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NESTING HENDERSON REED-WARBLERS (*ACROCEPHALUS VAUGHANI TAITI*) STUDIED BY DNA FINGERPRINTING: UNRELATED COALITIONS IN A STABLE HABITAT?

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ABSTRACT.—Using DNA fingerprinting we studied Henderson Reed-Warblers (*Acrocephalus vaughani taiti*), which are confined to Henderson Island in the central South Pacific. During the single study season, the birds had a well-defined nesting period from late August to early January. About one-third of nesting groups comprised three, not two adults. The members of trios, which could include two males and one female, or one male and two females, were unrelated. However, all members of trios contributed to incubation and/or feeding the young, whether or not they were parents of the chicks. The output of young per adult was slightly but not significantly higher in pairs than trios. We suggest a compensating advantage for members of trios: in the stable island habitat, young birds may be more readily able to secure a nesting territory when belonging to a trio than when in a pair. *Received 16 August 1993, accepted 21 November 1993.*

ABOUT 3% OF BIRD SPECIES are known to breed in groups (Stacey and Koenig 1990). Studies of this phenomenon have proliferated in the past 20 years as research workers have tried to pinpoint the costs and benefits to individuals of group membership. In some cases the benefits appear clearcut. In the Seychelles Warbler (*Acrocephalus sechellensis*), young birds reared on high-quality territories tend to remain there to help raise probable relatives. This strategy offers greater lifetime reproductive success than the alternative of dispersal, probably to a poorer territory (Komdeur 1992). At the other extreme there may be no benefit to group membership per se. Instead, group breeding by some Dunnocks (*Prunella modularis*) arises as a consequence of unrelated males and females pursuing their individual and divergent interests on a variable territorial patchwork (Davies 1992). In between these extremes are examples of group breeding of exceptional complexity and interest, such as found in Acorn Woodpeckers (*Melanerpes formicivorus;* Koenig and Stacey 1990) and fairy wrens (*Malurus* spp.; Brooker et al. 1990, Mulder et al. 1994).

In general, however, group breeding is associated with lack of dispersal by one sex or both, and this has led to studies addressing whether or not group breeding is adaptive (Craig 1984) and, if it is adaptive, what might be the benefits of helping in the natal group (Emlen et al. 1991). These explanations invoke either direct fitness benefits to the philopatric helper or indirect benefits, such as increased production of nondescendant kin. However, the direct benefits of group breeding need not depend on natal philopatry. For example, if a bird allied to nonrelatives fared better in competition for territorial space than a lone bird (Ligon and Ligon 1990) or, if an allied bird experienced lower mortality (Faaborg and Bednarz 1990), group breeding could be favored even in the absence of natal philopatry. Our study of the Henderson Reed-Warbler (*Acrocephalus vaughani taiti*), a species confined to the central Pacific island of Henderson, evaluates further the possibility that group breeding without natal philopatry may arise because of intrinsic advantages of group breeding.

In a more perfect world we could honestly write that we set forth to test the hypothesis that Henderson Reed-Warblers bred in unrelated groups. However our interest in the Henderson Reed-Warbler arose because it, like the Seychelles Warbler studied by Komdeur (1992),

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is a generalist insectivore living in a stable, low-latitude forest where territories were potentially limiting. Such conditions may favor group living (Emlen 1982). Our first question, therefore, was whether the Henderson Reed-Warbler, like its Indian Ocean counterpart, is also found in groups. The answer was unknown because ours was the first study of the species' breeding biology. When the answer was positive we asked, via DNA fingerprinting, whether the group members were related. Only when the answer to that question was negative did we begin to explore whether group breeding might have benefits not predicated upon relatedness. Thus, our study, using DNA fingerprinting, explores the mating system of the Henderson Reed-Warbler, and considers some benefits that may accrue to birds breeding in groups of unrelated individuals.

STUDY AREA AND METHODS

Our study was carried out during the Sir Peter Scott Commemorative Expedition to the Pitcairn Islands, which lasted from January 1991 to March 1992. Thus, fieldwork on uninhabited Henderson Island (24°20'S 128°20'W), which at 3,700 ha is the largest island of the Pitcairn group, spanned a single breeding season, roughly from late August 1991 through early January 1992. Because Henderson Island is a raised limestone island that is unusually pristine ecologically, it has been designated as an UNESCO World Heritage Site. It is the home to four endemic landbirds: a flightless rail (*Nesophylax ater*), a fruit dove (*Ptilinopus insularis*), a lorikeet (*Vini stepheni*), and the Henderson Reed-Warbler. Thus, the reed-warbler, the island's only passerine, is free of avian predators. It is a robust *Acrocephalus* species with a catholic diet (Graves 1992). The main nest predators probably are Polynesian rats (*Rattus exulans*).

Field methods.—The reed-warbler occurs over essentially all of Henderson Island: in the coastal woodland characterized by the introduced hardwoods *Thespesia populnea* and *Cordia subcordata*; and in the mixed woodland of the plateau, some 25 m above sea level. The latter woodland, with canopy about 6 m, is exceptionally thick. E. H. Quayle, assistant field naturalist on the 1922 visit by the Whitney South Sea Expedition, wrote "No-one can imagine the impenetrability of the bush on the flat top." This constraint meant that nests, both in the coastal and the plateau woodland, were found opportunistically.

Nests typically were placed in slight, spindly trees, often isolated from other trees; therefore, nest contents usually were checked by mirror. To reach chicks for blood sampling, two people held a ladder while a third ascended to the nest. Since the chicks were handled only on this one occasion, they were not weighed, nor was growth followed in detail.

If nests were found before or during incubation, 1-h incubation watches (one to three per nest) were conducted to assess the contribution to incubation of the birds attending the nest. For each watch the time during which each adult incubated was scored, as was the (relatively short) time during which the eggs remained uncovered. Similarly, 1-h feeding watches (one to three per nest) were undertaken to assess relative feeding effort. During watches the number of feeds delivered by each adult was noted. Feeding watches were carried out in the middle part of the day (starting times between 0700 and 1600) when the young were at least six days old.

Individual identification of reed-warblers was greatly facilitated by their variable, partial albinism (Holyoak 1978). This attribute meant that at most nests individuals were readily identifiable by plumage features alone. However, the birds could not be sexed until capture.

Although some adult reed-warblers were caught before or during incubation, the majority were captured by a mist net placed alongside the nest when the young were about nine days old, after the bulk of nest observations had been completed. At capture, the number of wholly or partially white remiges (left wing for convenience) and rectrices (total, since two sides not always symmetrical) was tallied. Birds were sexed by the presence (indicating a female) or absence of a vascularized brood patch and by the shape of the cloacal protuberance (Svensson 1992). A blood sample of about 0.05 mL was taken from the brachial vein and preserved in 1 mL absolute alcohol for subsequent DNA fingerprinting. Similar blood samples were taken from young aged seven to nine days.

To estimate insect abundance a Malaise trap was operated in the plateau woodland for 10 days per month for 11 months (May 1991–March 1992). The data analyzed were from five two-day periods per month, and the data presented (Fig. 1) represent the sum of the 10-day samples collected in the given month. Statistical tests are two-tailed unless indicated otherwise.

DNA fingerprinting.—Techniques for multilocus DNA fingerprinting of birds have been well described elsewhere (Bruford et al. 1992). In our study undertaken at the Department of Zoology, University of Leicester, DNA derived from blood was digested with *Mbo*I restriction enzyme and filters were then probed with Jeffreys' probe 33.15, labelled with $\alpha\{^{32}P\}$-deoxycytidine triphosphate by primer extension from single stranded M13 vectors (Jeffreys et al. 1985a, b). All chick samples were run on the same gel as the full-grown birds attending the chick's nest to avoid the need to compare fingerprints between gels.

Bands between approximately 23 and 3 kilobase (kb) pairs were inspected and scored as identical when their centers were within 0.5 mm of each other and

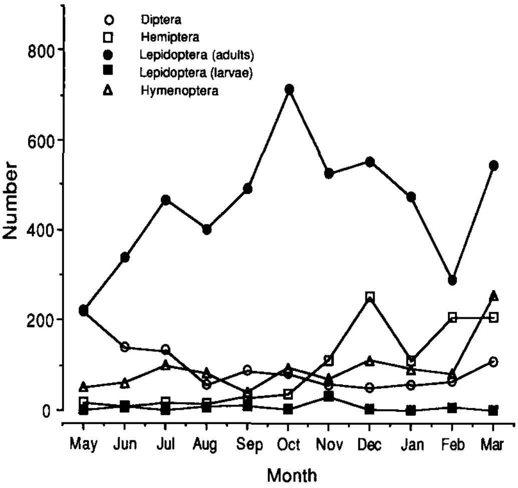

Fig. 1. Total number of insects belonging to four orders caught in greatest numbers in a Malaise trap on Henderson Island. Lepidoptera are split into adults and larvae, the latter likely to be especially important in diet of young Henderson Reed-Warblers. Each point represents aggregate number of insects caught over a 10-day sampling period in given month.

any difference in intensity was less than two-fold. The band-sharing coefficient (s) between two individuals (a and b) was calculated using the formula:

$$s = 2N_{ab}/(N_a + N_b), \tag{1}$$

where N_{ab} is the number of shared bands, and N_a and N_b are the number of scored bands in the fingerprints of a and b, respectively (Wetton et al. 1987). Background band-sharing was calculated from 10 dyads of apparently unrelated individuals (chicks from different nests or chicks/adults from different breeding coalitions) run in adjacent, or next-to-adjacent, tracks on a gel. No individuals were used more than once in the calculation of background band-sharing. Band-sharing coefficients were calculated for all pairwise comparisons between offspring within a nest, between offspring and the birds attending that nest, and between the attending birds.

Mean band-sharing coefficients of first-order relatives (parent-offspring and full siblings) generally will slightly exceed 0.5 (Jeffreys et al. 1985a, b) because of band-sharing between unrelated individuals. Half-siblings will have band-sharing coefficients roughly midway between the values for first-order relatives and for unrelated individuals.

Parentage was assigned to most chicks when both putative parents were available for fingerprint comparisons. Where only one putative parent was available, we compared band-sharing coefficients against the 95% confidence ranges of band-sharing values for dyads of unrelated individuals. This comparative approach does away with the need for a segregation analysis of a large family (e.g. Westneat 1990, Hunter et al. 1992, Hartley et al. 1993) and any linkage, even if present, is unlikely significantly to affect the results (Amos et al. 1992).

RESULTS

Nesting sites and season.—During the study 27 nests with contents (eggs/young) were found, at a mean height of 3.6 ± SD of 1.19 m (range 1.7–7.0). The nests typically were sited in spindly individuals of a wide variety of tree species: *Xylosma suaveolens* (7), *Thespesia populnea* (5), *Nesoluma st-johnianum* (3), *Ixora fragrans* (3), *Eugenia reinwardtiana* (2), *Pisonia grandis* (2), *Psydrax odorata* (2), *Celtis pacifica* (2), and *Glochidion pitcairnense* (1).

As described by Graves (1992), nests were made of various fibers and lined with finer material. They were rather bulky. The mean dimensions of five were: external depth, 132 ± 12.8 mm; external diameter, 114 ± 6.2 mm; cup depth, 52 ± 7.3 mm, cup internal diameter at rim, 59 ± 8.4 mm.

First-egg dates in the study nests fell during September (6), October (6), November (14) and December (1). The November sample includes one known repeat of a failed clutch. Otherwise, the laying dates could refer to first or repeat clutches. However there are probably no true second broods, since the young remain partly dependent for at least six weeks postfledging (see below).

Casual observations suggested that caterpillars and adult moths (Lepidoptera) were the main dietary items of nestling reed-warblers. The numbers of these insects caught in the Malaise trap showed significant monthly variation (moths, $F_{10,44} = 4.48$, $P < 0.001$; caterpillars, $F_{10,44} = 7.59$, $P < 0.001$); these insects were most abundant during the period October–December when most young were in the nest (Fig. 1). Of the other most-numerous insect groups caught in the trap, bugs (Hemiptera) also varied from month to month ($F_{10,44} = 17.8$, $P < 0.001$) and were most abundant during the latter part of the breeding period, when dipteran numbers fell ($F_{10,44} = 6.44$, $P < 0.001$). Hymenopterans, over 95% of which were ants that are perhaps unsuitable as nestling food, showed monthly variation ($F_{10,44} = 3.78$, $P = 0.001$), but no clear seasonal trends. These data suggest that reed-warblers timed breeding to coincide with a period of high abundance of suitable food.

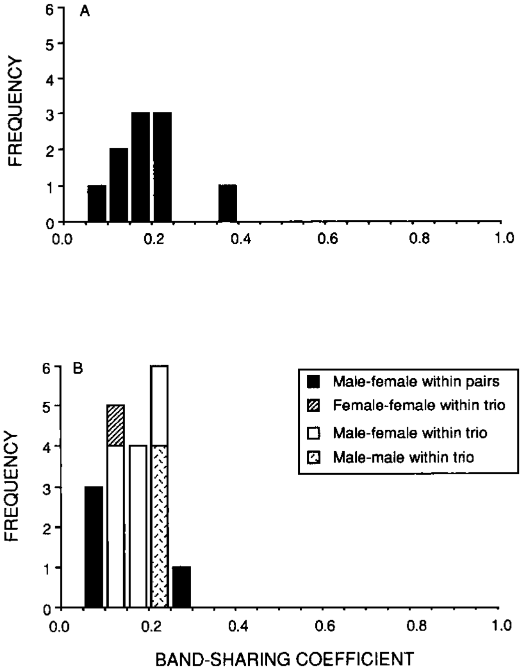

Fig. 2. Frequency distributions of band-sharing coefficients between dyads of: (A) apparently unrelated individuals (n = 10 dyads; 20 different individuals); and (B) adults within breeding coalitions, split by sex and number of adults attending the nest (n = 19). Band-sharing coefficients of dyads of adults within breeding coalitions all are within 95% range of apparently unrelated dyads (range 0.008-0.367; $\bar{x} \pm t$SD).

Territory size.—Warblers defended exclusive territories during the breeding season and probably during the remainder of the year (Graves 1992). Although territories were not mapped in detail, the nests of six groups with contiguous territories were found in the roughly linear strip of coastal woodland near our North Beach campsite. The six nests were separated by an average of 108 m. Territories with a circular boundary of radius 54 m would have an average size of 0.92 ha. If territory sizes are similar in the coastal and plateau woodland, then the 3,700-ha island contains about 4,020 territories. With an average of 2.36 birds per breeding group (next section), the breeding population would be 9,500 birds. Graves (1992) estimated a total postbreeding population of 10,800 birds.

Pairs and trios.—Territorial groups in August sometimes included four birds. However, judging by behaviors and the wholly brown plumage indicative of young birds (see below), these groups included young from the previous breeding season. Several group members then participated in nest building, but this phase of the breeding cycle was not studied in detail. By the time incubation was underway, there was no indication that groups larger than three incubated or fed young, nor that group members remained on territory during the breeding attempt without participating at the nest.

During detailed nest watches, either two or three birds participated in both incubation and feeding of the young or, more rarely, only in feeding. Relevant data were collected at 22 nests. At 14 nests (64%), a pair was present. For six nests, both the male and female incubated and then the nest failed; for two nests, both the male and female incubated and then both fed the young; and in six nests found after hatching, both fed the young.

At eight nests (36%), three birds participated. Of this latter group, four were watched during incubation and, subsequently, during the rearing of the young. At two of the four nests, all members of the trio incubated and fed the young. At the other two, only two birds (a male and female) incubated, but the third was in regular attendance and then helped feed the chicks. A fifth trio nest failed before hatching, but all three birds incubated. The final three trio nests were watched only during the brood stage when three birds fed the young.

All birds in five trios were caught and sexed. Four trios included two males and one female (polyandrous trio), while one involved one male and two females (polygynous trio). We were able to calculate 15 within-trio band-sharing coefficients. The mean value (0.172 ± 0.05) does not differ significantly from that (0.189 ± 0.08) derived (see Methods section) from 10 dyads of unrelated birds (t = 0.67, df = 23, $P > 0.05$; Fig. 2). No dyads from the within-trio group had band-sharing coefficients above the upper 95% range for the band-sharing coefficient of apparently unrelated birds, while the band-sharing coefficients of all dyads fell outside (below) the 95% range for first-order relatives (see legend of Fig. 4). Although nonnormal distributions of band-sharing coefficients are known (T. Burke pers. comm.), it appeared that, regardless of gender, Henderson Reed-Warblers within trios were unrelated.

Clutches and incubation.—The egg of the Henderson Reed-Warbler, like that of the Pitcairn Reed-Warbler (*A. v. vaughani*; Williams 1960), is pale green-blue, spotted with large distinct spots of black and brown. There is rather little diffuse marking. Five eggs from clutches of three and two were measured. Their mean length and breadth were 21.9 ± 0.78 mm and 15.7 ± 0.43 mm, respectively.

Considering only those 18 nests found at the egg stage, the mean clutch size was 2.44 ± 1.04, with no significant differences between the nests attended by two and three birds ($n = 8$ and 6, respectively). Most clutches were of two and three eggs ($n = 12$ and 3, respectively). There was a single nest with one egg, and two with five eggs. Both of the latter were remarkable.

At nest H, two eggs had been laid by 3 November when incubation had not started. By the next check on 6 November, five eggs (two bluer and three greener) were being incubated by three birds. The nest was depredated two days later and the adults never caught. However it seems very likely that two females laid in the nest.

Events at nest 3, tended by a trio of one male plus two females, were more startling. The nest was found after two chicks had hatched, so the contents were not checked in detail until 18 November, when those chicks were blood sampled at 10 days old. The contents also included a newly-hatched chick, a pipping egg, and another egg. The following day the pipping egg had hatched and the small chick died. The nest could not be disturbed again until the young fledged. When they did, there was no sign of small chicks or eggs. DNA fingerprinting indicated that the male fathered both large chicks, one of which was the offspring of each female. Thus, two females laid in the nest. Moreover, one or both females laid in two episodes, and heat provided by the earlier chicks apparently sufficed to hatch the eggs laid in the second episode. This observation resembles Tarburton and Minot's (1987) report of nestling White-rumped Swiftlets (*Aerodramus spodiopygius*) incubating and hatching eggs.

During incubation a bird would normally sit for 10 to 20 min and rarely more than 30 min until relief. Incubation watches were undertaken at three nests attended by two sexed birds. The male and female, respectively, undertook an average of 6.3 and 93.7% of incubation (i.e. percent of total time eggs were covered). Incubation watches were undertaken at five nests attended by four polyandrous trios. At this stage, one male was visibly subordinate, often being jostled off the eggs by the dominant male or the female. By contrast, the subordinate male never supplanted the dominant male on the eggs. The average contributions to incubation of dominant male, subordinate male, and female were 36.5, 4.2, and 61.5%, respectively. The totals do not sum to 100% because sometimes two birds sat on the eggs side by side! Females in pairs contributed more to incubation than females in polyandrous trios (Mann-Whitney $U = 0.0$, $P < 0.05$). The time from clutch completion to hatching was about 15 days.

Breeding success.—All observed broods contained either two or three chicks. The mean brood size was 2.41 ± 0.62 ($n = 17$; all nests with chicks) and the mean number of fledglings per successful nest was 2.29 ± 0.47 ($n = 17$). In fact, the only recorded chick losses were those described for nest 3 above. In general, therefore, losses occurred during the egg stage. Once hatched, chicks mostly fledged.

The mean number of fledglings produced per nest for the 17 nests followed from the egg stage was 1.47 ± 1.18. At 15 of these nests, the number of adults was recorded. Where two adults attended the nest, the mean output was 1.25 ± 1.39 fledglings ($n = 8$). When three adults attended the nest the mean output was 1.43 ± 0.98 ($n = 7$) fledglings, which is higher but not significantly so ($P > 0.05$).

Relationships within broods, and between broods and adults.—Fingerprints were obtained from 13 complete broods containing 29 chicks and also from attendant trios (5), attendant pairs (4), and the attending female of a pair (1). We fingerprinted 53 birds. However, we failed to catch any adults and obtain their fingerprints at three nests (one with a trio, two with pairs) with sampled broods.

Parentage was assigned when all bands in the offspring fingerprint could be found in the fingerprint of one or other of the putative parents. Parentage was excluded when there were several mismatching bands. In the reed-warbler fingerprints, there were either no mismatches ($n = 20$) or from 5 to 15 mismatching bands ($\bar{x} = 9.0 \pm 3.6$, $n = 11$). Parentage, therefore, was easily assigned.

When potential parents are related in breeding trios (e.g. a son, helping his mother and father, might gain paternity), there is a problem with using band mismatches to assign parent-

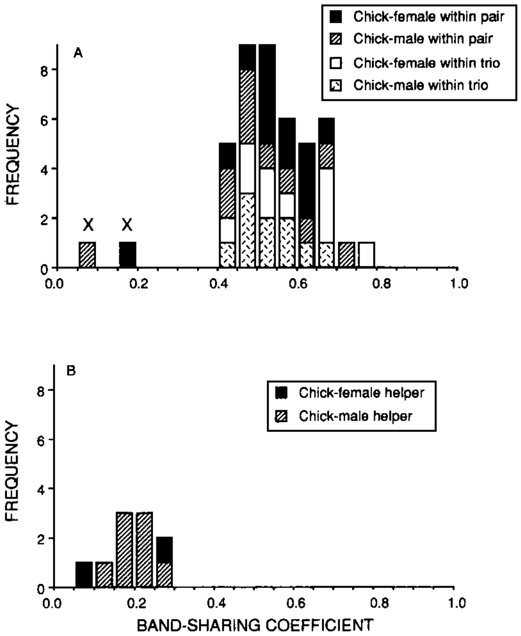

Fig. 3. Frequency distributions of band-sharing coefficients between dyads of: (A) chicks and most related male and most related female, split by the number and sex of attendants; and (B) chicks and the least related adult of trios. Dyads marked with X represent one chick (from brood of three) unrelated to either putative parent of attending pair; this chick most likely was product of dumped egg. Band-sharing coefficients of dyads of chicks and the least-related adult in trios fall within 95% range of apparently unrelated dyads (Fig. 2A).

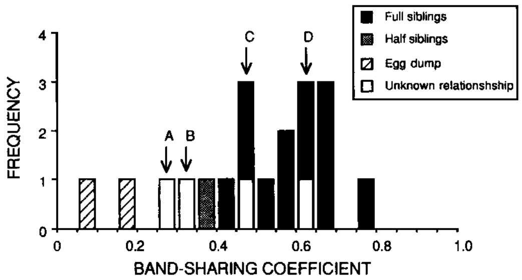

Fig. 4. Frequency distributions of band-sharing coefficients between dyads of chicks within nests. Parentage determined by presence or absence of mismatching parental bands in fingerprint of chicks for all but four dyads; these four dyads are represented by chicks from four broods of two offspring and are indicated by letters A to D in figure. Dyads A and B fall within 95% range of apparently unrelated dyads (Fig. 2A) and are discussed further in text. Dyads C and D fall outside 95% range of apparently unrelated dyads (Fig. 2A) and within 95% range of known full-siblings (0.343–0.831; $\bar{x} \pm t$SD, $n = 12$ dyads from 8 nests, so degrees of freedom for t are 7) suggesting that chicks within dyads C (only female fingerprinted) and D were not of mixed parentage.

age. Bands inherited from the mother's son or his father cannot be distinguished in the fingerprints of his offspring. However, we already have shown that adults breeding in trios are unrelated (Fig. 2B), so the problem does not arise in this case.

Band-sharing coefficients between offspring and putative parents are shown in Figure 3A. All 10 chicks tended by fingerprinted trios were the offspring of group members, and we could readily determine which members of trios gained parentage and which did not (Fig. 3). In the one polygynous trio, the two females each mothered one chick, while the male fathered both chicks. The other four completely sampled trios were polyandrous. In all four cases the female in the trio was mother to both chicks in her nest. However, in each case only one male secured paternity. In three cases he was the behavioral subordinate (judged on incubation behavior) and, in the fourth, he was the dominant male in the trio. If, lacking data on copulation frequency and any knowledge of the type of sperm precedence in this species (Birkhead and Møller 1992), we assume that both males in a trio are equally likely to secure paternity, then the probability of observing four (of four) single-father broods of two is not significantly low ($P = 0.06$); however, the sample size is insufficient to show a difference.

At the sixth fingerprinted-trio nest, the adults were not sampled. However, the band-sharing coefficient (0.625) of the two chicks in this nest, as in the other four polyandrous trio nests, indicated that they were probably full siblings (Fig. 4; dyad D). Thus, every chick ($n = 12$) tended by a trio was the offspring of trio members.

Thirteen nestling fingerprints were derived from five pair nests with fingerprinted adults. In 12 cases, fingerprinting confirmed the parentage of the adults (Fig. 3A). In the thirteenth case, the band-sharing coefficients were low for both the offspring-male (0.054) and the offspring-female (0.154) comparisons, and fell within the 95% range for the band-sharing coefficients between unrelated birds (Fig. 2A). In the absence of any observation hinting at a third, unsampled adult on this territory, we suggest this chick hatched from a dumped egg.

Four other chicks were fingerprinted in two pair nests where the adults were not sampled. The band-sharing coefficients of the two chick pairs were 0.261 and 0.303 (Fig. 4; dyads A and B). Both of these coefficients fall below the lower 95% confidence limit for full-sibling dyads. They fall within the upper 95% confidence limit for unrelated dyads (Fig 2A) and close to the band-sharing coefficient of a known half-sibling from the trio nest with two females (0.367; Fig. 4). Without data on the adults at these pair nests, we cannot determine whether these two chicks arose from dumped eggs or whether they were half-siblings. If the latter, we guess that the most likely origin of half-siblings is via a common mother and two fathers—as would arise if the female copulated with an extrapair male. In summary, the 17 chicks from nests tended by pairs included 14 that were the offspring of the pair, 1 from a dumped egg, and 2 of uncertain origin. Those two may have been the offspring of one pair member, but probably were not the offspring of both pair members.

Nest visiting rates in pairs and trios.—Within pairs, the feeding rate was not detectably influenced by whether there were two or three young in the nest. No trios fed three young. Thus, we can directly compare nest visiting rates of pairs and trios. The two groups did not differ in the total number of feeds delivered to the nest in an hour (pairs, $\bar{x} = 21.7 \pm 6.96$, $n = 18$; trios, $\bar{x} = 21.3 \pm 6.32$, $n = 17$; $t = 0.276$, df = 33, $P > 0.05$). It follows that the per adult hourly visiting rate was higher in pairs ($\bar{x} = 11.3 \pm 7.21$, $n = 26$) than within trios ($\bar{x} = 6.5 \pm 3.46$, $n = 42$; $t = 3.62$, df = 66, $P < 0.001$).

Feeding-rate data are available from four polyandrous trios. In two, the subordinate male did not incubate, but did assist with feeding young. Grouping the data into dominant-male feeding rate, subordinate-male rate, and female rate, there was no indication of differences (Friedman two-way ANOVA; $X^2 = 1.5$, $P = 0.653$). Regrouping the same data according to whether the male had gained paternity in the brood, the paternal-male feeding rate, the non-paternal-male rate, and the female rate were not significantly different (Friedman two-way ANOVA; $X^2 = 1.5$, $P = 0.273$). In the one polygynous trio we watched, the two females fed at a similar rate.

We conclude that birds belonging to trios delivered food to nests at similar individual rates, regardless of parentage or social status. Since pairs deliver food at a similar total rate to trios, it follows that all members of trios share equally (in comparison with members of pairs) in the per-capita reduction in nest-visiting rate.

Young reed-warblers continued to receive part of their food from adults for at least six weeks after fledging. In fact, the dependent period may be substantially longer since apparent family groups were seen together in August 1991, some seven months after the presumed end of the previous breeding season. Whatever the precise length of the period, its duration probably suffices to prevent second broods.

White feathers.—The tails of 12 breeding males and 11 breeding females were scored. The mean numbers of white feathers were 5.5 ± 3.7 and 1.8 ± 2.3, respectively (Mann-Whitney $U = 22.5$, $P < 0.05$). Males also were more likely to have at least one white feather in the left wing; 9 of 13 did in contrast to 2 of 11 females ($X^2 = 4.36$, df = 1, $P < 0.05$). Evidently, there is sexual dimorphism in the extent of albinism. In contrast, Williams (1960) believed there was no linkage between albinism and sex in the Pitcairn Reed-Warbler.

All fledglings seen lacked white feathers; thus, albinism is probably related to age (Holyoak 1978, Graves 1992) as well as gender. However, a longitudinal study is needed to define the relationship.

If more white feathers are acquired with age and if older birds tend to breed in pairs, (where per-adult output of fledglings may be higher than in trios), we predict pair males will possess more white feathers than trio males. The mean number of white tail feathers in four males breeding in pairs was 7.8, whereas the mean for eight males breeding in trios was 4.4 (Mann-Whitney $U = 7.0$, one-tailed, $P = 0.077$); the difference is not statistically significant, but suggests that pair breeding is more likely in older males. Within the four polyandrous trios, there was no indication of a relationship between dominance and white tail feathers, or between paternity and white tail feathers.

DISCUSSION

The principal findings of our study are that Henderson Reed-Warblers breed in either pairs or trios. Trios, consisting of either two males and one female ($n = 4$) or two females and one male ($n = 1$), commonly contain unrelated birds. However, all members of trios contribute to feeding of young, even when they are not related to those young. Judged by rate of food delivery, nests provisioned by trios and pairs receive the same amount of food, so individual trio members work less at food gathering than pair members.

Because the data from one study season are inevitably limited, there are less secure findings as follows. While the breeding output of trios (1.43 fledglings) was higher than that of pairs (1.25), the difference was not statistically significant. The reproductive success of adults breeding in pairs (but apparently not in trios) is devalued by egg dumping and possible extrapair offspring. Thus, the output of offspring per adult is 0.48 in trios and a maximum of 0.62 in pairs. The males within polyandrous trios may be younger than pair males, judging by the extent of albinism. How may these facts be reconciled?

In the subtropical habitat of Henderson Island a young reed-warbler can disperse or remain in the natal territory to help rear relatives. The young of the ecologically similar Seychelles Warbler often follow the latter course, which brings the greater lifetime reproductive success (Komdeur 1992). Henderson Reed-Warblers do not follow the latter course, presumably because the gain of that strategy—0.18 additional first-order relatives (i.e. 1.43-1.25)—is less than the potential gain from breeding elsewhere in either a pair or a trio. A possible ecological contrast between Cousin Island, where Komdeur (1992) worked, and Henderson Island is that there are differences in territory quality across Cousin, whereas such differences are not obvious on Henderson Island. The Cousin interterritory differences could promote natal philopatry, especially in Seychelles Warblers raised on high-quality territories.

We do not know the annual survival of breeding Henderson Reed-Warblers but suspect it may be as high as 85 to 90% (Diamond 1980, Komdeur 1992). If so, territorial vacancies may be scarce, and a means for dispersing younger birds to increase their chances of securing a territory could be to form coalitions of more than two birds, namely, trios. In mammals, larger coalitions of male lions (*Panthera leo*) are more likely to gain and retain control of prides than smaller coalitions (Packer et al. 1988).

While a male reed-warbler would surely benefit genetically from allying with his brother, only 50% of males fledging from modal broods of two will fledge with a brother. If first-year survival is around 35% (Komdeur 1991), the chance that a first-year male can ally with another male from his brood becomes 0.175. The same argument applies to alliances between young females and their sisters. Therefore, it is unremarkable that we failed to detect related birds in the five trios we fingerprinted; however, we would expect to do so in a larger sample. Vehrencamp (1983) pointed out how the availability of relatives can influence group-living strategies.

Beside the possibility that trios may be more likely to secure territories than pairs, we have identified two possible advantages of trio breeding that could compensate for the slightly lower per-adult output of offspring. First, trio females contribute less to incubation than pair females. Second, trio breeding requires a lower chick feeding rate of the adults. If younger breeders are less skilled at feeding than older reed-warblers (Desrochers 1992), trio breeding would then particularly benefit younger breeders. As these birds age, they may "graduate" to pair breeding—as hinted by the albinism data. That transition could arise actively, by the eviction of one bird, or passively when the trio was reduced by mortality (Faaborg and Bednarz 1990).

In four fingerprinted broods tended by polyandrous trios, there was no case of shared paternity. Perhaps this resulted from the modest sample. Notwithstanding, the two males shared equally the task of feeding the young. This might be explained if the two males had had equal access to the female during her fertile period, and used that access to guide their feeding effort (Davies 1992).

In polyandrous trios, the two males may compete for paternity by attempting to gain greater access to the female. The combined mate-guarding attention of the two males perhaps explains why, in polyandrous trios, there was no instance of extratrio offspring (0/12). In pairs, where only one male could guard the female, there were instances of apparent extrapair young (3/17).

In polygynous trios, the two females could each build their own nest. This was neither observed nor suspected and might not be a viable option if male incubation is essential for successful hatching. Alternatively, the two females may compete for parenthood by both laying in the same nest. This probably led to the large clutches described for nests 3 and H.

While Henderson Reed-Warblers may be unusual in forming breeding groups of unrelated birds, we suggest their propensity to form groups is a direct consequence of the island's stable habitat, a climax forest in a geographical region where annual temperature and rainfall variation is not high (Spencer 1995). In that sense, therefore, the reed-warblers fit the paradigm that relates group living to a stable, saturated habitat (Emlen 1982). On Pitcairn Island, an inhabited island 200 km from uninhabited Henderson Island, the closely-related Pitcairn Reed-Warbler lives. Our casual observations on Pitcairn suggested that the reed-warblers there bred only in pairs. This possible behavioral difference might be related to the greater anthropogenic disturbance and consequent year-to-year instability of the habitat on Pitcairn, at least if that instability were associated with greater territorial flux and a reduction in the relative advantage of trio membership during territory acquisition.

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