

Group structure, mating system and extra-group paternity in the co-operatively breeding White-breasted Thrasher *Ramphocinclus brachyurus*

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Avian co-operative breeders show a diverse range of social and reproductive systems. Here we combined microsatellite genotyping with field observations over three consecutive breeding seasons to investigate the social structure and mating system of the White-breasted Thrasher *Ramphocinclus brachyurus*. Co-operative breeding was facultative in this species, with approximately one-third of nests having helpers. Breeding groups comprised a pair of breeding adults and up to three helpers of either sex. Within co-operative groups, age was associated with parentage in both sexes. Helpers were retained offspring and either rarely or never achieved parentage in current broods. There was no evidence of egg dumping and a relatively small percentage of chicks (7.5%, $n = 67$) were fathered by males from outside the co-operative group. The White-breasted Thrasher is a globally Endangered species with a very small and declining population. A captive breeding programme for this species is not recommended at present, but may become necessary in the future, and any such programme should take account of our findings regarding breeding behaviour and group structure.

Keywords: co-operative breeding, kinship, Lesser Antillean Islands, mating system, microsatellites, Mimidae, St Lucia.

Co-operatively breeding birds are species in which social groups are made up of at least three individuals that all contribute to offspring care at a single nest (Ekman *et al.* 2004). In the majority of co-operative breeders, social groups are made up of closely related individuals (Dickinson & Hatchwell 2004), and the decision to help is usually explained in terms of inclusive fitness benefits (Hamilton 1964, Emlen 1997, Clutton-Brock 2002). By contrast, in most co-operatively breeding birds where social groups are made up of unrelated individuals, help is only given by individuals who have reason to believe that they may have direct parentage of at least part of the brood (Davies 2000; but see *inter alia* Reyer 1986 and Cockburn 2004 for other reasons why unrelated

birds may help). Subordinates may share in reproduction by mating with the dominant female in the group (Rabenold *et al.* 1990, Whittingham *et al.* 1997), by egg dumping (Komdeur 1994) or by nesting independently within a plural group structure (Curry 1988a, 1988b). In some co-operative species supernumerary birds may gain direct benefits through shared reproduction at the same time as receiving indirect benefits by increasing the production of non-descendant kin (Curry 1988a, 1988b, Whittingham *et al.* 1997, Richardson *et al.* 2002).

The presence of multiple sexually mature adults within the same social group sets the scene for reproductive conflict. Co-operatively breeding birds show a multiplicity of mating systems (reviewed by Cockburn 2004), with widely varying degrees of reproductive skew, ranging from sharing egg-laying or fertilization opportunities in an egalitarian fashion (Jamieson *et al.* 1994, Faaborg *et al.* 1995, Winterbottom *et al.* 2001), to complete monopolization of breeding opportunities by a 'despotic' dominant pair

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(Quinn *et al.* 1999, Legge & Cockburn 2000). One series of reproductive skew models proposes that subordinate reproduction is under dominant control, but that dominants may 'trade' a share in group reproduction to secure the subordinate's continued assistance. A second series of reproductive skew models posits that dominants have incomplete control over subordinate reproduction, and that reproductive partitioning within groups depends on the outcome of competition between dominants and subordinates. The outcome of these models depends on a number of parameters, including the degree of relatedness between group members (Magrath *et al.* 2004), and more empirical data are required to test them (e.g. Jamieson 1997).

Another feature of avian mating systems that has been revealed by modern molecular techniques is the near-ubiquity of extra-pair fertilizations (EPFs). Extra-pair paternity has been found in the majority of avian species that have been subject to parentage analyses (Birkhead & Møller 1998), and co-operative breeders are no exception (Pruett-Jones 2004). In populations of co-operatively breeding birds, reported rates of extra-group fertilization (EGF) range from 0% (e.g. Bruce *et al.* 1996, Quinn *et al.* 1999, Legge & Cockburn 2000) to 82% (Hughes *et al.* 2003). EPFs and EGFs are of particular interest in explaining the dynamics of co-operative systems, as female EGF can erode indirect benefits for related helpers (Dunn *et al.* 1995), and reduce the amount of within-group reproduction for group members to 'trade' (as per concessionary models of reproductive skew) or to compete over. Although females may obtain direct material benefits from copulation with multiple mates, it is generally considered that females seek extra-pair matings to improve the genetic quality of their offspring (reviewed by Birkhead & Møller 1992, 1998, Møller 1998, Petrie & Kempnaers 1998, Griffith *et al.* 2002). Recent studies have suggested that females may use EPF to avoid the deleterious effects of inbreeding (Keller *et al.* 1996, Crnokrak & Roff 1999, Slate *et al.* 2000, Keller & Waller 2002) or of extreme outbreeding (Veen *et al.* 2001). Blomquist *et al.* (2002) showed a positive relationship between genetic similarity of social mates and incidence of EPF in three species of shorebird, although their findings remain controversial owing to concerns over sample size, methodology and choice of model species (Griffith & Montgomerie 2003). Eimes *et al.* (2005) showed the same relationship in the Mexican Jay *Aphelocoma ultramarina*, and further examples exist in non-avian taxa (Amos

et al. 2001). More empirical tests of a link between genetic relatedness of social mates and incidence of EPF in birds are required.

We studied the influence of group composition and individual relatedness on reproductive skew and extra-group paternity in the White-breasted Thrasher *Ramphocinclus brachyurus* (Vieillot 1818), a terrestrial passerine bird endemic to the West Indies which is classified as Endangered according to IUCN Red List criteria (BirdLife International 2000, 2006) and has been described as one of the highest-priority bird species in the neotropics for research and conservation action (Stotz *et al.* 1996). The Thrasher was previously assumed to be a monogamous pair-breeder (Collar *et al.* 1992), although during the course of our research on this species it rapidly became clear that roughly one-third of nests had helpers. Nothing was previously known about the social organization or mating system of the species, excepting the observation that 'it is constantly to be met with in pairs, or in small mobs' (Semper & Sclater 1872). Here we use behavioural observations and microsatellite genotyping to investigate the social structure and mating system of the White-breasted Thrasher.

METHODS

Study species

The White-breasted Thrasher is a medium-sized (52–66 g), omnivorous passerine belonging to a monotypic genus in the family Mimidae (Cody 2005). Like many mimids, White-breasted Thrashers are adapted to terrestrial foraging, having a long tail, long, strong legs and a robust, elongated and curved bill that enables the bearer to 'thrash' through accumulated plant detritus in search of prey. White-breasted Thrashers are also typical of their family in being sexually monochromatic within the visible spectrum (many seemingly monochromatic birds are sexually dichromatic within the UV range of the spectrum; for example, see Eaton & Lanyon 1998, Bridge *et al.* 2008; it is not known whether this is the case in the Thrasher). Both male and female are strikingly coloured, with dark chocolate-brown upperparts, white plumage below and a deep red eye. White-breasted Thrashers on St Lucia breed between April and September, laying clutches of two eggs (93% of clutches, $n = 96$), which hatch after 14 days of incubation. Nestlings fledge after about 12 days and remain flightless for several days after leaving the nest. Multiple broods are common,

with females laying as many as five clutches and fledging as many as three successful broods over the course of an extended breeding season (Temple 2005).

Study population

The White-breasted Thrasher is restricted to approximately 13 km² of semi-arid coastal woodland on the Lesser Antillean islands of St Lucia and Martinique. Its total population has been estimated at 1300–2600 individuals (Temple 2005) and the species is considered to be globally Endangered (BirdLife International 2000, 2006). Only one other avian co-operative breeder, the Floreana Mockingbird *Nesomimus trifasciatus*, faces such a high threat of extinction (BirdLife International 2004), although other threatened species may be found to breed co-operatively in the future. During three field seasons (April–June 2002, March–August 2003, April–September 2004) we studied a population of White-breasted Thrashers resident in a 680-ha remnant of scrub woodland on the east coast of St Lucia, between the settlements of Dennery and Praslin (13°55'N, 60°55'W). Detailed behavioural data and complete sets of blood samples were collected for 30 unique groups, and a further 33 groups were monitored less intensively. These 63 groups were spread over one main study site and four satellite sites, occupying a total area of c. 100 ha.

Behavioural observations and sample collection

We caught birds in mist-nets, attached individual combinations of coloured plastic leg-rings and individually numbered metal leg-rings, and took 10–50- μ L blood samples. Blood samples were taken from the brachial vein and stored in lysis buffer at room temperature. Juveniles were ringed and sampled on the nest once they reached 7 days of age. Over three seasons, 100 adults and 119 chicks from 63 groups were caught and uniquely colour-ringed. The 100-ha study area held an estimated total of 70 groups and 170 resident adults, so we sampled approximately 60% of the adult population within the study area. We ringed a further 19 adults and 23 juveniles at sites outside the core study area. Standard biometric measures were taken, and adult birds were aged as first-years (born in the previous calendar year) or full adults (born at least 2 years previously) based on plumage characteristics and eye colour,

following the method of Temple (2005). Full adults had pale brown edging on the greater coverts and a deep brownish-red eye, whereas yearlings had greater coverts edged with russet chestnut-brown and a muddy-brown eye (Temple 2005). These differences are subtle and can only be seen in the hand.

Complete sets of samples (i.e. all adults plus offspring) were obtained for 30 unique groups, comprising 30 principal males, 30 principal females, 10 male helpers and seven female helpers. These 30 groups were distributed throughout the study area. Access problems meant that the study area used in 2002 was slightly different from that used in subsequent years (although the areas largely overlapped), so some groups could not be followed in subsequent years. Of the 30 completely sampled groups, three groups were observed for three successive breeding seasons, 12 groups were observed for two successive breeding seasons and 15 groups were observed for one breeding season. For four of these groups, we obtained complete sets of samples in two successive years, and for the remaining 26 groups we obtained a complete sample set in one year only. Parentage of nestlings was determined exclusively from those 30 completely sampled groups, where DNA for every potential breeder was available. To avoid pseudo-replication, for the four groups where full sample sets were available for two consecutive years, one year was chosen at random to be included in the parentage analysis. We determined group composition using the 30 completely sampled groups, because White-breasted Thrashers can be aged and reliably sexed only after capture and molecular sexing (Temple 2005). Data on group size and recruitment of helpers come from all study groups ($n = 26$ in 2002, $n = 63$ in 2003, $n = 23$ in 2004).

Groups were visited several times a week to check for the presence of individuals and to look for signs of nesting during the three study seasons. Nests were found by direct searching (Thrasher nests are large, conspicuous and placed at low heights), and were monitored approximately every 4 days, or more often if hatching or fledging was imminent. During these regular visits, information was collected on group membership and the movement and dispersal of individuals. The location of colour-ringed birds was recorded using a hand-held Garmin 12XL GPS receiver. To discover more about the behaviour of group members, nests were observed from a hide positioned 15–20 m from the nest tree. Up to three observation periods were recorded for each

group, timed when nestlings were 4–10 days old. Observation bouts took place between 07:00 and 12:00 h and lasted from 1.5 to 3 h. There were too few behavioural observations to quantify dominance interactions within groups. However, a male and female were considered to be the principal pair if, by comparison with other group members of the same sex, they performed the majority of chick care (Temple 2005) and tended to be the first to return to the nest following disturbance. In all cases, the oldest birds of each sex in each group were classed as the principal pair.

DNA extraction, microsatellite typing and DNA-based sexing

Total genomic DNA was extracted from the blood samples using standard overnight proteinase K digestion followed by phenol/chloroform extraction and ethanol precipitation (Sambrook *et al.* 1989). All DNA samples were then genotyped for four dinucleotide-repeat and two tetranucleotide-repeat microsatellite loci, developed specifically for this study (Jin *et al.* 2006). The polymerase chain reaction (PCR) amplification and screening of microsatellite loci followed Hoffman and Amos (2005). One sample failed to amplify at more than two loci and was excluded from the dataset.

Microsatellite genotyping and scoring errors can seriously impact upon estimates of parentage, especially where putative fathers are excluded based on a mismatch at a single locus (Marshall *et al.* 1998, Taberlet *et al.* 1999, Hoffman & Amos 2005). A common source of error involves the incorrect assignment of alleles, due for example to the presence of stutter bands, weak PCR amplification or alleles appearing blurry on autoradiographs (Hoffman & Amos 2005). Consequently, whenever we encountered a potentially ambiguous genotype, the sample was re-genotyped at that locus. In addition, we also estimated the genotyping error rate for our dataset by extracting, independently genotyping and blind-scoring 24 individuals for which duplicate blood samples had been obtained.

A PCR-based method (Griffiths *et al.* 1998) was used to sex all sampled birds. The accuracy of this technique was checked using a control group of 36 adult females who were caught at the nest-site whilst brooding and sexed according to the presence of a brood patch (birds lacking a brood patch cannot be sexed with certainty without dissection, laparotomy or molecular sexing).

Parentage analysis and relatedness

Before analysing parentage, we tested the genotype data for deviation from Hardy-Weinberg equilibrium and for linkage disequilibrium using Genepop version 3.1d (Raymond & Rousset 1995). All tabulated probabilities were corrected for continuity using the Bonferroni method (Rice 1989), with an α level of $P < 0.05$. Genepop was also used to calculate expected heterozygosity and the frequency of null alleles (Dakin & Avise 2004). Finally, we calculated the probability of paternal exclusion (Weir 1996), a measure of the ability of a genetic test to exclude non-fathers from paternity. This was very high at 0.967, implying that few, if any, of our paternity assignments are likely to arise due to chance.

We used the program NEWPAT XL (Worthington-Wilmer *et al.* 1999) to verify that the resident female's genotype matched that of the chicks hatched by the group, and thereafter to assign paternity using an exclusion approach. Any mismatches between resident females and their putative chicks were double-checked and, where the discrepancy could be attributed to an obvious scoring error (see earlier section), the genotype was adjusted accordingly. Paternity analysis employed NEWPAT XL to search for matches between candidate males and the deduced paternal alleles of each offspring. Two analyses were conducted, using different levels of stringency. In the first analysis, we allowed a maximum of two un-scored loci and no mismatches. In the second, to guard against males being excluded through scoring errors or mutations, we allowed up to two mismatches, and in all cases where a resident male and a chick were mismatched, the original autoradiograms were re-checked. We searched for candidate fathers amongst all sampled males ($n = 105$), and putative matches were tested using Monte Carlo simulation. To test the hypothesis that helpers are retained offspring from previous years, a parentage analysis identical to the one described above was carried out, considering all full adults (i.e. individuals at least 2 years old) that were part of the group to be the potential parents of any resident yearlings.

Relatedness (r) is a continuous measure of overall identity by descent (Blouin 2003). We calculated Queller and Goodnight (1989) estimators of r for all social pairs in the study population using KINSHIP (Goodnight & Queller 1999). This statistic has the desirable property of being approximately normally distributed about a mean of 0.5 for first-order relatives and zero for unrelated individuals.

RESULTS

Group size and composition

Groups ranged in size from two to five, with an overall mean of 2.44 ± 0.06 (mean \pm se (for all cases hereafter), $n = 112$, range 2–5, Table 1). Group size varied little between years, with consecutive means of 2.54 ± 0.15 ($n = 26$), 2.35 ± 0.08 ($n = 63$) and 2.61 ± 0.17 ($n = 23$) in 2002–04. On average, 37.2% of groups had helpers in any given year. The composition of the group by age was determined for 30 different groups (age composition could be determined only for groups where all individuals had been captured and examined in the hand). Eighteen of these (60%)

were lone pairs, eight were trios and four were quartets (Table 2). In all 18 cases, both members of a lone pair were full adults. Yearlings were never encountered breeding independently or with an adult partner.

Table 1. Size of White-breasted Thrasher breeding groups on St. Lucia in 2002–04.

Year	Group size			
	2	3	4	5
2002	15	9	1	1
2003	44	17	1	1
2004	14	4	5	0

Table 2. Size, composition and identity of group members for 30 unique groups of White-breasted Thrashers studied in 2002–04. Values of relatedness (r) between members of the principal pair, occurrence of extra-group fertilizations (EGFs) and number of chicks sampled in each group. Group size is defined as the total number of yearlings (age = 1) and full adults (age > 1) present throughout the breeding season. Individuals are identified by the number on their metal leg-ring. No individual was a member of more than one group.

Group	Year studied	Group size	Relatedness between principal pair	EGF recorded?*	Helper(s) present? (M = male, F = female)	No. of chicks sampled
2	2002	2	-0.212			2
5	2002	2	0.126			2
15	2002	2	0.489	Y		1
34	2002	2	-0.083			1
1	2003	3	0.000	Y	M	2
3	2003	2	0.200			1
9	2003	3	0.166		F	1
38	2003	2	0.117			2
53	2003	3	0.096		M	2
59	2003	3	0.217		M†	2
64	2003	2	-0.198			2
80	2003	2	0.012			2
115	2003	2	-0.440			2
B	2004	4	-0.060		M, F†	2
C	2004	2	0.508			2
D	2004	2	0.221	Y	F†	3
E	2004	3	0.197	Y	F	4
G	2004	2	0.682			2
H	2004	3	-0.123		M	3
I	2004	3	0.282		M†	3
J	2004	2	-0.333			5
L	2004	4	-0.029		M, F†	3
M	2004	2	0.261			4
O	2004	2	0.241			2
Q	2004	3	0.262		M†	2
R	2004	4	-0.261		M, F	1
T	2004	2	-0.136			1
U	2004	2	0.217			2
V	2004	4	-0.185		M, F	3
W	2004	2	0.338			3

*Y denotes groups that raised at least one chick fathered by a male from outside the group.

†Indicates helpers that were ringed as chicks and that are known (independently of any genetic analysis) to have stayed on as helpers in their natal group.

Co-operative groups almost invariably consisted of a pair of full adults accompanied by one or two first-year birds; there was just one trio that was made up entirely of older birds (two males and a female).

Recruitment and turnover of helpers

We observed 22 banded yearlings of known origin that stayed as helpers. Birds never dispersed into another group to become a helper. Both sexes acted as helpers, although there was a slight bias towards males (10:7 for the 30 completely sampled groups). Only one individual (a male) remained as a helper for two consecutive years. In two cases, offspring from the previous year overwintered with the natal group even though they did not stay on as helpers in the next breeding season (our study may have underestimated this phenomenon because monitoring did not take place in the winter months, and only started just before the beginning of the breeding season).

Turnover of principal birds

Principal pairs were usually stable from year to year, and opportunities to fill a vacancy in an established breeding group occurred infrequently. In 29 group-years, four vacancies for males and two vacancies for females arose (in all of these cases the previous incumbent disappeared from the study site; there were no 'divorces'). Territory inheritance, where a helper inherits the principal role, occurred on one occasion, when a 2-year-old male helper inherited the territory following the disappearance of his father. This did not result in an incestuous mating because the principal female had been replaced by the principal female from the neighbouring group

before the start of the breeding season. In the other five cases where vacancies arose, either there were no helpers in the group at the time (two cases), or the helper(s) present was not of the appropriate sex to fill the vacancy. Three male helpers subsequently settled as full adult breeding birds directly adjacent to their natal group, but no female helpers were observed to settle near to their natal group (see Temple *et al.* 2006 for more information on male and female dispersal patterns). Helpers that did not stay on to help for a second year and that did not inherit a territory or settle nearby all disappeared, and their fate is not known.

Genotyping and error rates

A total of 253 White-breasted Thrasher blood samples were genotyped for six microsatellite loci. The frequency of missing single-locus genotypes in the dataset was 0.024. There was no evidence of linkage disequilibrium, although two loci showed significant deviation from Hardy-Weinberg equilibrium (Table 3). Estimated null allele frequencies were also high (> 5%) for these two loci, which potentially could have caused problems for the parentage exclusion analysis. However, it transpired that no principal males or helpers were excluded from parentage of offspring on the basis of a single mismatch at either of these loci (possible null allele mismatches involve both putative father and offspring being homozygous for different alleles).

Genotyping errors may represent a major cause of mismatches between offspring and their true parents (Marshall *et al.* 1998, Hoffman & Amos 2005a). By repeat genotyping 24 randomly selected samples at six loci, an error rate of 0.0074 per reaction or 0.0046 per allele was calculated (four reactions were

Table 3. Summary of microsatellite loci used in this study, including polymorphism characteristics for the White-breasted Thrashers genotyped.

Locus	No. of alleles	Size range (bp)	H_e^*	Null allele frequency	Hardy-Weinberg equilibrium probability†	Paternal exclusion probability
WB2	6	213–223	0.740	+0.0164	0.850	0.506
Th3	6	136–156	0.736	−0.0295	0.230	0.524
WB5	8	168–202	0.773	+0.0705	0.0014	0.588
Th6	6	144–164	0.655	+0.0293	0.393	0.399
Th12	2	153–155	0.342	+0.1285	0.0005	0.141
Th15	4	151–159	0.602	+0.0451	0.0988	0.330
Overall	5.33	136–223	0.641	+0.0433		0.967

*The level of heterozygosity expected under Hardy-Weinberg equilibrium (HWE).

†Probabilities in bold type remain significant after the sequential Bonferroni correction is applied (Rice 1989).

mistyped and five out of 1080 alleles were scored incorrectly). Of the five alleles mistyped, two were due to data entry errors and three were attributable to scoring inconsistencies, which occurred because the autoradiograph for that reaction was faint or ambiguous. In all three cases it had already been recognized that scoring was problematic, and they were 'flagged' in the dataset so that the scores would be treated with caution. These three cases were also consistent with the dropout of a single allele during PCR amplification (Gagneux *et al.* 1997, Goossens *et al.* 1998). Previous studies report error rates of 0.001–0.127 per reaction (reviewed by Hoffman & Amos 2005a). The error rate found in this study falls at the lower end of this range, and we can consequently be relatively confident in the relatedness and parentage estimates presented here. The genetic sexing method was found to be 100% accurate: in all 36 cases where an individual could be sexed as female due to the presence of a brood patch, molecular sexing returned an identical result.

Mother–offspring pairs

In every case ($n = 67$ chicks, 40 nests, 30 groups), the genotype of the nestling matched that of the putative mother (i.e. the oldest female, in cases where there was both a full adult and a yearling female in the group). Of the 16 chicks born in groups where there were two resident females ($n = 7$), the younger female (a yearling in all seven cases) could be excluded from the parentage of the majority of chicks produced (9/16 or 56.25%). Remaining chicks matched both resident females. Given that helpers were daughters of the principal female (and hence siblings or half-siblings of the current year's offspring), it is unsurprising that many of the chicks matched both the principal and the helper female. There was no evidence of brood parasitism by conspecific females from outside the social group.

Paternity analysis

After scoring errors were corrected, 92.5% of chicks (62/67) were found to have genotypes matching that of the principal male. The remaining 7.5% of chicks (5/67) were found to mismatch all males in their group, and were concluded to have been fathered by extra-group males (Table 4). As was the case for females, sharing of parentage between principal and subordinate same-sex group members was either rare or absent. In the 10 groups with two

Table 4. Summary of paternity exclusion analysis of $n = 67$ offspring and $n = 105$ candidate fathers. The majority of chicks matched the principal male in their natal group. All resident principal males were sampled. Likelihood was calculated based on Monte Carlo simulation using NEWPAT XL.

Result of exclusion analysis	No. of offspring
Principal male is the only match	15
Principal male is most likely of multiple matches	14
Principal male matches, but is not most likely	33
Principal male mismatches offspring	5

resident males, 63.6% of chicks (14/22) matched the adult male but not the yearling male. The remaining 36.3% of chicks matched both resident males. NEWPAT was used to search for candidate fathers for the five chicks that were sired by extra-group males. For three of the five, none of the sampled candidate males matched the chick. For one of the remaining two individuals there were eight matching males, none of which was a close neighbour of the cuckolded male. For the final chick, there were two potential fathers, including a male from an adjacent group.

Identity of helpers

Within the 30 completely sampled groups, there were seven female helpers and 10 male helpers. Every helper matched the principal pair at all loci, in accordance with the hypothesis that helpers are philopatric offspring from the previous year and with observational data where six of the 17 helpers were already known to be the previous year's offspring of the principal pair because they were ringed as nestlings.

Reproductive skew within groups

We tested whether male or female helpers ever share reproduction with the principal pair using a combination of genetic analyses and behavioural observations. In the case of females, all offspring matched the principal female while female helpers mismatched at least one chick in 5/7 groups. Behavioural observations showed that the mean clutch size of co-operative groups was no larger than that of unassisted pairs (1.98 ± 0.03 for 61 clutches laid by 54 unassisted pairs versus 1.94 ± 0.04 for 35 clutches laid by 26 co-operative groups). Behavioural observations

also revealed that in all five cases where two females were mist-netted at the same nest at the same time, the principal female had a distinct brood patch whereas the female helper had no brood patch.

Male helpers mismatched 14/22 chicks. In every case where the principal male mismatched a chick, the male helper mismatched as well and we concluded that the chick was the result of extra-group copulation. However, in one group in 2004 the older male disappeared during the breeding season, and the helper male (thought to be his son based on genetic paternity analysis), who mismatched both chicks in the first brood, acquired principal status and matched the second-brood chick.

Extra-group paternity and parental relatedness

If females use EGFs to avoid the deleterious effects of inbreeding (Blomquist *et al.* 2002), then we would expect to find a positive correlation between the occurrence of EGFs and the genetic similarity of social mates. Pairs in which the male was cuckolded were more closely related to each other on average ($r = 0.227 \pm 0.100$, $n = 26$) than pairs in which the female remained faithful ($r = 0.064 \pm 0.052$, $n = 4$), but this difference was not statistically significant: logistic regression showed that the Queller and Goodnight (1989) relatedness (r) of social mates was not a significant predictor of EGF ($\chi^2 = 1.43$, $df = 1$, $P = 0.23$). However, the sample size was very small for EGF pairs, and more data are needed to test the inbreeding avoidance hypothesis in this species conclusively.

DISCUSSION

Social system

White-breasted Thrashers studied on St Lucia lived in groups consisting of a pair of breeders, both of which were at least 2 years old, and up to three helpers, the vast majority of which were yearlings. All helpers of known origin were recruited from young fledged in the group; none was an unrelated immigrant. In this respect, White-breasted Thrashers are typical of the majority of avian co-operative breeders in which groups form via the retention of philopatric offspring (Dickinson & Hatchwell 2004). Both males and females acted as helpers in roughly equal proportions. This contrasts with the majority of co-operatively breeding birds in which helpers are

predominantly or exclusively male (Cockburn 1998, Heinsohn 2004). In another co-operatively breeding mimid, the Galápagos Mockingbird *Nesomimus parvulus*, both sexes can act as helpers but whether they do so or not depends on the operational sex ratio (Curry & Grant 1990).

In some co-operatively breeding birds, including most other mimids known to be co-operative breeders (e.g. Galápagos Mockingbird, Española Mockingbird *Nesomimus macdonaldi*, Floreana Mockingbird *N. trifasciatus*, Tropical Mockingbird *Mimus gilvus*; Curry 1989, Morton *et al.* 2004, Botero & Vehrencamp 2007), territories may be shared by multiple breeding units, resulting in plural breeding. Social groups may include multiple breeding birds of either sex, usually with each female having her own separate nest but with all females and their social mates and helpers belonging to a social group that defends a single collective territory (Curry & Grant 1990). In plural-breeding species, subordinates may share in reproduction by nesting independently within the territory occupied by the social group, and in some species individuals may act as helpers while simultaneously breeding at another nest (Curry 1988a, 1988b). Our study did not allow us to determine conclusively whether or not White-breasted Thrasher breeding units aggregate to form collective territorial groups, because to do so would require detailed mapping of movements of individuals and more thorough, direct measures of dominance/subordinate relationships (e.g. see Curry 1988b). However, we can state with a reasonable degree of confidence that White-breasted Thrasher helpers in our study did not share in reproduction by nesting independently within a plural group structure. In contrast with Galápagos Mockingbirds, which are capable of breeding in their first year (Curry 1988b), White-breasted Thrashers were never observed to breed as yearlings (and almost all helpers were yearlings). Whereas Galápagos Mockingbirds may help at one nest at the same time as breeding at another (Curry 1988a, 1988b), no White-breasted Thrasher in this study was observed to attend two different nests simultaneously. However, co-operation between as well as within breeding units may be important in the Thrasher. Spatial autocorrelation analysis showed highly significant fine-scale genetic structure in our study population (Temple *et al.* 2006), with levels of relatedness between principal males in neighbouring breeding units comparable with that seen within co-operative groups in many species where kin selection is cited as a cause of co-operation. The mean relatedness

between male neighbours was between that expected for cousins ($R = 0.125$) and that expected between uncles and their nephews, grandfathers and their grandsons, or half-siblings ($R = 0.25$) (Temple *et al.* 2006). Further research is required to show how far cooperation between neighbouring breeding units extends.

Mating system

No instances of egg dumping or unequivocal joint nesting between the principal female and female helpers were recorded. Likewise, there was no conclusive evidence that male helpers ever shared parentage of broods. However, the fact that subordinate birds are expected to be older siblings of the current brood made parentage testing difficult (Double *et al.* 1997), particularly with the small number of loci we were able to develop. The pattern we found was one in which, for both sexes, whenever one or more adult birds from the group match a chick, the principal bird is also included. That the converse is not true (subordinate birds never match when the principal bird does not) suggests that the principal birds get most parentage. To get a feel for how often helpers are likely to match by chance, we conducted simple Monte Carlo simulations, generating pairs of unrelated birds by drawing alleles randomly from the observed allele frequency distributions and then asking how often a chick is genetically consistent with being the offspring of its true mother and any of one, two or three full-sibling helpers. We found frequencies of 34, 50 and 62%, respectively, well in line with the rates we found where both the principal and a female helper match (44% of chicks, average = one female helper per group) and where the principal and a male helper match (36% of chicks, average = one male helper per group). Consequently, our data appear consistent with helpers rarely or never reproducing at the expense of the principal bird in the group. Rates of EGF were also relatively low.

Extra-group mating

A female bird may experience a wide range of benefits from engaging in extra-group matings (Andersson 1994), although it is generally considered that the most important benefit is that of obtaining better genes for her offspring (Birkhead & Møller 1992, 1998, Møller 1998, Petrie & Kempenaers 1998, Griffith *et al.* 2002). Some co-operatively breeding birds exhibit very high levels of extra-group

paternity (e.g. Mulder *et al.* 1994, Richardson *et al.* 2001), although others do not (e.g. Haydock *et al.* 1996, Quinn *et al.* 1999, Legge & Cockburn 2000, Hatchwell *et al.* 2002), including our study species. Rates of EGF may be linked to the degree of genetic variance between males. Island populations are expected to exhibit low levels of genetic variability due to a combination of founder effects, inbreeding, genetic drift, and low rates of immigration and emigration (Wright 1931, Jaenicke 1973; Frankham 1997), and it has been argued that such genetically depauperate populations should provide females with little incentive to engage in extra-pair copulations (Petrie & Kempenaers 1998). Alternatively, if there is persistent intense competition for limited breeding space, successful males might be of uniformly high genetic quality and females may gain little or no benefit from extra-group fertilizations (Quinn *et al.* 1999).

Females who solicit extra-pair matings may do so because they are seeking 'compatible genes' rather than just 'good genes' (Mays & Hill 2004, Puurtinen *et al.* 2005). One form of genetic compatibility between partners is achieving an optimal degree of outbreeding (Bateson 1983), and it has been suggested that females who are closely related to their social mates should use EGF to avoid inbreeding (Keller & Waller 2002). We found no significant relationship between the genetic similarity and the occurrence of EGF in the present study, but our sample size was too small to confirm or refute the inbreeding avoidance hypothesis conclusively.

Within-group reproductive skew

There was no unequivocal evidence that reproductive sharing between principal birds and helpers ever occurred in this study. Although the possibility of some subordinate reproduction cannot be ruled out, the results suggest that reproductive skew in White-breasted Thrasher groups is high. Joint nesting by females in avian social groups is unusual (Vehrencamp & Quinn 2004), although it happens fairly often in several mimid species (e.g. Curry 1988b, Curry & Grant 1991). Why, then, is there apparently no within-group reproductive sharing in White-breasted Thrasher breeding groups?

Incest avoidance may place an important constraint on reproductive sharing in many co-operative societies (particularly those formed by the retention of philopatric offspring), but it has not yet been incorporated into any formal reproductive skew model (Magrath *et al.* 2004). There is evidence of

incest avoidance and possibly inbreeding depression in some co-operative breeders (Koenig & Haydock 2004), with groups in some species, such as the Acorn Woodpecker *Melanerpes formicivorus*, going to the length of forgoing breeding entirely if the only reproductively mature pair in the group is closely related (Koenig *et al.* 1999). However, in a small number of species it seems that incest (defined as mating between first-order relatives) forms a routine part of the breeding strategy (Koenig & Haydock 2004). The extent to which incest occurs and its adaptive (or maladaptive) significance are controversial topics (Koenig & Haydock 2004), not least because, even with modern molecular techniques, incest remains hard to detect (McRae & Amos 1999, Parker *et al.* 1999). Because of the low rates of extra-pair paternity and the high stability of pair-bonds between breeders, White-breasted Thrasher helpers are almost invariably first-order relatives of the breeders that they assist. Given the potential costs of inbreeding (Hedrick 1994, Lacy & Ballou 1998), there may be a strong selection pressure for helpers to exercise restraint and make no attempt to copulate with the opposite sexed breeder.

Alternatively, dominant birds may exert control over subordinates, as suggested in many models of reproductive skew. Control may be complete (as in Vehrencamp's (1979, 1980, 1983) original 'optimal skew' model) or incomplete (as in Johnstone's (2000) synthetic model). The results of this study were consistent with the predictions of both of these models, in that helpers were closely related to breeders ($r = 0.5$ on average), helpers seldom or never bred independently, the presence of helpers was correlated with significantly higher breeding success (Temple 2005) and reproductive skew was high. Because almost all helpers were first-order relatives of the principal pair and there were very few stepfamilies, it was not possible to test the hypothesis that the degree of reproductive skew should vary according to the degree of relatedness between principals and helpers.

Most reproductive skew models concern only interactions between the competitive sex (usually males), although there is empirical evidence that the choosy sex (usually females) may have the ability to regulate the degree of reproductive skew in their own interest (Davies 1992, Whittingham & Dunn 1998). In the case of the White-breasted Thrasher, high reproductive skew may result from the female abstaining from mating with helpers because she is involved in a social contract with the principal male

in which paternal care is traded for fidelity. This has been suggested as an explanation for low levels of extra-pair and extra-group paternity in other avian species (Warkentin *et al.* 1994, Negro *et al.* 1996), including co-operative breeders (Legge & Cockburn 2000). Several studies have shown that males of a range of species adjust their provisioning effort in proportion to their confidence that they have fathered the brood (see Wright 1998). In the White-breasted Thrasher, male parents perform the majority of chick-feeding duties, whereas helpers provision the brood at a much lower rate than either the breeding male or the female (Temple 2005).

A final possible explanation for the high reproductive skew observed in White-breasted Thrasher social groups is that yearling helpers may be physiologically incapable of sharing reproduction because they have not yet reached sexual maturity. Some passerine birds, particularly long-lived tropical species, do not reach sexual maturity until the age of 2 years (e.g. Collias *et al.* 1986), and in some co-operatively breeding species helpers show low levels of primary sex steroid hormones that may physiologically and behaviourally inhibit reproduction (or that may result from the absence of necessary stimuli, Schoech *et al.* 1991, 1996). White-breasted Thrasher yearlings were never encountered breeding independently, or with an older partner, in this study. However, whether this is due to physiological or ecological constraints is unknown.

Conservation implications

Social organization and mating systems have an impact upon the extinction risk of populations (Caro 1998). Conspecific aggregation can render populations at greater risk from threats such as disease and overexploitation by humans (Dobson & Poole 1998), and mating systems, extra-pair paternity and reproductive skew can all have a marked influence on effective population size (N_e) (Nunney 1993, Waite & Parker 1996) by increasing the variance of mating success (Møller 2001). Species with high reproductive skew will also tend to be more inbred (Møller 2000), and inbreeding can potentially have an adverse effect on small and declining populations (Spielman *et al.* 2004). Although this study found no evidence of strong skew between principal males in different groups, within-group reproductive skew was very high. Consequently, this study suggests that N_e is markedly lower than the actual population size in the White-breasted Thrasher: indeed, it may be

appropriate to exclude yearling birds when calculating population size in this species. Many conservation priority-setting systems use data on population size to assess the relative extinction risk of different species, and hence the relative urgency of action to protect them (Mace & Collar 2002). According to IUCN Red List criteria, 'Population is defined as the total number of mature individuals, i.e. the number of individuals known, estimated or inferred to be capable of reproduction' (IUCN 2006). As yearling Thrashers appear to breed neither independently, nor with older partners, nor by reproductive sharing within co-operative groups, we would argue that they fall outside this definition.

The White-breasted Thrasher is an Endangered species and is directly threatened *inter alia* by the construction of a major tourist resort and golf course, 'Le Paradis', which is being built on our research site. Calls have been made to establish a captive population of White-breasted Thrashers (C. Ijsselstein unpubl. data), although Collar *et al.* (1992) rightly described this as premature: for species that have not yet reached critically low population levels, effective (and cost-effective) conservation should focus on protecting and augmenting wild, *in situ* populations rather than on establishing *ex situ* breeding facilities (Balmford *et al.* 1995, Snyder *et al.* 1996, Jones 2004). However, as the Martinique population of the White-breasted Thrasher may number as few as 200 individuals, and as the St Lucia population of 1100–2200 is inferred to be declining (Temple 2005), such measures may become necessary in the future. Any captive breeding programme should take into account our findings regarding mating system and group structure.

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