Using these assumptions, the best least-squares fit to the data is obtained for $\sim$45% of lithospheric extension (Fig. 2*b*), and leads to a relative variation in P_n velocity of $\sim$4%, which is similar to the observed anisotropy. As discussed earlier, the curve in Fig. 2*b* provides only minimum estimates of the anisotropy of P_n velocity and lithospheric extension because of the uneven distribution of data. It follows that, besides the alignment of the fast direction of seismic velocity with the direction of present-day extension, the magnitude of the extension measured from the observed anisotropy ($\sim$45%) is within the range of the amount of Cenozoic extension measured from surface geology[24,25]. These observations favour the interpretation that the observed anisotropy is due to Cenozoic extension of the lithosphere rather than to the cumulative signature of the earlier tectonic phases. Thus, only a few million years have been sufficient to reset the old lattice preferred orientation of the mantle-lid minerals and record the signature of the present tectonic regime. Clearly, many simplifying assumptions have been made to reach this conclusion and it may therefore not be unique. Our observations strongly suggest, however, that the pervasive surface rifting of the Basin and Range is not only a crustal process but also affects mantle-lid deformation. ☐

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Shared paternity revealed by genetic analysis in cooperatively breeding tropical wrens

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POSTPONEMENT of dispersal and breeding to assist in rearing others' young may be favoured if helpers' contributions to the production of close kin exceed their likely reproductive success had they dispersed[1,2]. Young adult stripe-backed wrens (*Campylorhynchus nuchalis*) remain in natal groups and greatly enhance reproductive success of close kin. Long-term behavioural observations suggest that only the dominant male and female in a group breed[3]; however, extra-pair parentage has been confirmed biochemically in apparently monogamous birds[4,5], including some social species[6,7]. DNA fingerprinting of wren groups shows that behaviourally dominant males sometimes share paternity with auxiliary males previously thought to be nonreproductive, whereas dominants are the only reproductives among females. Reproduction by auxiliary males (but not females) helps explain the long tenure of males in helper status and the contrasting combativeness of females in competition for breeding positions outside the natal group[8,9], but reproduction by auxiliaries cannot alone explain helping behaviour.

We analysed parentage for 69 offspring produced by 22 social groups. Blood was collected from 260 birds in 1988–89; 110 constituted complete breeding-season membership of 17 social groups that reproduced during those years and 28 additional samples provided tests for 5 other groups in previous years. Histories of group membership and behavioural status were available for the previous 4–12 years.

For each group, genomic blots of *Hae*III and separate *Hin*fI digests were hybridized with Jeffreys' probes 33.6 and 33.15 (ref. 10). *Alu*I blots were also analysed for large families. Five scorers located bands exclusive to each adult on autoradiographs and recorded their presence in offspring lanes. For 53 of 68 offspring, 1 adult female and 1 adult male in the group provided a minimum of 2 exclusive bands (range 2–18, mean 5.9±3.4 for *Hae*III blots with both probes) and the entire offspring banding pattern could be derived only from those two adults. Then, two of us tallied the number of bands for each offspring that were unattributable to each adult combination of potential parents[5] (intragroup) (Fig. 1). The parents assigned by minimizing unattributable bands in no case contradicted parents assigned by matching exclusive adult bands. The second technique was important for large families with several closely related potential breeders (brothers accumulate because of high natal philopatry in males; Fig. 2) and allowed assignment of parentage for all but one

TABLE 1 Parentage in stripe-backed wrens

Group composition	No. group-years	No. Young	Parentage		
			PM-PF	PF-AM	Outside
2 PRINS only	5	10	9	NA	1
2 PRINS + AM	10	23	19	4	0
2 PRINS + AF	1	2	2	NA	0
2 PRINS + AM and AF	18	34	32	2	0
Totals	34	69	62	6	1

Groups are composed of principal males (PM), principal females (PF) (PRINS for both), auxiliary males (AM) and auxiliary females (AF).

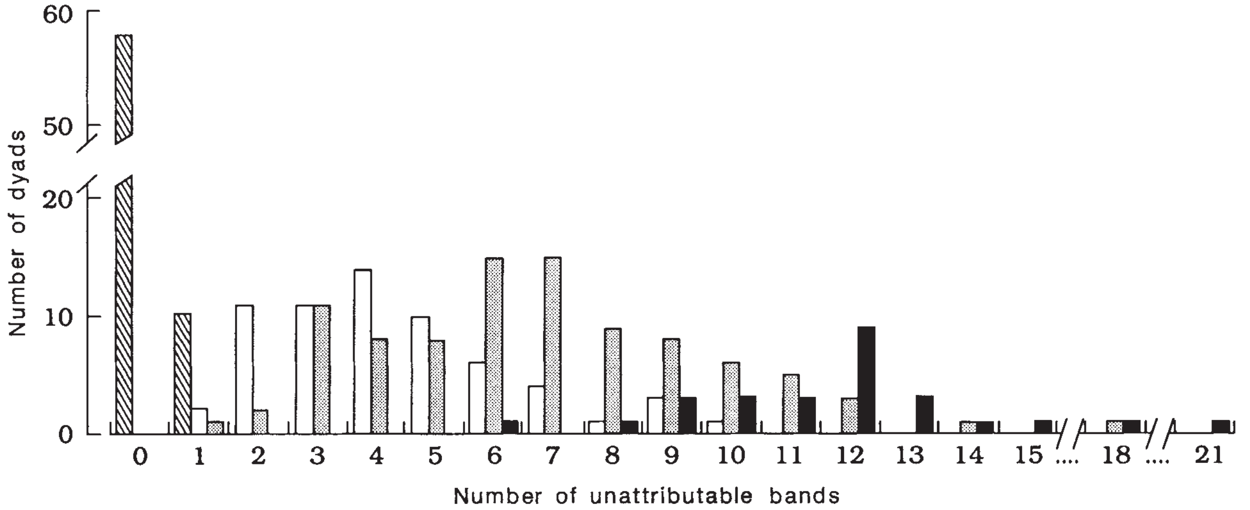

FIG. 1 Distribution of unattributable bands produced by considering every possible adult male–female dyad within groups as potential parents of each offspring, summing across probes 33.6 and 33.15 (ref. 10) with *Hae*III. Assigned parents (hatched bars) produce an average of 0.15 ± 0.36 unattributable bands in juveniles ($n = 68$); combinations of first-order relatives (open bars) excluding parental dyads (for example, mother–brother or brother–sister pairs) produce 4.9 ± 4.0 unattributable bands ($n = 64$); first-order relatives with lesser relatives (for example, sister–uncle pairs) (stippled bars) produce 7.4 ± 6.9 ($n = 92$); and dyads of less than first-order relatives (for example, uncle–immigrant pairs) (solid bars) produce 11.8 ± 3.3 ($n = 22$). Even combinations of first-order relatives are usually distinct from best-fit dyads. Among the 68 offspring with assigned parents, 58 had banding patterns entirely and uniquely derivable from the parental banding patterns. Ten offspring had one novel band unattributable to either assigned parent; we consider these novel fragments mutations. Occasional unattributable bands in offspring are expected because of high mutation rates in these hypervariable regions of the genome[10], between 0.003 and 0.05 mutations per locus per generation for humans[12] and 0.0035 for house sparrows[13]. We calculate the mutation rate for stripe-backed wrens, based on the occurrence of 10 novel bands in 68 offspring, each of which had on average 54.4 bands across both probes on *Hae*III blots, as (10/68)/54.4 or 0.0027 mutations per locus per generation. The distribution of the best fit (parental assignments) category does not differ from random expectation (Poisson) ($G = 1.394$, $p > 0.5$). The expected frequency of individuals showing two or more unattributable bands derived from the actual parents is 0.0098. With a probability of <0.01 that actual parents would produce two or more unattributable bands, we call any adult combinations producing two or more unattributable bands in offspring a misassignment.

juvenile (Fig. 3*b*).

Of the 69 young produced in 34 group-years, 62 (90%) were offspring of the principal male and principal female of their group, and 6 were offspring of the principal female and an auxiliary male. In no case was an auxiliary female identified as the parent of a juvenile and in only one case was extra-group parentage suggested (Table 1). The 4 reproductive auxiliary males were found in 4 of the 13 groups in which an auxiliary male helped a brother or father and an unrelated principal female who had immigrated during the auxiliary's lifetime. Parentage in three of these four groups was obvious on the basis of matching exclusive adult bands (Fig. 3*a*). Assignment in the fourth group (Fig. 2) relied on analysis of unattributable bands. In all four groups, paternity was shared with the principal male: 1/2, 2/4, 1/2 and 2/3 juveniles were sired by the auxiliary.

The opportunity for older subordinate males to breed helps to explain the long tenure of auxiliary males in queues for dominant status in their natal groups. Overt challenges to principals are rare, although recent behavioural observations show increased conflict among males in groups with immigrant breeding females (W.H.P., unpublished data). We had previously thought that the genetic benefits of helping behaviour were both indirect (the production of siblings) and direct but delayed

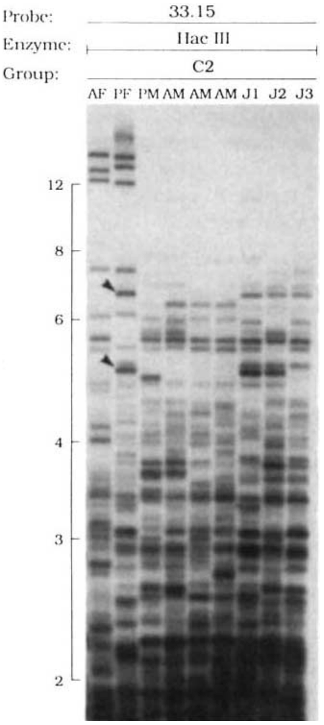

FIG. 2 DNA fingerprints from a large group consisting of two adult females (sexed behaviourally as well as by the presence of female-specific bands above 12 kb; ref. 14), the principal male and three of his male offspring by a previous principal female. The mother is easily assigned to all three juveniles by band-matching; arrows indicate bands important in this assignment. Paternity was tested by pairing the mother with each male in turn and counting the number of unattributable bands produced by each combination for each offspring. For offspring 1 with this probe-enzyme combination, the female in lane 2 (the mother) paired with males in lanes 3, 4, 5 and 6, produced 2, 0, 4 and 5 unattributable bands, respectively. For offspring number 2, the same combinations produced 0, 1, 5 and 6 unattributable bands, and for the third offspring, 2, 0, 7 and 6. The same scoring technique applied to the other five probe-enzyme combinations (using *Hin*f1 and *Alu*I) produced similar results. Using 33.6 with *Hae*III resolved parentage of offspring 2 and using *Alu*I with 33.6 clearly revealed the parentage of offspring 3. The male in lane 4 sired the first and third offspring, whereas the male in lane 3 sired the second. DNA sizes (kb), on the left-hand side.

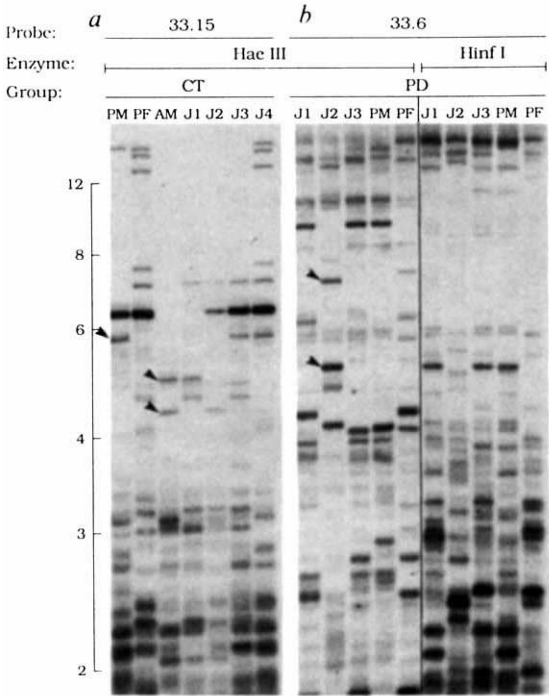

FIG. 3 DNA fingerprints from two groups of stripe-backed wrens. *a*, (Group CT): The principal male (PM) and principal female (PF) were identified as parents of juveniles 3 and 4, whereas juveniles 1 and 2 were offspring of the auxiliary male (AM) and principal female. Arrows indicate obvious exclusive adult bands confirming this assignment. *b*, (Group PD): Juvenile 2 is the only juvenile of 69 examined not closely related to the rest of its group. Arrows indicate obvious nonmatching bands. Assignment of parents for this juvenile has not been possible among adults in the 10 neighbouring groups. Extra-group parentage is possible, as are juvenile adoption (previously recorded in this population) or accidental capture of a wandering juvenile. DNA sizes (kb), on the left-hand side.

METHODS. Blood samples, stored in phosphate-buffered saline, were incubated overnight at 55 °C after adding SDS to 0.8% and 200 μg Proteinase K, extracted several times in phenol/phenol:chloroform:isoamyl alcohol, then dialysed against TNE_2. DNA (5 μg) were digested with excess restriction endonuclease at 37 °C. Resulting fragments were separated through a 0.8% agarose gel (22 cm) at 20 V for 65 h until all fragments smaller than 1,600 base pairs (bp) were run off, and then transferred to nylon by Southern blot in 10 × SSC buffer. The probes were radiolabelled by primer extension with $[^{32}P]dGTP$. Hybridizations were run overnight at 62 °C in 1.5 × SSC, 0.1% SDS, 5 × Denhardt's solution, and 6% w/v polyethylene glycol. Hybridized filters were washed 4 × 30 min at 62 °C in 1.5 × SSC, 0.1% SDS, and exposed to x-ray film at −80 °C. Using *Hae*III with probe 33.15, a mean (f) of 24 scorable bands were produced per lane, 30 with 33.6. The proportion of bands shared (x, calculated as $2e/(2e+a+b)$ where e is the number of fragments of equal mobility and intensity in each pair of adjacent lanes, a is the number of fragments distinct to one of the pair, b the number distinct to the other) among a sample of 24 birds related at a level less than cousins (based on long-term pedigrees assuming monogamy) was 0.27 using 33.15, and 0.26 using 33.6. Assuming independent segregation, the mean population allele frequency (q), where $x=2q-q^2$, is 0.15 for 33.15 and 0.14 for 33.6 with *Hae*III. The expected proportion of bands shared between siblings $(s)=(4+5q-6q^2+q^3)/4(2-q)$ or 0.62 for the wrens[15]. In groups containing two adult brothers, the probability of misassigning the uncle as the father (P_u) is s^c, the likelihood that the uncle and father share all exclusively paternal bands c, where $c=(f)[1-(1+q-q^2)/(2-q)]$. For *Hae*III with 33.15, $c=9.3$ and $c=12.2$ with 33.6, so $P_u=0.62^{9.3}$ or 0.012 for 33.15, and 0.003 for 33.6. Using both combinations, the probability that the uncle would share all exclusively paternal bands in an offspring with the actual father is 0.00004. But, there are often more than two first-order male relatives as potential fathers in a group. The likelihood that an offspring band could be attributed to only one adult male in a group with n first-order male relatives (assuming the true father is included) is $(1-s)^{n-1}$. For wren groups with four first-order male relatives, a paternal band in an offspring lane could be assigned with certainty to a single male with a frequency of 0.055. With $c=21.5$ for both probes, only one exclusive band should match any particular male with an offspring in such a group. Matrices of unattributable bands for each combination of potential parents provide much greater resolution, as mother-uncle dyads should produce $c(1-s)$ or 8.2 unattributable bands on average.

(improved future fecundity because of the production of young to reciprocate as helpers when the current auxiliary male becomes a principal in that group)[3]. We have now demonstrated that immediate direct benefits can also accrue. The tendency for older auxiliary males to contribute more to feeding young[3] can now be interpreted as a reflection of increasing probability of parenthood, rather than just as investment in future helpers.

Our previous estimate of the indirect component of fitness has been revised downward. If, as in our sample, auxiliary males sire 10% of the offspring in the population, each can expect to sire an average of 0.08 young per yr (demographic data for 1986–1989, $n=212$ auxiliary male-yrs). In the subset of groups in which principal females are recent immigrants, auxiliary males sire on average 0.24 young yr^{-1}. The alternative of attempting breeding outside the natal group (unaided pairs are the only option for dispersing males) yields on average 0.26 young yr^{-1} (1986–1989 data, $n=91$ male-yrs). We have previously shown that indirect contributions to genetic representation by increasing sibling production are considerably higher: 0.64 siblings yr^{-1} (ref. 3). For auxiliary males helping unrelated principal females, we now estimate the indirect component of this enhancement as (0.64 (total) − 0.24 (direct)) devalued by half because the remainder are half-siblings, or 0.20 offspring equivalents. Combined preliminary estimates for immediate direct and indirect benefits accruing to such male auxiliaries then yield 0.44 offspring equivalents per yr (full accounting will include delayed effects). Neither the chance of breeding in auxiliary status nor sibling production would be sufficient, even for this subset of auxiliary males, to favour staying in auxiliary status compared to dispersing to attempt breeding; however, these two factors in combination are sufficient to compensate deferred dispersal.

Auxiliary females, unlike males, were never observed to reproduce and apparently derive no direct fitness benefit from helping. The absence of breeding alternatives for females helps explain their investment in fighting over principal positions in non-natal groups with many helpers[9]; they are competing for an opportunity that is valuable in part because it can be monopolized[11]. The window on genetic relatedness provided by DNA technology allows us to see more clearly the divergence between the sexes, and the importance of ontogeny, in dispersal tendencies and routes to biological fitness. ☐

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