

Reproductive success and helper effects in the cooperatively breeding grey-crowned babbler

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Abstract

Cooperative breeding, where some individuals help to raise offspring that are not their own, is a relatively rare social system in birds. We studied the breeding biology of a declining cooperative breeder, the grey-crowned babbler *Pomatostomus temporalis*, with the aim of isolating the social factors that affect its reproductive success. Most breeding pairs were assisted by philopatric offspring, although pairs could breed successfully without helpers. Females laid up to four clutches (usually three eggs per clutch) per season. Male (but not female) helpers increased the number of young fledged from individual nests and the likelihood of re-nesting, resulting in higher seasonal fledgling production. Helper effects on brood size and fledgling production were greater in the second year of the study, which was also characterized by higher nest failure. This suggests that helpers enhance reproduction more in poor conditions. Our study demonstrates the interacting effects of social and ecological factors on reproductive success, and that retention of offspring is not always beneficial for the breeders in cooperative species.

Introduction

The grey-crowned babbler *Pomatostomus temporalis*, one of the five Australo-Papuan babblers (*Pomatostomidae*), is a highly social, cooperatively breeding woodland bird. It exhibits life-history traits shared with many Australasian passerines of the parvorder Corvida, such as a small clutch size, long breeding seasons, multibrooding and extended parental care (Ford, 1989; Rowley & Russell, 1991). Among some families of the Corvida, there is also a tendency towards cooperative breeding (Cockburn, 1996), an otherwise rare phenomenon among the avifauna (*c.* 3% of birds, 23% of the Corvida; Hatchwell & Komdeur, 2000; Cockburn, 2003). In cooperatively breeding birds, some individuals assist the nesting attempts of others. Such 'helpers' boost reproductive success in many species, to the extent that some (white-winged chough *Corcorax melanorhamphos*, Heinsohn, 1992; apostlebird *Struthidea cinerea*, Woxvold & Magrath, 2005) cannot breed successfully as unassisted pairs.

Helpers often increase the reproductive output of others through additional provisioning of young, but they may also help by reducing the efforts required of parents (Brown *et al.*, 1978; Brown & Brown, 1981), deterring predators (e.g. Rabenold, 1990) or intraspecific intruders (Lennartz, Hooper & Harlow, 1987), or by continuing to rear young after a breeder dies. Much research into cooperative breeders has focused on why helping occurs when it can be costly to the

provider (Heinsohn & Legge, 1999). Through helping, individuals may acquire skills necessary for independent survival or breeding (e.g. Komdeur, 1996), or may signal their suitability as a future breeder (Carlisle & Zahavi, 1986) or coalition partner (Boland, Heinsohn & Cockburn, 1997). Where social groups are kin-based, helpers may accrue indirect fitness benefits by producing more relatives (Hamilton, 1964; Brown, 1987). Irrespective of kin selection, boosting the production of future group members may confer fitness benefits associated with living in a large group, such as better territory defence (Woolfenden & Fitzpatrick, 1984) or foraging efficiency (Rood, 1990), decreased predation risk and greater survival (Waser, Creel & Lucas, 1994; Clutton-Brock *et al.*, 1999; Ekman, Bylin & Tegelström, 1999).

The grey-crowned babbler was the first species in which the presence of helpers was shown experimentally to increase breeding success (Brown *et al.*, 1978; Brown & Brown, 1981). Most breeding pairs are assisted by subordinate helpers that are usually offspring from previous broods (Brown *et al.*, 1978; Blackmore & Heinsohn, in press), and therefore related to the offspring they help raise. In most cooperative breeders, the members of one sex, usually the males, are more philopatric (Dickinson & Hatchwell, 2004). However, grey-crowned babblers are unusual in that offspring of both sexes are equally philopatric and dispersive (Blackmore, 2006). Where both sexes are philopatric, one sex of the helper may nevertheless contribute more than the

other (e.g. Legge, 2000), and the relative contribution of males and females may vary between stages of the nesting cycle (Woxvold, Mulder & Magrath, 2006).

Formerly abundant through eastern and northern Australia, grey-crowned babblers are declining in south-eastern Australia where their woodland habitat has been subjected to widespread land clearing, and surviving populations are believed to be threatened primarily by the effects of habitat fragmentation on their social dynamics and breeding success (Garnett & Crowley, 2000). However, our knowledge of the factors that determine their reproductive success remains limited. Although a positive helper effect has been firmly established (Brown *et al.*, 1982), not all helpers feed nestlings (Brown *et al.*, 1978), and previous workers lacked the molecular techniques necessary for determining sex and relatedness as possible causes of differential helper effects. Here, we examine for the first time all the social factors likely to influence the reproductive success of grey-crowned babblers at different stages of nesting, including extra-pair parentage and the relative contribution of each sex of the helper. Our study aims to provide both a comprehensive analysis of helper effects in this species and base line information for the future study of the impact of habitat fragmentation on their social dynamics.

Methods

Study species and site

The grey-crowned babbler weighs *c.* 80 g and maintains its woodland territories of 1–53 ha year-round (Higgins & Peter, 2002). Most socially monogamous breeding pairs (84%) are assisted by 1–11 subordinate helpers (median group size is four, $n = 85$) and most (62%) helpers are male (Blackmore, 2006). All group members contribute to the provisioning of young and the building and repair of their large domed nests used for both raising young and roosting (Dow & King, 1984). Incubation lasts 17–25 days, nestlings are fed and brooded until fledging at 17–23 days and fledglings are dependent on group members for food and protection for *c.* 3 months (Higgins & Peter, 2002).

We studied a population of the subspecies *Pomatostomus temporalis temporalis* in the east Pilliga Nature Reserve (PNR; 149°30'E, 30°53'S) from July 2003 until March 2005. The study area covered *c.* 8000 ha of the 84 000 ha PNR, north-east of Coonabarabran, New South Wales. The reserve is part of the 'Pilliga Scrub', which has an approximate area of over 450 000 ha.

General methods

Babblers were attracted into mist nets with territorial call playback and a robotic model of a male babbler. Birds were banded with a numbered metal leg band and three coloured plastic leg bands for individual recognition. A small sample of blood (10–70 μ L) was collected from the brachial vein. Adults and nestlings were sexed from blood samples using

the molecular technique described by Griffiths *et al.* (1998). Procedures for genotyping and parentage assignment are described elsewhere (Blackmore & Heinsohn, in press).

In 2003 and 2004, the nesting attempts of 20 colour-banded groups (the term 'group' refers to a social unit, and includes pairs without helpers) in contiguous territories in the PNR and two on private land nearby were monitored at least fortnightly between 1 July and the end of the following March. All nests were watched at least every 2 days at the end of the nestling period to determine whether the nest failed or fledged, the fledging date and to count fledglings. As birds less than a year old were rarely observed to feed nestlings (Brown *et al.*, 1978), we use the term 'helpers' to refer only to subordinate group members that fledged in previous years and 'group size' to refer to the breeding pair and helpers. Sixty-four breeding events were recorded. Clutch sizes were obtained for 17 nests and brood sizes for 21 nests. We use 'brood size' to refer to the number of young that hatched successfully, as distinct from the number of young that fledged.

Statistical analyses

All statistics were calculated using Genstat Eight Edition (Release 8.2; Lawes Agricultural Trust, 2005). We used generalized linear mixed models (GLMM) for binomial response variables and restricted maximum likelihood models (REML) for continuous response variables. All models incorporated the random term 'group' to avoid pseudoreplication from repeated sampling of groups within and between years. Simpler generalized linear models (GLM) were used when there were no repeated measures or when the within-term correlation associated with the random term 'group' was negligible. Variables and their interactions were progressively excluded from models if dropping that term did not result in a significant change in deviance. We used the Wald statistic, which approximates a χ^2 -square distribution, to interpret all GLMMs and REMLs. Significant factors in GLMs were determined by an *F*-statistic for continuous data or a χ^2 -squared statistic for binomial data. Residuals were examined to confirm whether data in the final models were distributed normally.

We analysed the proportion of nests that were successful and the proportion of females that re-nested (binomial responses), and the number of nestlings, fledglings and independent young produced (continuous responses). We included the social factors that might influence reproductive success as explanatory variables of interest: group size and the number of male and female helpers to determine helper effects, and the presence of young resulting from extra-pair fertilization or laying by a second female to examine with the effects of parentage. We also included seasonal and timing factors that might affect reproductive output (year and month of clutch initiation). We examined the effect of the dominant females' breeding experience (first time or experienced) although this was only known for the second year of the study. Group size and helper numbers reflect group composition at the point of laying.

Results

Of the 22 groups studied, 16 were monitored in 2003 and 17 in 2004, with 11 groups monitored in both years. Five groups from 2003 left the study area. In 2004, two were replaced by immigrant groups, two immigrant groups formed new territories in the study area and two groups were added by extending the study area. Group size varied between years for most groups (82%, $n = 11$ groups) and between nesting attempts in 52% of 21 group-years where groups made more than one attempt.

Clutch size and multiple brooding

All groups attempted at least one nest in each season that they were studied. Breeding commenced in July. The last observed broods fledged in January in 2003 and February in 2004, with one additional brood fledged between 1 April and 8 July 2004 after monitoring ceased.

Clutches typically consisted of three eggs (59%, $n = 17$). Two nests contained one egg (12%), three had two-egg clutches (18%) and two nests had four eggs (12%). The latter comprised one known and one suspected case of joint nesting by a helper female (Blackmore & Heinsohn, in press), and so it is unlikely that single females laid more than three eggs. Three (23%) of 13 clutches that survived to hatching contained unhatched eggs.

Most groups attempted one (35%; $n = 31$ group-years) or two (42%) nests; 13% attempted three and 10% attempted four nests in a season. Fifty-two per cent of the females re-nested following a successful first attempt ($n = 21$), and females always re-nested if the first attempt failed ($n = 10$). The probability of re-nesting when the first nest fledged ($n = 21$ group-years) was first considered in a GLMM. However, the within-term correlation associated with the random term 'group' was negligible ($r = 0$) and so the analysis was simplified to a GLM. The probability of re-nesting increased with the presence of additional male helpers ($\chi^2_1 = 5.72$, $P = 0.017$; Fig. 1) but not female helpers ($\chi^2_1 = 0.05$, $P = 0.823$). Females with two or more male helpers always re-nested (Fig. 1). The dominant female was known to be a first-time ($n = 4$) or experienced ($n = 4$) mother in only eight group-years. First-time mothers never re-nested following a successful first nest, but three (75%) of the four experienced mothers did. Both the number of male helpers ($\chi^2_1 = 4.5$, $P = 0.034$) and maternal experience ($\chi^2_1 = 5.55$, $P = 0.019$) significantly increased the probability of re-nesting in the reduced dataset, but this should be interpreted cautiously, given the small sample sizes.

Reproductive success and helper effects

Most nests (81%, $n = 64$) were attended by up to six helpers, but some unassisted pairs bred successfully. Half of the nesting attempts made by unassisted pairs fledged, and one-third produced independent young ($n = 12$).

Maternal experience did not significantly affect the probability of nesting success ($\chi^2_1 = 2.42$, $P = 0.120$) or the number of fledglings produced from a nest ($F_{(1,13)} = 1.55$,

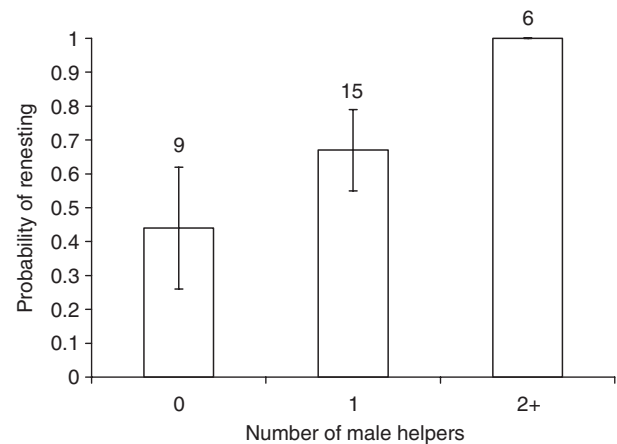


Figure 1 Probability (\pm SE) of re-nesting following a successful first nest in groups with zero to four male helpers ($n = 30$). Groups with two, three or four male helpers are pooled. Data labels indicate sample sizes.

$P = 0.235$). The presence of young sired by extra-pair males did not affect brood size ($\chi^2_1 = 2.56$, $P = 0.109$; $n = 18$) or the number that fledged from a nest ($\chi^2_1 = 0.19$, $P = 0.659$; $n = 32$).

Group size ($\chi^2_1 = 0.95$, $P = 0.329$), male ($\chi^2_1 = 2.90$, $P = 0.089$) and female helpers ($\chi^2_1 = 0.93$, $P = 0.334$) did not significantly affect the probability of nest success. However, year of study was significant ($\chi^2_1 = 4.09$, $P = 0.043$): the probability of successful fledging was 0.80 (± 0.08 SE) in 2003 (20/25) compared with 0.54 (± 0.08 SE) in 2004 (21/39). The random factor 'group' showed a high within-term correlation ($r = 0.57$) and was retained in the final model.

Group size had a positive effect on brood size ($\chi^2_1 = 8.41$, $P = 0.004$; $n = 21$) and broods were smaller later in the season (month of clutch initiation: $\chi^2_4 = 8.43$, $P < 0.001$). Year alone did not affect the number of nestlings ($\chi^2_1 = 0.50$, $P = 0.478$) but did interact with group size ($\chi^2_1 = 4.91$, $P = 0.027$). Increased group size had a positive effect on the number of nestlings in 2004, but not in 2003 (Fig. 2), although this effect may have been driven by small sample sizes (2003: six broods; 2004: 15 broods). Substituting the number of male and female helpers for group size did not improve the model ($\chi^2_5 = 0.24$, $P = 0.999$). The random term 'group' showed a high within-term correlation ($r = 0.35$).

Group size ($\chi^2_1 = 0.23$, $P = 0.629$), year ($\chi^2_1 = 1.68$, $P = 0.195$) and the month initiated ($\chi^2_6 = 1.05$, $P = 0.388$; $n = 58$) did not significantly affect the number of fledglings produced from a nest. However, when the number of male and female helpers were considered separately, male helpers increased the number of fledglings ($\chi^2_1 = 4.80$, $P = 0.028$, $n = 61$; Fig. 3). Neither the main effect of female helpers ($\chi^2_1 = 2.02$, $P = 0.155$) nor the interaction with male helpers ($\chi^2_1 = 0.16$, $P = 0.686$) were significant. The female effect was close to significant when the order of terms was reversed ($\chi^2_1 = 3.66$, $P = 0.056$). The random term 'group' again showed a high within-term correlation ($r = 0.57$).

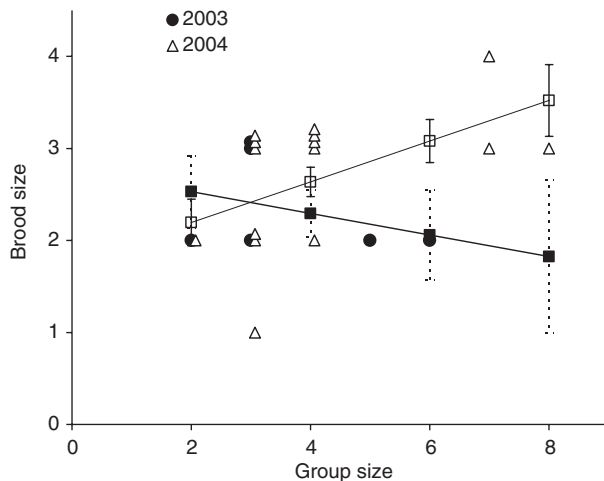


Figure 2 Relationship between group size and brood size in 2003 (closed circles) and 2004 (open triangles; $n=21$). Closed (2003) and open squares (2004) show values predicted from linear regression (\pm SE).

To isolate helper effects from territory or breeder quality (Brown *et al.*, 1982), we compared the reproductive success of the same breeding pairs when they were helped on two occasions by different numbers of male and female helpers. Sample sizes were low; however, seven matched pairs in which the number of males varied between nesting attempts (attempts were spread across both years, and included three increases and four decreases in helper number) showed a non-significant but suggestive positive effect of more male helpers on the number of young fledged (Wilcoxon matched pairs test = 2.5, $P = 0.078$). By contrast, six matched pairs in which the number of female helpers changed (three increases, three decreases) gave no indication that groups produced more fledglings when they had more female helpers (Wilcoxon matched pairs test = 9.5, $P = 0.969$).

Male helpers also had a strong positive effect on the total number of fledglings produced over an entire season ($\chi^2_1 = 10.98$, $P < 0.001$; $n = 32$; Fig. 4). Seasonal fledgling production was not affected by female helpers ($\chi^2_1 = 0.68$, $P = 0.409$) or year ($\chi^2_1 = 0.29$, $P = 0.592$), but when seasonal fledgling production from 2003 and 2004 was analysed separately in linear regression, male helpers had a positive effect in 2004 ($F_{(1,15)} = 9.59$, $P = 0.007$; $n = 17$) but not in 2003 ($F_{(1,13)} = 1.03$, $P = 0.329$; $n = 15$).

We found no explanation for variation in the number of young to reach independence (3 months post-fledging): group size: $\chi^2_1 = 0.27$, $P = 0.601$; year: $\chi^2_1 = 0.09$, $P = 0.762$; month of clutch initiation: $\chi^2_6 = 1.80$, $P = 0.094$ ($n = 58$); male helpers: $\chi^2_1 = 2.53$, $P = 0.11$; female helpers: $\chi^2_1 = 3.29$, $P = 0.070$ ($n = 62$).

Discussion

Like most cooperatively breeding species (Pruett-Jones, 2004), unassisted pairs of grey-crowned babblers can breed

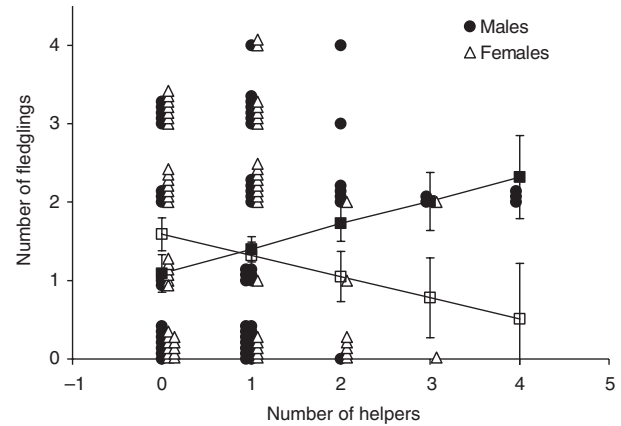


Figure 3 Relationship between the number of male and female helpers and the number of fledglings produced from nests ($n=61$). Closed squares show predicted male values (\pm SE), and open squares show predicted female values (\pm SE) from linear regression.

successfully. However, larger groups produced more fledglings. Group size did not affect the survival of young that reached independence, and so the helper effect on reproductive success appears to operate only through increased fledgling production. Groups with more male (but not female) helpers were more likely to re-nest and fledged more young, suggesting that males are of greater value to breeders.

Only male helpers had a positive effect on fledgling production, boosting both the number of young fledged from individual nests and the total seasonal production. In many cooperative species, helpers have an 'additive' effect on productivity by increasing the amount of food delivered to the nest and reducing nestling starvation (e.g. acorn woodpecker, Koenig & Stacey, 1990; Seychelles warbler, Komdeur, 1994). Breeders may also benefit from 'compensatory' help, in which the presence of helpers allows them to reduce their own effort (Hatchwell, 1999). The two are not mutually exclusive (Hatchwell, 1999), but in grey-crowned babblers previous evidence suggested that help is largely compensatory. Brown *et al.* (1978) found that helpers did not increase total feeding rates to nests, but reduced the feeding rates of parents, and Brown & Brown (1981) reported that helpers enabled females to accelerate re-nesting, a result consistent with a 'load-lightening' effect. Our study further showed that male helpers increased the production of fledglings from individual babbler nests, suggesting that at least some help is 'additive'. Dominant grey-crowned babblers appear to reinvest any saved energy in the production of new clutches, showing that cooperative breeders can benefit from both additive and compensatory effects in the same breeding season.

With the benefit of genetic sexing not available to previous workers, our results suggest that the positive effect of helpers reported by Brown *et al.* (1982) may have been due to the contributions of male helpers alone. This adds to a growing body of evidence showing that the benefits of cooperative breeding are contingent on helper sex when both sexes are routinely philopatric. In laughing

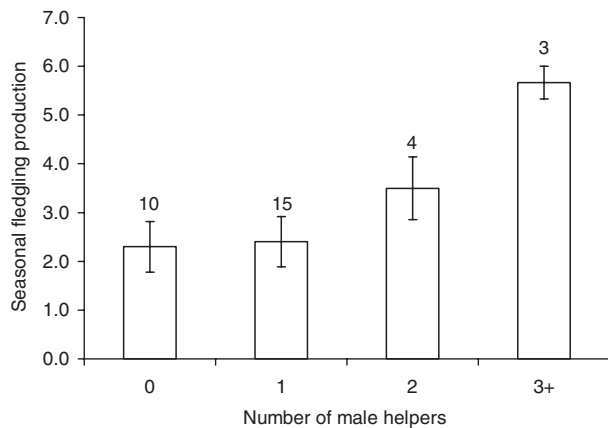


Figure 4 Mean (\pm SE) number of fledglings produced across all nests in a season in groups with zero to four male helpers. Groups with three ($n=2$) and four ($n=1$) male helpers are pooled.

kookaburras *Dacelo novaeguineae*, for example, group size was positively correlated with fledging success and male helpers provisioned more than their female counterparts. However, male helpers had a neutral impact and female helpers a negative impact on fledging success once breeder and territory quality were taken into account (Legge, 2000). Male Galápagos mockingbirds *Nesomimus parvulus* were also more likely to help than females, but this plural breeding species is dissimilar to babblers in that most groups have more than one breeding female (Curry & Grant, 1990). In the apostlebird, male helpers have a greater role in preventing nestling starvation (Woxvold *et al.*, 2006), and in the splendid fairy-wren *Malurus splendens*, female but not male helpers increase the reproductive success of breeders (Brooker & Rowley, 1995). Green woodhoopoes *Phoeniculus purpureus* (Ligon & Ligon, 1990) and hoatzins *Opisthocomus hoazin* (Strahl & Schmitz, 1990) are similar to grey-crowned babblers in that both sexes help but male helpers provide greater compensatory care.

Correlations between the number of helpers and reproductive success should be interpreted carefully. In philopatric species, group size may be either a cause or effect of reproductive success, and a correlation could arise due to other confounding variables such as the quality of the breeding pair or the territory (e.g. Brown *et al.*, 1982; Emlen, 1991). However, in grey-crowned babblers, two lines of evidence suggest that helper effects occur independently of other factors. First, our matching of the same pairs with and without more helpers suggested a positive effect of male helpers, although the result was non-significant ($P = 0.078$), possibly as a result of low sample sizes. By contrast, there was no indication that female helpers had any effect on reproduction. Second, although there were insufficient data to test the overall effect of female age, we found no evidence that maternal experience influenced the production of young in each breeding attempt. Maternal experience did, however, affect a female's decision to re-nest. Further, our findings that group size correlates with reproductive success concur

with those of Brown *et al.* (1982), who demonstrated with a removal experiment that helpers improved seasonal fledgling production in grey-crowned babblers.

As other studies have shown that each male's parental effort may vary with his share of matings (e.g. Davies & Hatchwell, 1992; Hartley *et al.*, 1995; Briskie *et al.*, 1998), we hypothesized that reproductive success could be lower in cases of extra-pair fertilization. However, we did not find a correlation between extra-pair paternity and reproductive success. As most offspring result from monogamy (Blackmore & Heinsohn, in press), babblers may use the general rule that they are feeding offspring or relatives (e.g. Wright, Parker & Lundy, 1999). Alternatively, other individuals may compensate for reduced paternal investment.

In addition to helper effects, ecological factors are likely to have a profound impact on reproduction in this species. Larger groups produced more nestlings and male helpers boosted seasonal fledgling production in 2004, but not in 2003. In many cooperative species, helpers only affect reproductive success in some years or have a stronger effect when breeding conditions are poor (e.g. Hatchwell, 1999; Magrath, 2001). Conditions in 2003 were better than in previous and subsequent years, as relatively high rainfall temporarily eased drought conditions in the study area (Bureau of Meteorology). Brown & Brown (1981) reported that environmental factors such as temperature and rainfall affected feeding rates in grey-crowned babblers, and our findings support his suggestion that the benefits of helpers become more apparent when conditions are poor (Brown *et al.*, 1978).

Much of the current theory about the evolution of cooperative breeding and helping behaviour can be traced to early work on the grey-crowned babbler. However, it now appears that the benefits of cooperative breeding for this species fluctuate with helper sex and ecological conditions. Both sexes of helper stand to gain similar indirect fitness benefits and face analogous constraints on independent breeding (Blackmore & Heinsohn, in press), but only one sex boosts the production of nondescendent kin. Our understanding of varying levels of helping within species is poor (Heinsohn & Legge, 1999), and species where the sexes are similarly philopatric but differentially helpful provide an unusual opportunity to isolate motivation for cooperative breeding.

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