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Flexible Helping Behaviour in the Azure-Winged Magpie

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Abstract

Helping to rear the offspring of others may be a way for younger birds to gain access to future reproduction especially when turnover of breeding opportunities is low. However, this explanation is not applicable to cases where adults also help, or when roles shift between helpers and breeders. Over a period of 6-yr, we studied a marked population of azure-winged Magpie (*Cyanopica cyanus*) breeding in a non-territorial, colonial system. Magpies bred in a highly flexible cooperative system, in which individuals helped at different stages of the breeding cycle, including nest building, feeding the incubating female and feeding the young and removing the faecal sacs. On average, 50% of hatched nests were assisted by helpers-at-the-nest, and nest success appeared to be positively related to the presence of helpers. Helpers were predominantly males. Although juveniles were more likely to help, both juvenile and adult birds helped. Individual birds behaved as helpers either as a first-option or after having attempted their own breeding (second-option helpers). An individual helper may assist more than one nest during the same breeding season and in different breeding seasons. Reversals between breeder and helper roles were common in both directions, within a breeding season and between years. Helping behaviour is an option for almost any member of the colony. Therefore, hypotheses related to the enhancement of future breeding opportunities for juveniles can be discarded as general explanation of helping in this species. Although the decision to help appeared to be influenced by proximal environmental conditions hindering successful breeding, the associated benefits of helping as opposed to simply recovering for future reproduction, especially for former breeders, deserve further study.

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Introduction

Cooperative breeding systems are those in which more than one pair of individuals show parent-like behaviour towards young of a single nest or brood (Brown 1987). Such reproductive systems are rather rare, and among birds they are known to occur in only about 3% of the world's approx. 9700 extant species (Down 1980; Brown 1987; Edwards & Naeem 1993; Cockburn 1996; Arnold & Owens 1998).

Recent reviews propose that helping behaviour is promoted by both ecological constraints and life history traits reducing the turnover of breeding opportunities (Arnold & Owens 1998, 1999; Hatchwell & Komdeur 2000; Pen & Weissing 2000). Testing the validity of this approach as a general explanation for the distribution of helping among taxa, rests on both comparative analyses and detailed studies of bird populations differing in life history and ecology.

Reproductive limitations commonly affect young individuals more strongly. As a consequence, helpers are typically juveniles that have not reached the reproductive status (e.g. Brown 1987; Stacey & Koenig 1990). Thus, besides a potential increase in their inclusive fitness, helping might benefit young individuals by increasing their chances for future reproduction. However, this view is challenged by the reports of helping by adults or subadults in different taxa such as fishes (e.g. Taborsky 1984; Martin & Taborsky 1997), mammals (e.g. Clutton-Brock et al. 2001, and references herein) or birds (e.g. Emlen 1990; Dickinson et al. 1996). Hence cooperative systems appear to be more complex that previously assumed (e.g. Kokko et al. 2001).

The Azure-winged Magpie (*Cyanopica cyanus*) is a social corvid (Cramp & Perrins 1994), occurring in eastern Palearctic Asia and the Iberian Peninsula (Spain and Portugal) (Goodwin 1986). Its breeding system is colonial and the presence of helpers at the nest has been reported in the Japanese subspecies (Hosono 1983; Komeda et al. 1987). Komeda et al. (1987) confirmed the presence of 0–2 helpers, of unknown age and sex, in seven nests monitored during a single breeding season. In the Iberian subspecies (*C. cyanus cooki*) Araujo (1975) and Cruz (1988) observed that four or more magpies simultaneously visited and fed nestlings in one nest. These observations suggested the possible presence of helpers at the nest, although individuals in neither of these two populations (Avila and Badajoz, respectively) were colour-ringed. Here we present the results of monitoring a marked population for a 6-yr period, with the objective of studying the environmental, social and individual conditions related to the occurrence of helping behaviour in this species.

Methods

Study Area and Population

The study area is located 22 km north of the city of Badajoz (39°03′N, 6°48′W), in the middle of the species' Iberian distribution (Sacarrao 1967). The predominant habitat is a dehesa (open holm oak *Quercus ilex* woodland). The climate is typically Mediterranean, with dry-hot summers and mild-wet winters. Azure-winged Magpies in this area breed between late Mar. and early Jul.

Data Collection

Since 1992, Azure-winged Magpies in this population have been captured and marked with metal and coloured plastic rings. Data are presented from the years 1992 to 1997. At the beginning of the nesting period (late Mar. or early Apr. depending on the year) each tree in the area was inspected. If it contained a nest, it was marked. Field work lasted until the last chicks fledged, usually in early Jul. The whole area was searched for nests at least once per week, and different portions of the area were searched every 2 d, in a way that every tree in the entire area was inspected at least twice a week. Each nest found was monitored (at least once every 2 d) and intensively observed until fledging. Observations on nests were carried out with a telescope from a hidden position during at least 1 h every second day. Nests were included in the analyses only when both members of the breeding pair were identified. In cases where only one member of the pair was marked, we assumed that the other member remained the same because pairs proved to be highly stable during the breeding season (during the 6-yr of study we have only registered one case of divorce within the current breeding season). The sex of breeders was assigned according to their behaviour, being recorded as females those individuals that incubated the eggs and brooded the young (Hosono 1966; Goodwin 1986; Komeda et al. 1987). Two age-classes were distinguished on the basis of plumage (Cruz et al. 1992; see also Cramp & Perrins 1994), juveniles (up to 1-yr-old birds, presenting partial moult, duller plumage and whitish fringes to tail-feathers) and adults (more than 1-yr-old, showing complete moult, rich azure-blue wings and brighter plumage).

Observations of individual nests were intensified during the days just after they were found (up to 3 h of continuous observation), in order to identify the members of the pair. In some instances nests were abandoned either before completely built or before any egg was laid. In these cases it was not possible to be sure about the identity of the breeding pair and the helpers. Consequently, helping behaviour before hatching (for instance nest building) or after fledging (feeding or defending fledglings) was less frequently observed. Most observations refer to helpers at the nest, from hatching to fledging.

Definitions

As suggested by Brown (1987), we use the term ‘helper’ (except if otherwise stated) for those individuals besides the breeding pair that collaborated in feeding the young and removing the faecal sacs. Helpers-at-the-nest may be individuals that behave as such from the beginning of the breeding season instead of attempting to breed by themselves. We refer to them as first-option (FO) helpers, as opposed to those individuals that shifted to helping behaviour after their own breeding attempt (regardless whether it failed or not), for which we use the term second-option (SO) helpers. The term 'redirected helpers' was used by Emlen (1981) for those birds that decided to help after failing a breeding attempt. We prefer to use the term SO helpers to include also individuals that decided to help after successfully rearing a brood. Komeda et al. (1987) distinguished frequently-visiting helpers in contrast to rarely-visiting helpers that did not feed the chicks. We observed some instances of individuals that approached the nest but did not participate in any parental tasks. In some cases these individuals were even attacked by the male of the breeding pair. Since they did not actually contribute to parental care we decided to exclude them from the category of helpers.

Data Analysis

For those analyses where breeding pairs were used as independent cases, we included only those pairs with at least one known member, in order to avoid double counting as a result of replacement clutches within a season. Likewise, to avoid pseudoreplication (Hurlbert 1984) when considering the amount of birds monitored in the whole period of study, each individual was included only once and assigned to classes (juvenile–adult, FO–SO) according to the year when it was first recorded in our study area. Meteorological data were obtained from the Valdesequera Meteorological Station (situated within the study area). The meteorological variables used were (1) mean temperature during Mar., and (2) total rainfall during the 3 mo before the beginning of the breeding season (Jan. to Mar.). In arid environments, rainfall is the main environmental constraint affecting the availability of very different kinds of food, either vegetal or animal (Mooney et al. 1974; Mooney 1981). Therefore, we decided to use rainfall as an indirect index of interannual differences in food abundance and of general constraints for reproduction. Non-parametric tests were used when the distribution of data differed from normality. Kolmogorov–Smirnov normality test was used with probability level $p > 0.1$. The effect of independent variables on the decision of helping was analysed by logistic regressions. Comparison between two proportions followed the procedure in Zar (1984). Statistical tests were performed with STATVIEW 5.0. Values reported below are mean ± SD.

Results

Helping Before Hatching

In addition to the breeding pair, some other individuals were observed participating in nest building or providing food to the breeding female during incubation. At least 19 instances of helping behaviour during nest building were recorded in the 57 nests observed during the nest-building phase during the whole study. This involved 18 individuals, both males and females. Up to four different individuals were observed collaborating in building a single nest. Of the 18 individuals, three were not identified, three were females and 12 were males.

The subsequent role of these nest-building helpers varied. Two females bred in another nest during the same season and the other one was missed until the next year when she was observed as a breeder in the colony. Four males were missed after nest building, three bred in another nest and five were helpers during the same season either in the same nest they collaborated to build (one case) or in different nests (four cases).

In 17 further instances (involving 12 individuals) helping consisted of providing food to the breeding female during incubation (126 observed nests). Three of these helpers were not identified. One individual helped to feed the incubating female, and when the clutch was lost and the pair laid a replacement clutch in another nest, the same helper collaborated in feeding both the female during incubation and the young after hatching in the new nest. Most birds that helped during the incubating phase continued to help after hatching (10 cases; in five more cases the nest were predated before hatching), so the helpers had no opportunity to continue. Only in one case, the helper at incubation did not continue helping after hatching, despite the chicks survived to fledging.

Helpers at the Nest: Proportion of Nests Assisted and Number of Helpers per Nest

During the 6-yr of study, a total of 110 nests with individually recognizable breeders and with at least one hatched egg were intensively observed to fledging. Table 1 shows the number of hatched nests that had or had not helpers, and the number of helpers per nest in each year of the study period. The number of nests where eggs hatched with and without helpers did not differ for the 6-yr of study ($\chi^2_5 = 4.86$, $p = 0.43$). On average, 49.1% of hatched nests were assisted by helpers, with a maximum of 73.3% in 1995.

Nests could be assisted by more than one helper. The number of helpers per nest was not significantly different between years (Kruskal–Wallis $H_5 = 7.68$, $p = 0.17$). However, in 1995 (1) the modal number of helpers per nest was 1 instead of 0 as in all other years, and (2) at maximum nine helpers were present at a nest (Table 1).

Table 1: Frequency distribution of the number of helpers per nest for hatched nests (total) in every year of study

Year	Total	0 Help	1 Help	2 Help	3 Help	4 Help	5 Help	9 Help
1992	19	11 (57.9)	5 (25.3)	2 (10.5)	0	1 (5.3)	0	0
1993	20	12 (60.0)	5 (25.0)	3 (15.0)	0	0	0	0
1994	15	7 (46.7)	5 (33.3)	2 (13.3)	0	1 (6.7)	0	0
1995	15	4 (26.7)	5 (33.3)	1 (6.7)	1 (6.7)	2 (13.3)	1 (6.7)	1 (6.7)
1996	16	9 (56.3)	6 (37.5)	0	1 (6.3)	0	0	0
1997	25	13 (52.0)	5 (20.0)	4 (16.0)	2 (8.0)	0	1 (4.0)	0
Comb.	110	56 (50.9)	31 (28.2)	12 (10.9)	4 (3.6)	4 (3.6)	2 (1.8)	1 (0.9)

Parentheses indicate the percentages with respect to total hatched nests. Comb. = 6 yr combined.

Table 2: Total number of breeders and helpers in the colony for every year of study

Year	Breeders/helpers		Male	Female	p-Value	Juveniles	Adults	p-Value	FO	SO
1992	B	30 (29)	15	14		2	16			
	H	11 (27.5%)	5	1	0.207	7	3	0.003	10	1
1993	B	30 (28)	11	17		2	15			
	H	7 (20.0%)	4	1	0.152	4	2	0.020	5	2
1994	B	34 (33)	17	16		3	22			
	H	9 (21.4%)	5	0	0.061	3	6	0.306	8	1
1995	B	44 (40)	19	21		8	25			
	H	26 (39.4%)	12	1	0.008	6	15	0.758	17	4
1996	B	54 (51)	25	26		7	37			
	H	9 (15.0%)	8	1	0.033	1	8	1.000	6	3
1997	B	42 (39)	19	20		3	33			
	H	16 (29.1%)	11	1	0.009	6	6	0.004	9	3

Besides the total number of breeders, the number of those breeders that did not help as a second-option is shown in brackets. The percentage that helpers represent with respect to the total individuals participating in the breeding tasks (only breeders + helpers) is shown in brackets. Figures are shown for males, females, juveniles and adults. Probabilities (p) after Fisher exact test for the null hypothesis that helping or breeding is independent of sex (first p column) and age (second p column). FO: number of individuals that behaved as helpers as a first-option; SO: number of individuals that behaved as helpers as a second-option. Discrepancies between partial and total figures are due to not well identified individuals that could not be accurately assigned to a particular category.

Table 2 shows the number of breeding individuals recorded for every year of study, together with the total number of helpers for that year. On average, 25.4% of individuals that contributed to the breeding tasks were helpers. There were differences between years in the relative number of individuals that behaved as helpers ($\chi^2_5 = 11.31$, $p = 0.04$), the highest percentage of helpers being recorded in 1995 (39.4%).

Breeding Success with and without Helpers

The number of fledglings per hatched nest was significantly higher for nests with helpers ($\tilde{x} = 3.5$; $n = 54$) than for nests without helpers ($\tilde{x} = 0$; $n = 56$; Mann–Whitney U-test $Z = 2.985$, $p = 0.003$). Moreover, the number of fledglings per nest increased with the number of helpers (Kruskal–Wallis $H_3 = 15.194$, $p = 0.0017$; Fig. 1).

These differences in the number of fledglings cannot be explained by differences in brood size. Nests that were assisted by different numbers of helpers did not differ in the number of eggs laid (ANOVA $F_{3,106} = 0.636$, $p = 0.593$) but they differed marginally in the number of hatched chicks (ANOVA $F_{3,106} = 2.611$, $p = 0.055$).

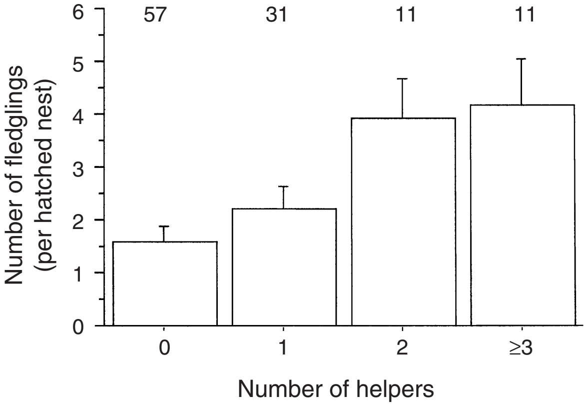

Fig. 1: Reproductive success in hatched nests as a function of the number of helpers that assisted the nest. Figure shows the number of fledglings (mean and standard error) in nests without helpers (0) and in those that received help from one (1), two (2) or more than two (≥3) helpers. Sample sizes (number of nests) are shown over the bars

Helpers appeared to contribute to a reduction of complete brood losses through predation ($\chi^2_3 = 8.849$, $p = 0.031$; Fig. 2). In addition, the number of fledglings was still related to the number of helpers that assisted the nest, in nests that completed the nesting phase to fledging (ANOVA $F_{3,52} = 3.187$, $p = 0.031$; Fig. 2).

Iterative Helping

Helpers may help in more than one nest during a single breeding season. This happened either after the nest was predated or after the chicks fledged. We did never observe a case of helping at more than one nest simultaneously. The number

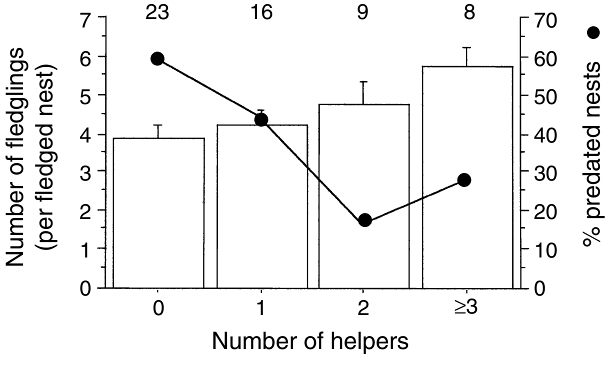

Fig. 2: Proportion of hatched nests that were predated, and the reproductive success in those nests that succeeded to fledging, as a function of the numbers of helpers that assisted them. Sample sizes for the proportion of predated nests are those in Figure 1. Sample sizes for fledged nests are indicated over the bars

of nests at which individuals helped in a season varied between 1 and 4 (mode 1), and there were no significant differences between years (Kruskal–Wallis $H_5 = 6.054$, $p = 0.30$). Individuals may act as helpers in more than one breeding season. Fifty-two individuals helped at least during one breeding season. Seventy-five per cent of individuals (39) helped only in one breeding season, 19.2% (10) did so in two breeding seasons and only 5.8% (three) helped in three breeding seasons. Hence, helping in only one breeding season was more common than helping during two or more breeding seasons (Comparison between proportions: $Z = 5.10$, $n = 52$, $p < 0.001$).

We also considered the number of times that individual helpers acted during the period of study, i.e. including several times per year if that was the case. Of 52 individuals that helped within the six study years, 32 (61.5%) did so only once, 10 (19.2%) in two occasions, four (7.7%) individuals helped three times, another four (7.7%) did so on four occasions, one (1.9%) in five and one (1.9%) helped six times. More individuals helped on only one occasion compared with more than one (Comparison between proportions: $Z = 2.36$, $n = 52$, $p < 0.05$).

Sex and Age of Helpers

Males were more likely to be helpers (27 of 93) than females were (four of 81) (Fisher exact test, $p = 0.0001$), although when data were analysed separately for years the male predominance did not reach significance for all years of study (Table 2). Females never helped for more than one breeding season, and we never observed females helping in more than one nest per season. The average sex ratio in the colony was 1.3 ± 0.2 SD males per female in the six study years. This sex ratio was neither significantly different from 1:1 for the whole period ($\chi^2_5 = 1.885$, $p = 0.865$) nor for any of the years included (χ^2_1 one group, $p > 0.05$ in all cases).

In two cases (one in 1995 and another in 1997), a young that fledged in the colony was observed to act as a helper already in the same breeding season. The proportion of juveniles that behaved as helpers (27 of 52) was higher than the proportion of adults that did so (20 of 91; Fisher exact test, $p = 0.0004$), although the difference was not significant in each study year (Table 2).

Eighteen individuals were monitored as juveniles and at least in one more year as adults. Most of them (10) acted as helpers both as juveniles and adults, four did so only as juveniles, one helped only as adult, and three never helped (i.e. only bred both as juveniles and adults).

Logistic regression showed that both sex and age influenced the decision of helping, but that the effect of sex was more important (male help was 11.4 times more likely than that of females) than the effect of age (3.6 times in juveniles compared with adults) ($r = 0.465$, $n = 127$, $p = 0.001$; Table 3).

First-Option Helpers, Second-Option Helpers and Role Reversals

The decision to help might be chosen as a FO or following a breeding attempt. Considering only the first time that each helper was recorded to behave

Table 3: Logistic regression on the effect of age and sex on the probability to help or not

Independent variables	Coefficient	Chi-square	p-value
Age	−2.635	6.941	0.0084
Sex	4.094	16.761	< 0.0001

Table 4: Logistic regression on the effect of temperature and rainfall on the probability to help or not

Independent variables	Coefficient	Chi-square	p-value
Temperature	2.400	5.759	0.016
Rainfall	−1.891	3.574	0.059

as a helper, FO helpers were more common than SO helpers both over all study years (42 FO vs.10 SO, χ^2_1 one group = 19.69, $p < 0.001$) and in each single year (Wilcoxon Z = −2.20, p = 0.03, Table 2).

First-option and SO helpers did not differ in age (FO: 16 adults, 24 juveniles; SO: four adults, three juveniles; Fisher exact test: p = 0.438), but they did with respect to sex (FO: 24 males, 0 females; SO: three males, four females; Fisher exact test: p = 0.001). All female helpers were SO helpers.

Role reversals of breeders to helpers occurred not only within a single breeding season (i.e. SO helpers) but also between breeding seasons (breeder to FO helper in next year: seven individuals; FO helper to breeder next year: 11 individuals). One individual helped in one season, bred in the next one, and then helped again in the following season. In two further cases individuals alternated roles during four breeding seasons.

Environmental Conditions and Helping

The number of individuals choosing the option of helping was affected by the environmental conditions in a particular year. Mean temperatures of Mar. (start of egg laying) ranged from 12.6 to 17.4°C ($\bar{x}$ = 14.2 ± 1.7, n = 6), and total rainfall during the 3 mo before the beginning of the breeding season (Jan. to Mar.) ranged from 57.7 to 349.8 mm ($\bar{x}$ = 140.0 ± 109.3, n = 6). When temperature and rainfall were considered in a logistic regression with helping as a dependent variable (logistic regression r = 0.214, n = 201, p = 0.005), temperature was the main factor positively affecting the probability to help, and rainfall was marginally, negatively related to helping (Table 4).

Discussion

Helping behaviour in our study population was remarkably flexible both in its timing during the breeding season and during lifetime of the helpers. It occurs at all stages of the breeding period such as nest building, feeding the incubating female, and feeding the young during the nestling period. It can be performed by any bird, even by adults, and it can be used flexibly by all members of the colony when their own breeding possibilities are low or when a previous breeding attempt has finished (either failed or not).

Helping during the building of nests or nest cavities has been previously observed in other cooperatively breeding species (e.g. Lennartz & Harlow 1979; Reyer 1980; Emlen 1990). However, it is not clear whether the birds observed collaborating in these tasks behaved only as helpers or bred later on in the season. Our observations indicate that individuals collaborating in building another pair's nest did not necessarily participate in feeding the chicks in that or any other nest, and they could even breed by themselves. In fact, both sexes were observed collaborating in nest building, and since females never behaved as FO helpers, this indicates that breeding females, other than the breeding pair, also collaborated in nest building.

As in some other cooperative breeding species (e.g. Reyer 1980; Poiani 1992) incubating females were fed by other individuals different from her mate, and these helpers tended to continue helping this same nest after hatching.

The percentage of nests with helpers in the colony was high (around 50% during most years and even 70% in 1995). These figures are within the range mentioned for this species by Komeda et al. (1987; 40–93%). The year 1995 was exceptional in the percentage of nests with helpers (over 70%), the percentage of helpers in the colony (39.4%), and the average number of helpers per helped nest (2.9 ± 2.5) and per hatched nest (2.1 ± 2.5). Also we recorded the highest number of helpers assisting a single nest (nine) in this year. The breeding season of 1995 took place at the end of a long period of draught that lasted for 5-yr. Also rainfall was very low in 1995. This suggests that the presence of helpers may have been influenced by climatic factors either in the year 1995 or in the previous years. The presence or absence of rainfall might affect both the availability of resources and thereby the physical condition of birds.

Mediterranean ecosystems, as inhabited by this species, are characterized by their high interannual variability in rainfall, which affects the composition and productivity of the vegetal cover and thereby that of the whole ecosystem (Mooney et al. 1974; Mooney 1981; Peco 1989). Insufficient food resources (e.g. Orians et al. 1977) or unpredictable environmental conditions (e.g. Emlen & Wrege 1991; Wrege & Emlen 1991) may promote helping behaviour. Our results show that helping was favoured under drier environmental conditions (low rainfall and high temperature) which are the least favourable in these ecosystems (Mooney et al. 1974; Mooney 1981; Peco 1989). However, factors other than meteorological variables also affect the presence of helping. For instance, the fate of the ongoing breeding attempts may also affect the number of SO helpers. Thus, the flexibility of the breeding system in this species makes the amount of help received per nest positively depend on the difficulties of bringing up the brood successfully.

Our results show that helping is much more influenced by gender than by age. Females rarely help and if they do, they act as SO helpers. In most bird species, the female is the dispersing sex and there are several reasons why they may be less prone to help in others' nests. For example, (1) they are not related to the members of the group where they breed, and (2) they are likely to suffer higher mortality than males, which leads to male sex ratio bias and higher breeding opportunities for females (Woolfenden & Fitzpatrick 1984; Brown 1987). However, in our study population sex ratio was not significantly biased to males, and most importantly, even females helped after losing their own nests, indicating that competition for breeding opportunities is not a general explanation.

A key question in cooperatively breeding species is whether helpers actually increase the success of helped nests. Many correlational studies indicate that helpers may contribute to the success of the nest, although this does not appear to be always the case (see reviews in Innes & Johnston 1996; Hatchwell 1999; Legge 2000). Experiments revealed that high success and the presence of helpers may be correlated with environmental factors such as territory quality, without a direct effect of helpers on nest success (e.g. Leonard et al. 1989; Nias & Ford 1992). In other cases, however, experimental results provide evidence for an increase in productivity because of alloparental care (Mumme 1992; Boland et al. 1997). In our study population, the absence of environmental differences between pairs because of a lack of territoriality, coupled with the high success associated with the presence and number of helpers, indicate that a direct effect of helping behaviour on nest success is likely. Alternatively, better parents might produce more offspring to fledging and at the same time attract more helpers, which would have produced an association between the number of helpers and fledging success. This could explain the marginal association found between hatching success and the presence of helpers. Although these alternatives can only be distinguished with the help of experiments, data on feeding rates (J. Valencia, unpubl. data) show that helpers actually contribute to increase the total rate of food delivered to the nest. Also, the effect of helpers in reducing the impact of predation supports that their contribution is relevant.

Our data show that some birds helped in more than one nest during a single season, but not simultaneously, or during several breeding seasons. Most remarkably, role reversals were common during our period of study. Switching back and forth between helping and breeding was commonly recorded for individual birds either within one breeding season or between years. This flexibility is not common among cooperative breeding birds (Brown 1987; Stacey & Koenig 1990), although it has been reported for some species (e.g. Emlen 1990; Lessells 1990; Dickinson et al. 1996).

When asking for the functional significance of helping, two questions need to be answered separately: why individuals do not breed, and why they do help. Answers to the first question are usually better understood (e.g. Brown 1987). In our species, unfavourable environmental conditions may increase the likelihood of helping. For the second question, enhancing inclusive fitness was proposed as one possible answer (Hamilton 1964). Previous work in the azure-winged Magpie suggests that helping behaviour does not occur between the most highly related individuals within the group (González 1996), although the average degree of relatedness within the group is high (González 1996). Also, genealogical data from our marked birds show that in most cases (75%: J. Valencia, unpubl. data) helpers and helped were not close kin (parent–offspring or siblings). Hence, although a role of kin selection cannot be fully discarded (see e.g. Keller 1997; Russell & Hatchwell 2001), it seems unlikely as the main explanation for helping in this species.

Helping by young individuals that have not yet attained social status or experience to breed (Brown 1987; Emlen 1990) can also be discarded for our study population. Instances of helping behaviour occurred as early as a few days after fledging (two cases observed in 1995 and 1997) but helping was also very common among adult birds. A single individual may act as a helper for several years, but also some juveniles bred themselves without previously helping, which indicates that helping is not a prerequisite to reach the breeding status.

Unlike other cooperatively breeding birds, helping in the azure-winged magpie appears as a feasible option for most birds in the colony. Social groups in this species are stable (Hosono 1968; Cruz 1988; González 1996), highly cooperative in many respects such as in food searching (Cruz 1988; González 1996) and in antipredatory defence (Hosono 1975; Ueta 1999), and include complex social relationships (J. Valencia, unpubl. data). Helping at the nest in this species may improve the success of social groups, and a currently debated question is whether group benefits may favour the evolution of cooperative behaviour (see e.g. Dugatkin & Reeve 1993; Kokko et al. 2001). Further studies should discriminate between competing hypotheses on the kind of benefits obtained by individual helpers, especially by adults that become helpers after having bred by themselves.

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