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Reproduction by subordinates in cooperatively breeding Arabian babblers is uncommon but predictable

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Abstract In a genetic analysis of the mating system of cooperatively breeding Arabian babblers (Timalidae: *Turdoides squamiceps*), we identified which individuals in the population are breeding, and how reproductive success was distributed among group members with respect to their dominance rank, for both males and females. The population was characterized by an asymmetrical distribution of reproductive success; behaviorally dominant males produced 176 of 186 (95%) of the offspring in 44 social groups analyzed, and alpha females produced 185 of 186 (99.5%). We evaluated models of reproductive skew by examining genetic and demographic correlates of reproduction by subordinates. Subordinate (beta) males that sired young were more likely to be recent dispersers from their natal groups or members of newly formed groups than betas that did not reproduce. Breeding beta males had spent smaller proportions of their lives with the current alpha male and female as alphas than had beta males that did not sire young. One consequence of the linkage of dispersal with breeding in newly formed, nonnatal groups is that beta males that sired young had significantly lower genetic similarity to the alpha males in their groups (based on band-sharing coefficients using multilocus minisatellite DNA fingerprinting) than those that did not sire young. This pattern may occur generally in species in which group membership accrues both through nondispersal of young (forming groups of relatives) as well as through dispersal involving coalitions that sometimes include nonrelatives.

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Introduction

Cooperative breeding has been described for at least 220 species of birds (Stacey and Koenig 1990), and many species of invertebrates (Hamilton 1964; West-Eberhard 1975) and mammals (Moehlman 1979; Rood 1980; Owens and Owens 1984). In addition to the possible benefits of sociality and cooperation, there is usually some competition and conflict among members of social groups (Alexander 1974). One way in which competition occurs is over access to breeding opportunities, resulting in variable distributions of reproductive success among members of social groups of different societies (Vehrencamp 1983; Keller and Reeve 1994; Emlen 1982, 1995). Vehrencamp (1983) and Emlen (1982) defined conditions under which reproduction among members of a cooperatively breeding group should be biased in favor of dominant group members, or divided approximately equally among group members. Conflicts between dominant individuals and subordinates over reproductive opportunities will be resolved according to the opportunities available to the subordinate if it leaves, the benefits to the dominant of maintaining current group size, and their relative fighting abilities (Vehrencamp 1983; Keller and Reeve 1994; Emlen 1982, 1995).

Genetic relatedness between group members should also influence the resolution of this conflict. As genetic relatedness between dominant and subordinate individuals increases, so should reproductive bias favoring dominants (Vehrencamp 1983; Keller and Reeve 1994; Emlen 1982, 1995). This skew can be explained by the subordinate's increased tolerance of manipulation by the dominant due to the high indirect fitness benefit of rearing kin (Vehrencamp 1983; Keller and Reeve 1994). As the fitness value of staying increases, it is less likely that this value will be exceeded by the benefits of leaving.

In the current study, we used multilocus minisatellite DNA fingerprinting (Jeffreys et al. 1985) to describe the mating system of cooperatively breeding Arabian babblers (*Turdoides squamiceps*) by identifying the breeding individuals in the population and describing the distribution of reproduction by members of social groups according to dominance rank for both sexes. We compare the reproductive success of participants in groups consisting of apparent nuclear families to that of individuals in more complex groups containing more than one possible pair of unrelated adults. In addition, we investigate whether any variation exists among groups in the monopolization of reproductive success by dominant individuals, and whether this variation is correlated with relatedness between dominants and subordinates or with other demographic patterns.

Methods

Study population

The study population is part of a marked population undergoing long-term investigation, located at Hatzeva, Israel, approximately 30 km south of the Dead Sea. Social groups maintain year-round territories in the desert and nest along dry river beds (for a complete description of the habitat and social structure see Zahavi 1989, 1990; a brief description follows). Territories are frequently occupied by the same groups for many years, and offspring may remain as auxiliaries on the natal territory for as many as 5 years before dispersing. Dispersal is sex biased: females, on average, disperse farther, while males may attain breeding status within their natal territory or on an adjacent territory. Females lay three to five eggs in a single nest within the group territory, and a group may produce from one to three, or rarely four, broods in one breeding season.

Social groups consist of 2–20 individuals and are variable in composition. Most groups in the study population are simple groups (Zahavi 1989), apparent nuclear families composed of one presumed unrelated male-female pair with retained offspring of previous years as auxiliaries (single male-single female, or SMSF, groups). Complex groups (Zahavi 1989) contain two or more possible mating combinations of presumed unrelated adults, with or without auxiliary members. Most commonly, these groups contain two or more males, usually brothers or fathers with sons, with an unrelated female (multiple male-single female, or MMSF, complex groups). Less frequently, complex groups consist of two or more females (usually sisters) and two or more males to which they are not related (multiple male-multiple female, or MMMF, complex groups). All members of the social group assist in territory defense, sentinel activity, mobbing, nest-building, incubation, and provisioning of young from a single nest.

Assignment of dominance rank

The main study population is under year-round observation; most groups are censused on a weekly to monthly basis during both the breeding and nonbreeding seasons. Group history records extend as far back as 20 years for some groups, and provide information about age, sex, and group membership of individual babblers. An age-structured dominance hierarchy exists, and rank is assigned based on observations of social interactions, including allofeeding, allopreening, and aggressive interactions (Zahavi 1989, 1990; Y. Perl and A. Zahavi, unpublished data).

Assignment of breeding status within groups is based on observations of dominance, courtship behavior, and group history information. Any individual that is unrelated to at least one group member of the opposite sex (according to group history records), or that is observed engaging in courtship and copulations with other group members, is considered a potential member of a mating combination. Those individuals that display no courtship behaviors within the group, and that were reared in the same group as all of the opposite-sex adult members of their current group, are not considered potential members of a breeding pair within the group.

Field methods

Blood samples were collected from 625 adults and offspring from 29 SMSF, 18 MMSF, and 4 MMMF groups. Birds in the study population are regularly marked with unique combinations of colored leg bands. Since 1993, two small (50–75 μl) blood samples were collected from each bird at the time of banding. The samples were preserved in 1 ml of lysis buffer (100 mM Tris, pH 8.0, 100 mM EDTA, 10 mM NaCl, 0.5% SDS; Longmire et al. 1988) at 4 °C for 2–26 weeks until DNA could be extracted. Unmarked adult birds (or fledglings) that joined marked groups, and unmarked groups in areas not previously included in the study population were live-captured, marked, and sampled either in early winter prior to the onset of courtship and breeding, or in late summer after breeding was complete.

Parentage exclusion analysis

Multilocus minisatellite DNA fingerprinting (Jeffreys et al. 1985) analyses of parentage and relatedness were performed using restriction endonuclease *Hae*III and Jeffreys' probes 33.15 and 33.6 in established protocols (Rabenold et al. 1990). Parentage was determined for 186 of 215 offspring analyzed, representing 44 group-years for 1993, 1994, 1995, and retrospectively for 1991–1992 when appropriate samples were available. The parentage of 16 offspring could not be determined because we did not have samples from the putative parents or the samples were degraded. Results for the remaining 13 offspring were ambiguous (see below). Analysis differed between simple and complex groups in the following manner.

Simple (SMSF) groups

Due to low levels of polymorphism within the population (mean band-sharing between nonrelatives = 0.66 for *Hae*III/33.6, 0.65 for *Hae*III/33.15), it was difficult to exclude as parents some dyads that included auxiliary individuals in simple groups (where auxiliaries are themselves putative offspring of dominants, and thus also putative siblings of the offspring in question). For 50 offspring of such simple (SMSF) groups, analysis was completed using dyads composed of second-ranking males or females paired with the dominant individual of the opposite sex, in addition to testing the dominant pair. The principal pair was not excluded in any of the 50 cases, and test pairs of one dominant and one subordinate could not be excluded as parents in 16 cases. Behavioral evidence indicates inbreeding avoidance between first-order relatives (Zahavi 1989); therefore, we did not test every possible dominant-subordinate pairing in simple groups, but limited our analysis to a systematic exclusion analysis of the dominant pair. In cases of ties between the dominant pair and a dyad containing one or two subordinates, the behaviorally dominant pair was not excluded as parents in a simple group.

Complex (MMSF or MMMF) groups

All male-female adult dyads were considered in complex (MMSF or MMMF) groups. When more than one dyad was not excluded after analysis with *Hae*III and both probes, families were analyzed using a second restriction endonuclease (42 cases). In 18 cases, more than one dyad was not excluded after analysis using Jeffreys' probes with both *Hae*III and *Hinf*I. These blots were hybridized with M13 phage DNA (Vassart et al. 1987), and the number of unattributable bands was summed across all three probes for each enzyme. In cases where the best fit produced one unattributable band after analysis with all six enzyme-probe combinations, that adult dyad was not excluded. When more than one dyad of unrelated adults produced a score of zero or one, the results were deemed inconclusive (13 cases).

Exclusion criteria

Except for rare mutations, offspring bands should be entirely attributable to their parental dyad (Jeffreys et al. 1988); therefore, any band present in an offspring lane which was not present in the adult dyad was scored as "unattributable" (Rabenold et al. 1990). Of the 186 offspring for which parentage was decided, 178 had banding patterns derived entirely from the parental dyad. Eight had one novel band not attributable to the parental dyad. We calculated the mutation rate for the study population as the rate at which novel bands appear per band scored in assigned offspring, or [8 novel bands/(186 offspring × 64.1 bands/offspring across Jeffreys' probes 33.6 and 33.15 with *Hae*III)], or 0.0007. Using this estimated mutation rate, the expected Poisson frequency with which an offspring should have two or more unattributable bands derived from the actual parents is 0.00098. Therefore, we excluded as parents any dyad producing two or more unattributable bands.

Band-sharing and confidence calculations

The proportion of bands shared was calculated as $2N_{AB}/(2N_{AB}+N_A+N_B)$, where N_{AB} is the number of bands shared by two individuals, N_A represents the number of bands unique to individual A, and N_B the number unique to individual B (Wetton et al. 1987; Lynch 1990). Band-sharing coefficients were used to calculate the probability of misassigning various categories of adult group members as parents (Jeffreys et al. 1985, Georges et al. 1988). Based on mean band-sharing values between nonrelatives of 0.66 (with probe 33.6) and 0.65 (with probe 33.15) and on mean number of bands scored, 34.5 and 32.3, the probability of mistaking an unrelated individual as a parent after analysis with *Hae*III and both probes is 0.0022, while the likelihood of misassigning a first-order relative is 0.048. Calculations of confidence were made using values for *Hae*III with 33.6 and 33.15, the minimum analysis for each family, although full analysis in many cases involved up to six enzyme/probe combinations.

To check the uniformity of our exclusion criteria across types of social groups, we compared the distributions of unattributable band scores produced using *Hae*III with Jeffreys' probes 33.6 and 33.15 for dyads consisting of the assigned parents, and of the mother paired with the excluded first- or second-ranking adult male group member, across simple and complex groups, using Mantel's matrix comparison text (Mantel 1967; Schnell et al. 1985; Rohlf 1990). We also used Mantel's test to check the uniformity of our exclusion criteria across types of social groups, by comparing the genetic similarity between nestlings and excluded and nonexcluded alpha and beta males.

To test the prediction that reproductive bias is larger when group members are more closely related, we used Mann-Whitney *U*-tests to compare the genetic similarity between alpha and beta males from complex groups in which paternity was shared to that between alpha and beta males from simple and complex groups in which all offspring were attributed to the alpha male. To compare genetic similarity and other demographic features of the focal set of alpha and beta males from complex groups in which paternity was shared to those from complex groups in which all offspring were attributed to the alpha male, we used Mann-Whitney *U*-tests. In these comparisons, we considered the alpha-beta pair the primary sampling unit. None of the 18 males (9 unique alpha-beta pairs) of simple groups is used in more than one dyad. Of the 23 males of complex groups used in this analysis, 5 are used in more than one pair, as they moved between groups and/or their status changed; however, every pair comprises a unique combination of males.

Results

Parentage analysis

In both simple and complex groups, production of young was primarily attributed to the dominant pair. All 112 offspring of 22 SMSF groups, and 64 of 74 (86.4%) offspring of 22 complex groups were attributable to the dominant pair (Table 1). Ten offspring were attributed to beta males, and of these, one nestling was also attributed to a beta female. Of the nestlings produced during 18 group-years in groups containing two or more males with one unrelated female (MMSF complex groups), 58 of 62 (93.5%) were the offspring of the alpha male with the alpha female. In the four MMMF groups, behaviorally dominant alpha males contributed 50.0% of total paternity (6 out of 12 offspring produced). Table 2 summarizes the decision criteria (all relevant band-sharing and unattributable band scores) used for the ten young attributed to parents other than the behaviorally dominant pair. Three of the offspring attributed to a beta male with an alpha female were the offspring of a single nest (ATD 94); neither the alpha nor the beta male could be excluded as father of the fourth nestling in the brood.

Table 1 Results of the parentage analysis, by group composition [*M* male, *F* female, *numbers* correspond to the dominance rank of the adult, *U* cases where the rank of one or more subordinate adults was unknown; 0, no young were attributed to any adult dyad of that type, –the combination did not occur (complex groups) or was not systematically scored (simple groups) see text for definitions of MMSF and MMMF]

Group composition	Group years	Number of young	Parentage					
			M1-F1	M2-F1	M3-F1	MU-F1	M1-F2	M2-F2
Simple	22	112	112	0	–	–	0	–
Complex MMSF	18	62	58	2	0	2	–	–
Complex MMMF	4	12	6	5	–	0	0	1
Total	44	186	176	7	0	2	0	1

Table 2 Criteria used to exclude the alpha male/alpha female pair as parents, for each juvenile attributed to one or more subordinate adult group members (*n/a* not applicable, see legend to Table 1 for further details)

Group-year	Nestling	Band-sharing: offspring with adults				Parentage	Total number of unattributable bands							
		M1	M2	F1	F2		M1-F1		M2-F1		M1-F2		M2-F2	
							*Hae*III	*Hinf*I	*Hae*III	*Hinf*I	*Hae*III	*Hinf*I	*Hae*III	*Hinf*I
ATD 94	AHTZ	0.79	0.85	0.82	0.67	M2-F1	0	2	0	0	2	1	2	0
ATD 94	CATS	0.71	0.87	0.82	0.58	M2-F1	1	1	0	0	2	1	1	1
ATD 94	HMTM	0.73	0.82	0.71	0.67	M2-F1	2	0	0	0	2	2	2	1
EST 94	THAL	0.80	0.88	0.86	n/a	M2-F1	2	0	0	0	n/a	n/a	n/a	n/a
EST 94	HATV	0.68	0.79	0.85	n/a	M2-F1	2	1	0	0	n/a	n/a	n/a	n/a
SVA 93	LCTZ	0.62	0.79	0.84	0.70	M2-F1	4	1	0	0	4	2	1	2
TLM 94	CATA	0.83	0.83	0.68	0.84	M2-F2	4	n/a	3	n/a	2	n/a	0	n/a
TLM 95	ATMZ	0.78	0.83	0.71	n/a	M2-F1	2	n/a	0	n/a	n/a	n/a	n/a	n/a
TLM 95	CTMH	0.63	0.75	0.79	n/a	M2-F1	4	n/a	1	n/a	n/a	n/a	n/a	n/a
ZMM 93	ALTT	0.57	0.73	0.85	n/a	M2-F1	2	n/a	0	n/a	n/a	n/a	n/a	n/a

Multiple paternity was detected in four nests (involving four different group-years) of complex groups in which paternity could be assigned for all offspring. All instances of shared paternity occurred during the first successful nesting attempt of the year. In one group-year (EST 94), the beta male sired one of three nestlings in the first nest, and the only nestling of the second. In three nests, 50% (one of two) of offspring were sired by the beta male. In one of these group-years (ZMM 93), seven nestlings of three subsequent nests were attributed to the alpha male; in all, the alpha sired eight of nine offspring produced.

During the years of our study (1993–1995), approximately two-thirds (43 of 65 groups for which information was available) of the groups in the study population were SMSF groups, while one-third were complex (either MMSF or MMMF). Approximately 40% of nests observed (35 of 87) were those of complex groups. In the genetic analysis, complex groups are overrepresented with respect to their frequency in the population. After corrections are made for the actual frequency of complex groups in the population, subordinate males sired approximately 3% of the young produced in the population. Subordinate females produced, on average, only 0.3% of the young in a given year. Additionally, multiple paternity occurred in approximately 11% of broods produced by complex groups, and in only 5% of broods across the population.

Uniformity of exclusion criteria

We compared unattributable bands (*Hae*III with Jeffreys' 33.6) for nestlings paired with the alpha or beta male that was assigned paternity versus the one that was excluded in the parentage analysis (Fig. 1). We found that the distribution of unattributable bands for the alpha male fathers was different from the corresponding distribution for excluded beta males (Fig. 1A; $P = 0.001$; Mantel's matrix comparison test). The distributions for beta male fathers and the corresponding

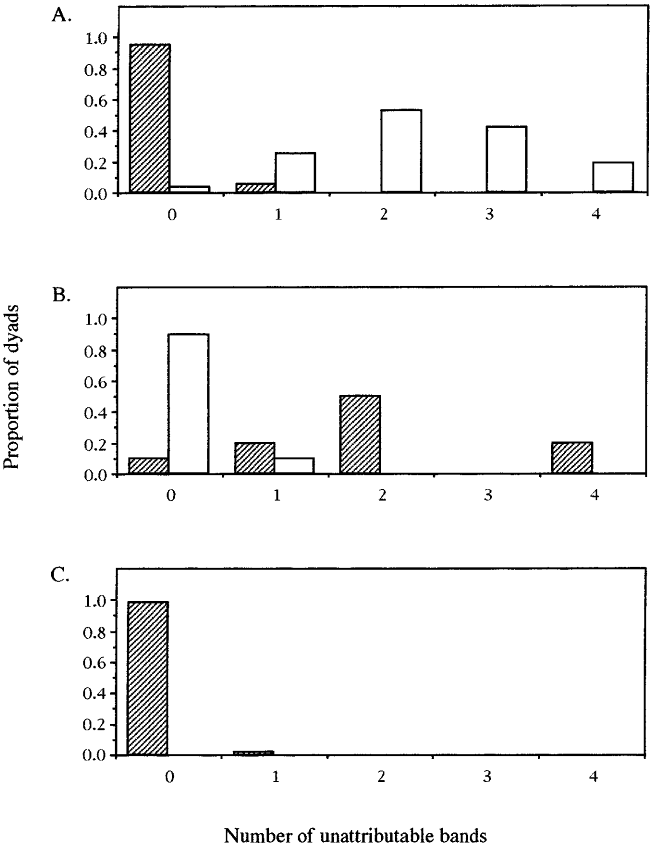

Fig. 1A–C Distributions of unattributable bands produced using *Hae*III with Jeffreys' probes 33.6 and 33.15 for offspring scored against dyads consisting of their actual mother paired with their actual father, and with the excluded alpha or beta male. **A** distributions of unattributable bands for the offspring of complex groups that were attributed to the alpha male ($n = 64$). Alpha males are represented by *hatched bars*, and beta males by *open bars*. **B** Distributions for the offspring of complex groups that were sired by beta males ($n = 10$). **C** Distribution for the offspring of simple groups, all of which were attributed to the dominant pair of their natal groups ($n = 112$)

excluded alpha males were also different (Fig. 1B; Mantel $P = 0.001$). The distributions of unattributable bands for non-excluded males were similar whether they represented alpha or beta males in complex groups (left-hand modes of Fig. 1A, B), or nonexcluded alpha males of simple groups (Fig. 1C). These findings indicate that the exclusion criteria used were consistent for males of different dominance ranks. In a similar manner, we compared band-sharing scores using *Hae*III with Jeffreys' probe 33.6 for dyads composed of nestlings paired with the alpha or beta male that was assigned paternity versus the one that was excluded (Fig. 2). Average band-sharing for alpha male fathers with their offspring in complex groups was 0.81 ± 0.057, for beta male fathers, 0.81 ± 0.049, and for alpha males of simple groups, 0.82 ± 0.062. Average band-sharing with nestlings was similar for excluded alpha and beta males of complex groups (alpha males: mean = 0.71 ± 0.088; beta males: mean = 0.68 ± 0.079). The distribution of band-sharing for alpha male fathers with their offspring was different from the distribution for the same offspring paired with the beta males that were excluded as their fathers (Fig. 2A; Mantel $P = 0.001$). Average band-sharing for beta male fathers with their offspring was also different from the average for alpha males that were excluded as their fathers (Fig. 2B; Mantel $P = 0.001$).

Genetic relatedness of males, history of association, and beta male paternity

We calculated band-sharing scores (*Hae*III with Jeffreys' probe 33.6) between alpha and beta males of all simple (SMSF) and complex groups. Genetic similarity between alpha and beta males, as estimated by band-sharing, was significantly lower in complex groups in which beta males sired young (mean = 0.65 ± 0.09, $n = 5$) than in complex groups in which alpha males monopolized paternity (mean = 0.77 ± 0.09, $n = 10$; $P = 0.037$, Mann-Whitney $U = 42.0$; Fig. 3A, Table 3). Genetic similarity was also higher between the two highest-ranking males of SMSF groups (mean = 0.85 ± 0.06, $n = 9$; Fig. 3B) than the overall mean between the two highest-ranking males of complex groups (mean = 0.73 ± 0.10, $n = 15$, Fig. 3A; $P = 0.002$, Mann-Whitney $U = 16.5$). In complex and simple groups combined, the distributions of male-male band-sharing scores were different between groups where alpha males sired all young (mean = 0.81 ± 0.084; $n = 19$) versus those where beta males sired young (mean = 0.65 ± 0.091, $n = 5$; $P = 0.008$, Mann-Whitney $U = 10.5$).

Using information from records of group history, we examined the relationship between beta male paternity

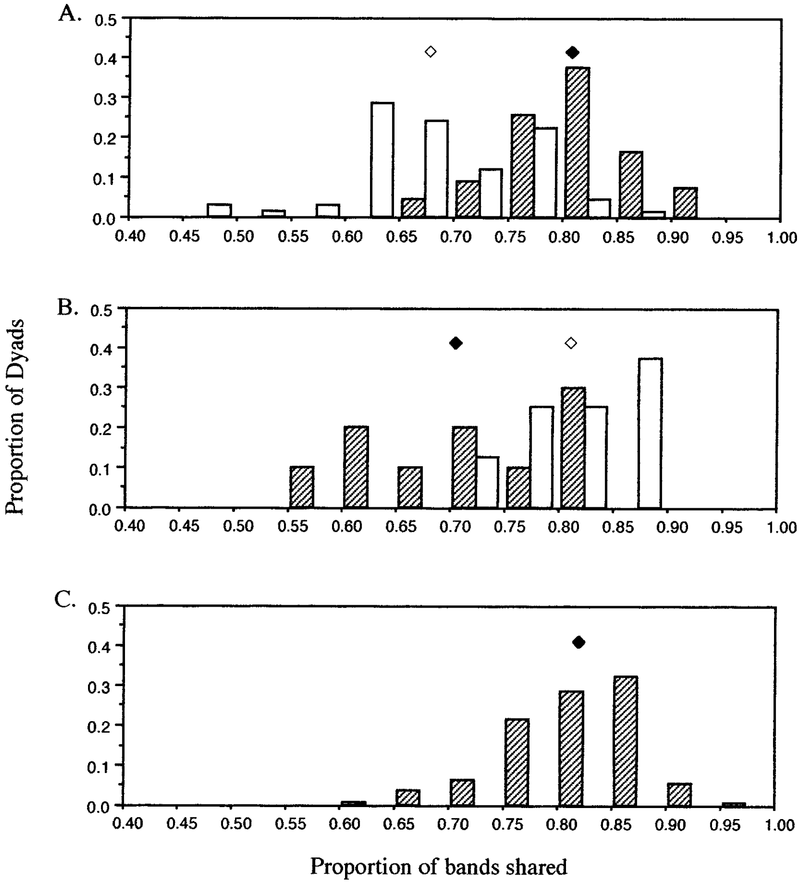

Fig. 2A–C Distributions of band-sharing values using *Hae*III with Jeffreys' probes 33.6 for dyads consisting of young paired with their genetic fathers, and with excluded alpha or beta males in complex groups. Scores for alpha males are represented by *hatched bars* (average marked with *solid diamond*); *open bars* (and *open diamonds*) represent beta males. **A** Distributions for hatchlings sired by alpha males ($n = 64$), paired with their fathers (mean = 0.81 ± 0.06) and the beta males excluded as fathers (mean = 0.68 ± 0.08). **B** Distributions for offspring of complex groups that were sired by beta males ($n = 10$). Scores of genetic similarity are shown for offspring paired with their beta male fathers (mean = 0.81 ± 0.05) and the alpha male excluded as the father (mean = 0.71 ± 0.09). **C** Distribution for simple groups, in which only one pair of unrelated adults is present (mean = 0.82 ± 0.06)

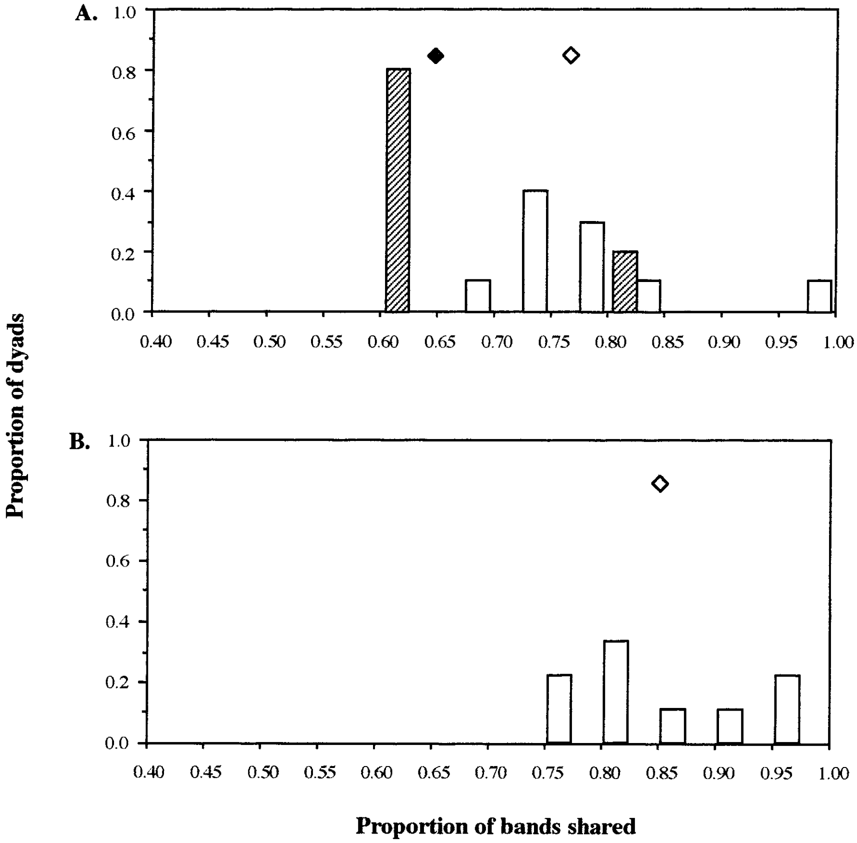

Fig. 3A,B Distributions of band-sharing (*Hae*III with Jeffreys' probe 33.6) between alpha and beta males of social groups in which alpha males sired all young produced, and in which beta males sired young. **A** Distributions for complex groups. *Hatched bars* represent those complex groups in which beta males received paternity ($n = 5$, mean = 0.65 ± 0.09; average marked with *solid diamond*). *Open bars* represent the distribution of band-sharing between the males of groups in which the alpha male sired all of the young ($n = 10$, mean = 0.77 ± 0.09; average marked with *open diamond*). **B** Distribution of band-sharing values for single male single female groups; all offspring of these groups were attributed to the alpha male with the alpha female ($n = 9$, mean = 0.85 ± 0.06). Those groups in which the same alpha and beta males were present for more than 1 year were counted only once

Table 3 Age and length of association of beta males with alpha males and females of complex groups (*Y* yes, *N* no)

Group	Presumed relationship M1-M2	M1 age (months)	M2 age (months)	Proportion M2 life with M1	M1-M2 age difference (months)	Proportion M2's life with M1 as M1	Proportion M2's life with F1 as F1	Proportion bands shared M1-M2	M2 in natal group
Complex groups in which alpha male sired all young									
BMS 94	Father-son	94	46	1	48	1	1	0.71	Y
BOK 94	Second order	97	47	0.89	50	0.66	0.04	0.67	Y
BOT 94	Brothers	34	34	?	0	?	?	0.79	Y
BOT 95	Second order	47	13	1	34	0.92	0.83	0.76	Y
DRB 95	Unrelated	48	12	0.75	36	0.42	0.75	0.78	N
MBS 93–95	Father-son	85	11	1	74	1	1	0.73	Y
MTE 94	Father-son	?	?	?	?	?	?	0.70	Y
MZR 94A	Father-son	96	58	1	38	1	0.79	0.74	Y
MZR 94B	Brothers	60	37	1	23	0.05	0.38	0.98	Y
MZR 95	Father-son	108	47	0.77	61	0.77	0.51	0.82	Y
ZMM 95	Beta unknown								Y
Mean		74	34	0.93	40	0.73	0.66	0.77	
SD		27	18	0.11	22	0.34	0.33	0.09	
Complex groups in which the beta male sired young									
ATD 94	?	?	?	?	?	?	?	0.60	N
EST 94	?	?	?	?	?	?	?	0.61	?
SVA 93–94	Second order	63	37	1	26	0.59	0.05	0.81	Y
TLM 94–95	Brothers	36	11	1	25	0.09	0.09	0.60	N
ZMM 93–94	Brothers	31	24	1	7	0.04	0.04	0.63	N
Mean		43	24	1	19	0.24	0.06	0.65	
SD		17	13	0	11	0.30	0.03	0.09	
Mann-Whitney *U*		22	19	7.5	22	21	21.5	42	
P-value		0.12	0.31	0.25	0.12	0.064	0.051	0.037	

and age in months of both alpha and beta male, age difference (in months) between alpha and beta males, and proportion of beta male's life spent with the alpha male, and with the alpha male or the alpha female in the dominant position (Table 3). We compared the data in each of these categories between complex groups in which alpha males sired all young and those in which beta males sired young. There was a tendency, although not significant, for alpha males to be older and for the average age difference between alphas and betas to be larger in groups in which alphas monopolized paternity than in groups in which betas sired young (Table 3). There was no significant relationship between male paternity and either beta male age or the proportion of life the beta male had spent with the alpha male. Betas that sired young had spent a smaller proportion of their lives with the current alpha in alpha position for both male ($P = 0.064$, Mann-Whitney $U = 21.0$) and female ($P = 0.051$, Mann-Whitney $U = 21.5$) alphas compared to betas that did not sire young (Table 3). In the five groups in which paternity was shared, three were known to be newly formed groups of recent dispersers breeding away from their natal territories (and a fourth less well known group could have been as well), and one group had a newly arrived female on the beta males' natal group. In contrast, in the groups in which reproduction was monopolized by the alpha male, 10 of 11 were breeding on their natal territories in longer-established groups.

Discussion

Mating system

The genetic analysis of parentage in Arabian babblers has revealed relatively low levels of reproduction by subordinate group members across the population, confirming expectations based on behavioral observations made by Zahavi (1988, 1989, 1990). Our results also reveal an asymmetrical pattern of reproductive success similar to those that characterize some other cooperatively breeding species (stripe-backed wren, *Campylorhynchus nuchalis*, Rabenold et al. 1990; the European bee-eater, *Merops apiaster*, Jones et al. 1991; the Tasmanian native hen, *Tribonyx mortierii*, Gibbs et al. 1994; red-cockaded woodpecker, *Picoides borealis*, Haig et al. 1994; bicolored wren, *C. griseus*, Haydock et al. 1996). In these species, multiple parentage within groups is infrequent. Extragroup parentage is rare or nonexistent in *C. nuchalis*, *M. apiaster*, and *P. borealis*, although extragroup parentage was found in bicolored wrens (Haydock et al. 1996) and at relatively high frequencies in fairy wrens, *Malurus spp* (Brooker et al. 1990; Dunn and Cockburn 1998). Other cooperatively breeding species are characterized by a more egalitarian sharing of parentage among unrelated group members (dunnock, *Prunella modularis*, Burke et al. 1989; pukeko, *Porphyrio porphyrio*, Jamieson et al. 1994; Galapagos hawk, *Buteo galapagoensis*, Faaborg et al. 1995).

Reproductive skew

Models predict that reproductive skew will favor dominants, especially those closely related to subordinate group members (Vehrencamp 1983; Keller and Reeve 1994; Emlen 1982, 1995). Our study population supports this prediction; we found alpha and beta males of groups in which the alpha male sired all offspring to be more genetically similar, as measured by DNA fingerprinting, than the alpha and beta males of groups where the beta male sired young. This pattern is similar to that of cooperating male lions (*Panthera leo*; Packer et al. 1991) and white-browed scrub wrens (*Sericornis frontalis*; Whittingham et al. 1997), where groups in which males are closely related exhibit a large skew in the distribution of reproductive success (favoring dominant individuals), while those made up of less closely related individuals have a higher degree of shared paternity.

Sharing of reproduction among males occurred following dispersal or other major changes to group structure, such as the arrival of a new dominant, indicating an important relationship between the length of time that a group has been in its current configuration and the distribution of paternity. Among stripe-backed wrens, subordinate males were found to have high reproductive success soon after joining new social groups (Piper et al. 1995). In both this species and the Arabian babbler, the association between reproductive skew and the proportion of time that the beta male has spent with the current alpha male and female in the dominant position may reflect instability of the dominance hierarchy within newly formed groups. In contrast to the relative stability of the dominance hierarchy in more established groups created by delayed dispersal, the formation of new groups creates opportunities for reproduction by subordinates in unstable hierarchies that are also more likely to involve nonrelatives.

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References

Alexander RD (1974) The evolution of social behavior. Annu Rev Ecol Syst 5:325–383

Brooker MG, Rowley I, Adams M, Baverstock PR (1990) Promiscuity: an inbreeding avoidance mechanism in socially monogamous species? Behav Ecol Sociobiol 26:191–200

Burke T, Davies NB, Bruford MW, Hatchwell BJ (1989) Parental care of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. Nature 338:249–251

Dunn PO, Cockburn A (1998) Costs and benefits of extra-group paternity in superb fairy-wrens. In: Parker PG, Burley NT (eds) Avian reproductive tactics: Female and male perspectives. Ornithol Monogr 49. ADU, Washington DC, pp 147–161

Emeln ST (1982) The evolution of helping. J II. The role of behavioral conflict. Amer Nat 119:40–53

Emlen ST (1995) An evolutionary theory of the family. Proc Natl Acad Sci USA 92:8092–8099

Faaborg J, Parker PG, DeLay L, Vries TJ de, Bednarz JC, Paz SM, Naranjo J, Waite TA (1995) Confirmation of cooperative polyandry in the Galapagos hawk (*Buteo galapagoensis*). Behav Ecol Sociobiol 36:83–90

Georges M, Lequarre AS, Castelli M, Hanset R, Vassart G (1988) DNA fingerprinting in domestic animals using 4 different minisatellite probes. Cytogenet Cell Genet 47:127–131

Gibbs HL, Goldizen AW, Bullough C, Goldizen AR (1994) Parentage analysis of multi-male social groups of Tasmanian native hens (*Tribonyx mortierii*): genetic evidence for monogamy and polyandry. Behav Ecol Sociobiol 35:363–371

Haig SM, Walters JR, Plisser JH (1994) Genetic evidence for monogamy in the cooperatively breeding red-cockaded woodpecker. Behav Ecol Sociobiol 34:295–303

Hamilton WD (1964) The genetical evolution of social behaviour I & II. J Theor Biol 7:1–52

Haydock J, Parker PG, Rabenold KN (1996) Extra-pair paternity uncommon in the cooperatively breeding bicolored wren. Behav Ecol Sociobiol 38:1–16

Jamieson IG, Quinn JS, Rose PA, White BN (1994) Shared paternity is a result of an egalitarian mating system in a communally breeding bird, the pukeko. Proc R Soc Lond B 257:271–277

Jeffreys AJ, Wilson V, Thein SL (1985) Individual-specific "fingerprints" of human DNA. Nature 316:76–79

Jeffreys AJ, Royle NJ, WilsonV, Wong Z (1988) Spontaneous mutation rates to new length alleles at tandem-repetitive hypervariable loci in human DNA. Nature 332:278–281

Jones CS, Lessels CM, Krebs JR (1991) Helpers-at-the-nest in European bee-eaters (*Merops apiaster*): a genetic analysis. In: Burke T, Dolf G, Jeffreys AJ, Wolff R (eds) DNA fingerprinting approaches and applications. Birkhäuser, Basel, pp 169–192

Keller L, Reeve HK (1994) Partitioning of reproduction in animal societies. Trends Ecol Evol 9:98–102

Longmire JL, Lewis AW, Brown NC, Buckingham LM, Clark M, Jones D, Meinke LJ, Meyne J, Ratcliff RL, Ray FA, Wagner RP, Moyzis RP (1988) Isolation and characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. Genomics 2:14–24

Lynch M (1990) The similarity index and DNA fingerprinting. Mol Biol Evol 7:478–484

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27:209–220

Moehlman PD (1979) Jackal helpers and pup survival. Nature 277:382–383

Owens DD, Owens MJ (1984) Helping behaviour in brown hyenas. Nature 308:843–846

Packer C, Gilbert DA, Pusey AE, O'Brien SJ (1991) A molecular genetic analysis of kinship and cooperation in African lions. Nature 351:562–565

Piper W, Parker PG, Rabenold KN (1995) Facultative dispersal by juvenile males in the cooperative stripe-backed wren. Behav Ecol 6:337–342

Rabenold PP, Rabenold KN, Piper WH, Haydock J, Zack SW (1990) Shared paternity revealed by genetic analysis in cooperatively breeding tropical wrens. Nature 348:538–540

Rohlf FJ (1990) NTSYS-pc: numerical taxonomy and multivariate analysis system, version 160. Applied Biostatistics, Setauket, NY

Rood JP (1980) Mating relationships and breeding suppression in the dwarf mongoose. Anim Behav 28:143–150

Schnell GD, Watt DJ, Douglas ME (1985) Statistical comparison of proximity matrices: applications in animal behavior. Anim Behav 33:239–253

Stacey PB, Koenig WD (1990) Introduction. In: Stacey PB, Koenig WD (eds) Cooperative breeding in birds. Cambridge University Press, Cambridge, pp ix–xviii

Vassart G, Georges M, Monsieur R, Brocas H, Lequarre AS, Christophe D (1987) A sequence in M13 phage detects hypervariable minisatellites in human and animal DNA. Science 235:683–684

Vehrencamp SL (1983) A model for the evolution of despotic versus egalitarian societies. Anim Behav 31:667–682

West-Eberhard MJ (1975) The evolution of social behavior by kin selection. Q Rev Biol 50:1–34

Wetton JH, Carter RE, Parkin ET, Walter D (1987) Demographic study of a wild house sparrow population by DNA fingerprinting. Nature 327:147–149

Whittingham LA, Dunn PO, Magrath RD (1997) Relatedness, polyandry and extra-group paternity in the cooperatively-breeding white-browed scrubwren. Behav Ecol Sociobiol 40:261–270

Zahavi A (1988) Mate guarding in the Arabian babbler, a group-living songbird. Proc Int Ornithol Congr 20:420–427

Zahavi A (1989) Arabian babbler. In: Newton I (ed) Lifetime reproduction in birds. Academic Press, New York, pp 253–275

Zahavi A (1990) Arabian babblers: the quest for social status in a cooperative breeder. In: Stacey PB, Koenig WD (eds) Cooperative breeding in birds. Cambridge University Press, Cambridge, pp 103–130

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