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Coalitions of relatives and reproductive skew in cooperatively breeding white-winged choughs

Robert Heinsohn[1]*, Peter Dunn[2], Sarah Legge[1] and Michael Double[1]

[1]*Evolutionary Ecology Group, Division of Botany and Zoology, Australian National University, Canberra, ACT 0200, Australia* (*robert.heinsohn@anu.edu.au, sarah.legge@anu.edu.au, mike.double@anu.edu.au*)
[2]*Department of Biological Sciences, PO Box 413, University of Wisconsin–Milwaukee, Milwaukee, WI 53201, USA* (*pdunn@uwm.edu*)

We used DNA fingerprinting to examine reproductive skew in cooperatively breeding white-winged choughs, *Corcorax melanorhamphos*, which live in groups of up to 20 individuals. Before a severe drought, groups that had been stable for multiple years were characterized by long-term monogamy involving a single breeding pair (high skew). After the drought, new groups formed from the amalgamation of multiple individuals and coalitions of relatives. At most one member of each faction succeeded in breeding, such that skew was dependent on the number of unrelated factions, and not group size. In the new groups, dominant males and females with supporting relatives were always successful. Whereas most females without support also gained breeding positions, many males without family support failed to breed. Thus subordinates gain indirect fitness by first helping related males to secure a breeding position, and then helping to raise their young. Our study demonstrates the advantage of operating in coalitions, and suggests that the acquisition of future allies may be a major benefit of helping behaviour in this species.

Keywords: cooperative breeding; reproductive skew; coalitions; DNA fingerprinting

1. INTRODUCTION

Cooperative breeding, in which some individuals care for young that are not their own, is a relatively rare social system amongst vertebrates. In its simplest form, a cooperative group may consist of a breeding pair with one helper. The fundamental question of whether this helper should seek a share of reproduction, or merely be content to help, was pioneered by Vehrencamp (1980, 1983) and Emlen (1982), and has become known as optimal skew theory. Reproductive skew refers to the extent of shared reproduction amongst same-sex members of social groups. Reproductive benefits are shared in egalitarian societies (low skew), but monopolized by a few individuals in despotic societies (high skew). Optimal skew theory has recently undergone major expansions on two important fronts. First, although the original models were founded on limiting assumptions, a host of new models have been formulated that attempt to predict reproductive skew in a variety of real-life situations (e.g. Reeve *et al.* 1998; Cant & Johnstone 1999; Johnstone & Cant 1999). Second, recent molecular techniques are allowing precise determination of relatedness and reproductive success amongst group members (e.g. Rabenold *et al.* 1990; Packer *et al.* 1991; Dunn *et al.* 1995; Poldmaa *et al.* 1995; Quinn *et al.* 1999).

Although there has been much theoretical interest in reproductive skew, and molecular techniques have been applied to a range of cooperative species, there is still a major gulf between theory and empirical data (Magrath & Heinsohn 1999). One limitation of most models is that for reasons of tractability they are usually best applied to small groups with only two players of the same sex partitioning reproduction. However, many societies involve complex groups of large size and varying relatedness, and although interactions between multiple players can be difficult to model, an understanding of their dynamics is potentially very rewarding (e.g. Heinsohn & Packer 1995). The only attempt to model skew in multimember groups has been by Johnstone *et al.* (1999). Their analysis of three-member groups reveals complex patterns of predicted skew depending on group productivity and the three-way relationship between the dominant and subordinates, and suggests ever greater complexity with increasing group size.

One type of multimember system is found amongst cooperatively breeding birds and mammals in which dispersing individuals form coalitions to increase their chances of reproductive success (e.g. Zahavi 1974, 1990; Koenig & Pitelka 1981; Packer *et al.* 1991; Ligon & Ligon 1990; Rood 1990). Individuals in these coalitions face the dual optimization problem of having sufficient members to compete successfully against other coalitions for breeding vacancies, whilst assuring they gain a worthwhile share of either direct or indirect fitness for themselves within their own coalition.

In this paper, we report on the reproductive skew found within large groups of cooperatively breeding white-winged choughs, *Corcorax melanorhamphos*, formed through the amalgamation of dispersing individuals and coalitions. For many years we have viewed reproduction in this species as highly skewed with group productivity strongly enhanced by alloparental care from closely related individuals (Heinsohn 1992). However, a severe drought in 1994 caused high mortality in our study population, and many groups fragmented into smaller units. Here we use multilocus DNA fingerprinting to examine the reproductive success and skew of individuals and coalitions, as they joined others to form new cooperative groups.

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*Author for correspondence.

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Table 1. *Composition of 19 cooperatively breeding groups*

(Shown are group sizes, the number analysed with DNA fingerprinting, the number of factions of first-order relatives (based on DNA fingerprinting), faction composition, the number of offspring and number of group years, and the degree of skew for both males and females (see §2(e) for skew formula; also note that skew in the Green group was calculated before an additional male joined the group after the drought and sired one offspring). Factions are enclosed by parentheses, and include adult males and females (three years old, denoted by 'M' and 'F'), and juvenile males and females (denoted by 'm' and 'f') that presumably formed the group. Breeders are denoted by *, kidnapped group members by $^{\#}$, and breeding members that were not sampled but whose presence could be inferred are denoted by ^{1}. All offspring of these individuals are indicated by the values in the number of offspring column. Those groups which fragmented during the drought are denoted by ^{f}. The composition of these groups is shown before fragmentation.)

group	group size	finger-printed (N)	factions of relatives	faction composition	1995–1996 offspring	total offspring	male skew	female skew
long-term groups								
Farmers	11	11	2	(F*,f,M,M)(M*,M)	3	5 (2 years)	1	1
Yellow	11	8	4	(F*)(M*)(M)(f$^{\#}$)	6	7 (3 years)	1	1
Campbell Park Blue	10	10	2	(F*)(M*,M)	4	7 (3 years)	1	1
Green	10	9	3	(F*)(M*,M,M)(M*)	2	4 (2 years)	1	1
Black Mountain Blue	9	8	2	(F^{1*})(M*)	0	7 (4 years)	1	1
Orange^{f}	14	14	1	(F*,M*)	—	12 (5 years)	1	1
White^{f}	12	11	3	(M,M,f,f)(F,M,M, M,M,m)(M)	—	—	—	—
Red^{f}	6	5	2	(F,f,M,M,m)(F)	—	—	—	—
Small Orange^{f}	4	3	2	(F,m)(M)	—	—	—	—
Tidbinbilla^{f}	6	5	2	(F,F,M,m)(f)	—	—	—	—
new groups								
O'Connor 9	13	13	7	(F*,F,F)(F*)(F*) (M*)(M*)(M)(M)	4	4	0.67	0.58
Mafia	13	12	7	(F^{1*})(M*)(M*)(M*) (M)(M)(M)	6	6	0.69	1
Veterans	10	9	4	(F*,F,m)(M*)(M^{1*})	5	5	0.08	1
Haig Park	9	9	2	(F*,M,M,m) (M*,M,M,m)	1	1	—	—
WOB	9	9	5	(F*)(M*,f,f)(M*) (M)(M)	2	2	0.67	1
Bullies	9	9	5	(F*)(M*,M,m)(F) (M)(M)	2	2	1	1
White-orange	8	6	4	(F*)(M^{1*})(M)(M)	3	3	1	1
Village People	6	5	3	(F*,F)(M*)(M^{1*})	2	2	0	1
Athletes	4	3	2	(F^{1*}) (M*,M,m)	2	2	1	1
total	174	159	62	—	42	69	—	

2. METHODS

(a) *Cooperative breeding in white-winged choughs*

White-winged choughs are large (350–450g) passerines in which a single breeding pair are usually assisted by non-reproductive helpers. Unassisted pairs never succeed in reproducing; even trios have very low success. The number of young fledged increases across all larger group sizes (4–14 birds; Rowley 1978; Heinsohn 1992), and feeding experiments have shown that brood size is limited by foraging constraints on both breeders and helpers (Boland *et al.* 1997*a*). Group members assist the dominant pair in all aspects of reproduction from nest building and nest defence (Rowley 1978), incubating eggs (Heinsohn & Cockburn 1994) and feeding nestlings (Boland *et al.* 1997*a*) to extended care of fledglings (up to eight months; Heinsohn 1991*a*).

Young choughs (one to two years old) are inefficient foragers, but help raise young within their limited capacity (Heinsohn & Cockburn 1994; Boland *et al.* 1997*a*). Many sexually mature individuals (i.e. three or more years old) remain in the group as helpers and, until the events reported in this paper, dispersal from the natal group had been rare (Heinsohn 1992). Rowley (1978) observed that occasionally groups would fragment upon the death of a breeder, which he assumed was the male (but see §3(a)). These fragments would coalesce with others to form new breeding groups. Another way groups acquire unrelated members is by kidnapping and raising fledglings from other groups, which then become helpers (Heinsohn 1991*b*).

(b) *Study population*

Groups of white-winged choughs have been individually colour marked and studied in the woodlands near Canberra, Australia, from 1985 to 1989 (Heinsohn 1992), and again from 1993 to 1997. We collected blood samples (about 100 µl each) for DNA fingerprinting from 156 choughs living in 19 groups in Campbell Park, Black Mountain and Tidbinbilla Nature Reserves, ACT, Australia, from 1993 until 1997 (table 1). All groups were censused at least once every ten days from the beginning (September) to the end (March) of each breeding season. We aged, to the nearest six months, birds up to four years old based on eye colour (Rowley 1974); all choughs older than this were assigned the same age (four plus).

(c) *Molecular techniques*

Although the sex of choughs cannot be determined externally (Rowley 1978) we were able to determine their sex by amplifying a homologue of the *CHD* gene which is sex-linked in many non-ratites (Griffiths *et al.* 1998). Choughs do not usually reach sexual maturity until they are four (Rowley 1978), but we included all three-year-olds in our search for possible parents of nestlings within groups. Multilocus DNA fingerprints were made following standard methods (e.g. Bruford *et al.* 1992). Briefly, we digested 6 µg genomic DNA per individual with *Hae*III and added 6 ng of a molecular size marker to each sample, which was then subjected to electrophoresis at 70V for 45–50 h. The DNA was then Southern blotted onto Hybond-N+$^{\text{TM}}$ transfer membranes. All membranes were probed sequentially with radioactively labelled *per* (Shin *et al.* 1985), 33.15 (Jeffreys *et al.* 1985) and, lastly, molecular size marker to produce three separate autoradiographs. The molecular size markers allowed us to correct for distortions in the migration of DNA across the gel and to score similar size regions of the profile on each gel (above 2 kb).

(d) *Determining parentage and inferring relatedness between group members*

We attributed nestlings or fledglings to a pair of putative parents if (i) the DNA profile (both probes combined) of the parents contained all or most (two novel fragments) of the bands found in a nestling or fledgling, (ii) both parents shared a greater proportion of their bands with the nestling than an unrelated bird would have shared (see below), and (iii) all other potential parents in the group could be excluded through the presence of more than two novel fragments.

We also calculated the mean band-sharing coefficient and one-tailed 99% lower confidence interval for 24 independent dyads of first-order relatives (mother–offspring and father–offspring). This allowed us to estimate a lower limit of band-sharing for first-order relatives, and thus determine whether birds of unknown origin in the same group were close relatives (e.g. Piper & Rabenold 1992). We could also identify 15 independent dyads of unrelated individuals known to have originated from separate groups. From these dyads we calculated a mean band-sharing coefficient, and one-tailed 99% upper confidence interval. This allowed us to estimate an upper limit of band-sharing for determining whether individuals of unknown origin were unrelated to each other.

(e) *Estimating reproductive skew*

We used the formula of Pamilo & Crozier (1996) to calculate skew (S) in groups, $S=(N_{\text{T}}-Q_{\text{E}})/(N_{\text{T}}-1)$, where N_{T} is the total number of potential breeders. Q_{E}, the effective number of breeders, is defined as $Q_{\text{E}}=1/\Sigma p_i 2$, where p_i is the proportion of reproduction from the ith breeder (see also Jamieson 1997).

3. RESULTS

(a) *Drought and group fragmentation*

Although kidnapping has been frequent in the Canberra population (>20 cases noted in over 100 group-years (Heinsohn 1991*b*; unpublished data)), we never observed fragmentation of groups as reported by Rowley (1978) before 1994. All groups under observation from 1985 to 1989 showed stable membership over multiple years, augmented by retention of grown offspring, although some entire groups did disappear from the study area (R. Heinsohn, unpublished data). We first noted mixing of group membership during a period of severe drought in late 1994 that also coincided with high mortality across the entire study population. This drought occurred over the normal period of breeding (September–February), and was preceded by the coldest winter on record (150 years) in the Canberra region (Bureau of Meteorology, Canberra). The drought was also known to affect adversely the breeding attempts of a variety of other bird species (A. Cockburn, E. Krebs and R. Magrath, personal communication).

Approximately 14% of the colour-banded population ($N=21$) disappeared from the study area between August 1994 and March 1995. This compares with a much lower rate of annual mortality (<5%, R. Heinsohn, unpublished data) for all previous periods of our project. Critically, six out of the ten groups under observation since 1993 lost their breeding female over this period, whereas none lost their breeding male. The sex ratio of adult choughs sampled was 38 males to 26 females (approximately 1.5:1) after the drought, possibly reflecting greater mortality amongst females. Five of the six groups that lost their female broke up into smaller units of between one and four members. The group that remained together (Black Mountain Blue) did so in spite of having no female of suitable age within their group to fill the vacancy. They remained without a breeding female for two years.

Five out of eight coalitions of dispersing choughs were of one sex (see new groups, table 1). After a period of roving through the population, individuals and coalitions generally reformed with birds from other groups. There were repeated breakups and reformations between unrelated choughs; the dynamics of these are complicated and will be presented elsewhere (R. Heinsohn, unpublished data). Here we focus on the composition of cooperative groups after this period of instability, and the distribution of reproduction amongst groups composed of members of varying relatedness in their first breeding season after amalgamation. We refer to the varying individuals and coalitions of relatives within these new groups as 'factions' that represent divergent genetic interests during reproductive attempts.

(b) *Fingerprinting*

The mean (±s.d.) number of scorable bands above 2 kb was 17.9 ± 5.1 with *per* and 22.0 ± 5.3 with 33.15. A segregation analysis of bands in a family of 12 young revealed that, in general, bands for both probes were transmitted independently and inherited stably over five generations. We identified 11 female and 13 male parents for 51 out of the 69 juveniles through the most parsimonious combination of band-sharing coefficients and absence of novel fragments. In all except four cases, the pair of putative parents accounted for all bands, or all bands except one, present in the juvenile, and other potential pairs of parents produced lower band-sharing coefficients and at least three novel fragments. In two of the four exceptions, two juveniles each had two novel bands when compared with their putative parents. We considered these novel fragments to be mutations,

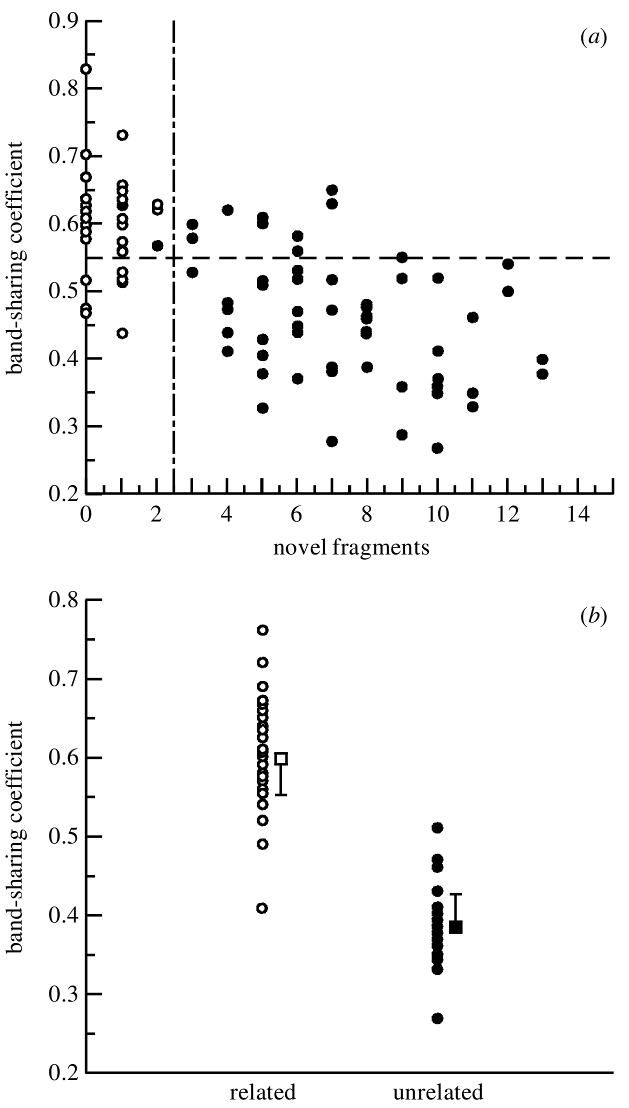

Figure 1. (*a*) Band-sharing coefficients of putative fathers versus the number of novel fragments. The lower confidence limit for first-order relatives (horizontal line), and the cut-off for excluding putative parents (vertical line) are shown. (*b*) Band-sharing coefficients between 24 dyads of known first-order relatives (open circles), showing the mean (open square) and lower 99% confidence interval, and 15 dyads of known non-relatives (filled circles), showing mean (filled square) and upper 99% confidence interval.

because these juveniles had high band-sharing coefficients with the putative parents (>0.625; figure 1) and we expect a few mutations to occur in a small proportion of offspring (1–5 per 1000 meiotic events; Burke & Bruford 1987). In the other two exceptions, two males each had high band-sharing with juveniles (0.57–0.64), and their profiles (in conjunction with the female's) accounted for all but one or two novel bands, suggesting that they should be considered parents. However, these males were excluded as parents, as in both cases there were other males with even higher band-sharing with the juveniles, and lower numbers of novel fragments. In figure 1*a*, the band-sharing coefficients are plotted against the presence of novel fragments, showing that even group members with band-sharing coefficients as high as those of parents to offspring (i.e. individuals that were clearly closely related to the juveniles) could be excluded based on the number of novel fragments.

Figure 1*b* shows the range of band-sharing coefficients between first-order relatives and between birds known to be unrelated. Also shown are the lower 99% confidence interval (0.54) for closely related birds, and the upper 99% confidence interval (0.44) for unrelated birds. We used these limits to assign a further five females and nine males as parents of the remaining 18 juveniles, in cases where a breeder of the opposite sex was missing from our sample. These assignments were conservative; for example, parentage was only assigned if there was one adult individual that had a band-sharing coefficient with the juvenile that was within the range of first-order relatives, and it was impossible that any missing birds were of the same sex (e.g. we knew we were only missing a breeder of known sex). We also used these confidence intervals to infer the relatedness between birds of unknown origin that joined known groups of choughs.

(c) *Group composition*

We studied 19 groups ranging in size from four to 14 members (table 1). These included ten groups for which we had long-term information (between two and five group years), and nine newly amalgamated groups that included previously banded birds. Four of the long-term groups that fragmented during the drought (White, Red, Small Orange and Tidbinbilla) were never observed breeding, but are included in table 1 to show group composition.

Within each group, we used band-sharing confidence intervals (figure 1*b*) to assign individuals to various factions (either single birds or coalitions) of first-order relatives. The number of such factions ranged from one to four in long-term groups (mean $= 2.40 \pm 0.47$ s.e.); in one case, the breeding pair were themselves closely related (Orange group, table 1). The number of factions in the new groups (range 2–7, mean $= 4.22 \pm 0.50$ s.e.) was significantly greater than that for long-term groups ($t_{17} = 2.65$, $p = 0.017$).

(d) *Reproductive skew*

All juveniles in the long-term groups were produced by monogamous pairs (41 young over 19 group-years), while multiple parentage (including polyandry and polygynandry) occurred in five out of nine new groups that formed after the drought (27 young over nine group-years; table 1). Thus, breeding skew for males was greater in long-term (mean $= 1.0$) than in new groups (0.64; Wilcoxon $\chi^2 = 5.1$, d.f. $= 1$, $p = 0.02$). There was no such trend for females (1.0 and 0.95, respectively; Wilcoxon $\chi^2 = 0.75$, d.f. $= 1$, $p = 0.39$).

In our sample of 61 factions of relatives, there was never more than one breeder of the same sex per faction (table 1). Thus, as the number of factions in each group increased, breeding was more likely to be shared among, rather than within, the factions. In other words, the number of breeders was related positively to the number of factions in the group ($F_{1,13} = 19.36$, $p < 0.001$, figure 2*a*), but this was not simply a consequence of group size ($F_{1,13} = 0.02$, $p > 0.50$, figure 2*b*). In the most extreme case of multiple parentage, which was also the only case where more than one female bred, one brood of four nestlings

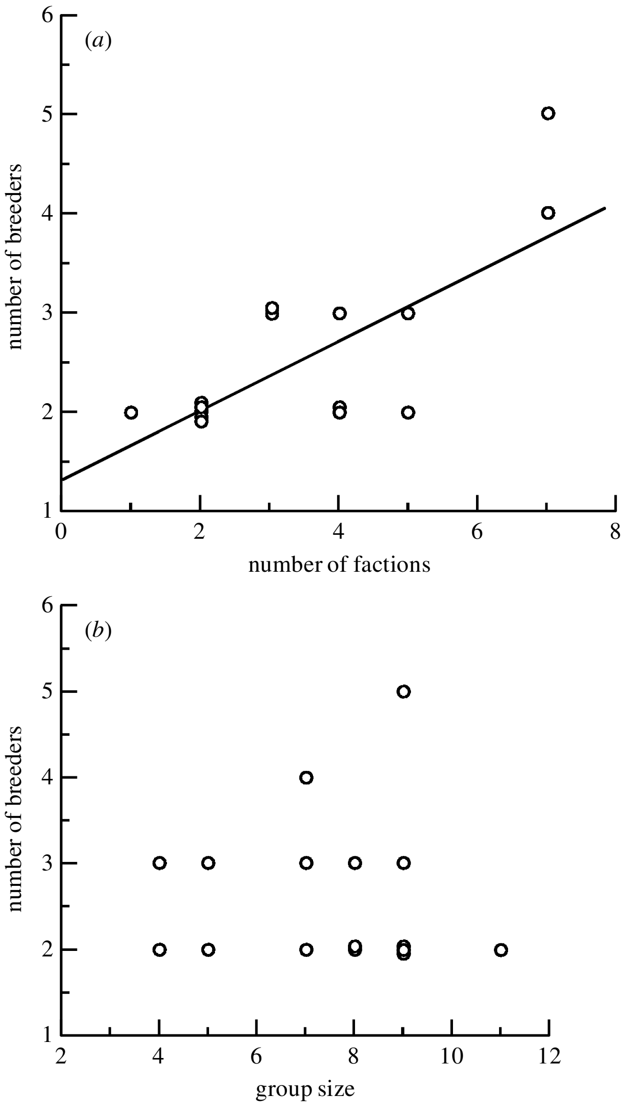

Figure 2. The number of breeders in a group during the breeding season 1995 compared across (*a*) the number of factions of relatives in the group, and (*b*) group size.

had three mothers and two fathers. Interestingly, the clutch on this occasion was unusually large, having seven eggs (a single female normally lays four), but this was reduced to four through egg-tossing. All other cases of within-sex sharing were by males.

Although usually of breeding age, 13 out of 17 non-breeding members of factions (new groups, table 1) were known to be younger than the breeders they were supporting. This age difference suggests they may have been behaviourally subordinate to the breeders. The remaining four individuals were caught as adults so it is uncertain whether they were also younger than the breeders in their coalition. Unlike adults, juveniles were always in multimember factions (table 1), and clearly do best to support relatives until they reach breeding age.

(e) *Reproductive success in new groups*

Overall the members of 12 out of 38 (32%) factions amongst the nine newly amalgamated groups failed to gain reproductive success, either directly or indirectly through relatedness to a breeder. Multimember factions always attained reproductive success for one of their members (eight out of eight cases; table 2). However, there were markedly different results for each sex when individuals did not have support from relatives (table 2). Only one out of eight females without support from relatives failed to gain reproductive success, compared with 11 out of 22 unsupported males ($G=3.85$, d.f. $=1$, $p=0.049$). Although sample sizes are too low to compare statistically, males without family support fathered a mean of 0.95 ± 0.23 s.e. young ($N=22$) in the first breeding season, compared with 1.50 ± 0.54 s.e. ($N=4$) for males with support. In contrast, females without supporting relatives appeared no less successful (mean $=2.25\pm0.64$ s.e. offspring, $N=8$) than females in multi-member factions (mean $=2.25\pm0.90$ s.e. offspring, $N=4$) because they nearly always gained a breeding position.

Table 2. *The success of single individuals, and coalitions supporting both male and female breeders, at gaining reproductive success within newly amalgamated groups in their first season together*

(Note that breeders in coalitions may be supported by individuals of either sex; thus 'total individuals' in coalitions includes both sexes. All values are calculated from data in table 1. The range of offspring produced per breeder is given in parentheses. See §3(e) for calculation of additional offspring equivalents per helper.)

	females		males	
	single	coalitions	single	coalitions
successful	7	4	11	4
unsuccessful	1	0	11	0
total individuals	8	12	22	13
offspring per breeder	2.25 (0–6)	2.25 (1–5)	0.95 (0–3)	1.50 (1–2)
additional offspring equivalents per helper	—	0.00	—	0.12

The major consequences of these results are (i) that males appear to benefit more than females by having supporting relatives, and (ii) that helping a related male, but not necessarily a female, has indirect fitness benefits. This amounts to an additional 0.12 offspring equivalents per helper in the average multimember faction, which is calculated as the difference in the breeder's expected success with (1.50) and without (0.95) support, divided by the number of helpers in the faction. This figure was then halved to allow for the fact that any additional young are only related by 0.25 (e.g. half siblings) rather than 0.5 (table 2).

4. DISCUSSION

High mortality during the 1994 drought appears to have broken down the usual fabric of chough society. This period of flux provided an excellent opportunity for assessing the factors affecting reproductive success and skew within groups, especially sex, relatedness and faction size. Before the drought in 1994, we had never observed groups to fragment, or even for individual choughs to disperse from their natal groups. It is clear, however, from our band-sharing coefficients that even most of our long-term groups (table 1) consisted of factions of closely related individuals that presumably originated from other groups. Choughs thus appear to be characterized by long-term stability, with occasional breakups and reformation of groups. All offspring from these groups were produced by monogamous pairs (i.e. skew was high) with the remainder of each group acting as helpers. In the most extreme case, one pair, who were themselves closely related, were the parents of all other 12 group members, spanning at least five years of reproduction. In contrast, the newly amalgamated groups after the drought were characterized by a larger number of factions, and faction number was a good predictor of the number of breeding individuals in a group (figure 2).

The large number of helpers distributed across varying sized factions of relatives makes testing predictions from models of skew in three-member groups (Johnstone *et al.* 1999) a dubious exercise. Instead, we draw attention to two apparently overriding rules for reproductive skew within these amalgamated groups. First, reproduction is shared between many (but not all) factions, consisting of either single choughs or coalitions of family, that represent distinct genetic interests. Second, at most one member of each faction succeeds in breeding, with subordinates relying instead on indirect reproductive benefits.

The advantages to male and female choughs of having support from relatives when new groups are formed can be analysed in terms of the total inclusive fitness gained. Although some of the classic studies of cooperative breeders have shown that individuals disperse in coalitions (Koenig & Pitelka 1981; Ligon & Ligon 1990), only one has used molecular techniques to evaluate reproductive skew within dispersing units. Packer *et al.* (1991) showed that male lions, *Panthera leo*, often disperse from their natal prides in coalitions of relatives. Males must be in coalitions of at least two to successfully takeover and maintain a pride of females and, if necessary, will form coalitions with unrelated males. Skew can be high in coalitions of relatives, but is always lower when coalitions are made up of non-relatives.

Choughs were only ever observed forming initial coalitions with related individuals, and like lions, skew between related coalition members was always high (table 1). However, most newly amalgamated chough groups had more than one rival male faction (either single males or coalitions supporting a male), possibly reflecting a general shortage of females (e.g. Pruett-Jones & Lewis 1990). Aggression was generally heightened in new groups, many potential collaborations failed (R. Heinsohn, unpublished data), and many males without factional support failed to gain reproductive success (table 2). Males, but not necessarily females, clearly do best if they are supported by relatives, and conversely, subordinates gain greater rewards if they help male relatives to secure a breeding position. Our analysis shows that, for a male, the potential rewards from competing alone are greater than those for helping. However, high variance caused by the large number of failures (i.e. 50%) makes competing alone a risky strategy. It is likely that both availability of help and individual quality (e.g. age) determine the costs and benefits of either joining a coalition or competing alone. Interestingly, many of the single males (e.g. most members of the Mafia) originated from groups consisting of close kin. Their reasons for not dispersing in coalitions (e.g. aggression–dominance interactions) remain unclear.

Sharing of reproduction between rival factions in new groups may simply reflect the lack of an established dominance hierarchy (e.g. Lundy *et al.* 1998). Alternatively, such mutual tolerance may reflect the disadvantages of being in small groups. Large groups (e.g. 12 birds) often destroy the nests and kidnap the young of smaller groups (e.g. four birds; Heinsohn 1988, 1991*b*); indeed one group (the Mafia, table 1) destroyed seven reproductive attempts of neighbouring groups before breeding themselves. There were also a small number of amalgamations of unrelated females, but in only one case did more than one female attempt to lay eggs in the same nest, and this involved egg-tossing. The willingness of males but not females to share reproduction probably reflects the greater difficulty and general rarity of dividing reproduction in females (Koenig *et al.* 1995; Cant 1998). It is, however, unclear from our data why a small number of adult females chose to support relatives, when their sex appeared to be in demand for breeding.

We have noted previously that unassisted pairs, and even pairs with one helper, have great difficulty in reproducing, and that reproductive success increases in all larger group sizes (Heinsohn 1992). Following Ligon (1983), we also hypothesized that older helpers aim to inherit at least some of the group to aid in their eventual reproduction (e.g. Heinsohn 1991*b*; Boland *et al.* 1997*b*). This paper confirms the dual advantages of both having help and, for a subordinate, helping a relative to gain a reproductive position. It is interesting that our long-term groups consisted of fewer factions (usually just two, table 1), most of which contained a successful breeder, whereas many of the newly formed groups had multiple factions with multiple parentage, together with many unsuccessful factions. Clearly, there is a period in which factions jostle for at least a share of reproduction, and those that fail may leave to try breeding elsewhere. An understanding of the factional politics behind such decisions will clearly be a rewarding area for study.

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