# PATERNITY AND THE RELATEDNESS OF HELPERS IN THE COOPERATIVELY BREEDING BELL MINER[1]

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*Abstract.* We used multi-locus DNA fingerprinting to determine the parentage of 13 broods of Bell Miner (*Manorina melanophrys*) nestlings. Despite very large contingents of male helpers attending individual nests and living in close proximity to breeding females, we found only one instance of extra-pair paternity in 24 nestlings. The genetic father of the extra-pair nestling was not among the males in our study population. The majority of helpers (67% of 52 cases) were close relatives ($r > 0.25$) of at least one parent of the brood being provisioned. Helpers were more often closely related to the male than the female parent. Only 17% of cases involved helpers that were apparently unrelated to either of the parents of the broods being aided. We conclude that Bell Miners do not mate promiscuously and that the majority of helpers are close relatives of the breeding pair. Cooperative breeding in Bell Miners seems to have evolved as a system of collateral kinship among the breeding birds and helpers.

*Key words: Bell Miner, communal breeding, cooperative breeding, DNA fingerprinting, helping behavior, honeyeaters, Manorina melanophrys, paternity analysis.*

## INTRODUCTION

Individuals expending time and energy caring for young that are not their own has long been recognized as a challenging problem for evolutionary theory. Since the 1970s, an increasing number of cases of aid-giving behavior has been documented in a wide range of taxa (Emlen 1991), including approximately 3% of bird species, where nonbreeding "helpers" appear to behave altruistically by helping to rear young that are not their own (Brown 1987). Such birds are said to exhibit cooperative breeding.

One hypothesis to explain the apparent altruism of cooperative breeding is that helpers increase their inclusive fitness by helping to raise their relatives' offspring (Hamilton 1964). This hypothesis has received support from a number of descriptive studies of cooperatively breeding birds in which aid-giving has been found to be preferentially directed toward close kin (Emlen and Wrege 1989, Komdeur 1994). However, helpers apparently contribute substantial aid to nonkin in some species (Clarke 1989, Walters 1990).

Dow (1978) suggested females of cooperatively breeding species might obtain care for their young by copulating promiscuously with multiple partners. This idea was extended by Haig et al. (1994) who suggested that frequent extra-pair copulations could be a component of the complex social structure found in cooperatively breeding species. Females may offer potential paternity to obtain care from otherwise unrelated helpers. In such cases, helpers should have paternity, but not necessarily be related to each other or the social parents at the nest. In almost complete contrast, Hartley and Davies (1994) concluded that the number of helpers at the nest in cooperatively breeding species is less when helping depends upon shared paternity rather than on collateral kinship with the broods.

The Noisy Miner *Manorina melanocephala* and the Bell Miner *M. melanophrys* have some of the largest group sizes described for any cooperative breeder, with up to 20 helpers attending a single brood (Põldmaa et al. 1995; D. Jones, unpubl. data.). Consequently, if Haig et al. (1994) are correct, these species should have

high frequencies of extra-pair matings, especially considering that in both species the vast majority of helpers are male (Clarke 1989, Dow and Whitmore 1990). Based upon field observations of promiscuous mating by Noisy Miners (Dow 1978), Dow and Whitmore (1990) suggested that the evolution of cooperative breeding in that species could have involved promiscuous matings by females. More recently, genetic analysis of parentage of Noisy Miners has indicated they have a monogamous, rather than promiscuous, mating system (Põldmaa et al. 1995).

Observational evidence of the mating system of the Bell Miner is equivocal. Whereas the species has only been observed copulating and breeding in socially monogamous pairs (Clarke 1988), some apparently unpaired male helpers are probably physiologically capable of mating (Poiani and Fletcher 1994), some have been observed engaging in apparent courtship feeding (Clarke 1988, Poiani 1992), and some appear unrelated to the "owners" of the nest at which they provide aid (Clarke 1989). There also has been one case of apparent intraspecific brood parasitism (Poiani 1993a). Because high levels of promiscuity have been found in cooperatively breeding species previously thought to be monogamous (Splendid Fairy-wren, *Malurus splendens* Brooker et al. 1990; Superb Fairy-wren *M. cyaneus,* Mulder et al. 1994), it is clearly inadequate to assume social parentage of young is an accurate reflection of genetic parentage.

Our aim in this study is to use multi-locus DNA fingerprinting to determine the parentage of Bell Miner nestlings and the degree of relatedness between parents and helpers at the nest. From these results we determine whether the extreme form of cooperative breeding in Bell Miners is associated with promiscuous mating and low levels of relatedness between helpers and the social parents at the nest, or a monogamous mating system, with high mean levels of relatedness among the members of the breeding unit.

## METHODS

### STUDY SPECIES

Bell Miners are a species of honeyeater (family Meliphagidae) that occur in discrete social units (colonies) comprising contiguous home ranges, each occupied by a breeding pair, the young raised on that home range, and varying numbers of apparently unrelated, sexually mature, non-

breeding helpers (Clarke and Fitz-Gerald 1994). Females build the nest and incubate their eggs alone. Clutch size is 1–3 eggs (mode = 2), and females may attempt to raise several broods in one year. Males are philopatric, whereas females disperse prior to gaining breeding status (Clarke and Heathcote 1990). Helpers may provision young belonging to several different pairs, either simultaneously or sequentially. Even members of a pair with dependent young of their own may act as helpers to another pair at the same time. For our analyses, we defined a family as a mother, her nestlings, their putative father, and any helpers that were observed bringing food to the nest. We grouped families that shared provisioners into coteries (Dow 1978).

### FIELD STUDY

We conducted this study within the Coranderrk Reserve at Healesville, southeastern Victoria, Australia (37°41'S, 145°31'E, see Poiani 1993b for a site description) from 27 October 1993 to 7 February 1994. When we found a nest, we determined its contents and used mist nets to capture the birds attending it. Each bird received a unique color combination of three colored and one metal leg band to permit identification at a distance. We collected 50–200 $\mu$l of blood from each bird in 75 $\mu$l nonheparinized capillary tubes by brachial venipuncture, and suspended it in 1 ml of Queen's lysis buffer (Seutin et al. 1991) and stored it at 4°C. The mother at a nest was identified by behavior and the presence of a brood patch (Clarke 1988). The putative father and helpers at each nest were determined from daily nest watches of 1–2 hr, during which we recorded each bird provisioning the nestlings. Watches were conducted from a hide, starting from the day of hatching or the time the nest was discovered and continued until the nestlings died or fledged.

### DNA FINGERPRINTING AND ANALYSIS

We performed DNA extraction and conducted DNA fingerprinting following Smith et al. (1991) and Põldmaa et al. (1995), at the Queen's Molecular Ecology Laboratory (QMEL). Fingerprints were organized so that a complete coterie appeared on a single gel. For each fingerprint we digested 5 $\mu$g of DNA per individual with *Hae* III and subjected it to electrophoresis on a 0.8% agarose gel for 40–44 hr, until fragments less than approximately 1.5 kb had mi-

grated off the gel. In each lane we also ran 20 ng of an internal size marker (lambda DNA; BstEII and HindIII/EcoRI - digested cocktail) to aid electronic scoring (Galbraith et al. 1991). The DNA was then Southern blotted onto Immobilon-N transfer membranes. All membranes were probed first with radioactively-labelled Jeffreys 33.6 (Jeffreys et al. 1985) and then *per* (Shin et al. 1985) and finally lambda, to produce three separate autoradiographs from each blot.

We scanned the autoradiographs as gray scale images and stored the images on a computer. We overlaid the standard band profiles from the lambda autoradiographs on the matching Jeffreys 33.6 and *per* autoradiographs and generated profiles of molecular sizes for each individual using Gelreader v2.05 (National Center for Supercomputing Applications, Champaign, IL). Subsequent electronic scoring followed Põldmaa et al. (1995) and Yezerinac et al. (1995). Compared across all autoradiographs, the majority of clearly resolvable bands appeared between 3,500 and 12,000 bp, so we scored only this range. We performed band-sharing analyses of the Gel-Reader output using two Visual Basic programs written by K. F. Conrad (copies of the compiled programs and source code available on request). Values presented are means ± SE.

## RESULTS

### DETERMINING EXTRA-PAIR YOUNG

The average number of fingerprint bands per individual for the 13 broods (10 females) we analyzed was 15.28 ± 0.29, $n = 83$ for Jeffreys 33.6, and 15.13 ± 0.34, $n = 83$ for *per*. The mean number of bands scored per lane did not differ significantly between the probes (paired $t_{82} = 0.40$, $P > 0.65$). In general, although both probes produced qualitatively similar results, Jeffreys 33.6 fingerprints were more consistent in their exposure, clearer, and easier to score. Therefore we concentrated our analyses on Jeffreys 33.6 fingerprints and used *per* only to confirm our results.

Among the 24 nestlings fingerprinted and probed with Jeffreys 33.6, all but 2 had some bands not shared with either parent (i.e., novel fragments; Burke and Bruford 1987). Surprisingly, the distribution of novel fragments among nestlings was skewed but not bimodal, suggesting that there were few or no extra-pair young (EPY; Fig. 1). Following Westneat (1990), we
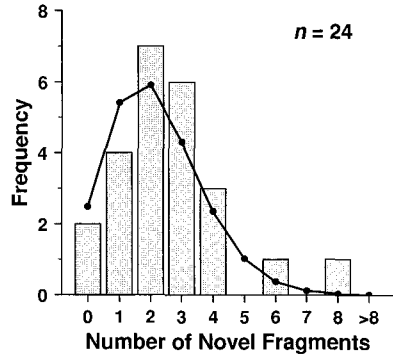


FIGURE 1. Distribution of novel fragments from Bell Miner fingerprints probed with Jeffreys 33.6. Bars are the observed frequency of novel fragments, connected points are expected values from a Poisson distribution calculated from the mean of the frequency of individuals having four or fewer novel fragments ($\bar{x} = 2.18$; see text). The distribution of novel fragments among birds with fewer than four novel fragments was not significantly different from the expected Poisson distribution ($\chi^2_4 = 1.52$, $P = 0.82$).

calculated the mean number of novel fragments for individuals having four or fewer novel fragments and fitted a Poisson distribution to the data (Fig. 1). Using this distribution, we calculated the probability of an individual having five, six, or seven novel fragments as 0.046, 0.017, and 0.005, respectively. Thus, in our sample of 24 nestlings, we would expect only a single individual with five novel fragments, possibly one individual with six novel fragments, and none with greater than six (Fig. 1). A similar result is obtained if the fitted distribution is based upon either individuals having three or fewer, or six or fewer novel fragments. Accordingly, we considered nestlings having more than four novel fragments to be potential EPY.

We then calculated band-sharing coefficients (D; % total bands common between two individuals; Wetton et al. 1987) of the offspring with their putative parents to determine whether the extra-pair nestlings resulted from extra-pair copulations or intraspecific brood parasitism (Westneat 1990). To estimate the level of band-sharing between unrelated individuals, we assumed that the putative parents of a family unit were not related and calculated the D-value (0.36 ± 0.03, $n = 13$) between them. From this we calculated the upper 95% confidence limit, D = 0.43, and used this as the cutoff between putative parents and descendent offspring (Fig. 2; Westneat 1990).
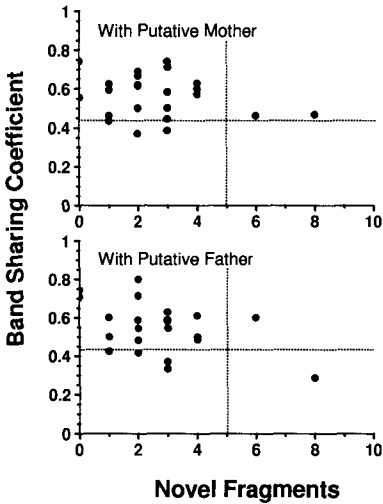
**FIGURE 2.** Distribution of band-sharing coefficients (D-values) between nestlings and their putative mothers (above) and fathers (below) versus the number of novel fragments nestlings possessed. Dashed lines occur at the cutoff limits of novel fragments (vertical) and D-values (horizontal) used for determining unrelated individuals.

Among the 24 nestlings, we found 2 nestlings that had more than four novel fragments (Fig. 1 and 2). The first had six novel fragments and D-values of 0.46 with its mother and 0.60 with its putative father. However, the high band-sharing with both the father and mother and the results from *per* (novels = 2, maternal D = 0.48, paternal D = 0.59) suggested to us it was not an EPY. The second nestling had eight novel fragments and D-values of 0.47 with its mother and 0.29 with its putative father. We therefore excluded the putative father and considered it to be an EPY. We then calculated the band-sharing statistics between the EPY and all males and helpers in our study, but could not find any male which resulted in it having four or fewer novel fragments when compared with its putative parents. The genetic father of the EPY was not among our samples.

In summary, we found only one family in 13 broods (8%) containing only one EPY (4% of 24 nestlings), but were unable to determine the nestling's actual father, either from within its own coterie, or from our overall sample of males. In the eight nests where multiple paternity was possible (clutch size > 1), we found all 8 broods were sired by only a single male.

## BAND-SHARING BETWEEN FULL-SIBLINGS AND RELATEDNESS OF HELPERS

We calculated D between each dyad of full siblings in our population (Fig. 3). The value obtained ($0.61 \pm 0.04$, $n = 15$ dyads) was reasonably close to the expected mean value of 0.68 (95% CI = 0.65–0.71), estimated from the level of background band-sharing (Quinn et al. 1994, p. 520). It also was not significantly different ($t_{36} = 1.00$, $P > 0.33$) from the mean value for parent-offspring dyads of $0.56 \pm 0.02$ ($n = 23$; Fig. 3) as might be expected because full siblings and parents and offspring have the same degree of relatedness ($r = 0.50$).

## RELATEDNESS OF HELPERS

In total, 39 individuals served as helpers to 13 broods. Among 91 helper-nestling dyads, the mean band sharing coefficient was $0.48 \pm 0.01$. This value is significantly lower than the mean band sharing coefficient between nestlings and
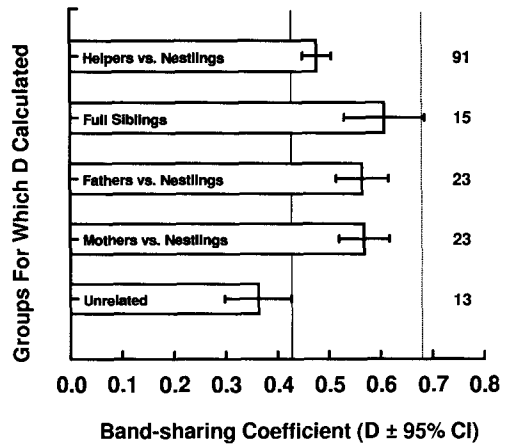


**FIGURE 3.** Mean band-sharing coefficients ($\pm$ 95% CI) among different groups of Bell Miners. D-values for unrelated individuals were calculated between the presumed unrelated parents of extended family units. Pair young (PY) had less than five novel fragments with their parents. The D-values between siblings were calculated for all pair-wise comparisons of band-sharing between PY within each family. Similarly, the D-values between helpers and nestlings were calculated for all pair-wise comparisons of band-sharing between helpers and the nestlings from nests at which they provided care. Sample sizes appear at the end of each bar and the solid vertical line indicates the maximum D-value we considered to indicate unrelated individuals. The expected mean value for full siblings ($r = 0.50$) was calculated based upon the level of background band-sharing (Quinn et al. 1994) and is indicated by the vertical dashed line.
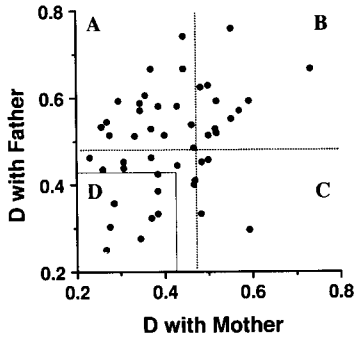
FIGURE 4.    Comparison of band-sharing coefficients with helpers between parents at the nests where the helpers provided care. Dashed lines indicating the estimated lower 95% confidence limit of D-values of second-order ($r$ = 0.25) relatives (estimated from background D, Quinn et al. 1994) divide the graph into quadrants A–D. The square delineated by the solid lines in quadrant D contains helpers apparently unrelated to both parents (D < 0.43). Helpers falling in quadrant A are at least second-order relatives of the father, but are unrelated to the mother. Helpers falling in quadrant C are at least second-order relatives of the mother, but are unrelated to the father. Helpers falling in quadrant B are at least second-order relatives of both parents. Note that most of the helpers in quadrant B fall above the line Y = X, suggesting that even these helpers are more closely related to the male than the female.

either of their putative parents ($t_{112}$ = 2.87, $P$ < 0.001; Fig. 3). Including overlap of helpers at multiple families and broods, we recorded a total of 52 instances of helpers assisting to raise a brood. For each of these 52 instances, we calculated D between the helper and the parents at the nest (Fig. 4). Based upon the cutoff value of D for unrelated individuals and the estimated ranges for full- and half-siblings (Fig. 3 and 4), 12 (23%) of these instances of helping involve first- or second-order relatives (i.e., $r$ = 0.50 or $r$ = 0.25) of both parents (Fig. 4). Nineteen (36%) were first- or second-order relatives of the father but not the mother, and only four (8%) were first- or second-order relatives of the mother but not the father. Of the remaining cases, eight (15%) seemed to be more distantly related to both parents, and nine (17%) appeared unrelated to either parent (Fig. 4). To summarize, 67% of instances of helping involved close relatives of the breeding male ($r$ > 0.25), and only 17% involved helpers apparently unrelated to either parent.

## DISCUSSION

Female Bell Miners do not appear to copulate promiscuously to assemble a contingent of unrelated helpers. The large contingents of helpers and the obligate nature of helping in the Bell Miner appear to be associated with a monogamous mating system and high levels of kinship between helpers and recipients of their aid (Hartley and Davies 1994). In our study, most helpers attending a nest were found to be close relatives of one or both members of the putative breeding pair. This situation is thought to be typical of many cooperative breeders (Brown 1987), although it has been verified by molecular analyses of relatedness in only a few species (Jones et al. 1991).

Our results are consistent with most genetic analyses of the parentage of young in other cooperatively breeding species. Six percent or fewer young were sired by a male from outside the group of individuals attending the nest in the Florida Scrub-Jay *Aphelocoma coerulescens* (Mumme et al. 1985), the Stripe-backed Wren (Rabenold et al. 1990), the European Bee-eater *Merops apiaster* (Jones et al. 1991), the Red-cockaded Woodpecker (Haig et al. 1994), the Noisy Miner (Põldmaa etal. 1995), and the Bicolored Wren *Campylorhynchus griseus* (Haydock et al. 1996). Two striking exceptions to this trend were found in the Splendid Fairy-wren and the Superb Fairy-wren in which 65% and 76% of young, respectively, were sired by males from outside the social group (Brooker et al. 1990, Mulder et al. 1994).

Given that there is only a low level of extrapair mating in Bell Miners and the fact that males are philopatric, while females disperse, it is not surprising that we found helpers were close relatives of one or both parents in the vast majority of cases (67%), as Clarke (1984, 1989) postulated from observation of individually marked birds. Furthermore, as expected from dispersal patterns (Clarke and Heathcote 1990), helpers appeared to be more closely related to the male (Fig. 4). The proportion of cases of Bell Miner helpers aiding nonrelatives was small (17%), but is consistent with estimates of aid-giving by nonrelatives obtained from an observational study of a nearby population (Clarke 1989).

That the vast majority of aid was provided by first- or second-order relatives is consistent with

the predictions of the indirect fitness benefit hypothesis (Hamilton 1964). It also is consistent with most observational studies of other cooperative breeders that have found that the majority of helpers are close relatives of the young they were aiding (see review by Brown 1987). However, one does need to be cautious with such generalizations, given the small number of species in which the relatedness of helpers has been examined using molecular techniques (e.g., Dunn et al. 1995). Whether the frequencies of aid-giving to nonrelatives should be regarded as fatal for the indirect fitness benefits hypothesis is best determined by calculating the costs and benefits of the behavior relative to those achieved by adopting alternative strategies. Hamilton's rule does not require that aid only be directed towards close relatives, but rather that on average, the benefits of attempting to direct aid towards close relatives exceed the costs (Dawkins 1979). Whether occasional aid-giving to nonrelatives represents a system where birds are following a fairly rough rule of thumb consistent with the indirect fitness benefits hypothesis (e.g., feed nearby begging nestlings because they are likely to be related), or whether they are gaining greater direct fitness benefits by helping nonrelatives (e.g., through increasing their chance of gaining a future mate; Reyer 1984) remains to be demonstrated.

We have shown that the extraordinary numbers of helpers (up to 20) assisting to raise a brood of just one or two nestlings in Bell Miners is not based upon a highly promiscuous mating system in which the female trades fertilizations for assistance at the nest. Hartley and Davies (1994) suggest that the number of helpers in a monogamous mating system may be limited by the diminishing benefits of increased care beyond what a certain number of helpers can provide. Although Clarke (1989) demonstrated that females with six or more helpers produced significantly more young per attempt than females with fewer helpers, the upper limit to the number of helpers that can usefully be deployed at a miner's nest remains to be determined. It seems unlikely that the indirect fitness benefits hypothesis alone will provide an adequate explanation for such extraordinary levels of sociality.

## ACKNOWLEDGMENTS

## LITERATURE CITED

BROOKER, M. G., I. ROWLEY, M. ADAMS, AND P. BAV-ERSTOCK. 1990. Promiscuity—an inbreeding avoidance mechanism in a socially monogamous species. Behav. Ecol. Sociobiol. 26:191–199.

BROWN, J. L. 1987. Helping and communal breeding in birds. Princeton Univ. Press, Princeton, N.J.

BURKE, T., AND M. W. BRUFORD. 1987. DNA fingerprinting in birds. Nature 327:149–152.

CLARKE, M. F. 1984. Cooperative breeding by the Australian Bell Miner, Manorina melanophrys Latham: a test of kin selection theory. Behav. Ecol. Sociobiol. 14:137–146.

CLARKE, M. F. 1988. The reproductive behaviour of the Bell Miner, Manorina melanophrys. Emu 88:88–100.

CLARKE, M. F. 1989. The pattern of helping in the Bell Miner (Manorina melanophrys). Ethology 80:292–306.

CLARKE, M. F., AND G. F. FITZ-GERALD. 1994. The spatial organization of the cooperatively breeding Bell Miner, Manorina melanophrys. Emu 94:96–105.

CLARKE, M. F., AND C. F. HEATHCOTE. 1990. Dispersal, survivorship and demography in the cooperatively-breeding Bell Miner, Manorina melanophrys. Emu 90:15–23.

DAWKINS, R. 1979. Twelve misunderstandings of kin selection. Z. Tierpsychol. 51:184–200.

DOW, D. D. 1978. Reproductive behavior of the Noisy Miner, a communally breeding Honeyeater. Living Bird 16:163–185.

DOW, D. D., AND M. J. WHITMORE. 1990. Noisy Miners: variations on the theme of communality, p. 561–592. In P. B. Stacey and W. D. Koenig [eds.], Cooperative breeding in birds. Cambridge Univ. Press, Cambridge.

DUNN, P. O., A. COCKBURN AND R. A. MULDER. 1995. Fairy-wren helpers often care for young to which they are unrelated. Proc. Roy. Soc. Lond. B 259:339–343.

EMLEN, S. T. 1991. Evolution of cooperative breeding in birds and mammals, p. 301–337. In J. R. Krebs and N. B. Davies [eds.], Behavioural ecology: an evolutionary approach. Blackwell Scientific, Oxford.

EMLEN, S. T., AND P. H. WREGE. 1989. A test of alternative hypotheses for helping behaviour in the

White-fronted Bee-eaters of Kenya. Behav. Ecol. Sociobiol. 25:303–319.

GALBRAITH, D. A., P. T. BOAG, H. L. GIBBS, AND B. N. WHITE. 1991. Sizing bands on autoradiograms: a study of precision for scoring DNA fingerprints. Electrophoresis 12:210–220.

HAIG, S. M., J. R. WALTERS, AND J. H. PLISSNER. 1994. Genetic evidence for monogamy in the cooperatively breeding Red-cockaded Woodpecker. Behav. Ecol. Sociobiol. 34:295–303.

HAMILTON, W. D. 1964. The genetical evolution of social behaviour. I and II. J. theor. Biol. 7:1–52.

HARTLEY, I. R., AND N. B. DAVIES. 1994. Limits to cooperative polyandry in birds. Proc. Roy. Soc. Lond. B 257:67–73.

HAYDOCK, J., P. G. PARKER, AND K. N. RABENOLD. 1996. Extra-pair paternity is uncommon in the cooperatively breeding Bicolored Wren. Behav. Ecol. Sociobiol. 38:1–16.

JEFFREYS, A. J., V. WILSON, AND S. L. THEIN. 1985. Individual-specific 'fingerprints' of human DNA. Nature 316:76–79.

JONES, C., C. LESSELS, AND J. KREBS. 1991. Helpers-at-the-nest in European Bee-eaters (Merops apiaster): a genetic analysis, p. 169–192. In T. Burke, G. Dolf, A. J. Jeffreys, and R. Wolf [eds.], DNA fingerprinting: approaches and applications. Birkhauser Verlag, Basel.

KOMDEUR J. 1994. The effect of kinship on helping in the cooperative breeding Seychelles Warbler (Acrocephalus sechellensis). Proc. Roy. Soc. Lond. B 256:47–52.

MULDER, R. A., P. O. DUNN, A. COCKBURN, K. A. LAZENBY-COHEN, AND M. J. HOWELL. 1994. Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. Proc. Roy. Soc. Lond. B 255:223–229.

MUMME, R. L., W. D. KOENIG, R. M. ZINK, AND J. A. MARTEN. 1985. Genetic variation and parentage in a Californian population of Acorn Woodpeckers. Auk 102:305–312.

POIANI, A. 1992. Feeding of the female breeder by male helpers in the Bell Miner. Emu 92:233–237.

POIANI, A. 1993a. A possible case of intra-specific brood parasitism in the Bell Miner. Corella 17:61–62.

POIANI, A. 1993b. Reproductive biology of the Bell Miner (Manorina melanophrys, Meliphagidae) at Healesville, southeastern Victoria. Wildl. Res. 20:579–598.

POIANI, A., AND FLETCHER, T. 1994. Plasma levels of androgens and gonadal development of breeders and helpers in the Bell Miner (Manorina melanophrys). Behav. Ecol. Sociobiol. 34:31–41.

PÕLDMAA, T., R. MONTGOMERIE, AND P. BOAG. 1995. Mating system of the cooperatively breeding Noisy Miner Manorina melanocephala, as revealed by DNA profiling. Behav. Ecol. Sociobiol. 37:137–143.

QUINN, J. S., R. MACEDO, AND B. N. WHITE. 1994. Genetic relatedness of communally breeding Guira Cuckoos. Anim. Behav. 47:515–529.

RABENOLD, P. P., K. N. RABENOLD, W. H. PIPER, AND S. W. ZACK. 1990. Shared paternity revealed by genetic analysis in cooperatively breeding tropical wrens. Nature 348:538–540.

REYER, H. U. 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the Pied Kingfisher (Ceryle rudis). Anim. Behav. 32:1163–1178.

SEUTIN, G., B. N. WHITE, AND P. T. BOAG. 1991. Preservation of avian blood and tissue samples for DNA analysis. Can. J. Zool. 69:82–90.

SHIN, H. S., T. A. BARGIELLO, B. T. CLARK, F. R. JACKSON, AND M. W. YOUNG. 1985. An unusual coding sequence from a Drosophila clock gene is conserved in vertebrates. Nature 317:445–448.

SMITH, H. G., R. MONTGOMERIE, T. PÕLDMAA, B. N. WHITE, AND P. T. BOAG. 1991. DNA fingerprinting reveals relation between tail ornaments and cuckoldry in Barn Swallows, Hirundo rustica. Behav. Ecol. 2:90–98.

WALTERS, J. R. 1990. The Red-cockaded Woodpecker: a 'primitive' cooperative breeder, p. 69–101. In P. B. Stacey and W. D. Koenig [eds.], Cooperative breeding in birds. Cambridge Univ. Press, Cambridge.

WESTNEAT, D. F. 1990. Genetic parentage in the Indigo Bunting: a study using DNA fingerprinting. Behav. Ecol. Sociobiol. 27:67–76.

WETTON, J. H., R. E. CARTER, D. T. PARKIN, AND D. WALTERS. 1987. Demographic study of a wild House Sparrow population by DNA fingerprinting. Nature 327:147–149.

YEZERINAC, S. M., P. J. WEATHERHEAD, AND P. T. BOAG. 1995. Extra-pair paternity and the opportunity for sexual selection in a socially monogamous bird (Dendroica petechia). Behav. Ecol. Sociobiol. 37:179–188.