

Territory configuration moderates the frequency of extra-group mating in superb fairy-wrens

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Abstract

The frequency of extra-pair paternity (EPP) in socially monogamous birds varies substantially between and within species, but ecological drivers of this variation remain poorly understood. Habitat configuration could influence EPP by moderating access to extra-pair mates, because species occupying territories in a clustered 'honeycomb' configuration have a larger pool of potential extra-group mates in their immediate neighbourhood than those living in linearly arranged territories (e.g. along narrow strips of riparian or fragmented habitat). We exploited variation in the spatial arrangement of territories due to anthropogenic modification of habitat of the cooperatively breeding superb fairy-wren *Malurus cyaneus* to test whether habitat configuration influenced the frequency of EPP. In this species, most paternity is obtained by males outside the social group [extra-group paternity (EGP)]. We found that the frequency of EGP among groups living in linear strips of roadside vegetation (41% of 44 offspring) was lower than it was for groups living in clustered territories within continuous habitat (59% of 70 offspring). Differences in group size and pair relatedness did not explain differences in EGP associated with territory configuration, although the frequency of EGP was negatively correlated with pair relatedness. Our finding suggests that territory configuration can influence rates of EGP and that anthropogenic habitat fragmentation has the potential to limit access to extra-pair mates, affecting mating systems and ultimately fitness.

Keywords: cooperative breeding, extra-pair paternity, habitat fragmentation, *Malurus cyaneus*, mating systems

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Introduction

Monogamy is the predominant social system among birds, but 86% of studied passerine species also mate outside the breeding partnership (Griffith *et al.* 2002). Extra-pair mating patterns are thus a focus for research on sexual selection in birds, often with the assumption that variation in extra-pair mating behaviour can be explained by variation in male signalling traits or benefits to females of extra-pair mating. However, correlations between rates of extra-pair mating and these factors may be eroded by ecological factors, if these influence opportunities to mate outside the pair bond. Understanding the effects of ecology on the frequency

of extra-pair mating is therefore essential for understanding mating systems, sexual signals and sexual selection.

Given that females obtain only sperm from extra-pair males, the main fitness benefits to females of extra-pair mating are presumed to be indirect and genetic. The 'good genes' hypothesis suggests that females pursue extra-pair fertilization from high-quality males to increase the viability of their offspring (Kempnaers *et al.* 1992), while the genetic compatibility hypothesis suggests females seek extra-pair fertilization from males genetically dissimilar to themselves to avoid inbreeding or maximize offspring heterozygosity (Zeh & Zeh 1996; Tregenza & Wedell 2000). Both predict reduced extra-pair paternity (EPP) in populations or species with low male genetic or phenotypic diversity because the incremental benefits of mating extra-pair should be

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diminished. Alternatively, limited dispersal may cause spatial clustering of kin and lead to higher rates of extra-pair mating to avoid inbreeding (Tregenza & Wedell 2000; Foerster *et al.* 2003).

Comparative analyses indicate that between-species variation in the frequency of EPP can be attributed largely to phylogeny and life history factors (Griffith *et al.* 2002; Westneat & Stewart 2003). For example, variation in male parental care can explain 54% of the variation in EPP frequency between bird species, with EPP higher when the male social partner invests little in the care of offspring (Møller 2000; Arnold & Owens 2002). However, ecological factors such as breeding density may also be important in explaining within-species variation in EPP (Westneat & Sherman 1997; Griffith *et al.* 2002). Where breeding density is high, both sexes are expected to have more opportunities for extra-pair copulation with lower costs, resulting in higher rates of EPP (Møller & Birkhead 1993).

Few studies have tested the effect of territory configuration on within-species variation in EPP, even though the spatial distribution of nests is likely to affect extra-pair mating (Canal *et al.* 2012; Taff *et al.* 2013). Access to nearby individuals of the opposite sex is a necessary prerequisite for mating outside the pair bond, and this access may be moderated by territory configuration or connectivity – for instance, if patchy habitat isolates some pairs from conspecifics. It has been hypothesized that territory configuration explains interspecific variation in extra-pair mating patterns among Australian fairy-wrens of the genus *Malurus* (Kingma *et al.* 2009). These cooperatively breeding birds typically exhibit high rates of mating outside their social group (54–76% of offspring; 55–95% of broods; Brooker *et al.* 1990; Brouwer *et al.* 2011; Double & Cockburn 2003; Mulder *et al.* 1994; Varian-Ramos & Webster 2012; Cockburn *et al.* 2013), with the exception of one species, the purple-crowned fairy-wren (*M. coronatus*), which has anomalously low rates of extra-group paternity (EGP) (2.6% of offspring and 5% of broods; Kingma *et al.* 2009). Kingma *et al.* (2009) proposed what we call the *territory configuration hypothesis* (TCH) to explain interspecific variation in EGP in fairy-wrens. According to this hypothesis, the linear arrangement of territories in purple-crowned fairy-wrens (a riparian specialist that lives along water courses; Rowley 1993) limits access to potential extra-pair mates, leading to low rates of EGP compared to other *Malurus* (which typically occupy territories in clustered honeycomb arrangements). For example, they estimated that a female purple-crowned fairy-wren would typically have only 7.6 males available within a two-territory radius, compared to 34.2 males for a congeneric female on a territory in a clustered configuration (Kingma *et al.* 2009).

The TCH predicts that, within species, the frequency of EGP should vary predictably with territory configuration. A recent study of red-winged fairy-wrens (*Malurus elegans*) found no difference in EGP associated with territory configuration (Brouwer *et al.* 2014). However, in this study, linear territories were in corridors of habitat extending out from continuous habitat, so sampled linear and clustered territories were closely connected (Brouwer *et al.* 2011). Here, we compared EGP in broods of the superb fairy-wren (*Malurus cyaneus*) in spatially separated, replicate configurations to test the prediction that EGP is lower in linearly arranged territories. Previous studies of this species in continuous habitat patches found that 60–76% of offspring may be fathered by males outside the group (Mulder *et al.* 1994; Dunn & Cockburn 1999; Cockburn *et al.* 2003; Colombelli-Negrel *et al.* 2009) from up to five territories away (84% from one or two territories away, Double & Cockburn 2000). Like *M. elegans*, *M. cyaneus* naturally occupies open woodlands to form mosaics of clustered territories where one group may be surrounded by up to eight neighbouring groups (Rowley & Russell 1997). However, *M. cyaneus* also occupies linear roadside habitat. The narrow width of this habitat (typically less than 50 m) imposes a linear configuration on territories, where the maximum number of neighbouring groups is 2. We analysed EGP in broods from three replicate sites with clustered territories in natural continuous habitat and four replicate sites in linear habitat, interspersed across two geographically distant populations.

Materials and Methods

Superb fairy-wrens (*Malurus cyaneus*) are small cooperatively breeding passerines that inhabit open woodland in southeastern Australia. Territorial pairs can be accompanied by up to four subordinate males and are resident year-round. Subordinate males are usually offspring from previous breeding attempts that remain on their natal territories and help feed subsequent broods (Mulder 1995). The oldest male on a territory has dominant status and is identifiable by an earlier moult into breeding plumage that is used during extra-territorial forays for courtship displays to nearby females (Mulder & Magrath 1994). Breeding females are usually unrelated to the dominant male and are believed to control extra-pair mate choice, as extra-pair copulations take place during predawn forays by females to the territories of extra-group males (Double & Cockburn 2000). We studied superb fairy-wrens in two populations 180 km apart, near the towns of Lara (38°01'00"S, 144°24'00"E) and Boho South (36°47'17"S, 145°48'09"E) in southeastern Australia, and sampled families from seven sites: three replicate sites of linear habitat

(McGearys Rd, Mackrells Rd, Creek Junction Rd) and one of continuous habitat (Kallara) at Boho South, and one linear site (Argoona Rd) and two continuous sites (Serendip South, Serendip North) at Lara. Within each population, sites were 0.8–17 km apart (Boho South: 2.1–7.4 km between sites, mean 4.4 km; Lara 0.8–17 km between sites, mean 11.3 km). Linear sites were bounded by agricultural grassland unsuitable for territory establishment (Fig. 1). Some linear sites were connected (e.g. by roadside vegetation) to larger fragments of habitat, but the nests we sampled were not close to these (based on Google Earth satellite view straight-line distance to closest patch of 1 km² or more of continuous habitat = 450 m McGearys Rd, 1.3 km Creek Junction Rd and 1.5 km Mackrells Rd at Boho, and 5.5 km Argoona Rd at Lara).

Field methods

We observed birds regularly over the breeding season (September 2011–March 2012) to locate nests. Mist nets were erected near each nest to capture all adult birds attending the nest. Nestlings and adults were fitted with a numbered aluminium band supplied by the Australian Bird and Bat Banding Scheme and a unique combination of three colour bands for individual identification. Each bird had morphometric measurements recorded, including body mass (grams) and tarsus length (millimetres). We used brachial venipuncture to collect small blood samples (10–50 µL) in heparinized capillary tubes and stored blood samples in 100% ethanol at room temperature. Each nest was observed for at least one hour to determine the composition and size of

the social group. The dominant male (putative father) on each territory was identified by comparing moult order and nest attendance (see: Cockburn *et al.* 2008; Dunn & Cockburn 1999).

We used a standardized playback survey to quantify differences in local neighbourhood density and to confirm that in linear habitat, there was only a single linear sequence of territories. We used the same playback tape for all sites, which contained a 20s broadcast of superb fairy-wren songs and calls from unfamiliar birds which we played back three times with an interval of around 1 min between broadcast pulses. At clustered sites, playback was broadcast at both 50 and 100 metres north, east, south and west of each nest, an area of 4 hectares centred on the nest. Similarly, at linear sites, playback was broadcast 50 and 100 metres from each nest both perpendicular and parallel to the vegetation's edge. The total number of birds heard or observed responding to playback at these eight survey points was recorded.

We quantified two measures of access to additional mates for each nest: the total number of neighbouring territories and the average distance (in metres) to the two closest neighbouring nests. Where the location of neighbouring nest(s) was unknown ($n = 8$ territories), we used the approximate centre of the neighbouring territory if known ($n = 6$).

Paternity analysis

We analysed paternity of 72 nestlings from 32 broods in clustered territories and 44 nestlings from 17 broods in linear territories. Genomic DNA was extracted from blood samples using a standard salt extraction method (Bruford *et al.* 1992). PCR and genotyping was performed by the Australian Genome Research Facility (Melbourne, Australia). Group members were genotyped at up to eleven polymorphic microsatellite loci (Table S1, Supporting information). Our combined exclusion probability was >0.999 at both Boho and Lara when mothers were specified as known parents (98% of 48 broods).

Paternity analyses were conducted using CERVUS (version 3.0.3, Kalinowski *et al.* 2007). We first conducted a simulation analysis to calculate critical values of likelihood ratios and determine confidence of subsequent assignments, using the following parameters: offspring 100 000; candidate males 35; candidate males sampled 0.9; proportion of loci typed 0.98 (Boho) and 0.83 (Lara); and proportion of loci mistyped 0.01, minimum typed loci 6. To determine whether offspring were sired by their putative fathers, we then analysed allelic mismatches between putative fathers, mothers and their offspring. We conservatively assigned parentage to the

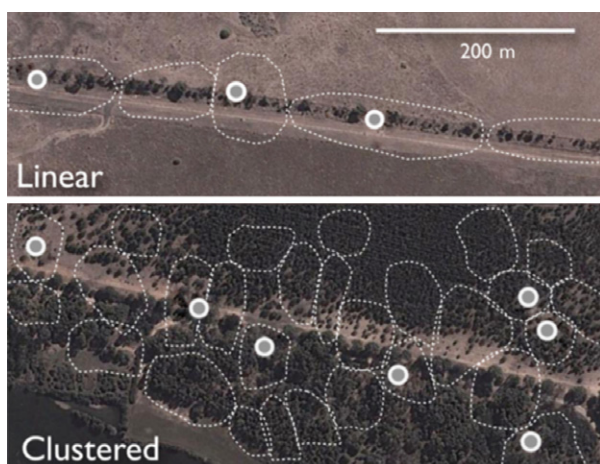


Fig. 1 Mapped territory boundaries superimposed onto satellite images illustrate sections of two sampling sites where territories are arranged linearly (top panel) and in clusters (bottom panel). Circles indicate locations of sampled nests.

social parent if it matched the offspring at all loci or mismatched at only one locus (to account for possible mutations). Offspring were considered extra-pair young when they mismatched the social father at two or more loci.

We attempted to identify sires of extra-pair offspring by comparing nonmaternal alleles to all other males in the population, including within-group subordinates. We assigned paternity to the candidate male with the highest LOD (log of odds) who did not mismatch the nestling at more than one locus. For two siblings in continuous habitat, a within-group subordinate male and male from a neighbouring territory were equally likely fathers; we conservatively assigned paternity to the within-group subordinate. Paternity assignments were manually confirmed through direct genotype comparison. Where no male fitted our criteria for paternity assignment, we specified the sire of nestlings as unknown.

Assessment of relatedness and allelic richness

We assessed how related females were to their social partners using Queller and Goodnight's relatedness coefficient (r) and the program COANCESTRY (version 1.0.0.1, Queller & Goodnight 1989; Wang 2011). For each site, we calculated mean allelic richness and gene diversity from genotypes of unrelated dominant birds ($n \geq 9$) using the program FSTAT 2.9.3 (Goudet 2001). Allelic richness can vary with habitat quality in this species (Harrisson *et al.* 2013).

Statistical analysis

We used Wilcoxon's rank-sum tests to confirm that linear and clustered territories differed as expected in

measures of neighbourhood density and to confirm that they did not differ with respect to other individual, environmental or social attributes (genetic diversity, allelic richness, pair relatedness, group size, mass of breeders and brood size). We assessed the effect of territory configuration (linear or clustered) on the proportion of extra-group nestlings within broods using a binomial logistic regression model with a logit-link function. We conducted the analysis at the level of the nestling because single broods in this species can contain offspring sired by multiple extra-pair males (Double & Cockburn 2000; this study). We included in the model covariates known to influence EGP in *Malurus*: relatedness (between the female and her social partner), the presence of helpers (pairs vs. groups) and population (Boho South or Lara). We tested whether differences between linear and clustered territories in number of neighbouring territories or distance between neighbouring nests underpinned configuration-related differences in EGP by substituting each variable in turn into the model and comparing AICs of the three models. As most of the data are not normally distributed, we present medians with interquartile ranges (IQR). All statistical analyses were performed in R v.3.1.0 (R Core Team 2014).

Results

Linear and clustered territories differed as expected in spatial arrangement and several measures of neighbourhood density, but not in other factors (descriptive statistics and comparisons detailed in Table 1). Playback attracted significantly more birds at clustered territories (Table 1) and confirmed that land adjacent to linear

Table 1 Wilcoxon's rank-sum analysis of differences between linear and clustered territories in neighbourhood density (number of birds responding to playback/4 hectares), number of neighbouring territories, average distance to the two nearest nests (metres), group size (number of birds), pair relatedness (r), allelic richness, genetic diversity, body mass (grams) of female and male breeders, and brood size. Sample sizes are numbers of territories (max 17 linear and 31 clustered; some missing data) for all variables except allelic richness and genetic diversity, which were site specific (4 linear and 3 clustered). Bolded values indicate $P < 0.05$

Variable	Median (IQR) n		W	P value
	Linear	Clustered		
Neighbourhood density	6 (0–13) 17	14 (5–20) 22	343	<0.001
Neighbour territories	2 (2–2) 16	3 (2–4) 30	416.5	<0.001
Neighbour nest distance	134 (122–157) 16	48 (38–58) 29	21	<0.001
Group size	2 (2–3) 17	3 (2–4) 31	324	0.17
Relatedness	0.08 (–0.03 to 0.12) 17	0.03 (–0.08 to 0.18) 30	242	0.78
Site allelic richness	7.89 (7.49–8.34) 4	6.83 (6.73–7.80) 3	4	0.63
Site genetic diversity	0.83 (0.81–0.84)	0.84 (0.80–0.86)	7	0.86
Female mass	9.38 (8.8–9.8) 16	9.75 (9.1–10.0) 30	307.5	0.12
Male mass	10.00 (9.7–10.5) 17	10.13 (9.6–11.5) 30	260.5	0.91
Brood size	3 (2–3) 17	2 (2–3) 31	192	0.09

habitat strips was unoccupied by fairy-wrens. Linear territories all had two neighbouring territories, while clustered territories had up to six adjacent territories, and neighbouring nests that were on average less than half as far apart. However, there was little evidence that potential indicators of habitat quality or group/individual attributes differed between linear and clustered territories (Table 1).

The proportion of extra-group offspring was lower in linear than clustered territories (41% of 44 offspring vs. 59% of 70 offspring; Fig. 2), and EGP tended to decrease with increasing pair relatedness, but did not vary with the presence of helpers or between populations (Table 2). In clustered territories, 21 of 31 broods (68%) contained extra-group young (13 entirely extra-group including 5 with 2 different extra-group sires and 1 with 3 different extra-group sires; 8 mixed within- and EGP with one within-group and one extra-group sire), one brood (3%) contained mixed within-group paternity (two within-group sires), and the remaining 9 broods (29%) had only within-group paternity by a single dominant male. In linear territories, 9 of 17 broods (53%) contained extra-group young (6 entirely extra-group including 1 with 2 extra-group sires; 3 mixed within- and EGP with one within-group and one extra-group sire). Overall, 61 of 114 offspring resulted from extra-group mating (53% EGP), and 5 offspring in 3 broods were sired by within-group subordinate males.

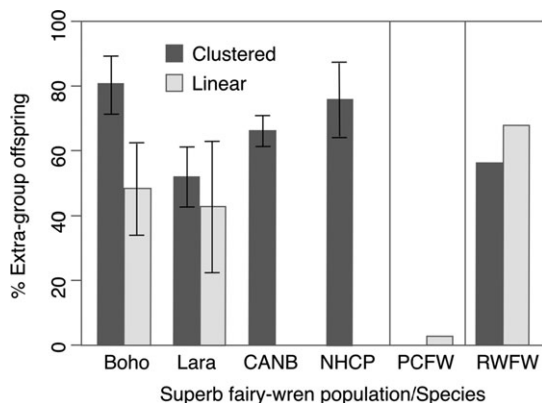


Fig. 2 The effect of territory configuration (dark bars = clustered, light bars = linear) on the percentage of extra-group offspring in superb fairy-wren (SFW, left panel) broods (mean \pm SE) at Lara and Boho South. For comparison, we also show data from other superb fairy-wren populations: CANB = Canberra (Mulder *et al.* 1994; Dunn & Cockburn 1999; Double & Cockburn 2003), NHCP = Newland Head Conservation Park (Colombelli-Negrel *et al.* 2009) and other studies on species in linear habitat: purple-crowned fairy-wrens (PCFW, Kingma *et al.* 2009) and red-winged fairy-wrens (RFWF, Brouwer *et al.* 2014).

Table 2 Binomial logistic regression analysis of how the proportion of extra-group offspring within broods is influenced by territory configuration, pair relatedness (r), population and the presence of helpers. Parameter estimates for factors are differences compared with the reference level (group in continuous habitat at Boho). Z-statistics and P-values are from the full model. Model AIC = 130.38. Bolded values indicate $P < 0.05$

Parameter	Estimate	SE	Z	P
Intercept	1.15	0.49	2.33	0.02
Configuration (Linear)	-0.93	0.47	-1.98	0.05
Relatedness	-2.28	1.20	-1.90	0.06
Population (Lara)	-0.71	0.47	-1.53	0.13
Helper presence	-0.44	0.41	-1.07	0.29

The proportion of extra-group offspring across the two study populations was relatively similar overall (49% EGP at Lara vs. 56% at Boho). Although the effect of territory configuration on EGP seemed stronger at Boho (linear: 48% EGP, clustered: 80% EGP) than at Lara (linear: 42% EGP, clustered: 51% EGP, Fig. 2), the interaction between configuration and population was not statistically significant (effect relative to clustered territories in Boho = 0.91 ± 0.99 , $Z = 0.92$, $P = 0.36$). There were more pairings between close relatives at Lara (Fig. 3), although pair relatedness did not differ significantly between populations overall (median (IQR) = 0.07 (-0.07 to 0.19) at Lara; 0.001 (-0.04 to 0.11) at Boho; Wilcoxon $W = 209$, $P = 0.39$). Median allelic richness and gene diversity were lower at Lara [allelic richness = 6.83 (6.73–6.83), genetic diversity = 0.83 (0.79–0.83)] than Boho [allelic richness = 8.43 (8.04–8.64), genetic diversity = 0.85

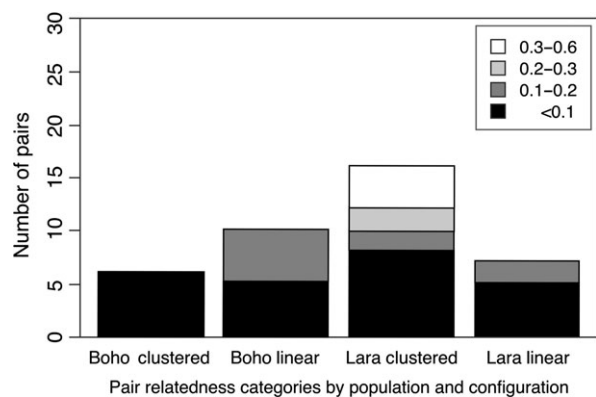


Fig. 3 Frequency of categories of relatedness between females and their social partner in linear and clustered territories at Boho and Lara. A score of 0 indicates the mean level of relatedness to be expected if two genotypes among the population were compared at random. Values range from +1 (individuals are genetically identical) to -1 (individuals diverge maximally from the population mean).

(0.82–0.87)], but not significantly so (allelic richness: Wilcoxon $W = 11$, $P = 0.11$; genetic diversity: Wilcoxon $W = 9$, $P = 0.40$, $N = 7$ sites).

Differences in neighbourhood density appeared to underpin EGP differences between territory configurations. Replacing 'Configuration' with 'Number of neighbouring territories' in the Table 2 model significantly improved the model fit (AIC changed from 130.38 to 125.09) and indicated that EGP increased as the number of adjacent territories increased (0.55 ± 0.22 , $Z = 2.45$, $P = 0.01$). Similarly, replacing 'Configuration' with 'Average distance to nearest nests' in the model significantly improved the model fit (AIC = 124.06) and indicated that EGP decreased as the distance between neighbouring nests increased (-0.012 ± 0.006 , $Z = -2.23$, $P = 0.03$).

We assigned paternity to 76% (31 of 41) of extra-group young in clustered territories and 67% (12 of 18) of extra-group young in linear territories. Extra-group sires were up to five territories from the offspring they sired, but in most cases (60%, 26 of 43), paternity was assigned to a male from a neighbouring territory (Fig. 4). The number of territories to the extra-group male did not differ significantly between linear (1.50 ± 0.23 territories) and clustered territories (1.97 ± 0.25 ; Wilcoxon $W = 395$, $P = 0.16$).

Discussion

Consistent with the predictions of the territory configuration hypothesis (TCH), we found lower frequencies of EGP in broods of superb fairy-wrens occupying linear territories (41%) than those living in clustered territories (59%). In contrast, factors thought to be associated with benefits of mating outside the social group in other fairy-wren species did not explain variation in the

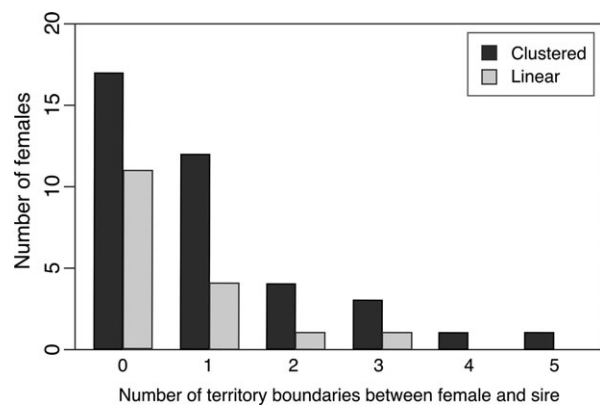


Fig. 4 The number of territory boundaries between females and sires (dark bars = clustered, light bars = linear) for all cases where the sire was identified.

frequency of EGP. We found no evidence that group size, which can influence rates of EGP in superb fairy-wrens (Mulder *et al.* 1994), differed across the two habitat configurations. Relatedness between partners was negatively, rather than positively, correlated with EGP and did not differ between the two habitat configurations. Finally, there was no evidence of any systematic difference between clustered vs. linearly arranged territories in male or female body mass, brood size, or site-specific genetic diversity or allelic richness. Our findings suggest that changes in territory configuration brought about by habitat fragmentation may reduce opportunities for EGP.

Females traversed a similar number of territories to reach extra-group sires in linear and clustered territories (Fig. 4), but probably had fewer potential mates to choose from. Linear territories had fewer neighbours than clustered territories, and neighbouring nests were also further apart, suggesting that birds in linear territory arrangements have on average fewer potential extra-pair mates within a similar distance. Because males advertise their availability for EGP with courtship displays during extra-territorial forays (Mulder 1997), reduced neighbourhood density will increase the distance males need to travel to visit a similar number of females, and presumably the risk and energetic cost of such excursions. Females in linear territories will also suffer costs because they subsequently travel to the territories of their chosen extra-group males to mate (Double & Cockburn 2000), and will have more limited options within a given radius of their territory. Travel costs may prohibit both sexes from compensating for the reduced pool of potential mating partners by travelling further. Although we did not know where in the extra-group male's territory mating took place, the fact that neighbouring nests were, on average, almost twice as far apart in linear vs. clustered territories suggests that females would have had to travel greater geographic distances to traverse a similar number of territories. Both the number of neighbouring territories and distance to closest nests predicted variation in EGP.

Extra-group paternity differences associated with territory configuration were not related to differences in group size. In another population of superb fairy-wrens, females with one or more helper males were more likely to mate extra-group than those without helpers (Mulder *et al.* 1994). Some social species have smaller group sizes in fragmented habitat (Banks *et al.* 2007), but we found no difference in group size between linear and clustered territories, and no effect of group size on EGP in broods.

Extra-group paternity differences associated with territory configuration did not appear to be driven by inbreeding avoidance. Although habitat fragmentation

can affect the frequency of inbreeding via constraints on dispersal (Banks *et al.* 2007) or effects on male philopatry (Stacey & Ligon 1991), we found no differences in pair relatedness between clustered and linear territories. Levels of genetic similarity between dominant pairs tended to be negatively, not positively, correlated with the frequency of EGP within broods in our study. This is in contrast to splendid (Tarvin *et al.* 2005), red-backed *Malurus melanocephalus* (Varian-Ramos & Webster 2012) and red-winged fairy-wrens *Malurus elegans* (Brouwer *et al.* 2011) where females were more likely to mate extra-pair as relatedness to their social partner increased, seeking extra-pair fertilizations from genetically dissimilar males. Assessing levels of relatedness may be more important for females in *Malurus splendens* and *M. elegans* because both sexes are philopatric, increasing the potential for inbreeding depression (Brouwer *et al.* 2011). The reason for the trend to low rates of EGP associated with higher pair relatedness in our study is unclear, but the pattern may have been driven by clustered territories at Lara where EGP was unusually low (Fig. 2), there were more pairings between relatives (Fig. 3), and allelic richness was lowest (AR = 6.6, and Table S1, Supporting information shows Boho had as many or more alleles than Lara in a smaller sample of birds). Low genetic diversity in a population is expected to reduce the benefits of EGP (Petrie & Lipsitch 1994).

Interspecific variation in the genus *Malurus* suggests that extra-group mating is influenced by a combination of habitat linearity and isolation, with the potential for severe fragmentation of naturally continuous habitat to influence mating systems. Red-winged fairy-wrens living in linear strips of habitat radiating out from a reserve did not have lower levels of EGP than birds living in clustered territories within the reserve (Brouwer *et al.* 2014). In our study, linear strips of habitat were not closely connected to larger habitat fragments, and the frequency of EGP in the superb fairy-wren was lower in linear than clustered territories, but still well above the 11% average for most socially monogamous birds (Griffith *et al.* 2002) and far higher than in purple-crowned fairy-wrens living in riparian habitat (Kingma *et al.* 2009). Purple-crowned fairy-wren habitat is patchy as well as linear (Skroblin & Legge 2010), so territories are often separated by gaps of hundreds of metres or even kilometres that impose an additional constraint on accessing extra-group mates. Furthermore, phylogenetic inertia may contribute to differences between these two species, as purple-crowned fairy-wren habitat is naturally linear and patchy, whereas fragmentation of superb fairy-wren habitat is anthropomorphic and recent (e.g. Harrisson *et al.* 2013). Nevertheless, despite striking differences

between the species, when costs of mating within-pair are very high in purple-crowned fairy-wrens due to inbreeding, rates of EGP increase to levels comparable with those of superb fairy-wrens in linear habitat (37.5% EGP in incestuously mated pairs; Kingma *et al.* 2013).

Our findings have potential applied relevance because they suggest that habitat modification can modify mating behaviour and influence fitness. Wildlife managers increasingly rely on linear wildlife corridors to connect habitat patches (Chetkiewicz *et al.* 2006), but despite extensive research on the effects of corridors on species richness, abundance and dispersal, consequences for mating behaviour have rarely been considered (Banks *et al.* 2007). In at least one other study of which we are aware (mountain brushtail possums *Trichosurus cunninghami*), a naturally monogamous mating system in forested expanses of habitat switched to polygyny in linear remnants of habitat (Martin *et al.* 2007), a finding consistent with expectations from changes in resource distribution and home-range overlap. Thus, in disparate taxonomic groups, there is emerging evidence that habitat alteration may influence mating systems.

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R.A.M. and M.L.H. conceived the study. G.C.B. carried out field work, collected samples and conducted genotyping. G.C.B., R.A.M. and M.L.H. wrote the manuscript. All authors commented on a final version of the manuscript.

Data accessibility

The source data and analysis scripts for this manuscript have been deposited in the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.pp67h>).

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1. Locus statistics for microsatellites used in analysis.