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Subordinate males are more likely to help if unrelated to the breeding female in cooperatively breeding white-browed scrubwrens

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Abstract Subordinates in communally breeding groups of birds usually help to provision nestlings, but in some species helping-at-the-nest is facultative. In species in which groups usually contain relatives, subordinates either always feed young or are more likely to do so when breeding dominants are close relatives, suggesting that benefits of helping collateral kin are important. In other species, adult group members are unrelated to each other and males may only feed young if they have gained paternity, showing that cooperation is related to the mating system. The white-browed scrubwren, *Sericornis frontalis*, is a communally breeding species in which most groups consist of a simple pair or a dominant pair with a subordinate male. Subordinate males either fed nestlings in a given nest at a rate comparable to the dominants, or did not feed them at all. Breeding groups usually formed through natal philopatry of males, so that about 80% of subordinates were closely related to one or both members of the dominant pair. However, because of death and dispersal, 54% of subordinates were unrelated to the resident female. Although subordinates with their mother fed nestlings in 48% of cases, they fed offspring in 75% of cases if their mother had been replaced by an unrelated female, suggesting that their decision to help is influenced by the opportunity to mate with the female. Supporting this conclusion, relatedness to the dominant male did not affect subordinate behaviour, and genetic studies showed that subordinates often gained paternity if unrelated to the female. Thus, paradoxically, provisioning nestlings is related to the opportunity for mating in a society in which there is natal philopatry and subordinates are usually related to one or both members of the dominant pair.

Key words Cooperative breeding · Mating systems · *Sericornis frontalis* · Helpers · Kin selection

Introduction

In most species of birds, only members of a breeding pair cooperate to provision young, but in "cooperative" (or communal) breeders, more than a single pair provision offspring from a brood (Brown 1987; Lack 1968). Potential benefits to subordinates of provisioning offspring involve direct benefits, or indirect benefits of increasing the reproductive success of relatives (Brown 1987; Emlen and Wrege 1989). Direct benefits to the subordinate can involve current reproduction within the group, or increased probability or success of future reproduction. Indirect benefits can involve increasing the current reproductive success of relatives or the probability that relatives survive to breed in future.

Breeding groups in cooperative species are most commonly established when young remain in their natal territory or colony (natal philopatry) as subordinates to a breeding pair (Brown 1987; Hartley and Davies 1994; Stacey and Koenig 1990), so that indirect benefits of provisioning young ("helping" following Brown 1987) are potentially important. Subordinates in these species usually help (Koenig and Mumme 1990), but in some species helping is facultative, with subordinates more likely to provision the young of breeders that are closer relatives (bell miner *Manorina melanophrys,* Clarke 1984; probably noisy miner *M. melanocephala*, Poldmaa et al. 1995; Galápagos mockingbird *Nesomimus parvulus*, Curry 1988; white-fronted bee-eater *Merops bullockoides*, Emlen and Wrege 1988; Florida scrub jay *Aphelocoma c. coerulescens*, Mumme 1992; Seychelles warbler *Acrocephalus sechellensis*, Komdeur 1994; western bluebird *Sialia mexicana*, Dickinson et al. 1996).

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In contrast to societies formed through natal philopatry, breeding groups in some species consist of individuals that are unrelated to each other (e.g. dunnock *Prunella modularis*, Davies 1992; alpine accentor *P. collaris*, Hartley et al. 1995; Smith's longspur *Calcarius pictus*, Briskie 1992; one population of pukeko *Porphyrio porphyrio*, Jamieson et al. 1994; brown skua *Catharacta lonnbergi*, Millar et al. 1994; Galapagos hawk *Buteo galapagoensis*, Faaborg et al. 1995). In these species, groups typically contain more than one male, and all adults are unrelated to each other because they come together after dispersing from their natal territories. Thus there is no possibility of gaining indirect benefits through the production of non-descendent kin. All males within a group may copulate with the female and DNA fingerprinting has shown that they frequently share paternity (where quantitative estimates were available, beta males sired from half as many to equal numbers of young as alpha males). In the dunnock and alpine accentor, whether a subordinate helps at a nest depends on whether he has copulated with the female, and is therefore likely to have sired offspring (Davies 1992; Hartley et al. 1995), showing that cooperation is related to the mating system. Benefits of cooperation in these species may also include those not directly related to reproduction (Faaborg and Bednarz 1990).

Facultative helping is potentially most informative about the evolution of cooperative breeding in species in which there is variation in relatedness of subordinates to members of the dominant pair, and where both indirect benefits and direct reproduction could be important. Recent genetic analyses have confirmed that male "helpers" sometimes gain paternity within their group even in species in which groups form through natal philopatry and therefore typically contain relatives. Reproduction by male subordinates usually occurs when their mother has been replaced by an unrelated stepmother, thereby lifting any incest restriction (stripe-backed wrens *Campylorhynchus nuchalis*, Piper and Slater 1993, Rabenold et al. 1990; bicolored wrens *C. griseus*, Haydock et al. 1996; superb fairy-wrens *Malurus cyaneus*, Dunn et al. 1995). Nonetheless, paternity gained by subordinates within groups is relatively uncommon in these species (2–10% of nestlings within groups overall) and is therefore unlikely to explain the evolutionary origin or maintenance of cooperation. Furthermore, helping in these three species is universal, not facultative, so the pattern of helping is not informative about the maintenance of cooperative breeding.

We studied the white-browed scrubwren, *Sericornis frontalis*, a cooperatively breeding species in which subordinates, which are male, may or may not help at the nest. Groups normally form through natal philopatry of males, so subordinates are usually related to one or both of the members of the dominant pair. Nonetheless, because of deaths, social re-arrangements and occasional natal dispersal of males, there is variability in relatedness among members of social groups. DNA-fingerprinting has shown that subordinate males can gain paternity in groups in which they are unrelated to the resident female, but not in groups with their mother (Whittingham et al. 1997). Thus helping by subordinates could be related to the indirect benefits of helping kin or to direct benefits through current or future reproduction. If cooperation was based solely on indirect benefits, subordinates should be more likely to help at the nests of their mother and father, than at nests where they are unrelated to one or both dominants. By contrast, if cooperation was based solely on mating opportunities, subordinates should help only at nests of unrelated females, possibly regardless of their relatedness to the dominant male. If both direct and indirect benefits were important, helping may be equally common regardless of whether the subordinate male is related to the female.

Materials and methods

Study population

We studied white-browed scrubwrens from 1992 to 1995 in the Australian National Botanic Gardens in Canberra. Scrubwrens are small (*c.* 11–15 g), largely-insectivorous passerines in the family Pardalotidae (Sibley et al. 1988), and are common throughout southern and eastern Australia in habitats with dense undergrowth (Blakers et al. 1984). Females, which have brown lores, lay three eggs in a clutch and fledge up to three broods during the breeding season (July–March). Males, which have black lores, do not help with nest-building or incubation but often feed young, which remain in the nest for about 15 days. All adults and their offspring in the population were marked with unique combinations of colour-bands and had a blood sample taken for DNA fingerprinting (Whittingham et al. 1997). The number of breeding groups ranged from 35 to 53 per year. Breeding seasons are identified by the year in which they started.

Breeding groups

The birds are resident throughout the year, and during the breeding season we visited territories at least three times a week to document group composition, dominance among males and reproductive attempts. A group was defined as all of those individuals sharing a common territory. We determined dominance ranks among males by recording interactions: dominant males displaced and sometimes chased subordinates. Dominance was stable during breeding attempts and from year to year, with older males being dominant to younger ones (unpublished).

Scrubwrens most commonly bred in pairs (46% of groups) or in trios consisting of a socially dominant pair and a subordinate male (44%), although 7% of groups had two subordinates, 2% had three and 1% had four. These figures refer to group composition at the time of hatching of the female's first brood for a season, including 169 group-years (number of groups in each year summed over years). Males often remained as subordinates on their natal territory (Results), while females always dispersed. Males rarely (1/62 yearlings) gained a breeding vacancy as a pair male or dominant (alpha) male in their first year.

DNA-fingerprinting carried out on a subset of groups in 1992 and 1993, showed that subordinates sired 32% of 50 nestlings in ten groups in which they were unrelated to the female; in these same groups alpha males sired 58% and unidentified extra-group males sired 10% of nestlings (Whittingham et al. 1997). By contrast, when the subordinate's mother was present in the group, the beta male did not sire any young within the group; all were sired by the alpha male ($n = 37$ nestlings in eight groups).

Provisioning of nestlings

We measured the rates that adults fed nestlings during hour-long watches, usually when the nestlings were 7–11 days old. Whenever possible, each nest was watched on three (occasionally more) different days, at 2-day intervals, although a high rate of depredation meant that many nests were watched on fewer occasions.

Age of subordinates

The decision by subordinates to help in cooperatively-breeding species can be influenced by their age (e.g. Curry 1988; Heinsohn and Cockburn 1994). Subordinates are likely to be older, on average, in groups in which members of the original family have died and been replaced by immigrants (e.g. Galápagos mockingbird; Curry 1988), and so age could easily confound the relationship between helping and relatedness. It is therefore important to consider age when examining the association between helping and kinship.

A subordinate's age was known if he was banded in the nest or if he had at least some juvenile plumage (Rogers et al. 1986) when first captured. A bird was considered to be "1 year old" throughout the breeding season following hatching, and so on for older ages. Only subordinates of known age were included in analyses in which the effect of age was assessed.

Relatedness of subordinates to dominant pair

We used a combination of pedigrees and band-sharing from DNA-fingerprinting to determine relatedness of subordinate males to members of the dominant pair (methods in Whittingham et al. 1997). Individuals were considered "unrelated" (not first-order relatives) if their band-sharing was <0.330, the lower, one-tailed 99% confidence limit for band-sharing between mothers and their (genetic) offspring. Individuals were considered to be "related" if their band-sharing was >0.346, the upper, one-tailed 99% confidence limit between females and their mates, which were assumed to be unrelated. Since there were no cases in which band-sharing was between these values, all females and dominant males could be classified as "related" or "unrelated" to each subordinate.

Pedigree and fingerprinting data were consistent in identifying whether the resident female was a subordinate's mother (n = 29 subordinate:female dyads). Furthermore, DNA-fingerprinting of 137 nestlings in 31 social groups revealed no egg-dumping in this population (Whittingham et al. 1997).

In pedigree analyses, we assumed that offspring raised by a group were first-order relatives (sons or brothers) of all resident males. To estimate the errors associated with this assumption, we examined subordinate:alpha dyads where both pedigree and DNA-fingerprinting data were available, assessing extrapolations from social to genetic relatedness and *vice versa*. Of 15 socially related dyads 12 were also genetically related. The three inconsistencies (20%) arose because the subordinates were sired by a different male in the natal group, which fingerprinting had shown to be unrelated to current alpha male. Both socially unrelated dyads were also genetically unrelated. Three of five (60%) genetically unrelated dyads were socially related; all 14 genetically related dyads were socially related.

Statistical analyses

We used the SPSS statistical package (Norusis 1995a,b) for all data management and most analyses, and Genstat 5 (Genstat 5 Committee 1993) for logit models of subordinate behaviour.

Subordinates were classified each year as "helpers" or "non-helpers" depending on whether they did or did not provision nestlings in at least one nest of a female in that breeding season (given the opportunity to do so). It was not possible to classify the behaviour of a subordinate in a year if the group had a string of reproductive failures before nest-watches could be carried out. Juveniles, which rarely fed nestlings and were usually still with their parents, were excluded from analyses.

We used logit modelling to examine the effect on helping (help or not) of relatedness to the female (mother or unrelated), relatedness to the male (close relative or not) and age (first-year or older). Age was dichotomized because there were few subordinates of known age over two years. A subordinate provided only one case in an analysis for any category relevant to the analysis. For example, in the analysis considering only the effect of the female on helping behaviour, a subordinate could be counted only once when in a group with his mother and only once when with an unrelated female, even if the subordinate was with the same female for several years or with different unrelated females in different years. Observations from different years were incorporated by modelling the proportion of years helped assuming a binomial error distribution. In analyses which considered more factors, we considered yearly values to be independent if there was a change between years in any factor. For example, a single subordinate would contribute three values to an analysis if he was in a group with his mother as "first-year" and then an "older bird", and then in a group with an unrelated female.

The effect of different factors on helping was assessed by first fitting full models, and then progressively eliminating non-significant terms. The effect of a "non-significant" variable of interest is reported as the effect of dropping that term from a model from which less-significant terms had already been eliminated. In all cases, the effect of a term was assessed as the change in deviance from dropping that term. As the deviance approximates a χ^2 distribution, values are reported as χ^2 values.

The logit analyses were complicated by missing values, so we assessed a series of models. We first assessed a model with all factors, but then repeated analyses after excluding the least significant variable ($P > 0.1$), making it possible to include more cases. The process was repeated to produce the simplest model, with the fewest cases excluded.

Results

Group composition and formation

Subordinates were related to both dominants (nuclear families) in 44% of groups, the female alone (stepfather group) in 2%, the alpha male alone (stepmother group) in 38%, and to neither dominant (unrelated group) in 16% (Table 1). Table 1 uses pedigree information if available and band-sharing if it is not (criteria given above).

While Table 1 shows true relatedness to the female, there are two sources of error in determining social and genetic relatedness of subordinates to dominant males. First, a dominant male shown to be a social relative by pedigree analyses may be genetically unrelated (estimated at 20%, above) and, second, a dominant male shown by DNA fingerprinting to be unrelated may be a social relative (estimated at 60%, above). We therefore used the observed discrepancies between social and genetic relatedness to estimate "true" social and genetic relatedness. For example, 17 of the 28 "nuclear" groups in Table 1 were classified as such from pedigree analyses alone, so we estimated that 3.4 (20%) of these were genetically "stepfather" groups. Similarly, 4 of the 10 "unrelated" were classified from fingerprinting alone, so we estimated that 2.4 (60%) of these were socially "stepmother" groups. Overall, we estimated that 86% of

Table 1 Composition and formation of scrubwren groups. Type of group is defined by social relatedness, from pedigree analysis if available, of subordinate to female and dominant male. Sample size is the number of unique subordinate:female:dominant male groups. When the history was unknown, group type was determined by DNA fingerprinting.

Type of group	*n*	%	How formed (with sample size)
Nuclear (mother and related male)	28	44	25 – Natal philopatry 3 – Unknown history
Stepfather (mother and unrelated male)	1	2	1 – Subordinate re-joined natal group after father replaced by immigrant dominant
Stepmother (unrelated female and related male)	24	38	18 – Mother replaced by immigrant 4 – Dominant & subordinate together joined unrelated female 1 – Adjacent territories coalesce after mother disperses 1 – Unknown history
Unrelated (unrelated female and unrelated male)	10	16	6 – Immigrated alone into group 1 – Immigrated with unrelated dominant (previous history unknown) 3 – Unknown history

subordinates were with a socially related alpha male and 88% with at least one social relative, and 69% with a genetically-related alpha male and 79% were with at least one genetic relative.

Natal philopatry of males led to nuclear families if there were no other social changes. Stepmother groups usually arose when the original female had been replaced by an immigrant, although occasionally related males dispersed together to an adjacent territory (Table 1). Groups in which males were unrelated arose primarily through immigration by males into subordinate positions in existing groups.

As expected from the mode of group formation, subordinates tended to be younger in nuclear families than other types of group. In nuclear families 72% of 32 subordinate-years involved first-year subordinates, while in other types of group only 46% of 35 subordinate-years involved first-year subordinates. (A "subordinate-year" is the datum from a subordinate in a given year; individuals were represented once for each year they contributed data.) Since this study started in the breeding season of 1992, most subordinates of known age were 1, 2 or 3 years old (one banded in a pilot year was known to be 4 years old), but records of birds of unknown exact age (n = 23 subordinate-years) showed that three males were subordinates when at least 5 years old.

Facultative helping behaviour

Subordinate males either fed nestlings at a rate comparable to the dominants, or they did not feed at the nest at all (Fig. 1). There was a mean number of 2.4 watches per nest for each of the 107 subordinate feeding rates represented in Fig. 1 (mode 3; range 1–5). An individual's behaviour (fed at nest or not) was consistent between watches at a nest: individuals did not differ between the first and second watches in 96% of 71 cases for females, 93% of 71 cases for alpha males and 94% of 88 cases for subordinates. Furthermore, individual subordinates behaved consistently at a nest. Given the overall probability of helping over the two watches for subordinates (P = 0.51), random variation between days would result in 50% consistency [i.e. $p^2+(1-p)^2$], significantly less than the observed 94% ($\chi^2 = 69, df = 1, P < 0.0001$; goodness-of-fit test with binomial expected frequencies of consistent and variable behaviour between watches).

Helping and relatedness

Relatedness to female and dominant male

Subordinates were *less* likely to help at nests of their mother than at nests of unrelated females (mothers: 48%, n = 30; unrelated: 75%, n = 38; χ^2 = 7.0, df = 1, P = 0.008).

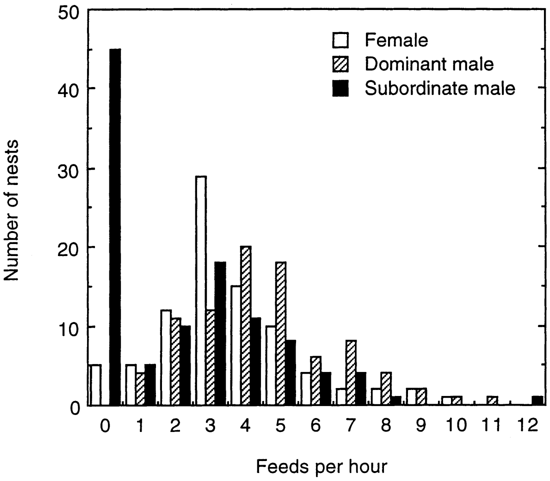

Fig. 1 Frequency distributions of feeding rates to nestlings by scrubwrens in groups which included one or more subordinates. Data were included only if the identity of feeders was know for at least 90% of visits to the nest, and come from 87 nests (n = 87 feeding rates by females and alpha males) associated with 107 feeding rates by subordinates, from 45 different dominant pairs and 55 different subordinates. The rounded mean number of feeds is shown if there was more than one watch at a nest

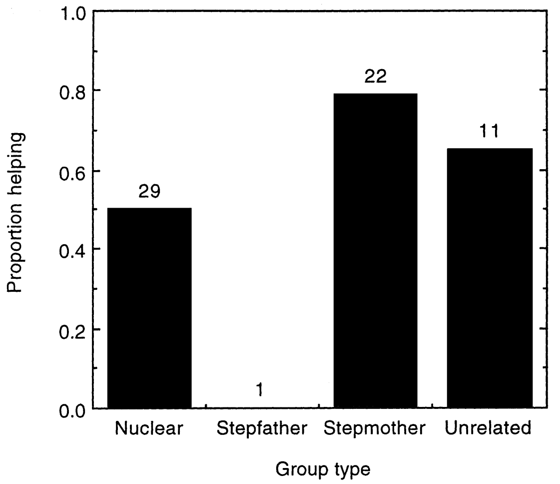

Fig. 2 Mean proportion of subordinate males feeding at nests according to the type of group in which they lived (*nuclear* mother and related male, *stepfather* mother and unrelated male, *stepmother* unrelated female and related male, *unrelated* unrelated female and unrelated male). *Sample sizes* are given above the *bars* (maximum of one case per subordinate in any one group type). See text for statistical analyses

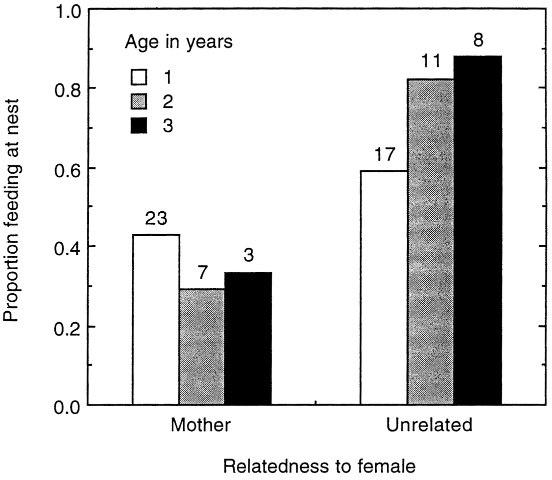

Fig. 3 Proportion of subordinate males of known age feeding at nests, according to their age and relatedness to the resident female. Sample sizes in subordinate-years are given above the bars. The single 4-year-old (a non-helper with an unrelated female) was grouped with the 3-year-olds

In analyses including the effect of relatedness of the subordinate to both the female and alpha male (Fig. 2; $n = 63$ cases), there was no effect of relatedness to the male either directly ($\chi^2 = 1.5$, $df = 1$, $P = 0.2$) or in an interaction with female relatedness ($\chi^2 = 0.8$, $df = 1$, $P = 0.4$). The interaction term was dropped before assessing the direct effect of male age.

The data shown in Fig. 2 also allow two contrasts, in which there is either a change in relatedness to the female or to the male. Subordinates were more likely to help in stepmother groups than in nuclear families ($\chi^2 = 6.0$, $df = 1$, $P = 0.01$), which involved a change only in female relatedness, but subordinate behaviour did not differ between stepmother groups and groups in which they were unrelated to both dominants ($\chi^2 = 0.9$, $df = 1$, $P = 0.3$), which involved a change only in male relatedness.

Does age confound the relationship?

Dichotomized age (yearling or older) had no effect on helping, either directly ($\chi^2 = 0.5$, $df = 1$, $P = 0.5$), through an interaction with female relatedness ($\chi^2 = 2.5$, $df = 1$, $P = 0.12$) or male relatedness ($\chi^2 = 0.2$, $df = 1$, $P = 0.7$). The effect of each term was assessed after dropping the terms that follow it in the list; $n = 61$ cases.

Although logit analyses found no effect of a subordinate's *dichotomized* age on his behaviour, there is still the potential for age to confound the relationship between helping and relatedness to the female. Dichotomizing age into "first-year" versus "older" could confound the relationship between helping and relatedness if 3-year-old subordinates were more likely to help than 2-year-olds and were over-represented in the sample of "older" subordinates with unrelated females. In fact, subordinates with their mother do tend to be younger (above), so it is important to examine the probability of helping for 2-year-old and 3-year-old subordinates separately.

Figure 3 shows that age does not confound the relationship between helping and relatedness to the female. At each age, subordinates were more likely to help unrelated females than their mother. Furthermore, if there is any (undetected) age effect, it lies between first-year and older birds, not within the "older" category.

Pairwise comparisons

We carried out pairwise comparisons of subordinate behaviour in their first and last years of observation, according to whether they lived only with their mother, or with their mother and an unrelated female in the different years. Of the seven subordinates in groups with their mother only, three fed nestlings in neither year, three fed in both years and one changed from not feeding in the first year to feeding in the last year. Of the other seven subordinates, one fed in neither year, three fed in both years and three fed at nests of unrelated females but not at nests of their mother. There was no case of a subordinate feeding at the nest of his mother and not feeding at the nest of an unrelated female. Overall, of these 28 cases (14 subordinates observed in 2 years), subordinates fed 48% of the time (10/21) when with their mother, and 86% of the time (6/7) when with an unrelated female, which are similar to the overall results, using all 68 cases, of 48% and 75% respectively (above).

Discussion

Helping is related to the mating system

This is the first description of an avian society in which subordinates in communal groups are *less* likely to help feed nestlings if they are more closely related to the dominants. Subordinates were less likely to feed their mother's nestlings (48% of cases) than those of an unrelated female (75%). A subordinate's age did not confound this relationship. Pairwise analyses of individual subordinates in groups with their mother and unrelated females in different years, although based on a small sample, showed the same pattern because some subordinates changed from not feeding nestlings of their mother to feeding nestlings of an unrelated female.

In the majority of communally-living species, philopatric young help if they are present, even if there is variable relatedness to the dominant pair. This issue is explicitly addressed in studies of stripe-backed wrens (Rabenold 1985) and superb fairy-wrens (Dunn et al. 1995). In those few kin-based societies in which individuals may or may not help, subordinates are *more* likely to help if they are more closely related to the dominants (Introduction).

Subordinate males were more likely to help feed nestlings if unrelated to the female, but were not affected by relatedness to the dominant male, which suggests that subordinates gain paternity in groups in which there is no incest restriction. This conclusion is supported by genetic analyses of paternity (Whittingham et al. 1997). In a subset of the groups included in this study, subordinates never mated incestuously, yet frequently gained paternity in groups in which they were unrelated to the resident female (above).

Subordinate behaviour could be affected by the mating system in two ways. First, subordinates might base their decision to help on their "estimate" of paternity in the current brood. For example, this is the case for dunnocks, where both the decision to help and the amount of help is related to a subordinate male's access to the female during her fertile period (Davies et al. 1992). Secondly, subordinate behaviour might be related to the longer-term opportunity for polyandry in that group type, without being related to an estimate of paternity in particular broods. For example, helping at the nest might increase the probability of copulating with the female in future breeding attempts, even in later years. Male pied kingfishers *Ceryle rudis* that act as helpers to unrelated breeders ("secondary helpers") are likely to pair with the female the following season (Reyer 1990). Carlisle and Zahavi (1986) and Wagner et al. (1996) have also argued that provisioning nestlings can be a sexually selected character that increases future mating success. Genetic and field work in progress will be used to assess the effect of realized paternity and opportunity for paternity on both the decision to help and quantitative variation in provisioning.

Subordinates help for more than one reason

Despite the overall pattern that feeding by subordinates is related to their opportunity for mating, half the subordinates did provision nestlings of their mother. In this circumstance subordinates never gained paternity, so that helping in these cases is not related to the mating system, and might be related to indirect benefits of helping kin or direct benefits other than mating within the group (e.g. helping may provide experience that translates into higher reproductive success in future breeding attempts; Komdeur 1996). Thus different subordinates help for different reasons, as both the mating system and other (unidentified) benefits appear to be important.

Subordinate behaviour is paradoxical

Scrubwren society is extraordinary in that subordinates often do not feed their mother's offspring, yet usually do help when they have the potential to sire some offspring. Thus cooperation is related to the mating system in a society in which subordinates are usually (about 79% genetically and 88% socially) related to one or both dominants. The occurrence of polyandry itself, given the lifting of an incest restriction, is not surprising. Polyandry has been confirmed in other kin-based societies (Introduction), and is incorporated into a general evolutionary model of the family (Emlen 1995). The real puzzle is why subordinates often fail to help close relatives, resulting in the paradox that helping tracks the opportunity for mating despite kinship of subordinates with one or both dominants in most groups.

The high opportunity for mating by subordinate scrubwrens (54% unrelated to the female) does not explain why subordinates often do not feed their mothers' offspring. Deaths and social fluidity can give similar mating opportunities in other kin-based societies, and yet the pattern of feeding does not follow the opportunity for mating. Amongst species in which male subordinates have been shown to gain paternity within the group, about 67% of stripe-backed wren groups had one or more helpers unrelated to the female (Piper and Slater 1993) and 47% of superb fairy-wren helpers were in groups with unrelated females (Dunn et al. 1995), yet helping is universal in both species.

We suggest that there is no strong, consistent benefit of "helping" kin. The fact that half the subordinates provisioned at nests of their mother suggests that there might be some benefit to helping kin, at least in some territories or years, but analyses of 4 years' data detected no overall effect of group size or feeding at the nest on reproductive success in scrubwren groups (Magrath and Yezerinac 1997). These data are correlational, but the most likely confounding variables in a society based on natal philopatry would emphasise rather than diminish a positive correlation between group size and reproductive success (Brown 1987). For example, pairs on better territories could produce more offspring, which then remain in following years as subordinates, leading to larger groups being found on better territories.

We do not know why half of the subordinates helped feed nestlings of their mother while others did not. We suggest that it could relate to variation in: (1) territory quality, (2) behaviour of dominants, (3) subordinate quality, (4) opportunities for gaining a breeding vacancy, or (5) a combination of these. For example, subordinates in good condition may be more able to "afford" to help, and thereby derive benefits such as gaining experience (e.g. Komdeur 1996). We do not yet have the data to test these ideas.

If helping by subordinates has little or no effect on the reproductive success of the group, why did subordinates usually feed the young of unrelated females? There are several possibilities (Emlen and Wrege 1989). For example, "helping" may be a form of courtship of the female which increases the chance of gaining copulations (above), or a compensation response to lower feeding rates by dominant males that have lost paternity (Davies et al. 1992).

General implications

These findings on scrubwren society have general implications for the study of communal breeding. First, they suggest it can be misleading to dichotomize (e.g. Hartley and Davies 1994) avian societies into those in which provisioning at the nest depends primarily (or partly) on non-descendent kinship and those in which helping depends on shared paternity. Acorn woodpeckers, *Melanerpes formicivorus*, also fit uncomfortably into any dichotomy, because of variability in the mating system, mode of group formation and relatedness among adult members of social groups (Stacey 1982; Koenig et al. 1984). Hartley and Davies' "dichotomy" may reflect end-points of a continuum in social behaviour, best analysed using recent models of family dynamics (Emlen 1995), or semi-discrete categories reflecting different evolutionary origins (Brown 1987).

Second, these findings suggest a novel hypothesis to help account for the puzzle that feeding at the nest by subordinates is often "universal" in kin-based societies, despite variation in relatedness of "helpers" to the dominant pair. Universal feeding has been interpreted to follow from some simple but imperfect "rule of thumb" for identifying relatives (Rabenold 1985), provide evidence that feeding is non-adaptive (Jamieson 1991), or be the result of dominants forcing subordinates to "pay rent" to be allowed to stay on the natal territory (Mulder and Langmore 1993; Dunn et al. 1995). We suggest that in many species universal feeding could be the result of different individuals feeding for different reasons, and that each individual's behaviour depends partly on a trade-off between kinship and mating benefits. When the dominant pair consists of close relatives, the benefits to subordinates of feeding can follow (at least partly) from non-descendent kinship, but with decreasing relatedness to the dominant pair the possibility of gaining reproduction within the group becomes an increasingly important reason for feeding. A contrast between kinship and (future) mating opportunities as reasons for feeding has been described for the colonial pied kingfisher, *Ceryle rudis* (Reyer 1990), supporting this general hypothesis.

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