

Unusually high levels of extrapair paternity in a duetting songbird with long-term pair bonds

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Abstract Previous studies suggest that extrapair young are very rare or absent in socially monogamous avian species that produce vocal duets. These results are generally consistent with functional hypotheses suggesting that duets may signal commitment between partners, or aid males as a paternity guard to ensure genetic as well as social monogamy. Additionally, species that exhibit social monogamy with the same partner across multiple breeding seasons tend to exhibit low levels of extrapair paternity, so duetting species that mate for life may be particularly likely to exhibit genetic monogamy. This study examined the social and genetic mating systems of California towhees (*Pipilo crissalis*), a duetting species thought to have life-long pair bonds. Observation of a color-banded population confirmed that California towhees exhibit long-term social monogamy. Known social families were genotyped at four microsatellite loci with high allelic diversity. Unexpectedly, paternity exclusion indicated that at least 13 of 31 (42%) nests contained extrapair young. All chicks exhibited maternal alleles, but 21 of 81 (26%) young were not the offspring of social fathers. Thus, in contrast to previous work, this study documents high frequencies of extrapair young among socially monogamous duetting birds with long-term pair bonds.

Keywords Extrapair paternity · Mating systems · Vocal duets · California towhee · *Pipilo crissalis*

Introduction

Avian vocal duets are temporally coordinated signals produced by pairs of birds vocalizing together (Farabaugh 1982). Duets are relatively rare vocalizations, likely occurring in only 3–7% of avian species (Benedict 2007c; Hall 2004). Duets may function as signals of commitment, helping to maintain strong pair bonds between mates (Wickler 1980). Additionally, males may guard paternity by participating in duets to signal the mated status of their females and to keep rival males away (Sonnenschein and Reyer 1983). Support for these hypotheses comes from several studies that have linked duetting with social monogamy, and potentially with genetic monogamy as well (Farabaugh 1982; Malacarne et al. 1991; Gill et al. 2005).

Analyses of paternity in five monogamous duetting species have found that extrapair young are uncommon. Three duetting species [Eastern Screech Owls (*Otus asio*), Dusky Antbirds (*Cercomacra tyrannina*), and Carolina Wrens (*Thryothorus ludovicianus*)] have no extrapair young, while extrapair fertilizations account for only up to 3% of young in two other species [Australian Magpie-larks (*Grallina cyanoleuca*) and Buff-breasted Wrens (*Thryothorus leucotis*); Fleischer et al. 1997; Gill et al. 2005; Haggerty et al. 2001; Hall and Magrath 2000; Klatt and Ritchison 1993; Lawless et al. 1997; Morton and Derrickson 1996; Shuler 1965]. Extragroup young are common among duetting Australian Magpies (*Gymnorhina tibicen*), however members of this species live in groups and are not socially monogamous (Brown and Farabaugh 1991; Durrant and Hughes 2005). The consistently low level of extrapair paternity among socially monogamous duetting species is surprising given that more than 75% of all socially monogamous avian species produce extra-pair young, and levels of extra-pair paternity below 5% are considered worthy of explanation (Bennett and

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Owens 2002; Griffith et al. 2002). The universally low levels of extrapair paternity observed so far among monogamous duetting species have led some authors to speculate that males of these species may not experience strong challenges to their paternity (Gill et al. 2005).

In addition to duetting, authors have suggested that the frequency of extrapair fertilizations varies in concert with certain avian life history characteristics. Species in which males provide significant amounts of parental care generally show low levels of extrapair paternity, possibly because females have more to lose if a male withdraws care when he suspects cuckoldry (Arnold and Owens 2002). Long-lived species and species with prolonged pair bonds also tend to exhibit low levels of extrapair paternity (Mauck et al. 1999; Wink and Dyrce 1999). Females of species with prolonged pair bonds may remain genetically monogamous to ensure commitment from their partners because divorce may be particularly costly in such species. Costs of divorce could exist either because experience improves breeding success because replacement mates are difficult to find, or because divorce causes loss of a territory or other resource (Mock and Fujioka 1990). Thus, it has been hypothesized that rates of extrapair copulations remain low in both of these contexts because the value of retaining a partner is high, and females act to minimize the risk of retaliation from their mates in the form of divorce (Arnold and Owens 2002).

This study examined the social and genetic mating systems of the California towhee (*Pipilo crissalis*), a permanent resident on the west coast of North America from Oregon south through Baja California. Mated pairs of California towhees produce vocal duets throughout the year (Marshall 1964; Quaintance 1941). Although only female California towhees build and incubate nests, parents of both sexes live year-round on a shared territory and care for offspring for up to 6 weeks before the young disperse from the territory (Kunzmann et al. 2002; LaBerteaux 1989). California towhees are believed to exhibit long-term monogamy, although this assumption is based on observation of a single marked pair (Kunzmann et al. 2002). Because they are a duetting species, I predicted that California towhees would show relatively low levels of extrapair paternity. This pattern is further expected if California towhees do prove to be socially monogamous across seasons.

Materials and methods

Field work was conducted at the Hastings Natural History Reservation in Carmel Valley, Monterey County, California between June 2002 and June 2006. The research area comprised roughly 6 ha surrounding two creek drainages.

Habitat in the area is predominantly oak woodland and chaparral (Griffin 1990).

Adult California towhees were trapped in Potter traps baited with cracked corn, and banded with a unique combination of three colored and one metal leg bands. Marked individuals were observed between March and June of each year, and social pairs were identified based on residence on the same territory, breeding attempts, and duetting behavior. Adults are sexually monomorphic but were sexed behaviorally during observation (only females build and incubate nests), or based on the presence of either a brood patch (females) or cloacal protruberance (males) at capture. Throughout all seasons, adults and fledglings were observed both opportunistically during population surveys and systematically during focal animal watches designed to monitor social behavior. All data used to assess territory occupation and social mating system came from 44 natural pairs. In 2005 and 2006 I removed males from established pairs as part of a separate manipulation. Pairs forming after male removals were not included in descriptions of the social mating system. For all pairs, I calculated an index of monogamy, which was the probability that two mates from year X that both survived to year $X+1$ would pair in year $X+1$.

Nesting attempts were monitored, and social families were designated as parents feeding at a nest and offspring contained within that nest. I did not sample offspring from all identified pairs due to difficulties finding or accessing nests and nest failure. This study includes 19 females, 25 males, and 81 chicks, from 31 known social families sampled across five breeding seasons. For 14 pairs I sampled a single nest. Of the remaining 17 nests, seven were from a single female in four seasons with three different social mates, four were from another female across four seasons with three different mates, four were from two different females in two seasons each with two different mates, and the remaining two were from one female across two seasons with one mate. Rates of mate switching among two of these females were artificially enhanced by male removal manipulations, but the EPP frequency for each female with pre- and post-removal mates did not differ predictably.

At the time of banding, 50 μ l of blood were obtained from the brachial wing vein of each adult. The chicks were banded with colored and metal leg bands from the nest at 7 days of age, and a 30- μ l blood sample was obtained from the brachial wing vein of each chick. Blood samples were stored in Longmire's solution at 20°C. Adult sex was confirmed using a PCR-based assay that amplifies dimorphic fragments on the Z and W sex chromosomes (Griffiths et al. 1998).

To assess parentage, individuals were genotyped at four nuclear microsatellite loci: Mme 1, Mme 2, Mme 7, and Mme 8. All loci were developed for song sparrows (Jeffrey

et al. 2001) but had high allelic diversity in California towhees (9 + alleles). DNA was extracted from blood samples using DNeasy tissue kits (Qiagen) and amplified with fluorescently labeled primers using polymerase chain reaction. Amplified DNA samples were processed on an ABI 3730 DNA analyzer, and genotypes were assigned based on peak location. Paternity exclusion analyses were performed by hand. The chicks were considered extrapair if they had allelic mismatches with a social parent at two or more microsatellite loci. All loci yielded clear peaks, but Mme 8 had single base pair shifts, and parents and offspring sometimes showed peaks that differed by a single base pair. As a result of this, I conservatively did not consider single base pair shifts as mismatches for Mme 8. The program CERVUS (Marshall et al. 1998) was used to test for null alleles, to calculate heterozygosity, to calculate exclusion probabilities, and to test that loci Mme 1, Mme 2, and Mme 8 were in Hardy-Weinberg equilibrium for the entire population. The same tests were run in CERVUS for males only at locus Mme 7 because it is Z-linked.

Results

Social mating system

California towhees displayed strong social monogamy both within and across breeding seasons. I identified 44 pairs of California towhees that inhabited the study site between 2002 and 2006. All the pairs were observed to duet. Among the pairs from which both individuals were known to be alive in subsequent seasons ($N=20$), the index of monogamy was 1.0. All the pairs from which both individuals survived over multiple breeding seasons remained paired for all of those seasons. This sample includes two pairs that bred together during 4 years, and two additional pairs that bred together for 3 years. Thus, pairs remained together, jointly defended a territory and jointly cared for offspring each year. Partner turnover did occur between breeding seasons if one partner disappeared from the study population. When a bird

disappeared, the surviving partner generally stayed on the original territory and was joined by a new mate.

Only once did I observe a confirmed case of divorce where both partners were seen alive, but not breeding together after they had done so previously. In this instance, a breeding female (A) was usurped by a neighboring female (B) who moved into female A's territory while female A, and her mate had chicks in the nest. The male continued to feed his small chicks, but both he and female B would chase female A from the territory when she tried to approach. The male immediately began to perform pair behaviors, including vocal duetting with female B. Soon after re-pairing, his original nest failed, and female B laid a new nest on the territory which also subsequently failed, apparently due to predation. Interestingly, after this brief period of divorce in one season, the male reunited with female A to breed together in the following season, and female B was not seen again. Therefore, this case of divorce did not affect the index of monogamy as calculated above.

I observed no evidence of polygyny, polyandry, or cooperative breeding. I also never observed an extrapair copulation, despite observing 19 within-pair copulations from six different pairs over the five seasons.

Genetic mating system

All four microsatellite loci were in Hardy-Weinberg equilibrium and had an average heterozygosity of 0.86 (Table 1). Null allele probabilities were ≤ 0.01 . The four microsatellite loci had a mean of 14.25 alleles/locus. The combined exclusionary power of all four loci when the mother's identity was known was 0.99. Leaving out locus Mme 8 because some alleles sometimes appeared shifted by a single base pair, the combined exclusionary power of the other three loci when the mother's identity was known was 0.95 (Table 1).

All putative offspring matched maternal alleles at every locus, but 21 of 81 (26%) chicks showed allelic mismatches to social fathers. All chicks that showed mismatches to social fathers did so at two or more loci, with the average

Table 1 Population genetic statistics for four microsatellite loci in 31 social families of California towhees sampled in Carmel Valley, California, USA, between 2002 and 2006

Locus	Number of individuals	Number of alleles	Observed heterozygosity	Expected heterozygosity	Estimated frequency of null alleles	Exclusionary power with mother known
Mme 1	122	9	0.81	0.76	-0.031	0.560
Mme 2	122	12	0.91	0.85	-0.037	0.709
Mme 7	65	11	0.86	0.81	-0.039	0.619
Mme 8	122	23 ^a	0.87	0.88 ^a	0.011	0.791 ^a

Summary statistics were calculated for all individuals at loci Mme 1, Mme 2 and Mme 8, but only for males at locus Mme 7 because it is Z-linked
^a Mme 8 alleles sometimes exhibited single base pair shifts, so the number of alleles, expected heterozygosity and exclusionary power with a known mother may be over-estimates

(\pm standard deviation) number of mismatched loci being 2.9 ± 0.7 per chick. There were 7 of 19 females (37%) that produced extrapair young in 13 of 31 nests (42%), and 10 of 25 males (40%) were cuckolded. Five nests, with brood sizes between one and three, contained 100% extrapair young. Across all broods that contained extrapair young, 20 of 32 (63%) chicks were sired by fathers other than the social father. These results are minimum estimates of extrapair paternity frequency because they do not take into account the relatively unlikely possibility that an extrapair male with a similar genotype to that of the social father (for example, a sibling) sired the young.

Females for which I sampled multiple nests showed varied levels of extra-pair activity (Table 2). All five females with multiple nests laid at least one clutch containing no extrapair young, but three females each laid between one and six clutches that did contain extrapair young (Table 2). On average, 37% of nests laid by these females contained extrapair young, and 43% of their mates were cuckolded.

Discussion

Results support earlier predictions and conventional wisdom suggesting that California towhees are socially monogamous with long-term pair bonds that may persist for the life of an individual (Kunzmann et al. 2002). Every pair of California towhees observed in this population remained together in subsequent seasons when both partners were present within the study site. Although I cannot rule out emigration as a cause of mate loss, birds within the study population exhibited extreme site fidelity, and it is likely that almost all partner changes were due to deaths (Benedict 2007a). Divorce is apparently rare among California towhees, and they exhibited no evidence of behavioral promiscuity or polygamy. Similar patterns of long-term monogamy have been documented in other duetting species, and evidence suggests that duetting species are more likely than non-duetting species to maintain long-term social pair bonds (Benedict 2007c; Farabaugh 1982; Gill and Stutchbury 2006).

Despite strong social monogamy among pairs, paternity exclusion analyses revealed that nearly 40% of females engaged in extrapair copulations, and that 40% of males were cuckolded. Female extrapair mating strategies were varied, with some females from which I sampled multiple nests persistently cuckolding a variety of extrapair mates, and others remaining genetically faithful to a mate in multiple years. The females do not appear to pursue a single strategy of always producing extrapair young or never producing extrapair young. For example, the most prolific female, which laid seven nests in 4 years with three different mates, was genetically unfaithful in the majority of nests but faithful in one. Her one nest that contained all within-pair young was preceded and followed by nests with the same social mate that contained extrapair young. A second female with the same social mate across two seasons produced a clutch in 2003 that contained only within-pair young and a clutch in 2004 that contained extrapair young. Thus, extrapair mating behavior among females appears to be plastic, and mating fidelity may be unrelated to pair bond duration. Future study would be informative in elucidating the factors influencing such behavior.

This study is the first to document a significant proportion of extrapair young in a socially monogamous duetting species. California towhees in this study produced extrapair young at a frequency roughly ten times greater than frequencies measured in other socially monogamous duetting species (Fleischer et al. 1997; Hall and Magrath 2000; Gill et al. 2005). Over 40% of nests contained extrapair offspring and more than a quarter of all young examined were extrapair. In contrast, the average frequency of extrapair offspring among all socially monogamous birds is only 19% of broods and 11% of offspring (Griffith et al. 2002). Thus, the frequency of extrapair young in California towhees is high relative to all socially monogamous species and must be considered exceptionally high given that this species produces vocal duets and shows long-term pair bonds with paternal care (Kunzmann et al. 2002; Marshall 1964; Quaintance 1941).

Extrapair young are relatively uncommon, but not unheard of in species with strong pair bonds (Segelbacher et al. 2005). It is possible that even in some such species, females do not have to limit extrapair copulations to ensure

Table 2 Descriptive statistics regarding production of extrapair young (EPY) and social mates cuckolded by five female California towhees for which multiple broods were sampled in Carmel Valley, California, USA between 2002 and 2006

Female ID	Number of years observed	Number of broods sampled	Percent of broods containing EPY	Number of mates	Percent of mates cuckolded
27	4	7	86%	3	100%
48	4	4	50%	3	67%
133	2	2	50%	2	50%
70	3	2	0%	2	0%
117	2	2	0%	1	0%

that males remain socially committed. This might be the case if males are unable to assess paternity, or if other mechanisms, such as population demographic characters, discourage males from divorcing unfaithful mates. Either situation could account for the frequent occurrence of extrapair young in California towhees despite long-term pair bonds and male parental effort. California towhees do not recognize particular offspring vocalizations, and are known to accept brood parasitic Brown-headed Cowbird (*Molothrus ater*) eggs and nestlings, suggesting little discrimination by adults (Benedict 2007b; Kunzmann et al. 2002). Furthermore, the study population at the Hastings Reservation between 2002 and 2006 appeared to have an abundance of unmated floater males, so it is possible that females were a limiting resource, such that divorce might be particularly costly to males (L. Benedict, unpublished data).

Compared with other duetting species, California towhees have some characteristics that might make them relatively likely to produce extrapair young, but none of these traits are in any way prescriptive. For example, California towhees are passerine birds, and passerines tend to have more extrapair young than members of other taxonomic groups (Arnold and Owens 2002; Wink and Dyrce 1999). Authors have suggested that other *Pipilo* species may exhibit extrapair paternity frequencies as high as 40%, but this estimate is based on sperm morphology, and molecular genetic analyses have not been performed on any congeners (Dobbs et al. 1998). Additionally, the majority of well-studied duetters live in the tropics where avian species generally exhibit low levels of extrapair paternity, while California towhees live in a temperate climate where species tend to exhibit more genetic promiscuity (Stutchbury and Morton 2001). These trends, however, have not been evident in previous tests of extrapair paternity among socially monogamous duetting species. Four of five socially monogamous duetting species tested thus far are passerines, and all showed low levels of extrapair paternity (Fleischer et al. 1997; Haggerty et al. 2001; Hall and Magrath 2000; Gill et al. 2005). Similarly, the two North American duetting species tested have shown perfect genetic monogamy (Haggerty et al. 2001; Lawless et al. 1997).

Why do California towhees produce significant numbers of extrapair young when other monogamous duetting species do not? If duets signal partner commitment in some species, males of these species may not experience strong challenges to their paternity (Gill et al. 2005). Clearly, male California towhees experience challenges to their paternity, despite the fact that all birds included in this study duetted with their partners. If these duets did, indeed, signal commitment, then duetting females that produced extrapair young were manipulating mates, and results argue against the hypothesis that California towhees use duets to honestly signal commitment to genetic monogamy (Hall 2004). Duets may also function as a paternity guard, and if

they are entirely effective, then levels of extrapair paternity should be low (Sonnenschein and Reyer 1983). Obviously, duet production by males did not completely prevent extrapair copulations by females in the study population. It is possible that males which duet more frequently with their females succeed in preventing more extrapair copulations, so further data examining the rates of duet production in conjunction with the frequency of extrapair young would be highly informative. Such data would also help to elucidate the role of duets in (honestly or dishonestly) signaling levels of commitment between partners.

Research has shown that duets function in a number of different contexts and may operate differently in different species (reviewed in Hall 2004). Thus, there are a variety of functions, other than signaling genetic commitment or mate-guarding, which California towhee duets are likely to serve. Avian species use duets to jointly defend resources, to signal quality, to prevent a partner from being usurped, to maintain contact with a mate, or to coordinate behavior with a mate (Cobb 1897; Dilger 1953; Hall 2004; Seibt and Wickler 1977; Smith 1994). All of these functions could be beneficial to duetting partners within a context of social but not genetic monogamy if, for example, maintaining a territory and mated status is a necessary prerequisite for any male reproductive success.

Existing evidence suggests that vocally duetting species with long-term social pair bonds are likely to exhibit genetic monogamy, but results presented here indicate that California towhees produce an unusually high number of extrapair offspring. This study confirms that social mating systems, genetic mating systems and communication behaviors vary along separate axes, highlighting the diversity of social systems among duetting species.

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