



The spatial organization and mating system of Horsfield's bronze-cuckoos, *Chalcites basalis*

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In theory, liberation from parental care in brood parasites should facilitate polygamous matings by both sexes. We used a combination of mtDNA and microsatellite analysis to reconstruct sibling groups of Horsfield's bronze-cuckoo chicks to infer the mating system of this species. By mapping the distribution of sibling groups we also inferred the breeding ranges and breeding duration of individual cuckoos. Genetic analysis revealed that individual female cuckoos laid distinctive egg types, enabling inclusion of data based on egg morphology. Pairs of Horsfield's bronze-cuckoos occupied exclusive breeding ranges encompassing clusters of host territories. There was a bimodal pattern in the timing and duration of breeding: early-arriving females laid eggs over a period of up to 5 weeks and were then replaced by late-arriving females, which continued laying periodically over at least 2 months. In other brood-parasitic birds polygamy is widespread. By contrast, Horsfield's bronze-cuckoo females were genetically monogamous, and males were either monogamous or sequentially monogamous. Polygamy may be constrained in Horsfield's bronze-cuckoos by the exclusive home ranges of females.

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Avian mating systems are closely associated with the degree of parental care required for the successful rearing of young (Emlen & Oring 1977; Burley & Johnson 2002). In theory, the likelihood of polygamy increases when one or both sexes are freed from the constraints of parental care (Emlen & Oring 1977). Obligate brood parasites lay their eggs in the nests of host species, and thus lack parental care altogether. Theoretical predictions of an increased incidence of polygamy in this group (Yokel 1986; Hauber & Dearborn 2003) have been partially supported by genetic analyses of the mating systems of three species of brood parasites. The common cuckoo, *Cuculus canorus* (Marchetti et al. 1998), the great spotted cuckoo, *Clamator glandarius* (Martinez et al. 1998a) and the brown-headed cowbird, *Molothrus ater* (Woolfenden et al. 2002; Strausberger & Ashley 2003) all have variable mating systems,

with substantial numbers of males and females having multiple partners. However, in all three species monogamy is still the prevalent mating system. Polygamous or promiscuous mating systems have also been observed through colour-banding studies on several other obligate brood parasites (orange-rumped honeyguide, *Indicator xanthonotus*: Cronin & Sherman 1977; village indigobird, *Vidua chalybeata*: Payne & Payne 1977; pin-tailed whydah, *Vidua macroura*: Barnard & Markus 1989).

Although emancipation from parental care provides the potential for polygamy, the exploitation of this potential depends on the spatial and temporal distribution of mates (Emlen & Oring 1977). For example, polygamy in common cuckoos is probably favoured by the clumped distribution of females, which converge on areas of high host density and occupy overlapping home ranges (Davies 2000; Vogl et al. 2004). By contrast, if females are uniformly distributed, as when they defend exclusive territories, the opportunity for polygamy is reduced (Emlen & Oring 1977; Hauber & Dearborn 2003).

We investigated the spatial distribution and mating system of a small, Australian cuckoo, the Horsfield's

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bronze-cuckoo. Extensive research has been conducted on the interactions between this species and its hosts (e.g. Brooker & Brooker 1992, 1996; Langmore et al. 2003), and detailed studies have been made at parasitized nests (e.g. Brooker & Brooker 1986, 1989a; Brooker et al. 1988; Payne & Payne 1998). However, studies of the social behaviour of brood parasites are exceptionally challenging, owing to the unpredictability of egg-laying sites, the furtive and brief nature of nest visits and the low densities and cryptic behaviour of adults. Furthermore, obtaining information about individual behaviour through colour-banding studies is problematic because of the nomadic and unpredictable movements of Horsfield's bronze-cuckoos (Higgins 1999). Thus most features of the social behaviour of adult Horsfield's bronze-cuckoos remain obscure. We used a combination of mtDNA and microsatellite analysis of sibling groups of Horsfield's bronze-cuckoo chicks to infer the mating system of the species. In addition, by mapping the distribution of sibling groups we inferred the breeding ranges and breeding duration of individual cuckoos. We also checked for evidence of host-specific races of Horsfield's bronze-cuckoo (as proposed by Brooker & Brooker 1992).

METHODS

Study Species

Horsfield's bronze-cuckoos occur throughout Australia. They primarily parasitize fairy-wrens, *Malurus* spp., but also use secondary hosts (Brooker & Brooker 1989b). They lay elongated, white eggs with reddish-brown speckles (Brooker & Brooker 1989b), which accurately mimic fairy-wren eggs (Langmore et al. 2003). They generally lay during the egg-laying period of the host, removing one host egg from the nest and replacing it with one of their own. The cuckoo chick hatches 1–2 days before the host chicks and ejects the host eggs or chicks from the nest within 2 days (Brooker & Brooker 1989b). Unlike many cuckoo hosts, fairy-wrens rarely reject cuckoo eggs (Brooker & Brooker 1989a; Langmore et al. 2003). However, around 40% of superb fairy-wren, *Malurus cyaneus*, females abandon cuckoo chicks in the first few days after hatching (Langmore et al. 2003).

Study Sites

The study was conducted in eucalypt woodland in Campbell Park, Canberra, in southeastern Australia (149°9' E, 35°16' S) from 1999 to 2005. In this region, Horsfield's bronze-cuckoos are migratory and arrive to breed in late winter or early spring. Their main hosts are superb fairy-wrens. Several Acanthizid species breed in the Park and are potential secondary hosts of Horsfield's bronze-cuckoos: yellow-rumped thornbills, *Acanthiza chrysorrhoa*, buff-rumped thornbills, *Acanthiza reguloides*, speckled warblers, *Pyrholaemus sagittatus*, and, at low densities, brown thornbills, *Acanthiza pusilla*, striated thornbills, *Acanthiza lineata*, and white-browed scrubwrens, *Sericornis frontalis*. A study of speckled warblers from

1997 to 2000 at the same site found no cases of parasitism by Horsfield's bronze-cuckoos in 84 clutches (Gardner 2002), so they were not considered further.

Each breeding season (September–January) we attempted to locate every superb fairy-wren and thornbill nest in the study site. Most nests were located during the building phase and were checked every 1–3 days until clutch completion. For parasitized nests that were found during the incubation or nestling stages, we calculated laying date retrospectively from the hatching date or stage of development of the nestling. Our estimates of the day on which a cuckoo egg was laid may thus be out by 1–3 days. Most parasitized nests were protected with a mesh cage that reduced depredation rates from 66 to 28% (Langmore et al. 2003). We also recorded the locations of parasitized nests, with a personal Global Positioning System receiver (Garmin GPS 12 XL; Garmin, Chicago, IL, U.S.A.) and these were used to calculate cuckoo breeding ranges in the software package Ranges 6 (Kenward et al. 2003). Cuckoo chicks were colour-banded and weighed 8–9 days after hatching. We colour-banded most fairy-wren adults and chicks, to map host territories.

Although our main study site was Campbell Park, we were also alerted to cases of Horsfield's bronze-cuckoo parasitism by Professor A. Cockburn's research group, which studied superb fairy-wrens in the Australian National Botanic Gardens (ANBG), 9 km from Campbell Park, during the same period (e.g. Cockburn et al. 2003). The ANBG research group usually identified parasitized nests only after the cuckoo chicks had hatched. Therefore we could investigate the genetic relationships between ANBG cuckoo chicks, but we did not have accurate data on parasitism rates, egg morphology or the duration of cuckoo breeding for the ANBG.

Egg Descriptions

Consistency of individual egg morphology of brood parasites has been confirmed using genetic techniques for brown-headed cowbirds (Fleischer 1985) and common cuckoos (Jones et al. 1997), although not for nonparasitic guira cuckoos, *Guira guira* (Cariello et al. 2004). Some variation has been reported in the egg morphology of Horsfield's bronze-cuckoos (Brooker & Brooker 1989b), which may be sufficient to distinguish between individual females (Brooker & Brooker 2003). Therefore, we made a detailed description of each cuckoo egg, comprising length and width (mm), density of speckling (sparse to dense), size of speckling (fine to blotchy) and distribution of speckling (e.g. denser band of speckling around middle of egg). Typical variation in the size of speckling is illustrated in Brooker & Brooker (2003).

Genetic Techniques

In genetic studies of brood parasites it is often more feasible to sample the offspring cohort than the parents (Strausberger & Ashley 2003). Strausberger & Ashley (2003) showed that it is possible to characterize reproductive patterns of unsampled adults by inferring sibling

relationships among offspring by using multiple highly variable microsatellite markers. In addition, mitochondrial DNA (mtDNA) sequences (which are inherited maternally) can be used to identify different maternal lineages, and thereby reduce the pool of potential mothers for each offspring sampled. Relationships inferred by using microsatellites can also be confirmed by testing whether pairs of individuals share mtDNA haplotypes.

From 2000 onwards, we collected (under licence from the Australian National University Animal Ethics Committee) a small blood sample (<50 µl) from the brachial vein of all cuckoo chicks that survived until day 8–9 of the nestling period together with corpses of deserted chicks. Additional samples from eastern Australia were included to improve estimates of population allele frequency: these comprised one dead juvenile from Gunning, New South Wales, blood samples from two individuals from Fowlers Gap, New South Wales, and tissue from two specimens from the Australian National Wildlife Collection, collected in Tasmania and Queensland (ANWC41743 and ANWC45415). We used the salting method of Bruford et al. (1992) to extract DNA from all samples.

Published techniques were used to amplify 12 microsatellite markers (Table 1). We isolated an unpublished locus, Cgm09, from a library made for the African black coucal, *Centropus grillii*, and amplified it with the conditions reported in Adcock et al. (2005) and the primers 5'-CAGAGCTGGTTTTGATTGTGC-3' and 5'-GAAACACATTGCCTTTCAGC-3'. The same 17 individuals chosen previously (Adcock et al. 2005) were used to evaluate summary statistics and tests of linkage disequilibrium and Hardy–Weinberg equilibrium (HWE) for Cgm09. For this, we used Genepop version 3.3 (Raymond & Rousset 1995).

Table 1. Microsatellite loci for relatedness assessment in Horsfield's bronze-cuckoo

Locus	N_A	All individuals		Alleles deduced from adults	
		H_O	H_E	H_E	Exclusion
Cba01	28	0.78	0.92	0.92	0.74
Cba02	10	0.61	0.75	0.79	0.43
Cba03	6	0.55	0.62	0.67	0.25
Cba04	20	0.92	0.89	0.91	0.69
Cba05	10	0.76	0.75	0.81	0.45
Cba06	7	0.79	0.77	0.75	0.36
Cba07	40	0.92	0.97	0.97	0.88
Cba08	13	0.92	0.85	0.85	0.55
Cba09	9	0.80	0.82	0.82	0.47
Clu02	19	0.92	0.90	0.92	0.71
Clu03	8	0.76	0.71	0.74	0.34
Tmm6	8	0.76	0.80	0.78	0.41
Cgm09	11	0.72	0.83	0.83	0.50

Number of alleles (N_A) is for all study and nonstudy samples. Observed (H_O) and expected (H_E) heterozygosity is given for all individuals, and H_E and the probability of exclusion when the other parent is not known are given for the data set constructed assuming that individuals sharing mt haplotypes are related. Amplification procedures: Adcock et al. (2005; Cba01–07), Adcock & Mulder (2002; Tmm6), Adcock et al. (2007; Cba08–09 and Clu02–03).

All PCR-amplified loci were visualized on an Applied Biosystems (ABI) 3100 genetic analyser and scored with ABI GeneMapper software (Applied Biosystems, Foster City, CA, U.S.A.).

A 429-base pair (bp) segment of the mitochondrial (mt) control region, reported to be highly variable in *C. basalis* (Joseph et al. 2002), was amplified with the primers CCRL1 and CCRH1 in the following reaction mix: 20-µl reactions in 0.2-ml tubes containing 50–100 ng of DNA, 2.0 mM of MgCl₂, 1× reaction buffer and 1 unit Taq polymerase (all from Promega Corporation, Madison, WI, U.S.A.) and 200 nM of CCRL1 and CCRH1. These were amplified on a Corbett Research Palm Cyclor (Corbett Research, Mortlake, NSW, Australia) using the following cycles: 94°C for 60 s then 38 cycles of 94°C for 20 s, 54°C for 20 s and 73°C for 90 s finishing with 73°C for 5 min. Amplified DNA was used as a template for sequencing following the methods in Adcock et al. (2005). Sequences were aligned by eye.

Parentage and Relatedness Analysis

We assigned individuals to sibling groups in three steps. (1) Significant pairwise relatedness estimates obtained from microsatellite data and shared mtDNA haplotypes were used to produce presumptive full-sib and paternal half-sib groups. (2) We examined the genotypes of individuals in these groups to check for conflicts with the hypothesized sibship. Related individuals that did not share a mitochondrial haplotype were examined to see whether they were likely to be half sibs (i.e. sharing a common father). (3) Field data were examined to confirm that the sib groups were consistent with the timing and location of laying and egg morphology.

Blouin (2003) recommended the use of two different relatedness estimators to check their concordance. We used the methods of moments algorithm in Kinship 1.2 (Goodnight & Queller 1999) to test hypotheses of full-sib or half-sib relationships versus a null hypothesis of unrelated. We then used simulation techniques (ML-Relate, Kalinowski et al. 2006) to estimate relatedness; we used a maximum likelihood approach calculated from the probability that two individuals share zero, one or two alleles at each locus for a particular hypothesized relationship. In all tests we used a minimum of 5000 simulated pairs.

Both methods of testing relatedness require an estimate of population allele frequencies. Since our sample is small and likely to contain a number of related individuals, an accurate estimate is difficult to obtain. Therefore for all calculations we used two estimates of population allele frequency. One estimate used all samples and the other assumed that all chicks from a single year that shared a mitochondrial haplotype were full sibs. For each locus, each of the alleles present in the group was added to the total.

A full-sib group was initially defined as one where all individuals shared a mitochondrial haplotype and where the relatedness of each pair of individuals fitted a primary hypothesis of full sibship with one or both of the methods described above. In presumptive full-sib groups of four

or more individuals, we determined the probability of detecting whether a chick was not a full sib to all other individuals in the group, assuming that all the others were full sibs. Where possible, we reconstructed all single-locus parental genotypes from the genotypes of the remaining group members. If the chick in question was not a full sib to the others then a mismatch in at least one parental genotype was possible. The formula used was $p_{\text{locus}} = 1 - (1 - p_{\text{ex}})^2$, where p_{ex} was the exclusion probability of one parent when the genotype of the other parent was unknown (equation 2a in, Jamieson & Taylor 1997). When we identified relatedness between all members of two groups we tested the probability that we could exclude them as half sibs. All the chicks in one group were used to reconstruct parental genotypes. The probability of detecting that a particular chick in the other group was not a half sib was the probability of excluding both parental genotypes (equation 3a in, Jamieson & Taylor 1997). For both these tests the total probabilities for all loci were calculated by using Fisher's method for summing probabilities.

Finally, we used KinGroup version 2 (Konovalov et al. 2004) to calculate the likelihood that different groups of individuals shared a particular relationship and a descending ratio algorithm to find the partitioning of individuals that maximized the likelihood.

RESULTS

Of 639 superb fairy-wren nests in which eggs were laid in Campbell Park between 1999 and 2005, 104 were parasitized by Horsfield's bronze-cuckoos (16.3%). Parasitism by Horsfield's bronze-cuckoos occurred during the first 4 years of the study only, and the parasitism rate for that period was 22.9%. One Horsfield's bronze-cuckoo chick was found in a buff-rumped thornbill's nest (1.3% of 77 buff-rumped thornbill nests in which eggs were laid), and no Horsfield's bronze-cuckoo parasitism occurred in 62 yellow-rumped thornbill and 16 brown thornbill nests in which eggs were laid. A further 18 Horsfield's bronze-cuckoo chicks and two eggs were found in superb fairy-wren nests in the ANBG. Three of the 125 parasitized nests contained two cuckoo eggs (2.4%). Of the 128 Horsfield's bronze-cuckoo eggs laid, 99 chicks hatched and 42 fledged.

Genetic Diversity

From the 42 chicks and one adult Horsfield's bronze-cuckoo from which genetic material was obtained, we found 11 mtDNA haplotypes (GenBank accession numbers DQ643404–DQ643414) and a diversity of 0.89 (assuming no related individuals). The number of haplotypes found per season was consistent (2000: 7 haplotypes/28 individuals; 2001: 4/11; 2002: 1/4). This is similar diversity (0.87) and number of haplotypes (12) to that found by Joseph et al. (2002) in his Australia-wide sample ($N=21$). One haplotype (F) occurred in both 2000 and 2001. The previously unreported locus Cgm09, with 11 alleles and diversity of 0.83, is comparable with

the other loci (average 14.8 alleles and 0.83 diversity). This locus was in HWE and not linked to the other loci.

Maternity and Sibship Estimates

All chicks that shared an mt haplotype at the same site and year also had pairwise relatedness (r) estimates that significantly ($P < 0.05$) fitted a hypothesis of full sibship better than one of being unrelated. These nine maternally related groups (Table 2) were also confirmed by the partitioning method used in KinGroup version 2 (Konovalov et al. 2004). The adult female caught in 2000 had mt haplotype B and could be rejected as a parent of all chicks apart from those born in 2000 with haplotype B. Further confirmation of these results was provided by examination of field data, which revealed that all the chicks that were identified as belonging to a particular full-sib group occurred in close proximity to one another both spatially and temporally (Fig. 1). Since there was no overlap in maternal haplotypes within years, we refer to the mothers of our cuckoo chicks and the full-sib groups by their maternal haplotype code (A–K) hereafter.

The significant values of r found between individuals with different haplotypes fell into two categories. First, where two full-sib groups had significant values of r , but different haplotypes (three pairs of full-sib groups), all members sharing a haplotype were significantly related to all individuals with a different haplotype. We examined these to determine whether they were half sibs (see below). The second category was where no pattern of relatedness could be seen; for example, a chick born in 2000 was the only member of its group to be related to a non-study individual. These cases were assumed to represent type I errors, presumably because of the overlapping distributions of r for full sibs and unrelated individuals. Assuming that relatedness is unlikely between years or with nonstudy individuals, the proportion of such errors was low (10/838).

The hypothesis that pairs of individuals were half sibs produced almost the same set of significant combinations as that for full sibship. Nevertheless, we are confident that these groups consist only of full sibs. First, in groups of three or more, no individual had genotypes that were inconsistent with full sibship. When other individuals, including possible half sibs, were added into full-sib groups of three or more individuals, we found inconsistent genotypes in at least four loci. In groups of four or more we were also able to compare each group member with the parental genotype calculated assuming that all other group members were full sibs. We determined the loci for which genotypes could be constructed and the combined probability of excluding at least one of the parental genotypes as being the parent of the group member in question. Table 2 shows the values for the chick in each group with the lowest probability of excluding a parent; all other members of the group had higher exclusion probabilities. Thus, in all groups with $N > 3$, there was a high probability of excluding the parental genotypes for every chick in the group. The three presumptive paternally related half-sib groups were A and C

Table 2. Summary of breeding information for 12 female cuckoos that bred in Campbell Park and the Australian National Botanic Gardens between 2000 and 2002, inferred from relatedness estimates of offspring and mapping of egg-laying sites of full-sib families

Maternal haplotype code	Distinctive features of egg pattern	No. offspring genotyped	Same mate as	No. eggs attributed	Relatedness range/mean*	MPI	MPE	Date first egg laid	Duration of laying (days)	Breeding range (ha)/no. host territories
Campbell Park										
A	—	3	C	0	0.38–0.50/0.43			1 Oct 2000	12	2.07/3
B	Dark, even, large	5		1	0.27–0.81/0.55	10	>0.99	14 Oct 2000	20	4.78/11
C	Sparse, blotchy	7	A	7	0.24–0.70/0.41	7	>0.99	31 Oct 2000	78	17.58/12
D	Fine, even	6		2	0.30–0.56/0.44	5	>0.99	7 Nov 2000	65	2.72/7
E	—	1		0				8 Nov 2000	—	—
F2	Almost immaculate white	3		4	0.28–0.68/0.43			27 Sept 2001	34	7.07/12
H	White halo at thin end	5	I	5	0.34–0.71/0.53	3	0.98	23 Sept 2001	32	11.81/14
I	Dark band in middle	2	H	4	0.45			2 Nov 2001	63	9.95/11
K	White tip	4		1	0.26–0.73/0.46	2	0.95	20 Nov 2002	—	27.4/15
Australian National Botanic Gardens										
F1	—	1	G	0				10 Nov 2000	—	—
G	—	4	F1	0	0.25–0.56/0.40	5	>0.99	10 Dec 2000	—	—
J	Large, dark, blotchy	1		2				5 Oct 2001	—	—

The minimum number of parental loci (MPI) was calculated from each group comprising at least three chicks, with one chick removed, and was used to calculate the minimum probability of excluding the reconstructed genotypes as parents of the removed chick (MPE).

*Range and mean of Queller & Goodnight's (1989) r .

(mean intergroup $r = 0.24$), G and F1 ($r = 0.16$), and H and I ($r = 0.28$). The fact that every intergroup pairwise value of r was significant in these pairs provides strong evidence that these were half sibs. No genotypic inconsistencies with this hypothesis could be found. For example, the combined number of alleles at each locus from all individuals in both groups never exceeded six. Reconstructed genotypes were not possible for groups F1 ($N = 1$ chick) and I ($N = 2$ chicks) but were possible from at least one of each pair of half-sib groups. The probability of excluding two parents and therefore the probability that our data could be used to exclude an individual as being a half sib was >0.99 for each comparison using six to eight reconstructed loci. When compared with those of other chicks from the same year, both genotypes were rejected for one or more loci for every chick; thus no other half sibs were present in the sample. The field data offered further support for these being half sibs. In every case the two paternally related, full-sib groups appeared, one after the other, in the same area (Fig. 1), suggesting that the male remained on the same territory and paired with two different females consecutively (see below). A further outcome of identifying these half-sib groups is that it offers further support that each of the five groups with more than one member consists of full sibs only. If unrelated or half sibs were present in a group, then at least one individual would share no parents with members of the other group.

For the two individuals in group I, the relatedness value alone did not distinguish between full or half sibship but the fact that both were related to all members of H suggests that the two individuals must have been full sibs.

Mating System

From these results we can infer that at least nine female cuckoos bred in Campbell Park and at least three female cuckoos bred in the ANBG between 2000 and 2002. Relatedness estimates indicated that all the chicks sharing the same maternal haplotype in the same year were full siblings (Table 2). Thus we have no evidence of polyandrous mating by female Horsfield's bronze-cuckoos.

By contrast, our results suggest that male cuckoos sometimes mated with two females, although temporal laying data suggest that they were sequentially monogamous rather than polygamous or promiscuous (see Timing and Duration of Breeding below, Fig. 1). Of five putative female cuckoos laying in Campbell Park in 2000, relatedness data indicated that two mated with the same male. The two putative females laying in the ANBG in 2000 also shared the same mate. Of the three females laying in Campbell Park in 2001, two shared the same mate. There was no overlap in the egg-laying periods of any females that shared a mate (see below). Overall, in 2000–2002, we can infer that seven males mated with nine

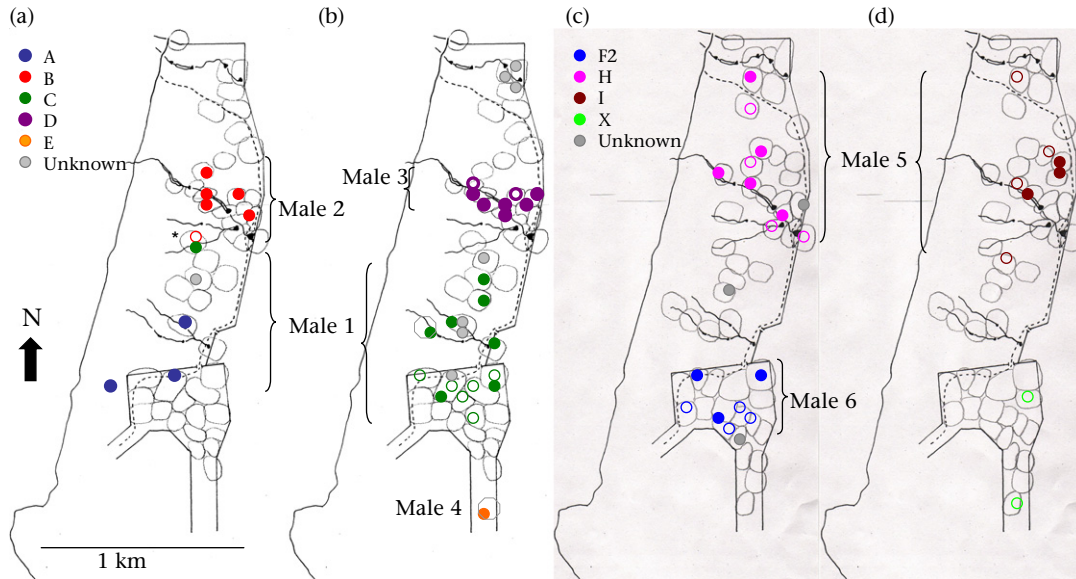


Figure 1. Breeding ranges of female and male Horsfield's bronze-cuckoos in Campbell Park in 2000 and 2001. The open, irregular circles represent the superb fairy-wren territories in that year. Each dot represents a cuckoo egg, and the key indicates to which full-sib cohort the egg belongs. Assignment of chicks to cohorts was based on genotyping (closed dots) and egg morphology (open dots). (a) Eggs laid between 1 October and 2 November 2000. During this period there were two monogamous pairs of cuckoos (female A and male 1, female B and male 2) laying in the Park. A third female, C, arrived at the end of October to replace female A and pair with her mate. She laid her first egg in the same nest as departing female B (nest indicated with an asterisk). (b) Eggs laid after 2 November 2000. In addition to female C and male 1, at least two more pairs commenced breeding (female D and male 3, female E and male 4). (c) Eggs laid from September to October 2001. Two monogamous pairs occupied discrete territories during this period. (d) November to January 2001. Female H had departed and female I paired with her mate and occupied her breeding range. Differences in egg morphology suggest that female F had probably also departed and been replaced by a new female 'X', although we do not have genetic material from those offspring.

females in Campbell Park and two males mated with three females in the ANBG.

Genotyping revealed that the Horsfield's bronze-cuckoo chick reared in a buff-rumped thornbill's nest was the offspring of a female cuckoo (A) that also laid eggs in two superb fairy-wren nests. This suggests that the egg was not laid by a separate thornbill-specific race of Horsfield's bronze-cuckoo.

Egg Morphology

Genetic material was collected only from those cuckoo chicks that hatched from 2000 onwards. A further 38 Horsfield's bronze-cuckoo eggs were laid in those years, but did not survive long enough for us to obtain genetic material. We used our genetic data to investigate whether egg morphology was consistent within females, allowing us to attribute some of the ungenotyped cuckoo eggs to particular female cuckoos.

From the genetic analysis we were able to confirm that each female laid eggs of a distinctive type (Table 2). For example, one female laid almost immaculate, white eggs, and another laid eggs with a white halo at the tip. Females were also fairly consistent in the size of their eggs (Fig. 2). Although descriptions were not always consistent within females (indicating some individual variability in egg morphology), some females had one or two consistent and distinctive features of egg patterning (Table 2). This allowed us to assign some of the ungenotyped eggs to

a particular female with a fair degree of confidence. Assignment involved first looking for a match between any distinctive feature of the pattern of an ungenotyped egg and the features of genotyped eggs that had been assigned to a particular female. Once a tentative assignment had been made, we compared the size of the ungenotyped egg with the range of sizes of the genotyped eggs (Fig. 2). If egg size also matched, we then compared the timing and location of laying of the eggs (Fig. 1). For

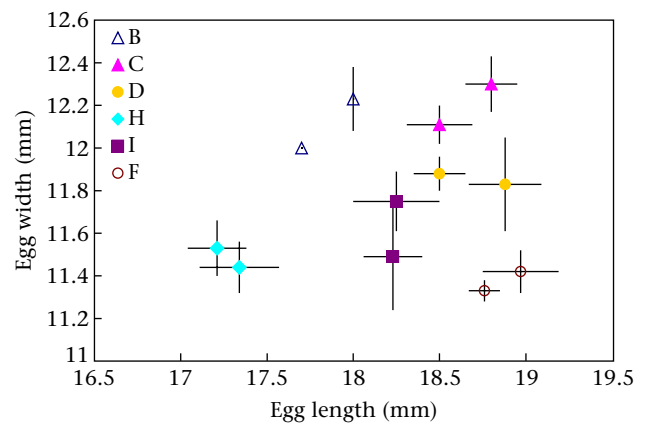


Figure 2. The mean \pm SE egg length and egg width of Horsfield's bronze-cuckoo eggs laid by six different females in Campbell Park. Each pair of symbols indicates the mean length and width of the eggs attributed to a particular female on the basis of genotyping and egg patterning.

many cases this was very convincing; the ungenotyped egg matched a group of genotyped eggs in pattern and size and they were laid in nearby fairy-wren territories within a few days of one another. If there were no distinctive features of egg pattern, or there were inconsistencies in the pattern or size, or in the timing or location of laying, we did not assign the egg. We were able to assign 26 of the 38 ungenotyped eggs to particular females. The egg morphology data also suggested that there might have been an additional female in 2001 from whose offspring no genetic material was obtained (Female X in Fig. 1).

Number of Eggs

The maximum number of genotyped offspring of a single female in a single season was seven. However, combining genetic analysis and egg morphology data, we found that a single female laid up to 14 eggs (Table 2). The average number of eggs laid per female \pm SE was 5.7 ± 1.1 ($N = 12$ females). We were confident of finding most of the eggs of only eight of those females (excluding ANBG females and female E on the edge of Campbell Park) and the average number of eggs laid by these females was 7.4 ± 1.2 .

Timing and Duration of Breeding

The genetic and egg morphology data indicated that female cuckoos had a bimodal pattern in the timing and duration of breeding in Campbell Park (Fig. 3). Those females that arrived and commenced egg laying early, between mid-September and mid-October, laid eggs over a relatively short period (12–34 days) and ceased laying within the study area by the beginning of November. By contrast, the females that replaced them in November continued laying periodically for at least 2 months (63–78 days, mean for both early and late females = 43.6

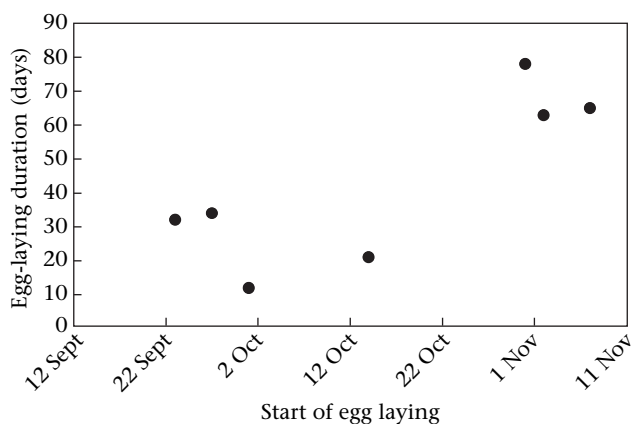


Figure 3. The start of egg laying in relation to the duration of egg laying for seven female cuckoos. We included only those females for whom we were confident of having found most of their eggs (excluded: ANBG females, one female that laid a single egg on the edge of the study area, and the 2002 female because of early cessation of field work).

days, Table 2). The fact that the eggs of late-arriving females began to appear in the breeding ranges of the early-arriving females (Fig. 1) suggests that the early-arriving females not only ceased breeding by November, but also departed from their breeding range.

We explored the possibility that early-arriving females departed because they had parasitized all available host nests. Female A laid three eggs in 12 days in a small breeding range overlapping three superb fairy-wren territories. No other clutches were available within her breeding range, although an additional six clutches were available in surrounding areas that were not occupied by another cuckoo. Female B parasitized six of 10 available clutches in 11 territories over 20 days. Female H parasitized nine of 12 available clutches in 14 territories during 32 days. Finally, Female F2 parasitized seven of 16 clutches within 12 territories over 34 days. Overall, females parasitized a mean \pm SE of $70 \pm 12\%$ of available nests.

We can infer minimum breeding duration of males, but this is less reliable as we do not know how long females might store sperm after a male has departed. Based on laying dates of eggs genetically assigned or attributed to particular males, males were breeding for longer than females (20–108 days, $\bar{X} \pm SE = 66 \pm 17.7$ days, $N = 5$). This enabled some males to pair with two females consecutively.

Breeding Ranges

Female cuckoos occupied discrete breeding ranges (Fig. 1). Minimum breeding range size varied between 2.1 and 27.4 ha ($\bar{X} \pm SE = 10.4 \pm 3$ ha; Table 2). The largest breeding range was occupied by female K, the sole breeding female in the Park in 2002. Cuckoo breeding ranges encompassed a mean \pm SE of 10.6 ± 1.4 superb fairy-wren territories (Table 2). Although there was substantial variation in the breeding ranges of different female cuckoos, the variation in the number of host territories encompassed was considerably less (Table 2), suggesting that the density and distribution of host territories influence the size of cuckoo breeding ranges.

Between 2000 and 2002, 12 superb fairy-wren groups experienced repeated parasitism events at different nests in a single breeding season; two territories were parasitized four times (Fig. 1). Repeated parasitism within a fairy-wren territory occurred either because the same cuckoo parasitized successive fairy-wren nesting attempts, or because there were two different cuckoos that did not overlap temporally. However, one fairy-wren nest received two cuckoo eggs during this period. Only one of the chicks from these eggs survived to be genotyped, but egg morphology suggested that they were laid by two different females (B and C, Fig. 1). Although the two females parasitized the same nest, they were otherwise separated spatially and temporally. The nest was on the border of their breeding ranges (indicated in Fig. 1) and the eggs were laid during the transitional period in late October when one of the females ceased breeding and the other had just begun. Two other cases of multiple parasitism occurred in 1999. In both cases the first cuckoo egg was laid before the

host began laying her clutch and was buried in the nest lining by the host. We do not know if the same female or two different females laid the two eggs in each of those nests.

Based on the areas in which males fathered chicks, male breeding ranges were also discrete areas (Fig. 1). The genetic evidence showed that pairs were monogamous for as long as the female continued breeding, and consequently male and female breeding ranges were the same size. Although three males obtained two mates, in every case the second female occupied the breeding range vacated by the first female. Thus males did not enlarge their breeding range to encompass the breeding range of a second female.

Recruitment

None of 25 Horsfield's bronze-cuckoo fledglings and one adult female colour-banded between 1999 and 2002 were observed to return to the study site in later years. Similarly, genotyping confirmed that none of the blood-sampled chicks returned to breed in subsequent years. Reconstructed parental genotypes from analysis of genotyped chicks also indicated that no adults bred in Campbell Park for more than 1 year of the study.

DISCUSSION

Horsfield's bronze-cuckoos in our study sites parasitized host nests within exclusive breeding areas. The lack of overlap in breeding ranges suggests that pairs defended a breeding territory. The largest breeding range occurred when only one female bred in the Park, suggesting that breeding range size might be constrained by competitive exclusion when multiple females are breeding. Only one confirmed case of breeding range overlap occurred, when two females laid eggs in the same nest. However, the nest was on the boundary between the breeding ranges of the females and parasitism occurred in a brief transitional period before one female departed and after the other arrived.

Few observations have been made of adult cuckoo social behaviour (Higgins 1999), but an observational study of the congeneric shining bronze-cuckoo, *Chalcites lucidus*, suggests that pairs also occupy discrete breeding territories in this species (Ford 1963). This differs from the spatial distribution of three other brood parasites, the common cuckoo, the great spotted cuckoo and the brown-headed cowbird. A radio-tracking study revealed that the home ranges of female common cuckoos overlap (Vogl et al. 2004), resulting in regular cases of multiple parasitism (up to 58% of parasitized nests, Moskat & Honza 2002). Similarly, in brown-headed cowbirds almost 40% of offspring shared a nest with offspring of a different female cowbird (Strausberger & Ashley 2003). In great spotted cuckoos, there were no exclusive female laying areas and 20% of nests were parasitized by more than one female (Martinez et al. 1998b). The lack of territoriality is particularly surprising in evicting cuckoos such as the common cuckoo, because their reproductive success is reduced if they lay eggs in nests that have already been parasitized

by another cuckoo. In evicting cuckoos, first-hatched cuckoo chicks evict all other eggs and chicks from the nest, so eggs laid by a second cuckoo are doomed to fail. However, in all these species, territoriality may be constrained by the disjunct distribution of breeding and feeding areas (Rothstein et al. 1984; Martinez et al. 1998b; Davies 2000; Vogl et al. 2004). In some populations, individuals travel several kilometres between breeding and feeding areas every day, and this might prevent effective defence of a breeding territory (Vogl et al. 2004). By contrast, there is no evidence of separate breeding and feeding ranges in Horsfield's bronze-cuckoos, which appear to forage within the territories of their hosts (personal observation). Combined breeding and feeding areas would allow Horsfield's bronze-cuckoos to defend territories, and thereby reduce the costs associated with multiple parasitism of the same nest by different females.

The genetic mating system of Horsfield's bronze-cuckoos in our study sites can be described as short-term monogamy. We found no evidence of females mating with more than one male. However, the bimodal pattern in the timing and duration of breeding among females suggests that they occupy more than one breeding site in a breeding season. This would require re-pairing for at least some females, because some males remained on the breeding site after the departure of early-arriving females and were present before later females arrived. Some males paired with just one female, but others were sequentially monogamous, as a result of their first mate departing and being replaced by a second female. Although the average duration of breeding at the study site was longer for males than females, some males gained reproductive success only for a short period of time, so it is possible that some males bred at more than one site.

Our evidence of short-term monogamy in females and sequential monogamy in males supports a prediction of Hauber & Dearborn (2003), who argued that the lack of parental care in brood parasites enables a change of partners at any stage during the reproductive cycle without disrupting the breeding effort. This predicts weaker seasonal pair bonds, more divorce and remating, and hence more sequential monogamy. Although several genetic studies have found evidence for polygamous mating in brood parasites (Marchetti et al. 1998; Martinez et al. 1998a; Woolfenden et al. 2002; Strausberger & Ashley 2003) only one study has attempted to distinguish between simultaneous polygamy and sequential monogamy (Martinez et al. 1998a). Martinez et al. (1998a) presented detailed data on the temporal laying patterns of individual females, but were unable to distinguish between simultaneous polygamy and sequential monogamy because females mated with multiple mates, and it was not known whether the sperm from different males was used sequentially. By contrast, our results show clear evidence of sequential monogamy in males, because when males mated with two females they were entirely separated temporally.

Barnard (1998) summarized the main factors that might promote monogamy in parasitic birds: cooperation to gain access to host nests; assurance of paternity and reduction of female harassment; and economic monopolization of

mates. Cooperation to gain access to host nests occurs when the male lures the hosts away from the nest to allow the female unobserved access to the host nest. Such behaviour has been reported for several species of cuckoo (e.g. Australian koel, *Eudynamis scolopaceus*: Barnard 1998; the great spotted cuckoo: Arias-de-Reyna 1998; Jacobin cuckoo, *Clamator jacobinus*: Gaston 1976) and may also occur in brown-headed cowbirds (Strausberger & Ashley 2003). This cooperative behaviour has not been reported for Horsfield's bronze-cuckoos, and was not observed during three cases of egg deposition (Brooker et al. 1988). Assurance of paternity in the form of mate guarding could benefit both sexes if harassment of the female is reduced, which might otherwise interfere with finding and parasitizing nests. However, this hypothesis has greatest application to socially gregarious parasites that are repeatedly exposed to multiple potential partners, such as the brown-headed cowbird (Barnard 1998).

The potential for economic monopolization of mates relates to the spatial and temporal distribution of potential mates, as well as the operational sex ratio (Emlen & Oring 1977). When potential mates are distributed uniformly in space there is little opportunity for monopolizing multiple mates, but as potential mates become clumped spatially the potential for polygamy increases (Emlen & Oring 1977). The contrasting distribution of female Horsfield's bronze-cuckoos with that of females of other cuckoo species suggests a possible basis for their contrasting mating systems. As discussed above, the distribution of females in several cuckoo and cowbird species is clumped, with overlapping female home ranges (Martinez et al. 1998b; Strausberger & Ashley 2003; Vogl et al. 2004), whereas our results show that Horsfield's bronze-cuckoo females occupy segregated breeding ranges. Thus, the spatial distribution of females in other brood-parasitic species appears to be more conducive to monopolization of multiple mates by males than that of female Horsfield's bronze-cuckoos. However, the bimodal pattern of breeding duration of female Horsfield's bronze-cuckoos (Fig. 3) allowed some males to monopolize more than one mate.

We are not aware of other cuckoo species with a bimodal pattern in the timing and duration of breeding like that of female Horsfield's bronze-cuckoos. However, Brooker & Brooker (1996) reported a bimodal pattern in parasitism of splendid fairy-wrens, *Malurus splendens*, by Horsfield's bronze-cuckoos in 2 years of their study, with a gap of 5–8 weeks in which no eggs were laid. This could reflect the departure of early-arriving females and their replacement by late-arriving females, such as we observed in Campbell Park. Our results show that early-arriving females exploited a high proportion of available clutches within their breeding range (ca. 70%). This suggests an adaptive explanation for the bimodal pattern of breeding that relates to saturation of available host nests. Horsfield's bronze-cuckoos, like other brood parasites (e.g. brown-headed cowbirds: Arcese et al. 1996; common cuckoos: Davies 2000), appear to depredate host nests, destroying the eggs (Brooker & Brooker 1996). This behaviour probably functions primarily to promote renesting by the host and thereby increase the number of nests available for parasitism, rather than to provide a meal, because only

females do it (Davies 2000). If a female Horsfield's bronze-cuckoo parasitizes all available host nests in one area, she could increase the number of host nests available for her next clutch by moving to a new site. There she could destroy more active host nests to promote renesting than at her old site, because none would contain her own offspring.

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References

- Adcock, G. J. & Mulder, R. A. 2002. Polymorphic microsatellite loci for paternity analysis in the Madagascar paradise flycatcher (*Terpsiphone mutata*: Aves). *Molecular Ecology Notes*, **2**, 287–289.
- Adcock, G. J., Langmore, N. E., Mulder, R. A. & Kilner, R. M. 2005. Microsatellite loci for population and behavioural studies of Horsfield's bronze-cuckoos (*Chalcites basalis*: Aves). *Molecular Ecology Notes*, **5**, 619–621.
- Adcock, G. J., Langmore, N. E. & Kilner, R. M. 2007. Polymorphic microsatellite loci for studies of bronze-cuckoo species (Genus *Chalcites*: Aves). *Molecular Ecology Notes*, **7**, 678–680.
- Arcese, P., Smith, J. N. M. & Hatch, M. I. 1996. Nest predation by cowbirds and its consequences for passerine demography. *Proceedings of the National Academy of Sciences, U.S.A.* **93**, 4608–4611.
- Arias-de-Reyna, L. 1998. Coevolution of the great spotted cuckoo and its hosts. In: *Parasitic Birds and Their Hosts. Studies in Coevolution* (Ed. by S. I. Rothstein & S. K. Robinson), pp. 129–142. Oxford: Oxford University Press.
- Barnard, P. 1998. Variability in the mating systems of parasitic birds. In: *Parasitic Birds and Their Hosts. Studies in Coevolution* (Ed. by S. I. Rothstein & S. K. Robinson), pp. 339–356. Oxford: Oxford University Press.
- Barnard, P. & Markus, M. B. 1989. Male copulation frequency and female competition for fertilizations in a promiscuous brood parasite, the pin-tailed whydah *Vidua macroura*. *Ibis*, **131**, 421–425.
- Blouin, M. S. 2003. DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. *Trends in Ecology and Evolution*, **18**, 503–511.
- Brooker, M. G. & Brooker, L. C. 1986. Identification and development of the nestling cuckoos, *Chrysococcyx basalis* and *C. lucidus plagosus*, in Western Australia. *Australian Wildlife Research*, **13**, 197–202.
- Brooker, M. G. & Brooker, L. C. 1989a. The comparative breeding behaviour of two sympatric cuckoos, Horsfield's bronze-cuckoo *Chrysococcyx basalis* and the shining bronze-cuckoo *C. lucidus*, in Western Australia: a new model for the evolution of egg morphology and host specificity in avian brood parasites. *Ibis*, **131**, 528–547.

- Brooker, M. G. & Brooker, L. C. 1989b. Cuckoo hosts in Australia. *Australian Zoological Reviews*, **2**, 1–67.
- Brooker, M. G. & Brooker, L. C. 1992. Evidence for individual female host specificity in two Australian bronze-cuckoos (*Chrysococcyx* spp.). *Australian Journal of Zoology*, **40**, 485–493.
- Brooker, M. G. & Brooker, L. C. 1996. Acceptance by the splendid fairy-wren of parasitism by Horsfield's bronze cuckoo: further evidence for evolutionary equilibrium in brood parasitism. *Behavioral Ecology*, **7**, 395–407.
- Brooker, M. G. & Brooker, L. C. 2003. Brood parasitism by Horsfield's bronze-cuckoo in a fragmented agricultural landscape in Western Australia. *Emu*, **103**, 357–361.
- Brooker, M. G., Brooker, L. C. & Rowley, I. 1988. Egg deposition by the bronze-cuckoos *Chrysococcyx basalis* and *Ch. lucidus*. *Emu*, **88**, 107–109.
- Bruford, M. W., Hanotte, O., Brookfield, J. F. Y. & Burke, T. 1992. Single locus and multi-locus fingerprinting. In: *Molecular Genetic Analysis of Populations: a Molecular Approach* (Ed. by A. R. Hoelzel), pp. 227–229. Oxford: IRL Press.
- Burley, N. T. & Johnson, K. 2002. The evolution of avian parental care. *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 241–250.
- Cariello, M. O., Lima, M. R., Schwabi, H. G. & Macedo, R. H. 2004. Egg characteristics are unreliable in determining maternity in communal clutches of guira cuckoos *Guira guira*. *Journal of Avian Biology*, **35**, 117–124.
- Cockburn, A., Osmond, H. L., Mulder, R. A., Green, D. J. & Double, M. C. 2003. Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren *Malurus cyaneus*. *Journal of Animal Ecology*, **72**, 189–202.
- Cronin, E. W. & Sherman, P. W. 1977. A resource-based mating system: the orange-rumped honeyguide. *Living Bird*, **15**, 5–37.
- Davies, N. B. 2000. *Cuckoos, Cowbirds and Other Cheats*. London: T. & A. D. Poyser.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.
- Fleischer, R. C. 1985. A new technique to identify and assess the dispersion of eggs of individual brood parasites. *Behavioral Ecology and Sociobiology*, **17**, 91–99.
- Ford, J. 1963. Breeding behaviour of the yellow-tailed thornbill in south-western Australia. *Emu*, **63**, 185–200.
- Gardner, J. L. 2002. Breeding biology of the speckled warbler, *Chthonicola sagittata*. *Australian Journal of Zoology*, **50**, 169–181.
- Gaston, A. J. 1976. Brood parasitism by the pied crested cuckoo (*Clamator jacobinus*). *Journal of Animal Ecology*, **45**, 331–345.
- Goodnight, K. & Queller, D. C. 1999. Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Molecular Ecology*, **8**, 1231–1234.
- Hauber, M. E. & Dearborn, D. C. 2003. Parentage without parental care: what to look for in genetic studies of obligate brood-parasitic mating systems. *Auk*, **120**, 1–13.
- Higgins, P. J. E. 1999. *Handbook of Australian, New Zealand and Antarctic Birds. Parrots to Dollarbird* Vol. 4. Melbourne: Oxford University Press.
- Jamieson, A. & Taylor, S. S. 1997. Comparisons of three probability formulae for parentage exclusion. *Animal Genetics*, **28**, 397–400.
- Jones, D. A., Gibbs, H. L., Matsuda, T., de L. Brooke, M., Uchida, H. & Bayliss, M. J. 1997. The use of DNA fingerprinting to determine the possible mating system of an obligate brood parasitic bird, the cuckoo *Cuculus canorus*. *Ibis*, **139**, 560–562.
- Joseph, L., Wilke, T. & Alpers, D. 2002. Reconciling genetic expectations from host specificity with historical population dynamics in an avian brood parasite, Horsfield's bronze-cuckoo *Chalcites basalis* of Australia. *Molecular Ecology*, **11**, 829–837.
- Kalinowski, S. T., Wagner, A. P. & Taper, M. L. 2006. ML-relate: a computer program for maximum likelihood estimation of relatedness and relationship. *Molecular Ecology Notes*, **6**, 576–579.
- Kenward, R. A., South, A. & Walls, S. 2003. *Ranges 6 v.1.2.: For the Analysis of Tracking and Location Data*. Wareham: Anatrack Ltd.
- Konovalov, D. A., Manning, C. & Henshaw, M. T. 2004. KinGroup: a program for pedigree relationship reconstruction and kin group assignments using genetic markers. *Molecular Ecology Notes*, **4**, 779–782.
- Langmore, N. E., Hunt, S. & Kilner, R. M. 2003. Escalation of a co-evolutionary arms race through host rejection of brood parasitic young. *Nature*, **422**, 157–160.
- Marchetti, K., Nakamura, H. & Gibbs, H. L. 1998. Host-race formation in the common cuckoo. *Science*, **282**, 471–472.
- Martinez, J. G., Burke, T., Dawson, D., Soler, J. J., Soler, M. & Møller, A. P. 1998a. Microsatellite typing reveals mating patterns in the brood parasitic great spotted cuckoo (*Clamator glandarius*). *Molecular Ecology*, **7**, 289–297.
- Martinez, J. G., Soler, J. J., Soler, M. & Burke, T. 1998b. Spatial patterns of egg laying and multiple parasitism in a brood parasite: a non-territorial system in the great spotted cuckoo (*Clamator glandarius*). *Oecologia*, **117**, 286–294.
- Moskat, C. & Honza, M. 2002. European cuckoo *Cuculus canorus* parasitism and host's rejection behaviour in a heavily parasitised great reed warbler *Acrocephalus arundinaceus* population. *Ibis*, **144**, 614–622.
- Payne, R. B. & Payne, L. L. 1977. Social organization and mating success in local song populations of village indigobirds, *Vidua chalybeata*. *Zeitschrift für Tierpsychologie*, **45**, 113–173.
- Payne, R. B. & Payne, L. L. 1998. Nestling eviction and vocal begging behaviors in the Australian glossy cuckoos *Chrysococcyx basalis* and *C. lucidus*. In: *Parasitic Birds and their Hosts. Studies in Coevolution* (Ed. by S. I. Rothstein & S. K. Robinson), pp. 152–169. Oxford: Oxford University Press.
- Queller, D. C. & Goodnight, K. F. 1989. Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.
- Raymond, M. & Rousset, F. 1995. Genepop (version 1.2): population genetics software for exact test and ecumenicism. *Journal of Heredity*, **86**, 248–249.
- Rothstein, S. I., Verner, J. & Stevens, E. 1984. Radio tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic brown-headed cowbird. *Ecology*, **65**, 77–88.
- Strausberger, B. M. & Ashley, M. V. 2003. Breeding biology of brood parasitic brown-headed cowbirds (*Molothrus ater*) characterized by parent-offspring and sibling-group reconstruction. *Auk*, **120**, 433–445.
- Vogl, W., Taborsky, B., Taborsky, M., Teuschl, Y. & Honza, M. 2004. Habitat and space use of European cuckoo females during the egg laying period. *Behaviour*, **141**, 881–898.
- Woolfenden, B. E., Gibbs, H. L. & Sealy, S. G. 2002. High opportunity for sexual selection in both sexes of an obligate parasitic bird, the brown-headed cowbird (*Molothrus ater*). *Behavioral Ecology and Sociobiology*, **52**, 417–425.
- Yokel, D. A. 1986. Monogamy and brood parasitism: an unlikely pair. *Animal Behaviour*, **34**, 1348–1358.