

1 **Effect of parentage and relatedness on the individual contribution to cooperative**
2 **chick care in carrion crows**

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4 Running headline: Canestrari et al.: Nestling care in cooperative crows

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1 Abstract

2

3 Carrion crows (*Corvus corone corone*) in northern Spain form complex cooperative
4 groups that contain non-dispersing offspring and immigrants. Reproduction is often
5 shared among group members, with polyandry prevalent over joint egg laying. However,
6 due to incest avoidance or sexual immaturity, reproduction is potentially available only to
7 a fraction of group members (“potential breeders”), while others do not breed (“non
8 breeders”). We combined molecular data with video-recorded observations at nests in
9 order to investigate whether potential breeders and non breeders adjust their individual
10 effort in nestling feeding respectively to their level of parentage and the relatedness with
11 the chicks. Overall, parents of at least one chick in the brood showed the highest feeding
12 rates. Among potential breeders, genetic mothers and fathers fed chicks at significantly
13 higher rates than individuals with no parentage, but they did not adjust their effort
14 according to the proportion of offspring generated. Current direct fitness benefits are
15 therefore important in determining a high provisioning effort, but crows may lack a
16 mechanism to finely assess their share of parentage. Among non-breeders, males
17 contributed more than females to chick feeding, but we found no significant correlation
18 between feeding rate and relatedness to the nestling. We discuss how the latter result can
19 be reconciled with the fact that kin selection has been shown to be important in shaping
20 the crow cooperative society.

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1 Cooperative breeding arises when more than two individuals contribute to raise the young
2 (Brown 1987). Members of cooperative groups might obtain indirect fitness benefits from
3 feeding the young of relatives by augmenting the production of non-descendent kin
4 (Hamilton 1964; Brown 1987), or they might obtain current direct benefits from raising
5 their own offspring. Furthermore, cooperation might grant future benefits such as access
6 to mating, inheritance of the territory, enhanced survival, or acquisition of skills that
7 facilitate later reproduction (Emlen 1991; Cockburn 1998). Individual contribution to
8 care of young by group members can help us to understand the evolution of cooperative
9 breeding, as individual effort is expected to reflect a trade-off between costs and benefits
10 of care (Cockburn 1998).

11 Cooperative societies can form through several routes (for a review see Cockburn
12 1998). Social groups can be extended families, where helpers do not breed and might
13 obtain indirect fitness benefits from feeding the young. If indirect fitness benefits
14 influence helping behavior, helpers are expected to vary their effort according to their
15 relatedness to the young (Emlen 1991) assuming that there is a mechanism for
16 determining who kin are. In other species, cooperation arises through polyandry, where
17 several unrelated males share matings with a female and contribute to feed the young.
18 Theory suggests that males in polyandrous groups should adjust their contribution
19 according to their level of parentage in the brood, if they have reliable clues about the
20 proportion of offspring sired (Whittingham et al. 1992; Westneat and Sherman 1993).

21 It is still unclear how current indirect and direct fitness benefits influence the
22 individual contribution to young care in cooperative societies. In some kin societies, such
23 as white-fronted bee-eaters *Merops bullockoides* (Emlen and Wrege 1988), Galapagos

1 mockingbirds *Nesomimus parvulus* (Curry 1988), long-tailed tits *Aegithalos caudatus*
2 (Russell and Hatchwell 2001) and Seychelles warblers *Acrocephalus sechellensis*
3 (Richardson et al. 2003), helpers are more likely to aid close relatives. However, no
4 correlation between relatedness and helping effort has been found in Arabian babblers
5 *Turdoides squamiceps* (Wright et al. 1999), laughing kookaburras *Dacelo novaeguineae*
6 (Legge 2000), and meerkats *Suricata suricatta* (Clutton-Brock et al. 2001). On the other
7 hand, the individual contribution to young care varies in relation to the share of parentage
8 in some polyandrous societies (dunnocks *Prunella modularis*, Davies et al. 1992; alpine
9 accentors *Prunella collaris*, Hartley et al. 1995; superb fairy-wrens *Malurus cyaneus*,
10 Dunn and Cockburn 1996) but not in others (pukekos *Pukeko pukeko*, Craig and
11 Jamieson 1985; Galapagos hawks *Buteo galapagoensis*, DeLay et al. 1996).

12 A society of carrion crows *Corvus corone corone* in northern Spain is an ideal
13 model to study the relative influence of direct and indirect fitness benefits on individual
14 contributions to cooperative care. Unlike most European populations, Spanish crows
15 breed cooperatively (Baglione et al. 2002a). Sociality arises through both delayed
16 dispersal of juveniles of both sexes that stay on the natal territory in association with one
17 or both parents (hereafter non-dispersing offspring), and through immigration of
18 individuals (mostly males) into territories where the dominant breeder of the same sex is
19 a relative (Baglione et al. 2002a, Baglione et al. 2003). In this complex society, different
20 group members obtain different benefits from group living. Some individuals, including
21 sexually immature immigrants and non-dispersing offspring associated with the parent of
22 opposite sex, have no access to reproduction within their group (non-breeders), but they
23 may gain indirect fitness benefits from raising related nestlings. Other group members,

1 including the dominant pair and all sexually mature immigrants, potentially have access
2 to reproduction within their group (potential breeders). Previous studies actually showed
3 that a substantial proportion of male mature immigrants mate with the dominant female
4 and gain direct fitness benefits, and that female immigrants may occasionally lay eggs
5 (Baglione et al. 2002a).

6 In this study we test: 1) if the work load differs between potential breeders and
7 non-breeders. Subsequently, we address variability in the provisioning effort within each
8 reproductive category, testing 2) how the share of parentage (proportion of offspring
9 generated) influences the feeding effort of potential breeders, and 3) how the relatedness
10 between non-breeders and nestlings influences their individual feeding rate. To do so, we
11 combined genetic information on parentage and relatedness between group members and
12 nestlings with video recorded observations of individual feeding rates.

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14 Methods

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16 Study population

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18 We have studied a population of carrion crows in a 45 km² rural area in Northern Spain
19 (42° N, 5° W) since 1995. The study area represents a traditional Spanish low intensity
20 agricultural landscape, with a mosaic of crops, meadows, poplar plantations, scrubs, oak
21 forest patches and uncultivated land. In this population, 75% of the territories (N = 236
22 group-years) are held by cohesive cooperatively breeding groups of up to nine birds
23 (mode = 3 birds). Groups form by delayed dispersal of offspring or immigration of

1 individuals that are related to the dominant breeder of the same sex (Baglione et al.
2 2002a; Baglione et al. 2003). Territories can therefore contain unassisted pairs (25% of
3 groups), families (a pair with non-dispersing offspring, 17% of groups), mixed groups (a
4 pair with both non-dispersing offspring and immigrants, 18% of groups) or pairs with one
5 or more immigrants (40% of groups). The sex ratio in the groups is male biased, but
6 supernumerary females are also found in the social groups. Immigrants of both sexes can
7 participate in reproduction within their group. Overall, within-group polygamy occurs in
8 67% of groups containing sexually mature immigrants, with polyandry prevalent over
9 joint egg laying. Molecular data suggested that extra-pair fertilizations by individuals
10 outside the social group do not occur in this population (Baglione et al. 2002b). Non-
11 dispersing offspring are usually associated with their parents and therefore unlikely to
12 breed within their natal territory due to incest avoidance. Both non-dispersing offspring
13 and immigrants can feed the incubating female and the nestlings, and can contribute to
14 nest sanitation, territorial defense and nest building. Egg incubation and brooding are
15 carried out by breeding females only. The maximum number of helpers at-the-nest
16 recorded in a group is three.

17

18 Classification of group members

19

20 Group members can be classified as “potential breeders” or “non-breeders” according to
21 whether or not they had potentially access to reproduction within the group (Table 1).
22 Based on incest avoidance criteria, we considered as potential breeders all sexually
23 mature group members that had at least one unrelated potential mate within the group.

1 This category includes the dominant pair and all immigrants of both sexes older than one
2 year (sexual maturity arises in the second year in crows, Cramp and Perrins 1994; Madge
3 and Burn 1999). Potential breeders would also include non-dispersing offspring older
4 than one year associated with a step-parent of the opposite sex, but these individuals were
5 not represented in our sample. According to molecular data (see below) we further
6 divided potential breeders into “parents” (genetic mothers or fathers of at least one
7 nestling in the brood) and “unsuccessful potential breeders” (those that generated no
8 nestlings). We classified as non-breeders all yearlings and non-dispersing offspring older
9 than one year that lived with both their genetic parents or at least with the genetic parent
10 of the opposite sex (parent-offspring associations were assessed on the base of molecular
11 data, see below and Baglione et al. 2002b). This classification is suitable for this study, as
12 it reflects the different kinds of current benefits that group members might derive from
13 cooperating at the nest.

14 To answer questions 1 and 3, we considered two possibilities for unsuccessful
15 potential breeders. The first is that they mated, but failed to gain a share of reproduction.
16 For example, a male may have gained copulations but lost out in the sperm lottery during
17 fertilization. The second is that they had no access to reproduction at all within the group,
18 and so were truly non-breeders (i.e. both genetically and socially). In crows, copulations
19 are difficult to observe and, so far, it has been impossible to identify other behaviors that
20 reliably indicate the share of paternity (e.g. time spent close to the breeding female during
21 the fertile period, see Davies et al. 1992). As field data could not contribute to refine our
22 classification of individuals, we answered question 1 by putting the unsuccessful

1 potential breeders in a separate category. To answer question 3 we ran two analyses, one
2 including unsuccessful potential breeders and one without, and we compared the results.

3

4 Molecular methods

5

6 In spring 1999, 2000 and 2003 we captured free flying carrion crows using two-
7 compartment walk-in traps and a snap trap specifically developed for this species (for
8 details on capture methods see Baglione et al. 2002a). We banded all the individuals with
9 a unique combination of color rings and wing tags. The birds were aged as one, two, and
10 older than two years according to the internal color of the upper mandible (Svensson
11 1992). The nestlings were banded with color rings just before they left the nest (30 days
12 after hatching).

13 We collected between 50 and 200 μ l of blood from the alar vein of each banded
14 individual. P2/P8 sexing method (Griffiths et al. 1998) provided the sex of the banded
15 birds. In a previous analysis, eight microsatellite loci (5.1 alleles on average, min-max =
16 2-8) were used to determine parentage in the groups (for details see Baglione et al.
17 2002b). According to our molecular data, we determined the number of offspring in the
18 brood generated by each potential breeder and calculated the proportion of nestlings
19 produced (also called “share of parentage” hereafter).

20 When possible, we assigned relatedness between group members and nestlings
21 based on the parentage analysis. In genetically monogamous groups, we assigned a
22 relatedness of 0.5 to group members that were offspring of both parents of the current
23 brood, and 0.25 when a step parent was present. Relatedness in groups with immigrants

1 was more complicated by the facts that a) relatedness between same-sex immigrants and
2 residents differs significantly from 0 (Baglione et al. 2003), and b) polygamous mating is
3 common. In those groups, we were unable to derive relatedness from the parentage
4 analysis. To assign r between potential breeders and non-offspring nestlings, and between
5 non-breeders and nestlings that were not their full brothers we relied on six microsatellite
6 loci (five alleles on average; min-max: 2-8) that could be scored unambiguously for all
7 the individuals and we estimated r by using the software Relatedness (Queller and
8 Goodnight 1989). The accuracy of r estimates was tested by calculating relatedness for
9 known categories, obtaining mean $r \pm SE = 0.48 \pm 0.02$ for parent-offspring ($n = 96$;
10 expected $r = 0.5$) and mean $r = 0.48 \pm 0.04$ for full siblings ($n = 67$; expected $r = 0.5$).
11 We obtained mean $r = 0.06 \pm 0.05$ for presumed non-relatives (members of breeding
12 pairs, $n = 17$). The final r values used in the analyses was the average relatedness
13 between an individual and all the nestlings reared in its territory.

14

15 Observations of individual feeding effort

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17 We placed video cameras 2 - 2.5 m away from the nests to record the nestling care
18 activities from day 11 after egg hatching (when breeding females brood only
19 occasionally) to the time of fledging on day 30. We used camouflaged micro-cameras
20 (size: 4×2×2 cm) commonly used for security systems and video-recorders placed at the
21 bottom of the nest tree. The birds never showed any visible reaction to the video cameras
22 and video recorded nests did not show a higher rate of brood failure (8/22) compared to
23 control non-video sampled nests (44/ 96, Yates corrected χ^2 test = 0.32, $p = 0.57$).

1 Recording bouts (four hours) were randomly distributed from 05.00 hours till 20.00
2 hours. The overall time of recording per nest varied between eight and 56 hours (Mean \pm
3 SE = 29.8 ± 1.83 for a total of 558 hours of observation) and data were collected over 2-
4 14 days per nest. Trapping, bird banding and blood sampling were authorized by the
5 Junta de Castilla y León.

6 Individual provisioning effort in birds is often measured as number and type of
7 food items brought to the nest or as number of feeding visits, but such methods are not
8 appropriate for carrion crows. Since carrion crows carry food in their crops, food items
9 are not visible in the recordings. Furthermore, a previous study showed that nest visits do
10 not always represent feeding events, as carrion crows sometimes fly to the nest but refrain
11 from feeding the chicks (Canestrari et al. 2004). We counted feedings to measure the
12 individual feeding effort. Feedings are conspicuous in the carrion crow and always
13 unequivocally visible in the video recordings. The crows carry food in their crops and
14 when they arrive on the nest, they put their beak in a nestling's open gape and regurgitate
15 part of the food, then they extract the beak and may repeat the act with the same nestling
16 or several others. We considered each of these events, which ranged between one and
17 five for each visit, as a feeding. To assess the assumption that the number of feedings per
18 visit is a good estimate of the amount of food that carrion crows carry to the nest in a
19 feeding trip, we performed the following test. We distinguished three different volumes
20 of feeding individuals' crop-loads of food on first arrival at the nest from the videotapes:
21 1, when no swelling of the crop was visible or when it was just detectable; 2, when the
22 swelling was prominent but it was less than half beak depth; 3, when the swelling was
23 more than half beak depth. We randomly chose 12 carrion crows and we took, for every

1 individual, repeated measures of the number of feedings for each defined crop's volume
2 (total number of deliveries = 226; total number of visits = 112). For every crow, we
3 calculated the mean number of feedings per visit (mean f) for each crop's volume and we
4 regarded these means as data points in the statistical analysis. Mean f increased with
5 crop's volume (Friedman ANOVA: Chi Square = 23, $n = 12$, $df = 2$, $p < 0.001$),
6 indicating that feedings are a suitable measure of nestling provisioning effort.

7

8 Statistical analysis

9

10 We calculated the number of feedings per hour (feeding rate) to characterize the
11 individual feeding effort. In three separate analyses, we used SPSS General Linear Model
12 (GLM) type III to test whether: 1) individuals of different categories differed in their
13 feeding effort. 2) feeding rate of potential breeders was influenced by parentage, and 3)
14 feeding rate of non-breeders varied with their relatedness to the chicks. In all models we
15 included sex, tarsus length (which in crows provides an estimate of dominance rank,
16 Richner 1989) and age of the individuals, and we controlled for territory's brood size and
17 number of adults providing care. Behavioral observations were carried out between day
18 11 and day 30 after hatching. We conducted a preliminary analysis to test whether chick
19 age had an effect on individual provisioning. For 23 individuals (15 adults and 8
20 yearlings) we compared the number of feedings per chick when nestlings were between
21 11-20 days and 21-30 days old. A Wilcoxon matched pairs test detected no statistical
22 difference among adults ($Z = -1.59$, $p = 0.1$) nor among yearlings ($Z = -0.6$, $p = 0.5$).
23 Therefore, we pooled the data of individual contribution to chicks aged between 11 and

1 30 days. Overall, we collected data on individual contribution of 30 parents (15 males
2 and 15 females), 8 unsuccessful potential breeders (5 males and 3 females), and 25 non-
3 breeders (15 males and 10 females) belonging to ten families, five mixed groups and five
4 pairs with immigrants. The small number of unsuccessful breeding females in our sample
5 reflects the rarity of female immigrants in the groups.

6

7 Results

8

9 Contribution to chick feeding by group members of different categories

10

11 Parents, unsuccessful breeders and non-breeders differed in their feeding effort (Table 2).
12 Tukey HDS post-hoc comparison indicates that parents' feeding rates were significantly
13 higher than those of unsuccessful potential breeders and non-breeders, while there was no
14 significant difference between the latter two categories. In general, females fed the chicks
15 at lower rates than males (Fig. 1). However, as the following models showed (see Table 3
16 and Table 4), the difference was statistically significant only among unsuccessful
17 potential breeders and non-breeders. Individual feeding rate was positively correlated
18 with brood size, but not with number of care-givers, age and dominance rank.

19 We also performed a Wilcoxon Matched Pairs Test to compare the feeding rates
20 of parents and non-breeders in 15 groups containing members of both categories. Within
21 the groups, parents showed a higher feeding rate than non-breeders ($Z = -2.5$, $p = 0.01$).
22 Similarly, in 5 groups containing parents and unsuccessful potential breeders, the former
23 exhibited higher feeding rates ($Z = -2.2$, $p = 0.028$).

1 Contribution to chick feeding by potential breeders

2

3 Potential breeders varied their feeding rate according to their parentage in the brood
4 (Table 3). Both males and females increased their provisioning effort with their share of
5 parentage (Fig. 2), but this effect was significant only if we included the individuals who
6 had no parentage (Table 3). By removing them, the analysis no longer detected any effect
7 of parentage, suggesting that parents do not fine-tune their contribution to the proportion
8 of offspring generated. Individual feeding rate increased significantly with brood size,
9 while sex, dominance rank, age and number of care-givers showed no significant effect.

10

11 Contribution to chick feeding by non-breeders

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13 The analysis was run two times, first considering only the true non-breeders and then
14 including the unsuccessful potential breeders (Table 4). Among non-breeders, only sex
15 had a significant effect on individual feeding rate. Male helpers made a greater
16 contribution to chick feeding than females (Fig. 1). Helpers did not significantly vary
17 their feeding rate according to their relatedness to the chicks (Fig. 3), nor with dominance
18 rank, age, brood size or number of care-givers. When we included unsuccessful potential
19 breeders ($n = 8$) in the analysis, the results did not change qualitatively. Again only sex
20 had a significant effect on feeding rate, with an increase in its F value (Table 4).

21

22 Discussion

23

1 Within the groups, parents fed the chicks at significantly higher rates than any other
2 group member, with no statistical difference between the contribution of mothers and
3 fathers. Unsuccessful potential breeders and non-breeders showed comparable feeding
4 rates, with males making higher contributions than females. The differences in
5 contributions do not seem to reflect a bias in parenting skills, since individual effort did
6 not increase with age. These results indicate that, among the benefits of care available to
7 different group members, current direct fitness benefits determined a higher individual
8 contribution to chick feeding. The patterns of provisioning effort of parents might explain
9 why within-group polygamy occurs. As parents make a higher contribution to chick
10 feeding, but they do not adjust their effort to the proportion of offspring generated,
11 dominant breeders may benefit more via the aid of a hard-working co-breeder than they
12 lose by allowing that co-breeder parentage. To assess this idea, we are currently
13 investigating the effect of the number and type of care-givers on the reproductive success
14 of crows. The importance of current direct fitness benefits in increasing the levels of help
15 has been also shown in western bluebirds, where helpers with a potential for copulatory
16 access showed higher feeding rates than helpers that had no breeding opportunity within
17 their group (Dickinson 2004).

18

19 Contribution to chick feeding by potential breeders

20

21 In species where polygamy occurs, individuals might care for young that are not their
22 own, and theoretical models suggest that they might reduce their effort in relation to a
23 perceived loss of parentage (Whittingham et al. 1992; Westneat and Sherman 1993). A

1 relationship between parentage and parental care is expected in species where there is a
2 trade-off between current and future reproduction (i.e. when parental care is costly) and if
3 individuals have reliable cues about their share of paternity (Sheldon and Ellegren 1998).
4 Furthermore, cuckolded individuals are especially expected to reduce their effort if they
5 are aided by helpers that can compensate for their decreased parental care (Davies and
6 Hatchwell 1992; Davies et al. 1992; Whittingham and Dunn 1998).

7 In cooperative carrion crows, reproduction is often shared between dominant
8 breeders and related adult immigrants of either sex (Baglione et al. 2002b). Among
9 potential breeders, the genetic contribution to the brood was important in determining the
10 individual feeding rate. However, although unsuccessful potential breeders showed
11 significantly lower feeding rates than parents, the latter did not seem to adjust their
12 contribution to their share of parentage. One possible explanation of the pattern observed
13 is that crows can assess the probability of having generated offspring (e.g. by relying on
14 whether or not they copulated), but they do not possess a finer mechanism to estimate
15 their share of parentage. This seems to occur in the pukeko (Jamieson et al. 1994) and in
16 the Galapagos hawk (DeLay et al. 1996), where all males in a group copulate with the
17 female and they seem to have no cues about their level of paternity within broods.
18 Alternatively, crows in polygamous groups might not lower their feeding rate because
19 parentage loss might be compensated by indirect fitness benefits, as co-breeders are
20 related (Baglione et al. 2003).

21

22 Contribution to chick feeding by non-breeders

23

1 The role of kin selection in shaping the crow society has been supported by evidence that
2 crows actively choose relatives to ally with when they become helpers at the nest
3 (Baglione et al. 2003). The fact that we did not find a statistically significant correlation
4 between relatedness and helping behavior supports the idea that individual provisioning
5 effort can be disjoint from the relatedness to the chicks, even when indirect fitness is
6 important in the maintenance of cooperative breeding. Besides the fact that the lack of
7 correlation in our data might be merely due to limited power of the analysis, there are
8 other four arguments behind this idea:

9 1) As shown by a recent mathematical model, the relatedness to the chicks might
10 be a poor predictor of individual helping effort when the inclusive fitness of provisioning
11 by helpers are calculated as a combination of relatedness and reproductive value of
12 helpers and young (i.e. the probability of becoming a breeder in the future) and when the
13 costs of helping are taken into account (Hardling et al. 2003).

14 2) The costs of lack of discrimination might be small in crows and the costs of
15 recognition errors large (failure to feed close relatives). In mixed groups, where
16 polygamy dilutes the degree of relatedness between non dispersing offspring and chicks,
17 reproduction is shared among close relatives (Baglione et al. 2003) and therefore the
18 average degree of relatedness between helpers and chicks remains high.

19 3) Individuals might lack a mechanism to finely assess their relatedness to the
20 young. We could not test whether there was a difference in contribution among helpers
21 that had obvious clues about their degree of relatedness with the chicks (e.g. non-
22 dispersing offspring aiding both parents versus those aiding a parent and a step-parent, or
23 non-dispersing offspring versus yearling immigrants). The number of non dispersing

1 offspring living in step families and yearling immigrants in our sample was too small to
2 perform such test.

3 4) Additional direct benefits of helping might compensate for the asymmetry in
4 the amount of indirect fitness benefits to helpers, resulting in a comparable provisioning
5 effort regardless of the differences in the relatedness with the chicks. In crows, future
6 direct fitness benefits are especially available to immigrants. Unlike non dispersing
7 offspring, immigrants find potential mates within the group (Baglione et al. 2003), and
8 they might obtain matings in the future if they signal their parental ability through help
9 (Zahavi 1995; Putland 2001). Furthermore, immigrants sometimes inherited the territory
10 after the death of the same-sex dominant, while offspring did not (Baglione unpublished
11 data).

12 The sex bias in helping behavior might indicate the importance of indirect fitness
13 among crow helpers. Assuming that kin selection is important in cooperative societies, it
14 has been shown theoretically that male biased cooperation could be favored by a
15 polyandrous mating system (Charnov 1981). If multiple males contribute to a clutch, a
16 female will be on average more related to her offspring than to her siblings. By contrast,
17 if male A sires proportion p of the nestlings, his average coefficient of relatedness to
18 these young will be $p/2$ when the other male is unrelated to him. Assuming that the father
19 of male A sired the same proportion p of nestlings, the relatedness between male A and
20 his sibs will be $(1+p^2)/4$, which is greater than $p/2$ whenever $p < 1$. The asymmetry holds
21 even when the male co-breeders are related, and could explain why crow female
22 offspring provide less food to the nestlings in the studied population, where polyandry is
23 common. A sex bias in helping effort might also be explained considering the difference

1 in reproductive value between helpers. If help is costly, current investment in help
2 reduces the future reproductive success of individuals. Individuals might adjust their
3 helping effort according to their expected future reproductive success, working less hard
4 the higher their probabilities to reach breeding status (Cant and Field 2001). In
5 cooperative crows, the sex ratio in groups is biased towards males (Baglione et al.
6 2002b). Although subordinate males can share in reproduction when they reach sexual
7 maturity, subordinate females have more chances to become dominant breeders. This
8 asymmetry might result in the observed male biased helping effort.

9 In this paper we have shown how different benefits lead to different investment in
10 nestling feeding by cooperative carrion crows. However, individual provisioning effort
11 can be influenced also by the costs of care (Heinsohn and Legge 1999), which might vary
12 among individuals. Future research will focus on these costs to fully explore cooperative
13 nestling rearing in this society.

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1 Figure legend

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3 Figure 1. Feeding rate (number of feedings per hour) by male and female parents,
4 unsuccessful potential breeders and non-breeders. Sample sizes are given above bars.

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7 Figure 2. Individual feeding rate (number of feedings per hour) of male and female
8 potential breeders plotted against the proportion of offspring generated in the brood of
9 their territory

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13 Figure 3. Individual feeding rate (number of feedings per hour) of male and female non
14 breeders and unsuccessful potential breeders plotted against the relatedness with the
15 nestlings

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Table 1.

Classification of group members

POTENTIAL BREEDERS (n = 38)		NON BREEDERS (n = 25)
<i>Parents (n = 30)</i>	<i>Unsuccessful potential breeders (n= 8)</i>	
group members that had: - at least one unrelated potential mate within the group - offspring in the current brood	group members that had: - at least one unrelated potential mate within the group - no offspring in the current brood	- yearlings - non dispersing offspring living with the parent of the opposite sex

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Table 2.

Factors affecting the relative individual contribution to nestling feeding by members of different categories (parents, unsuccessful potential breeders, non-breeders).

	F	d.f.	P
Category	4.4	2	0.02
Age	0.82	1	0.37
Sex	4.5	1	0.04
Tarsus length	0.64	1	0.43
Number of chicks	6.4	1	0.01
Number of care-givers	1.87	1	0.18
Category x Sex	0.35	2	0.71

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Table 3.

Factors affecting the relative individual contribution to nestling feeding by potential breeders and by parents only.

	All potential breeders			Parents only		
	F	d.f.	P	F	d.f.	P
Share of parentage	4.3	1	0.04	1.54	1	0.22
Age	0.34	1	0.56	0.62	1	0.44
Sex	0.71	1	0.4	0.05	1	0.83
Tarsus length	0.004	1	0.95	0	1	0.99
Number of chicks	8	1	0.008	7.9	1	0.01
Number of care-givers	0.42	1	0.51	2.1	1	0.16

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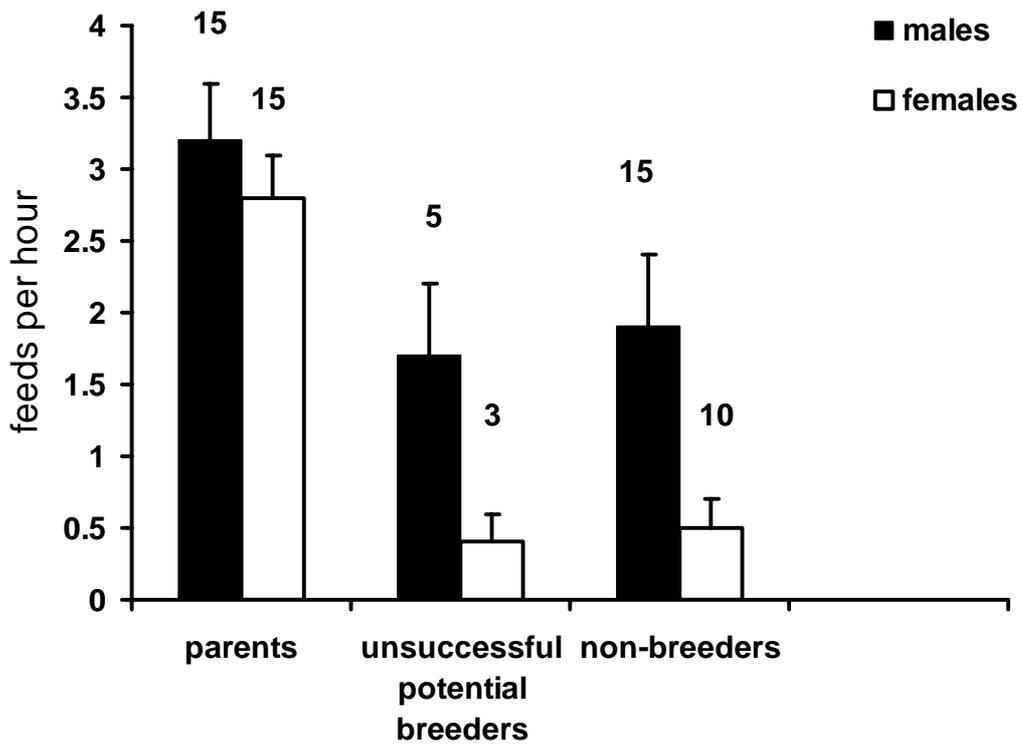
Table 4.

Factors affecting the relative individual contribution to nestling feeding by non breeders
and by non-breeders and unsuccessful potential breeders.

	Non-breeders			Non-breeders + Unsuccessful potential breeders		
	F	d.f.	P	F	d.f.	P
Relatedness	1.62	1	0.22	2.38	1	0.13
Age	1.56	1	0.23	2.41	1	0.13
Sex	6.89	1	0.02	9.65	1	0.005
Tarsus length	0.91	1	0.35	1.95	1	0.17
Number of chicks	0.68	1	0.42	1.13	1	0.29
Number of care-givers	0.004	1	0.94	0.06	1	0.8

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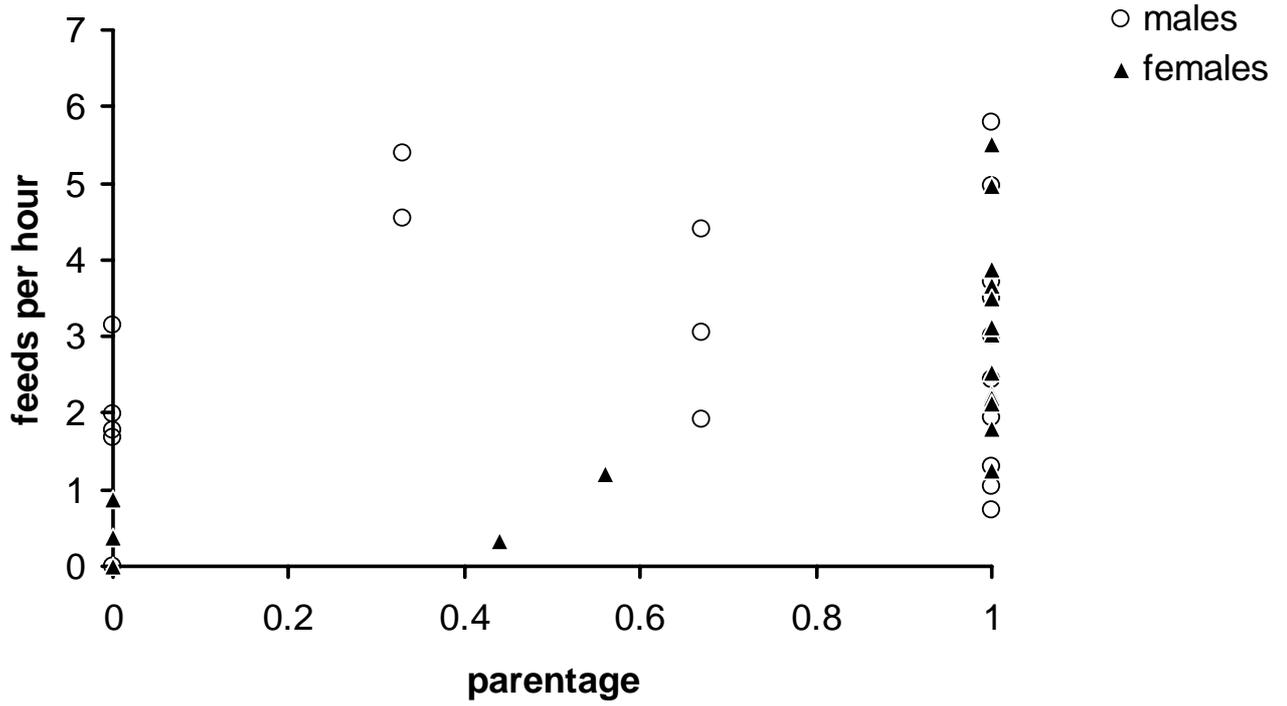
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Figure 1

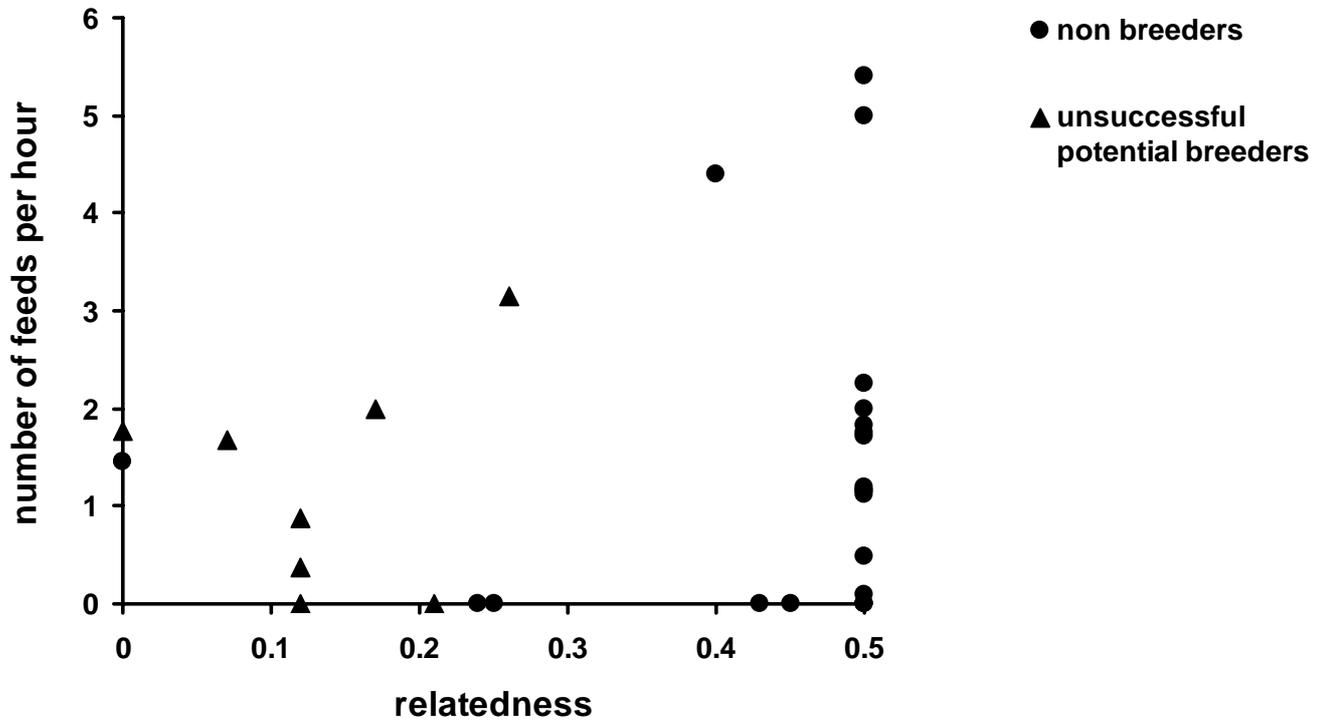
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Figure 2

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Figure 3