservation Biology*, **19**, 1537–1546.

Lande, R. (1998) Risk of population extinction from fixation of deleterious and revere mutations. *Genetica*, **102/103**, 21–27.

Lazaro-Perea, C., Castro, C.S.S., Harrison, R., Araujo, A., Arruda, M.F. & Snowdon, C.T. (2000) Behavioral and demographic changes following the loss of the breeding female in cooperatively breeding marmosets. *Behavioral Ecology and Sociobiology*, **48**, 137–146.

Legge, S. & Cockburn, A. (2000) Social and mating system of cooperatively breeding laughing kookaburras (*Dacelo novaeguineae*). *Behavioral Ecology and Sociobiology*, **47**, 220–229.

Ligon, J.D. & Ligon, S.H. (1990) Green woodhoopoes: life history traits and sociality. *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (eds P.B. Stacey & W.D. Koenig), pp. 31–65. Cambridge University Press, Cambridge.

Mossman, C.A. & Waser, P.M. (1999) Genetic detection of sex-biased dispersal. *Molecular Ecology*, **8**, 1063–1067.

Paetkau, D., Calvert, W., Stirling, I. & Strobeck, C. (1995) Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology*, **4**, 347–354.

Peakall, R., Ruibal, M. & Lindenmayer, D.B. (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. *Evolution*, **57**, 1182–1195.

Peakall, R. & Smouse, P.E. (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, **6**, 288–295.

Peakall, R., Smouse, P.E. & Huff, D.R. (1995) Evolutionary implications of allozyme and RAPD variation in diploid populations of dioecious buffalograss *Buchloe dactyloides*. *Molecular Ecology*, **4**, 135–147.

Pusey, A.E. (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution*, **2**, 295–299.

Pusey, A. & Wolf, M. (1996) Inbreeding avoidance in animals. *Trends in Ecology & Evolution*, **11**, 201–206.

Raymond, M. & Rousset, F. (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248–249.

Reed, J.M. (1999) The role of behaivor in recent avian extinctions and endangerments. *Conservation Biology*, **13**, 232–241.

Rowley, I. (1978) Communal activities among white-winged choughs *Corcorax melanorhamphus*. *Ibis*, **120**, 178–197.

Sæther, B., Ringsby, T.H. & Røskaft, E. (1996) Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos*, **77**, 217–226.

Schuelke, M. (2000) An economic method for fluorescent labelling of PCR fragments. *Nature Biotechnology*, **18**, 233–234.

Smouse, P.E. & Long, J.C. (1992) Matrix correlation analysis in anthropology and genetics. *Yearbook of Physical Anthropology*, **35**, 187–213.

Smouse, P.E., Long, J.C. & Sokal, R.R. (1986) Multiple regression and correlation extensions of the Mantel Test of Matrix Correspondence. *Systematic Zoology*, **35**, 627–632.

Smouse, P.E. & Peakall, R. (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. *Heredity*, **82**, 561–573.

Smouse, P.E., Peakall, R. & Gonzales, E. (2008) A heterogeneity test for fine-scale genetic structure. *Molecular Ecology*, **17**, 3389–3400.

Soulé, M.E. (1980) Thresholds for survival: maintaining fitness and evolutionary potential. *Conservation Biology, an Evolutionary-ecological Perspective* (eds M.E. Soulé & B.A. Wilcox). pp. 151–170, Sinauer, Sunderland.

Strahl, S.D. & Schmitz, A. (1990) Hoatzins: cooperative breeding in a folivorous neotropical bird. *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (eds P.B. Stacey & W.D. Koenig). pp. 131–155, Cambridge University Press, Cambridge.

Temple, H.J., Hoffman, J.I. & Amos, W. (2006) Dispersal, philopatry and intergroup relatedness: fine-scale genetic structure in the whitebreasted thrasher, *Ramphocinclus brachyurus*. *Molecular Ecology*, **15**, 3449–3458.

Walters, J.R. (1990) Red-cockaded woodpeckers: a 'primitive' cooperative breeder. *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (eds P.B. Stacey & W.D. Koenig). pp. 67–101, Cambridge University Press, Cambridge.

Walters, J.R. (2000) Dispersal behavior: an ornithological frontier. *Condor*, **102**, 479–480.

Walters, J.R., Cooper, C.B., Daniels, S.J., Pasinelli, G. & Schiegg, K. (2004) Conservation biology. *Ecology and Evolution of Cooperative Breeding in Birds* (eds W.D. Koenig & J. Dickinson). pp. 197–209, Cambridge University Press, Cambridge.

Waser, P.M., Creel, S.R. & Lucas, J.R. (1994) Death and disappearance: estimating mortality risks associated with philopatry and dispersal. *Behavioral Ecology*, **5**, 135–141.

Whitlock, M.C. & McCauley, D.E. (1999) Some population genetic consequences of colony formation and extinction: genetic correlations within founding groups. *Evolution*, **44**, 1717–1724.

Woolfenden, G.E. & Fitzpatrick, J.W. (1978) The inheritance of territory in group-breeding birds. *BioScience*, **28**, 104–108.

Woolfenden, G.E. & Fitzpatrick, J.W. (1980) The selfish behavior of avian altruists. *Proceedings of the 17th International Ornithological Congress*, **2**, 886–889.

Woolfenden, G.E. & Fitzpatrick, J.W. (1990) Florida scrub jays: a synopsis after 18 years of study. *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (eds P.B. Stacey & W.D. Koenig). pp. 241–266, Cambridge University Press, Cambridge.

Woxvold, I.A. (2004) Breeding ecology and group dynamics of the apostlebird. *Australian Journal of Zoology*, **52**, 561–581.

Woxvold, I.A. (2005) Social organisation, cooperative breeding and sex allocation in the apostlebird, *Struthidea cinerea*. PhD thesis, University of Melbourne, Melbourne.

Wright, S. (1931) Evolution in Mendelian populations. *Genetics*, **16**, 97–159.

Yaber, M.C. & Rabenold, K.N. (2002) Effects of sociality on short-distance, female-biased dispersal in tropical wrens. *Journal of Animal Ecology*, **71**, 1042–1055.