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## Confirmation of cooperative polyandry in the Galapagos hawk (*Buteo galapagoensis*)

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**Abstract** Without genetic tests of parentage, descriptions of mating systems must be considered hypothetical. Here we confirm the existence of cooperative polyandry in the Galapagos hawk (*Buteo galapagoensis*) using multilocus minisatellite DNA fingerprinting. In this species, breeding groups consist of one adult female and from one to eight males (the modal number of males is two). In polyandrous groups, all males copulate with the female and participate in the provisioning of the young. DNA samples from 66 individual hawks from ten breeding groups on the island of Santiago revealed mixed paternity in most groups. Multiple paternity was detected in five of six groups that produced two chicks in one breeding attempt (year). In addition, different males sired young in consecutive years in five of six groups in which male group membership was constant. Patterns of paternity suggest that reproductive success was randomly distributed among males within groups, with males apparently having equivalent probabilities of siring each young. Analysis of genetic similarity indicates that males within groups were typically not close relatives. These results demonstrate that the mating system of the Galapagos hawk is polyandrous, with relatively egalitarian relations among unrelated males belonging to the same breeding group.

**Key words** DNA fingerprinting · *Buteo galapagoensis* Paternity · Polyandry · Reproductive success

### Introduction

The mating system of the Galapagos hawk (*Buteo galapagoensis*) has been described as cooperative polyandry (Faaborg and Patterson 1982; Oring 1982). Social groups typically contain one adult female and two or three adult males, though groups with as many as eight males have been observed. Membership of such groups is relatively stable from year to year (Faaborg 1986), and all males within a group are known to deliver food to the nest and to copulate with the female. However, a more adequate description of the breeding system awaits a genetic analysis of paternity to determine whether multiple males sire young within a group and how any such mixed paternity is divided among group members.

Any interpretation of the selective forces maintaining this social organization (and apparent mating system) depends upon whether males belonging to the same group are typically genetic relatives. If they are typically related, group membership may confer an indirect fitness advantage upon nonreproductive males (Hamilton 1964), and we might expect our paternity analysis to reveal that Galapagos hawks actually have a typical cooperative breeding system, with an alpha breeding male and one or more nonbreeding helpers. However, if groups contain unrelated males, no indirect fitness gain would accrue to nonreproductive males, and paternity may be relatively evenly shared among males within groups (cf. Packer et al. 1991).

Here we use multilocus minisatellite DNA fingerprinting (Jeffreys et al. 1985a,b) to ask whether Galapagos hawk males within social groups tended to be related and whether multiple paternity occurred within groups, both within and between two consecutive breeding seasons (years). We also evaluated whether reproductive success was randomly distributed among

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males in a group, versus whether it was more evenly shared than expected on the basis of chance or whether processes such as sperm competition or behavioral dominance might have biased paternity in favor of some males.

## Methods

### Genetic analysis

#### Field methods

From one to three 50- $\mu$ l blood samples were taken by venipuncture of the brachial vein of each bird captured. Samples were put immediately into lysis buffer (100 mmol TRIS, pH 8.0, 100 mmol EDTA, 10 mmol NaCl, 0.5% SDS; Longmire et al. 1988) containing 0.2% sodium azide, shaken, and stored indefinitely at ambient temperature.

#### DNA extraction

DNA extraction began with addition of proteinase K (200  $\mu$ g) followed by incubation at 55 °C overnight. Subsequently, two extractions with phenol, two extractions with 25:24:1 phenol:chloroform:isoamyl alcohol, and one extraction with 24:1 chloroform:isoamyl alcohol were performed. Following the last extraction, the aqueous phase was dialyzed extensively against TNE<sub>2</sub> (10 mmol Tris, pH 7.4; 10 mmol NaCl; 2 mmol EDTA). Concentration and purity of extracted DNAs were assessed by spectrophotometry.

#### Digests, hybridizations and autoradiography

Three micrograms DNA from each individual were digested with  $\times 5$  excess restriction endonuclease (*Hae*III) at 37 °C for 3–5 h. 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) had been run off the gel], and were then transferred to nylon by Southern blot in  $\times 10$  SSC (3 M NaCl, 1 M C<sub>6</sub>H<sub>5</sub>Na<sub>3</sub>O<sub>7</sub>) buffer and fixed to the membrane by UV crosslinking. Jeffreys' multilocus minisatellite probes 33.15 and 33.6 (Jeffreys et al. 1985a,b) were radiolabelled by primer extension with [<sup>32</sup>P]dCTP. Hybridizations were run overnight at 62 °C in  $\times 1.5$  SSC, 0.1% SDS,  $\times 5$  Denhardt's solution, and 6% w/v dextran sulfate. Hybridized filters were washed for 4  $\times$  30 min at 62 °C in  $\times 1.5$  SSC, 0.1% SDS, and exposed to X-ray film at –20 °C for at least 24 h (see Fig. 1 for sample autoradiograph).

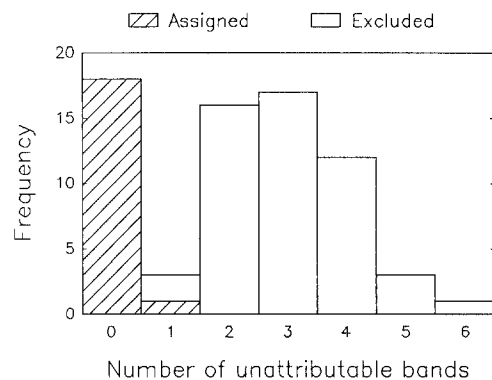
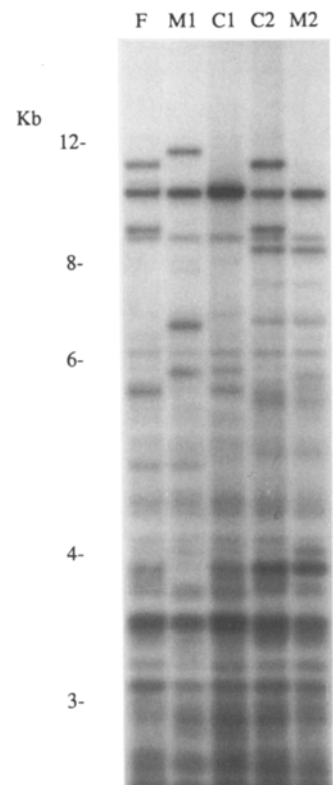
### Interpretation of autoradiographs

#### Unattributable band analysis

Within each social group, the resident female was paired with each adult male group member for consideration as the putative parents of each chick. The number of fragments present in an offspring's lane but not in either the male's lane or the female's lane was recorded as the number of "unattributable bands" (Rabenold et al. 1990). Except for rare novel bands (mutations producing alleles of new length; Jeffreys et al. 1988), banding patterns of offspring should be entirely attributable to the combination of banding patterns of their parents. Nonparental dyads should not account for all bands in an offspring's lane, provided sufficient variation is assayed.

The distribution of unattributable bands (Fig. 2) allows calculation of the rate of mutation (i.e., the rate of appearance of bands unattributable to parental dyads; Jeffreys et al. 1988; Westneat et al. 1990; Rabenold et al. 1990) and calculation of a criterion number of unattributable bands for exclusion of a dyad as parental.

**Fig. 1** DNA fingerprints of a Galapagos hawk social group consisting of one adult female (*F*), two adult males (*M1* and *M2*), and the two chicks they produced (*C1* and *C2*). *M1* was assigned as the father of *C1* and *M2* as the father of *C2*. This autoradiograph represents a genomic *Hae*III blot hybridized with Jeffreys' multilocus probe 33.6



**Fig. 2** Frequency distribution of the number of bands, in fingerprints of 19 Galapagos hawk offspring, that could not be accounted for by the mother's fingerprint combined with that of either the male that was assigned as the father (*open bars*) or with a male that was not assigned (i.e., was excluded; *shaded bars*) as the father. Unattributable bands were summed across probes (Jeffreys' 33.15 and 33.6)

Assuming mutations occurred randomly across nestlings and loci, the Poisson probability was 0.0012 that the combined fingerprints of the two genetic parents would fail to account for two or more bands in a nestling's fingerprint. (The mean occurrence of novel bands per chick was taken as the expected proportion and was calculated as one novel band among "best fit" dyads/19 young for which there was only one best fit, or 0.05.) Scoring across both probes and adding unattributable bands, 18 nestlings were found to match with single male-female dyads that produced no unattributable bands; all other male-female dyads produced one or more such bands. For one chick, the best fit parental dyad produced one unattributable band; all other male-female dyads in

the group resulted in two or more such bands. The smallest number of unattributable bands found for each of two other nestlings was two, but in each case one adult male group member had not been sampled. Finally, the father of one nestling could not be identified because three dyads produced zero unattributable bands.

#### *Band-sharing analysis*

To corroborate preliminary assignments made on the basis of unattributable bands, we calculated the proportion of bands shared by each pair of individuals within each group. This measure of genetic similarity (band-sharing score) was calculated as  $2S/(2S + A + B)$ , where  $S$  = the number of fragments of indistinguishable mobility and intensity in the two lanes under comparison,  $A$  = the number of bands unique to one member of the dyad, and  $B$  = the number of bands unique to the other member of the dyad (Wetton et al. 1987; Lynch 1990). We asked whether the distribution of mother-offspring band-sharing values was significantly different from the distribution of father-offspring values (it should not be if fathers have been correctly identified), and whether the father-offspring values were different from the distribution of band-sharing values representing dyads consisting of excluded males and young (father-offspring values should be higher than excluded male-young values if fathers have been correctly identified).

We used Mantel tests (Mantel 1967) to test for differences in location between sample distributions of band-sharing scores representing distinct inferential populations. Unlike conventional analyses which assume that data are independent, the Mantel test accounts for the interdependent nature of matrix data, where individuals are represented multiple times in pairwise permutations (Schnell et al. 1985). To perform these tests, we compared two symmetric similarity matrices, a matrix of band-sharing scores and a corresponding "hypothesis matrix" in which we designated one of the categories (inferential populations) with one numeral and the other category with another numeral (Schnell et al. 1985). We used a permutational analysis to assess the significance of the Mantel test result. This analysis was accomplished by randomly permuting the order of elements of one of the matrices, while holding constant the order of elements of the other matrix, and performing a Mantel test for each such permutation. The significance level was thus assessed by comparing the observed Mantel  $t$ -value with its permutational distribution (based on 1000 random permutations; Rohlf 1990). Nominal  $P$  values are reported. (Note that for those sample distributions that were used in two tests, Bonferroni-adjusted  $P$  values would be obtained by doubling the nominal  $P$  value).

To evaluate whether any of the dyads of males belonging to the same breeding group might have comprised close relatives, we assumed that the sample distribution of band-sharing scores for dyads of males belonging to different breeding groups was an accurate representation of genetic similarity between unrelated males. We then used the cumulative normal distribution function to obtain the probability associated with a single outlying band-sharing score from the within-group sample.

#### *Estimation of probability of assignment errors*

Using the results from band-sharing analyses, we computed probabilities of misassigning individuals as parents. We thus calculated the probability that a male other than the actual father could account for all of the exclusively paternal bands or that a female other than the actual mother could have provided all of the exclusively maternal bands. These calculations assume that bands assort in an independent fashion (i.e., they are neither linked nor allelic). Such probabilities were calculated for both unrelated individuals and first-order relatives.

#### *Calculation of expected parentage patterns*

We calculated the probability of two chicks in the same brood having the same father as  $1/n$ , where  $n$  = the number of adult males in the group, assuming all males have the same probability of fertilizing each egg. Therefore, the probability of the two chicks having different fathers is  $1-1/n$ , or  $(n-1)/n$ . For more than two chicks, as when the same social group breeds successfully in 2 years, the probability of  $y$  chicks having the same father is  $n^{-(y-1)}$ . In a preliminary attempt at evaluating whether reproductive success was biased in favor of some males, we compared these expectations of single versus multiple paternity to our findings. In addition, because mixed paternity was actually more common than expected under the assumption that reproductive success was randomly distributed among males within a group, we calculated the cumulative binomial probability of observing so few cases of unshared paternity.

## Results

### Samples used

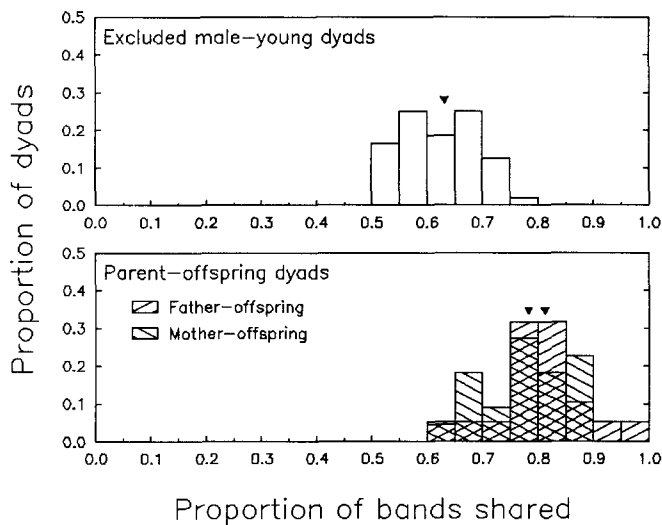
DNA was extracted from blood samples from 73 individual Galapagos hawks representing 12 social groups. Ten of the groups reside on Santiago Island and two on Santa Fe. Of the three chicks produced on Santa Fe in 2 years, paternity could be determined for only one chick; the other two chicks belonged to a group in which two adult males could not be distinguished genetically. Because of these complications, and to remove any other between-island differences, we include in this analysis only the hawks from Santiago ( $n = 64$  hawks in ten social groups). Eight of the ten Santiago groups were sampled in both 1990 and 1991, and the two remaining groups were first monitored in 1991. Nine groups produced at least two young during the 2 years combined. Each group contained one adult female and no female replacements occurred in the eight groups monitored for 2 years. The groups contained from two to eight adult males, for a total of 31 (blood samples collected from 29), and produced one or two chicks per year, for a total of 25 chicks. Three DNA samples from chicks were of such low concentration that a proper analysis could not be performed. The remaining 22 chicks from ten social groups formed the foundation of our assessment of patterns of parentage (Table 1).

### Determination of parentage

For 19 chicks, we were able to exclude all adult male group members except one. The dyads comprising the assigned father and the female accounted for all ( $n = 18$ ) or all but one ( $n = 1$ ) of the chick's bands, while all other female-male dyads within the group produced more attributable bands (Fig. 2). To corroborate these assignments, we compared the band-sharing values for assigned father-young dyads to those of mother-young dyads and to dyads consisting of excluded males and young (Fig. 3). The sample distribution of band-sharing scores representing mother-offspring dyads

**Table 1** Assignments of paternity within Galapagos hawk breeding groups. Males are identified by their band numbers

Group	Year	No. of males	No. of young	Fathers
B3	1990	8	2	B165, B164
	1991	8	2	B164, B163 or B156; B157
B4	1990	2	2	B338, B333
	1991	2	2	B333, B333
S1	1990	2	1	B078
	1991	3	1	B078
S2	1990	2	1	B152
S3	1990	2	1	B079
	1991	2	1	B059
S4	1991	3	2	B107, B105
S5	1991	2	1	B108
T1	1990	2	1	Not B166
T2	1990	2	1	A028
	1991	2	2	A028, D007
T3	1990	4	1	B161
	1991	3	1	Not B161 or B081



**Fig. 3** Distributions of band-sharing scores (proportions of bands shared) for dyads of Galapagos hawks taken from *HaeIII* digests hybridized with Jeffreys' probe 33.15. Each dyad consists of a nestling and an adult male excluded as that individual's father (*top panel*;  $n = 48$ ), and either an assigned father and his offspring ( $n = 19$ ) or a mother and one of her offspring ( $n = 22$ ; *bottom panel*). Triangles indicate means (*bottom panel*: father-offspring mean = 0.81, mother-offspring mean = 0.78)

( $\bar{x} = 0.78$ ) did not differ significantly from that representing father-offspring dyads ( $\bar{x} = 0.81$ ,  $P = 0.25$ ). The sample distribution of band-sharing scores representing father-offspring dyads was shifted significantly to the right of that representing dyads consisting of a chick and an adult male excluded as that chick's father ( $\bar{x} = 0.63$ ;  $P = 0.001$ , one-tailed; Fig. 3).

The three remaining chicks (of the 22 included in the analysis) resulted in ambiguous assignments. For two chicks in each of two groups, all adult males sampled were excluded as fathers on the basis of their producing two or more unattributable bands and having low band-sharing values, but in each case one adult male

group member had not been sampled (Table 1). Considering that fathers were found within all completely-sampled groups, the unsampled male may have been the father in both cases. The third chick of ambiguous parentage came from an eight-male group in which we were unable to exclude three of the eight males (each produced zero unattributable bands and band-sharing scores of 0.73, 0.70, and 0.71; Table 1).

#### Parentage: patterns within years

Six two-chick broods were sampled. Parentage was assigned for both chicks in five of these broods. Four (80%) of these broods had shared paternity (Table 1). An additional two-chick brood produced in group B3 in 1991 had one chick for which three males could not be excluded, but those three males did not include the male that sired the other chick in the brood. Thus, five of six broods showed mixed paternity.

#### Parentage: patterns between years

Across groups, eight males who were fathers in 1990 were still present in groups that produced offspring for which parentage was assigned in 1991. Four of these males were fathers in 1991, and three were replaced as fathers by other males (who had also been present in 1990; Table 1). In the case of the unassigned chick in B3, one of the males who had sired young in that group in 1990 was excluded, while the other successful breeder from 1990 remained as one of the three males not excluded as that chick's father. Of the six groups that produced young for which paternity was determined in both years, five showed changes in identity of males siring young.

#### Confidence in assignments

Mean band-sharing scores for dyads of unrelated individuals ( $x$  in Table 2) were used to derive  $q$ , the mean allele frequency across the family of loci screened by the probe. The derived  $q$  allows calculation of the probability of mistakenly identifying individuals as parents (Table 2; Jeffreys et al. 1985a; Georges et al. 1988). We calculated the probability that the fingerprint of an unrelated male could account for all of the exclusively paternal bands ( $p$  in Table 2), since we would assign as parents the members of any dyad whose combined fingerprints accounted for all bands in the chick's fingerprint (see above). This likelihood is equal to the probability that the misassigned male shared any band with the actual father (or  $x$ , the proportion of bands shared by unrelated individuals) raised to the number of paternally derived bands. The final probability of misassigning an unrelated bird is equal to the product of the probabilities produced by Jeffreys' probe 33.15 (0.12)

**Table 2** Summary of the calculation of error rates in assignments of parentage in Galapagos hawk groups, based on multilocus minisatellite DNA fingerprinting using two probes

Symbol	Meaning	Probe		
		33.15	33.6	Both
$x$	Mean proportion bands shared by nonrelatives	0.63	0.74	
$f$	Mean no. bands scored	18.8	19.1	
$q$	Mean allele frequency <sup>a</sup>	0.39	0.49	
$s$	Expected band-sharing between siblings <sup>b</sup>	0.79	0.85	
$o$	Expected parent-offspring band-sharing <sup>c</sup>	0.77	0.83	
$m$	No. maternal bands per chick ( $=fo$ )	14.5	15.9	
$p$	No. exclusively paternal bands ( $=f-m$ )	4.3	3.2	
$P_x$	Probability of misassigning an unrelated individual as parent ( $=x^p$ )	0.12	0.38	0.045
$Pr$	Probability of misassigning a first-order relative as parent ( $=s^p$ )	0.36	0.59	0.21

<sup>a</sup> Where  $x = 2q - q^2$  (Jeffreys et al. 1985a)

<sup>b</sup> Where  $s = [(4 + 5q - 6q^2 + q^3) / 4(2 - q)]$  (Georges et al. 1988)

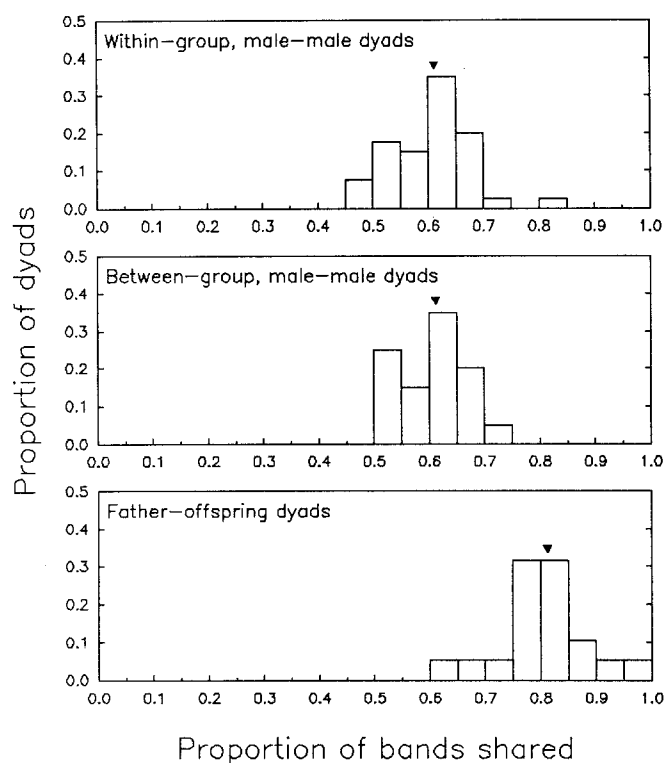
<sup>c</sup> Where  $o = [(1 + q - q^2) / (2 - q)]$  (Georges et al. 1988)

and probe 33.6 (0.38), since the probes detect different minisatellite sequences. The calculated probability (0.045) of misassigning paternity to an unrelated male is likewise the probability of mistakenly assigning an unrelated female as mother.

We also calculated the probability of misassigning as a parent some closely related adult, such as a brother of the actual father. We thus calculated the probability that the fingerprint of an uncle could account for all of the exclusively paternal bands in the fingerprint of his niece or nephew. Stated otherwise, we calculated the probability that the uncle shared any band with the actual father ( $s$ , the expected proportion of bands shared by siblings; Table 2) raised to the number of exclusively paternally derived bands. The calculated rate at which a first-order relative (e.g., brother) of the actual parent would be mistakenly identified as the parent, using both probes 33.15 and 33.6, is 0.21. However, we provide evidence below that males within groups were typically not close relatives.

#### Relatedness among adult males

We asked whether adult male group members appeared to be related by comparing band-sharing values of within-group male dyads to those of both presumably unrelated dyads (males from different groups) and to dyads consisting of assigned fathers and their offspring (Fig. 4). Although there is broad overlap among distributions of unrelated and first-order relatives, the distribution of band-sharing scores for within-group male dyads ( $\bar{x} = 0.61$ ) was statistically indistinguishable from that representing dyads of males belonging to different breeding groups ( $\bar{x} = 0.61$ ;  $P = 0.96$ , Fig. 4). Males belonging to the same group were typically less similar genetically than were fathers and their offspring ( $\bar{x} = 0.81$ ;  $P = 0.002$ , Fig. 4). Likewise, males belonging to different groups were typically less similar genetically than were fathers and their offspring ( $P = 0.001$ , one-tailed; Fig. 4). Overall, males belonging to the same breeding group appeared to be no more closely related than males belonging to different groups. However, one



**Fig. 4** Distributions of band-sharing scores (proportions of bands shared) for dyads of Galapagos hawks. Each dyad consists of two males belonging to the same breeding group (*top panel*;  $n = 40$ ), two males belonging to different breeding groups (*middle panel*;  $n = 20$ ), or an assigned father and one of his offspring (sex unknown; *bottom panel*;  $n = 19$ ). Triangles indicate means

dyad of males belonging to the same group had a band-sharing score (0.84) that fell above the mean father-offspring score (0.81) and fell well above the mean of the sample distribution of band-sharing scores for between-group, male-male dyads (0.61,  $P < 0.001$ , Fig. 4). These results suggest that one of the families (S5) contained two adult males that were close relatives (e.g., brothers or father and son). Otherwise, males did not appear to be associated with kin.

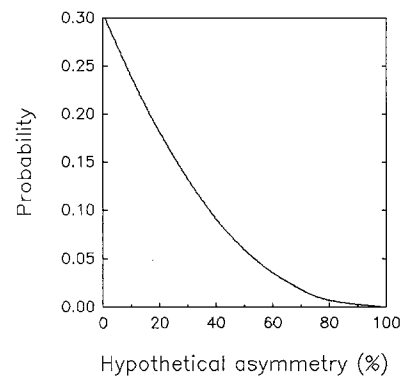
**Table 3** Binomial probabilities of unshared paternity in Galapagos hawk groups given the number of adult males and number of young produced, assuming males within groups have equal probability of siring each young. Whether paternity was unshared and number of assigned fathers are also shown. Groups (from Table 1) with at least two chicks within or between years are included

Group	Year	No. of males	No. of young	Probability same father	Same?	No. of fathers
B3	1990	8	2	0.125	No	2
	1991	8	2	0.125	No	2
	Combined	8	4	0.002	No	3-4
B4	1990	2	2	0.50	No	2
	1991	2	2	0.50	Yes	1
	Combined	2	4	0.125	No	2
S1	Combined	3	2	0.33	Yes	1
S3	Combined	3	2	0.33	No	2
S4	1991	3	2	0.33	No	2
T2	1991	2	2	0.50	No	2
	Combined	2	3	0.25	No	2
T3	Combined	4	2	0.125	No	2

### Evaluation of patterns of mixed paternity

Evidence for a mating system characterized by asymmetrical reproductive success among males of the same group would be provided by a high incidence of unshared paternity. However, among six two-chick broods (Table 3: B3, 1990; B3, 1991; B4, 1990; B4, 1991; S4, 1991; T2, 1991), in only one case (B4, 1991) did the two chicks have the same father. (Probabilities of both young being sired by the same male, calculated for each brood, are presented in Table 3.) This result is superficially suggestive of an egalitarian system in which reproductive success may be more evenly distributed among males than one would expect if every male in a group is assumed to have the same *random* chance of siring each young. To evaluate whether there were significantly fewer cases of unshared paternity (or, equivalently, more cases of mixed paternity) than expected under this assumption, we summed the probability of observing zero cases (the product of the six group-specific probabilities) and the six group-specific probabilities of observing one case [ $P(\leq 1 \text{ case of unshared paternity}) = 0.31$ ]. Similarly, the observation of one case of unshared paternity (S1, 1990 and 1991) among three cases where a group produced one young in each year (S1, S3, and T3) did not differ significantly from expectation ( $P = 0.67$ ). We thus conclude that the incidence of unshared paternity, in a small number of Galapagos hawk groups, was not significantly lower than expected assuming males of the same group are equally likely to sire each young.

Pronounced asymmetries in the reproductive success of males belonging to the same breeding group have been reported for other cooperatively breeding species (e.g., Rabenold et al. 1990). We therefore evaluated the probability of our finding of only one case of unshared paternity (among the six two-chick groups) for a continuum of hypothetical levels of reproductive asymmetry. In this evaluation, the advantage of any asymmetry accrued to one male, and the disadvantage was divided equally among all remaining males. Figure 5 shows a rapid decay in the probability of finding so little unshared paternity as the hypothetical degree of asymmetry increases. Findings like ours would be very unlikely



**Fig. 5** The probability of observing fewer than two cases of unshared paternity among six two-chick Galapagos hawk broods (Table 3: B3, 1990; B3, 1991; B4, 1990; B4, 1991; S4, 1991; T2, 1991) evaluated for a continuum of hypothetical asymmetries in the underlying probability that one male versus all others in the group will sire any given young. To clarify, if the hypothetical asymmetry were 0%, then each male in the group would have the same probability of siring any given young. If the asymmetry were 50%, then the probability for one male in a two-male group would be 0.75 and that for the other male would be 0.25. In an eight-male group, the probability for one male would be  $\sim 0.19$  and that for each of the seven other males would be  $\sim 0.12$

if actual reproductive success were even moderately asymmetrical among males within groups. Our results are thus consistent with the idea that males belonging to the same group had equivalent probabilities of siring any given young.

### Discussion

Our DNA-fingerprinting analysis of paternity in Galapagos hawks revealed extensive mixed paternity both within broods and across broods produced by the same group during consecutive years (Tables 1 and 3). In fact, only two cases of unshared paternity were found (Table 3). One of these involved a male within a two-male group who fathered two chicks in 1991 (B4). The other involved a male who fathered a single young in 1990 (when he was a member of a two-male group) and an-

other young in 1991 (when the group contained a third adult male).

This extensive "paternity-sharing" among Galapagos hawk males belonging to the same group was statistically consistent with the idea that paternity is randomly distributed among males within groups, with males apparently having equivalent probabilities of siring each young. In fact, the proportion of broods multiply sired (one of six) was actually less than the outcome expected to occur most commonly (two of six), assuming randomness. The finding of only one case of unshared paternity would be significantly less than expected if we were to assume that one male had even a relatively minor advantage over the others (Fig. 5). [A pronounced asymmetry in male reproductive success has been found in other cooperatively breeding birds (e.g., Rabenold et al. 1990).] Our results are thus consistent with behavioral observations that indicate little or no dominance structuring or mating advantage among male group members (L. DeLay et al; unpubl.), and in fact they prompt the speculation that paternity may actually be more evenly shared than expected under the assumption that each male in a group has the same *random* chance of siring each young.

Galapagos hawks usually fledge only one young per year. That individual disperses from its natal territory and joins flocks of nonbreeding birds until it is mature and able to establish itself in a breeding group. Thus, it is unlikely that adult males in a breeding group are relatives, as this would typically require their associating with kin with whom they have had no prior experience (Faaborg et al. 1980; Faaborg 1986). Our fingerprinting data support this supposition, as males belonging to the same group were not significantly more genetically similar than were males belonging to different groups but were significantly less similar to one another than were fathers and sons (Fig. 4). If groups are formed by wandering males who coalesce to establish new territories, related males could end up together in a group just by chance, but we would expect this to be uncommon. In our study, such an association between two closely related males might have occurred once (see top panel, Fig. 4).

The maintenance of cooperative polyandry in Galapagos hawks, therefore, cannot be ascribed to inclusive fitness gains resulting from interactions among kin (Hamilton 1964). Instead, this system appears to meet the conditions necessary for stable cooperation among unrelated individuals (e.g., Axelrod and Hamilton 1981; Lima 1989). Males remain in the same group year after year, and thus have repeated pairwise interactions and undoubtedly recognize one another. Given these long-term associations among males and considering our current findings, it will be of interest in future work to ask whether males actually share paternity more equally than expected under the assumption of randomly distributed reproductive success. Clarification of mechanisms that might promote such egalitarian paternity-sharing would also be of interest. One possibility is that

males alternate their copulations with the female, a schedule the female might control.

Any form of cooperation promoting little variation in male reproductive success might not be stable in groups that contain too many males. For one group, the unusually large eight-male group (B3), we have counted copulations by each male. The male that copulated the most times and the male that copulated the fewest times each sired one offspring in 1990 (L. DeLay et al., unpubl.). The male who copulated most in 1990 was not excluded as the father of one of the 1991 offspring, though this is the case where two other males also were not excluded, and the second 1991 offspring was sired by yet another male. Thus, we found that three males sired the four young produced by that group, despite the unusually high frequency of aggressive interactions among males and corresponding (minor) variation among males in copulation frequency. Virtually no dominance behavior was observed among males belonging to smaller groups, particularly two-male groups, and anecdotal observations suggest that copulations were approximately equally divided among males in these groups.

Although our results substantiate earlier reports describing the mating system of Galapagos hawks as a form of cooperative polyandry, larger samples over multiple years will be needed to determine whether paternity-sharing is truly egalitarian or whether subtle biases in male reproductive success exist. We have seen virtually no evidence of dominance interactions (including mate-guarding) in groups of the most common size; therefore, if such variation in male reproductive success is revealed by future work, sperm competition (Birkhead 1987; Birkhead and Moller 1992), including variation in male fertility, would be a plausible contributing mechanism. Future monitoring of both reproductive success and group reproductive behavior should allow us to better characterize the details of this interesting mating system.

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