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Social and Sexual Monogamy in Translocated New Zealand Robin Populations Detected Using Minisatellite DNA

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Most bird species are characterized as monogamous (Lack 1968, McKinney et al. 1984). However, recent research using genetic techniques has shown that social monogamy does not necessarily imply genetic monogamy. Although monogamous relationships involve social associations and often parental care shared by a male and female, they do not necessarily reflect the genetic contributions of attending adults to future generations (Davies 1991). Extrapair copulation (McKinney et al. 1984) and intraspecific brood parasitism (Yom-Tov 1980) cause discrepancies between apparent and realized reproductive success that are commonly missed in field observations.

Extrapair paternity is common in some species of socially monogamous birds (e.g.Westneat 1990, Yamagishi et al. 1992, Lifjeld et al. 1993), but uncommon in others (e.g. Burke et al. 1989, 1990; Decker et al.

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1993). Intraspecific brood parasitism (or egg-dumping) also is common in some socially monogamous species (e.g. Gowaty and Karlin 1984, Price et al. 1989). Detecting extrapair fertilization and intraspecific brood parasitism through parentage analyses is useful for characterizing the mating systems and for improving our knowledge of the biology of each species. This is not only of fundamental interest, but is important in the conservation of rare species. This study used minisatellite DNA profiling (Jeffreys et al. 1985a, b) to assess parentage among nuclear families of two island populations of New Zealand Robins (North Island, *Petroica australis longipes*; South Island, *P. a. australis*). New Zealand Robins are regionally threatened (Bell 1986), and both populations have been established by translocation.

New Zealand Robins are small insectivorous passerines considered to have a monogamous mating system (Oliver 1930; Fleming 1950a, b; Soper 1972; Powlesland 1983; Flack 1985). Despite strong territoriality, established adults are reported to move through other territories when foraging (Oliver 1930, Flack 1979). Therefore, the potential for extrapair copulation or intraspecific brood parasitism exists. In addition, occasional polygamous mating relationships have been recorded for the closely related Chatham Island Black Robin (*Petroica traversi*; Butler and Merton 1992). In general, however, socially monogamous robin pairs tend to stay close together (particularly during the prelaying period), and aggression is high, suggesting that the likelihood of frequent extrapair copulation and intraspecific brood parasitism is low.

Studies of different populations are a priority for research into avian mating systems (e.g. Westneat et al. 1990) because of the potential for identifying the factors influencing mating patterns under different circumstances. Both population density and sex ratios may affect the likelihood of extrapair copulations (Trivers et al. 1972, Westneat et al. 1990). If extrapair copulation typically occurs in a species, increased frequencies of this behavior might be expected in populations with higher densities, because paired individuals are more likely to encounter other birds. A higher frequency of extrapair copulations and extrapair fertilizations also may be expected if there is a male-biased sex ratio.

Differences in population densities and sex ratios between newly established populations of North Island and South Island robins facilitated a test of the influence of these factors on the mating system of the species. Population density was higher in the South Island population. Although sex ratios were male biased in both populations, the bias was considerably greater in the North Island population.

Materials and methods.—Parentage was studied in families of South Island robins on Motuara Island, and North Island robins on Tiritiri Matangi Island. The Motuara Island population (currently ca. 150 pairs; Maloney 1991) was established from five birds translocated from Nukuwaiata Island (also located at the northern tip of the South Island) in 1973 (Flack 1974).

The Tiritiri Matangi Island population was newly established at the time of sampling and had 31 to 35 birds at the start of the three breeding seasons during our study. The birds were translocated from a large population near Rotorua in the central North Island (Armstrong 1995), from which 44 birds were taken in April 1992 and 14 birds in June 1993. All samples came from these birds and their descendants. Robin densities during the seasons studied were about 1.5 birds/ha on Tiritiri Matangi (Armstrong unpubl. data) and about 6 birds/ha on Motuara (Maloney 1991). Although the sex ratio was slightly male biased on Motuara (Maloney 1991), it was more heavily biased towards males in the North Island robin population (77% males in the 1992 breeding season, 63% males in 1993, and 60% males 1994). The strong initial male bias resulted from the composition of the 1992 translocation (about two-thirds males), followed by higher mortality in females (Armstrong 1995).

Blood was obtained from South Island robin families in the 1992/93 breeding season (October 1992 to January 1993). North Island robins were sampled in the 1992/93, 1993/94, and 1994/95 breeding seasons. Twenty-one South Island and 16 North Island robin families were sampled, each comprising two putative parents and from one to three chicks (South Island, 33 chicks; North Island, 29 chicks). Putative parentage was assigned on the basis of paired adults feeding and brooding nestlings and provisioning fledglings. All pairs observed were socially monogamous (although opportunities for extrapair copulations appeared to exist).

Adults were caught using clap traps and hand nets, and chicks were either taken from the nest before fledging or caught with hand nets after fledging. Blood samples were collected as detailed in Ardern et al. (1994) and stored in liquid nitrogen for up to three weeks before being transported to the laboratory and subsequently held at $-80°C$.

A pilot trial assessing different enzyme-probe combinations is recommended for parentage analyses of each new species (Hanotte et al. 1992). Results of preliminary work (Ardern and Lambert unpubl. data) indicated that an optimal resolution of New Zealand Robin DNA fragments was achieved with *Hae*III digests in combination with probes 33.15 and 33.6 (Jeffreys et al. 1985a).

Total genomic DNA was extracted according to Ardern et al. (1997). DNA digestion, electrophoresis, Southern blotting, hybridization, and autoradiography were performed following the methods of Millar et al. (1992). Maternity and paternity was assigned by band matching, identification of unattributable fragments, and calculation of band-sharing coefficients between offspring and their putative parents (Westneat 1990, Decker et al. 1993, Graves et al. 1993). Band-sharing distributions were constructed for dyads of chicks with parental males and females, and chicks with unrelated males and females. Comparisons were restricted to individuals separated by six lanes or less on the same gel.

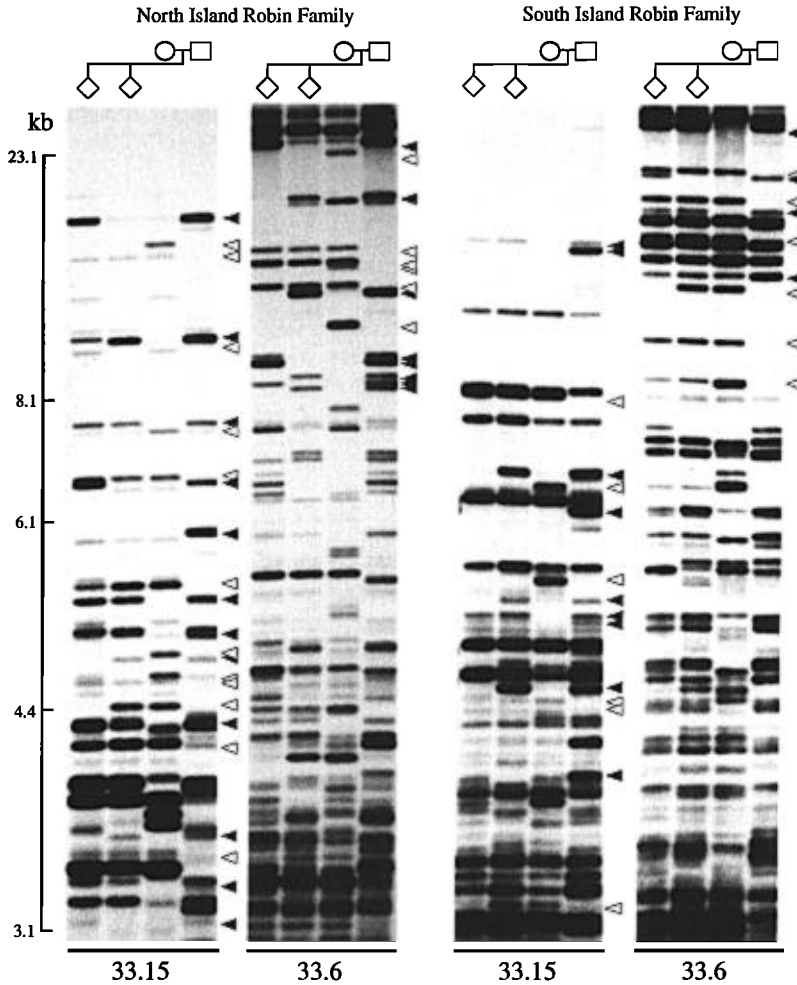North Island Robin Family   South Island Robin Family

Fig. 1. Minisatellite DNA profiles of individuals from a North and a South Island robin family produced by hybridization of minisatellite probes 33.15 and 33.6 to HaeIII-digested DNA.

The statistical significance of differences between numbers of fragments scored in males and females, and differences between expected and observed numbers of fragments shared between chicks and parents were tested using unpaired *t*-tests. Paired *t*-tests were used to test for differences in band-sharing (proportion of bands shared) between chick-female parent and chick-male parent dyads. A significance level of $P < 0.05$ was used in all statistical tests.

Results.—Complex and individual-specific minisatellite DNA profiles were produced by hybridization of both DNA probes (33.15, 33.6) to HaeIII-digested North and South Island robin DNA (Fig. 1). Fewer fragments were detected with 33.15 above 8kb. Therefore, the degree of overlap between the two probes was low in the regions scored (proportion of fragments scored that were detected with both probes: South Island, $\bar{x} = 0.01 \pm$ SD of 0.02, $n = 17$; North Island, $\bar{x} = 0.02 \pm 0.03$, $n = 15$).

Molecular weight range, number of fragments scored, and background band-sharing coefficients (see Table 1) generally were typical of measures reported for other species of birds (e.g. Burke and Bruford 1987, Lambert and Millar 1995). However, it should be noted that the background band-sharing was higher among South Island robins (0.43 ± 0.09, $n = 32$; combined probe results) than among North Island robins (0.20 ± 0.07, $n = 27$) .

For the North Island population, putative parentage was confirmed in band-matching analyses for all 16 families (29 chicks; lower confidence limit = 0.83). Taking each family as a replicate, this means that we are 95% confident that at least 83% of the broods in the population had no extrapair genetic contribution. The mean proportions of bands shared between chicks and male and female parents were 0.592 ± 0.079, ($n = 29$) and 0.6 ± 0.068 ($n = 29$), respectively. These proportions derived from an observed 19.8 ± 3.1 frag-

TABLE 1. Molecular weight range scored (kb), number of bands ($\bar{x} \pm$ SD), and band-sharing coefficients ($\bar{x} \pm$ SD) among apparently unrelated adult New Zealand Robins (North Island and South Island) for DNA profiles produced by hybridization of HaeIII-digested DNA with probes 33.15, 33.6, and both probes combined (numbers of individuals in parentheses).

	Probes		
	33.15	33.6	33.15/33.6
North Island (Tiritiri Matangi Island)			
Molecular weight range	>3	>8	>3/>8
No. of bands	24.5 ± 3.3 (15)	10.4 ± 2.2 (15)	34.9 ± 4.38 (15)
Proportion bands shared[a]	0.21 ± 0.07 (27)	0.18 ± 0.12 (27)	0.20 ± 0.07 (27)
South Island (Motuara Island)			
Molecular weight range	>3	>8	>3/>8
No. of bands	26.9 ± 3.3 (17)	9.9 ± 2.3 (17)	37.0 ± 4.6 (17)
Proportion bands shared[a]	0.44 ± 0.11 (32)	0.41 ± 0.16 (32)	0.43 ± 0.09 (32)

[a] Band-sharing calculated according to Wetton et al. (1987). Bands were considered shared if they differed no more than two-fold in intensity and if their centers were ≤0.5 mm apart (Bruford et al. 1992).

ments shared with males and 18.8 ± 3.5 fragments shared with females, neither of which differed significantly from the expected 20.3 fragments ($P < 0.1$, male and female parents).

For the South Island population, we found no evidence of extrapair genetic contribution in all 21 families (corresponding to 95% confidence that at least 87% of broods in the population had no extrapair contribution). However, our interpretation is more complex for this population due to DNA degradation and mutation (see below). For 28 of the 33 chicks (representing all 21 families), all fragments could be attributed to one or the other putative parent. For these 28 chicks, we produced band-sharing coefficients between offspring-male and offspring-female dyads (Fig. 2; similar results for North Island robins were obtained, data not shown). The mean proportions of fragments shared between chicks with male and female parents were 0.68 ± 0.07 ($n = 28$) and 0.72 ± 0.06 ($n = 28$), respectively (the latter higher than the expected value of 0.69). The difference between band-sharing coefficients for chicks paired with each parent was small, but approached significance (0.04 ± 0.05, $P = 0.065$). Observed numbers of fragments shared between offspring and parents were 25.9 ± 4.7 (male parents), and 28.3 ± 4.9 (female parents). Only the number of fragments shared between chicks and female parents differed significantly from the expected 25.4 fragments ($P < 0.1$ males; $P < 0.005$ females). These results suggested that some degree of sex-linkage is present in the form of Z-linked alleles in females (females being the heterogametic sex [Bloom 1974]). The range of values was greater for chick-male parent dyads, also suggesting possible sex-linkage as seen in the likely instance of sex-linkage among House Sparrows (*Passer domesticus*; Wetton et al. 1992). On average, a larger number of fragments was scored in females, but the difference between the sexes was not significant ($P = 0.194$).

Unattributable fragments were identified in five South Island robin chicks. The combined DNA profile (33.15/33.6) of one South Island chick contained five unattributable fragments, whereas the other four profiles contained only a single mismatched band. Several possible explanations exist for the occurrence of these mismatching fragments. Unattributable bands could be artifacts resulting from laboratory error in sample processing, incomplete digestion or sample degradation, or real effects of a mutation or mis-assigned putative parentage. To check for artifacts, a second DNA profile was produced from newly extracted DNA for this individual. The second profile indicated DNA degradation that appeared to have increased since the original extraction. We therefore could not confirm parentage exclusion, and this chick was excluded in subsequent analyses.

Because of the high mutation rates recorded for minisatellite regions in other avian species (typically ranging between 10^{-2} [Westneat 1990] and 10^{-4} [Burke et al. 1989]), a number of mutant bands could be expected in any large study. To determine whether the single mismatching fragments in the remaining four robins were likely to be the result of mis-assigned parentage or of mutation, band-sharing coefficients between the offspring and each putative parent were examined. All band-sharing coefficients between putative parents and chicks fell outside the range observed for chicks paired with non-relatives, and within the parent-offspring range (range 0.58–0.78 for males and 0.75–0.82 for females). Therefore, these fragments probably arose through mutation events. Actual mutation rates for North and South island robin populations, respectively, were calculated as 7.716×10^{-4} (1/1,296) and 3.273×10^{-3} (4/1,222) mutations per locus per generation.

After consideration of all the factors that can influence the possibility of mis-assigning parentage, it is reasonable to conclude that these data provide genetic evidence to confirm putative parentage among all robin families. No instances of extrapair fertilization
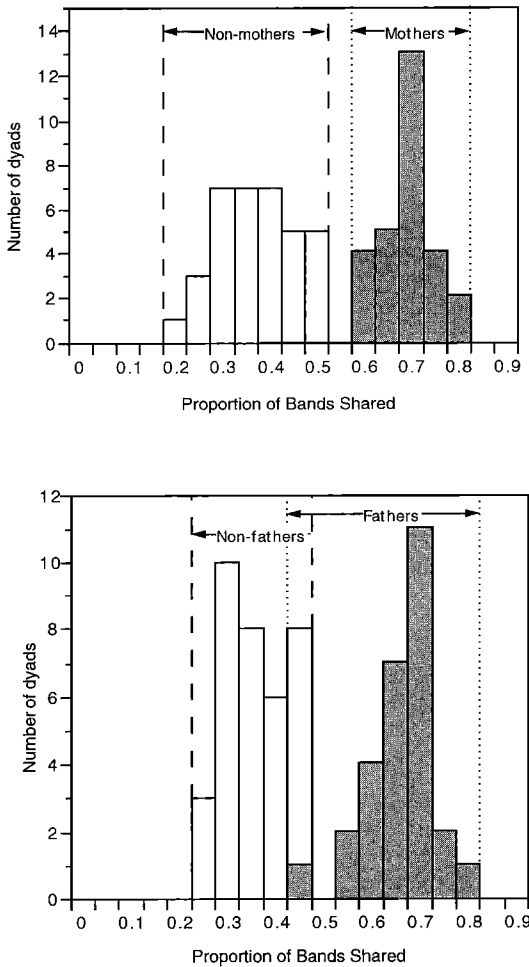
Fig. 2. Band-sharing distributions of South Island robin chicks with related and unrelated adults (upper, chicks paired with females; lower, chicks paired with males). Ranges of band-sharing values for the two groups are indicated at the top of each figure.

or intraspecific brood parasitism were identified, indicating social and sexual monogamy among all of the pairs we studied.

Discussion.—The parentage analyses presented here indicate that extrapair fertilizations do not appear to be common in New Zealand Robins. That is, social monogamy appears to be concordant with sexual monogamy. Intraspecific brood parasitism also appears to be uncommon. Field estimates of apparent reproductive success are therefore likely to reflect realized reproductive success accurately. This result was unaffected by differences between populations in density and sex ratios and also was unaffected by differences in the level of minisatellite DNA variation between the two populations.

Confirmation of putative maternity based on nest attendance suggests that egg dumping does not commonly occur among New Zealand Robins and that extrapair copulations are rare or extrapair matings are unsuccessful at achieving fertilizations. Even in cases where extensive field data on copulatory behavior are available, the relationship between extrapair copulations and extrapair fertilizations is not necessarily predictable (e.g. Lambert et al. 1994). Extrapair fertilizations appear to be common in some species in which no extrapair copulations have been observed (e.g. Yamagishi et al. 1992, Lifjeld et al. 1993). In contrast, observed extrapair copulations apparently have little or no genetic effect in other species (Gyllensten et al. 1990).

Aggression is a possible factor contributing to the maintenance of sexual monogamy in New Zealand Robins. Adult robins are fiercely territorial and display high levels of aggression towards intruders. Both sexes chase trespassing birds from their territories (Oliver 1930). They are rarely aggressive towards neighbors once territories are established (Armstrong 1995), but resident males will attack neighboring males that exhibit courtship behavior to the resident female (Armstrong pers. obs.). Also, in the closely related Chatham Island Black Robin, adult males sometimes evict females rather than attempt extrapair copulations (Butler and Merton 1992). Female-female aggression also may be important in the maintenance of sexual monogamy among New Zealand Robins. However, aggression in others species does not prohibit extrapair paternity.

The prevalence of sexual monogamy among New Zealand Robins has several implications for future research and conservation of this species. For example, biologists can now monitor levels of inbreeding in small populations based on nesting data alone, as is being done with the Tiritiri Matangi population. In addition, for future translocations, it will be possible to select individuals either closely or distantly related according to field observations alone, and to assess genetic contributions of founding individuals with a high degree of confidence.

In conclusion, sexual monogamy appears to predominate among breeding pairs of the socially monogamous New Zealand Robin. Aggression may be an important factor contributing to the occurrence of the socially and sexually monogamous breeding system in this species.

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Skin From Feet of Museum Specimens as a Non-destructive Source of DNA for Avian Genotyping

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The advent of the polymerase chain reaction (PCR) has revolutionized sampling possibilities in avian genetic studies. With PCR, many genetic markers of interest can be amplified from samples such as single feathers (Woodruff 1990, Taberlet and Bouvet 1991, Morin et al. 1994, Srikwan and Woodruff 1996) and museum bird specimens (Cooper et al. 1992), which contain minute quantities of DNA and/or highly degraded DNA. The potential of using museum specimens in particular has opened up new avenues for phylogenetic and population genetic research in birds, which are only just beginning to be exploited (Smith et al. 1991, Cooper et al. 1992, Cooper 1994, Morin and Woodruff 1996). Museum collections are now seen as valuable repositories of genetic material (Graves and Braun 1992), and requests to curators for the use of museum specimens for genetic research are growing. However, obtaining a sample for genetic analysis from a museum skin necessarily involves removing

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part of the specimen, and there is great concern that damage to specimens be kept to a minimum. Previous authors have described the use of small pieces of skin from the body (Smith et al. 1991); single remiges or rectrices (Ellegren 1991, Leeton et al. 1993); or pieces of muscle, tendon, and bone (Cooper et al. 1992). Here, we report on the use of small pieces of skin from the soles of the feet of museum specimens used in the context of a population genetics study of the Loggerhead Shrike (*Lanius ludovicianus*). Because the sole of the foot has not to our knowledge been used as a taxonomic character in birds, the damage done to the specimens for future research is negligible. Furthermore, because we successfully analyzed single-locus nuclear markers (microsatellites) with these samples, few genetic questions exist that cannot be resolved with this tissue.

Methods.—With a sterile scalpel blade, pieces of skin approximately 1.5 × 1.5 × 3 mm were cut from the ventral side of the proximal phalanx of the first digit of the feet from 19 specimens of the San Clemente Loggerhead Shrike (*L. ludovicianus mearnsi*) that