



Reproductive success increases with group size in cooperative carrion crows, *Corvus corone corone*

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The effect of group size and the number of helpers on reproductive success is crucial to understand the evolution and maintenance of cooperative breeding. In northern Spain, carrion crows form kin-groups (three to nine individuals) where up to five individuals contribute to rearing the young. Using data from 99 different territories, followed over 10 years, we showed that group size was positively correlated with the annual number of fledglings produced, after controlling for the potential confounding effect of territory quality. This occurred through: (1) an increased probability for larger groups of re-nesting after early nest failure; (2) a higher probability of nest success; and (3) a higher number of fledglings produced in successful attempts. Video-recorded observations at the nests showed that chicks received more food in larger groups during the first 10 days of life, when the risk of starvation is highest, suggesting a role of allofeeding by additional carers in augmenting the reproductive success of a group. In crows, indirect and direct benefits through increased production of young are therefore available to nonbreeding group members.

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In about 8% of bird species and 3% of mammals, more than two individuals cooperate to raise young from a single brood or litter (Emlen 1991; Cockburn 2003). Cooperative groups are often families, where offspring delay dispersal and help their parents to raise new broods on their natal territory. Associations of unrelated individuals, which frequently show polygamous mating, also occur in several species (Cockburn 1998). When groups form through the association of closely related individuals, additional carers usually do not breed and might obtain indirect fitness benefits by increasing the production of nondescendant kin (Hamilton 1964; Dickinson & Hatchwell 2004). To test whether helping in these species is

a kin selected trait, it is crucial to know whether the presence of helpers enhances the reproductive success of a group (Emlen 1991; Cockburn 1998).

The effect of the presence of multiple carers on reproductive success is difficult to assess, and available studies on cooperative species show contrasting results. In some species, for example, white-fronted bee-eaters, *Merops bullockoides* (Emlen & Wrege 1991) and white-winged choughs, *Corcorax melanorhamphos* (Heinsohn 1992), a positive correlation between group size and the number of young produced has been detected. However, simple correlations that do not take territory quality into account are difficult to interpret, especially in species where groups form as a result of juvenile delayed dispersal. Better territories might both produce and retain more offspring, leading to the formation of larger groups. Territory quality might therefore affect both reproductive success and group size, producing a noncausal positive correlation (Cockburn 1998; Dickinson & Hatchwell 2004).

Paired comparisons of the same territory in different years with or without helpers failed to find an effect of

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helpers on reproductive success in laughing kookaburras, *Dacelo novaeguineae* (Legge 2000), rufous vanga, *Schetba rufa* (Eguchi et al. 2002) and American crows, *Corvus brachyrhynchos hesperis* (Caffrey 2000a). However, this method might be biased against finding an effect of helpers, as pairs that go from being unhelped 1 year to having helpers the next year must breed successfully in the first year, while assisted pairs that become unassisted in the following year must have bred unsuccessfully in the first year. Therefore, this method intrinsically selects unassisted pairs with above average reproductive success and assisted pairs with below average breeding success (Dickinson & Hatchwell 2004).

An alternative approach is to experimentally remove helpers from a number of territories and to compare the reproductive success of reduced groups with that of unmanipulated ones. In Florida scrub jays, *Aphelocoma coerulescens* (Mumme 1992), Seychelles warblers, *Acrocephalus sechellensis* (Komdeur 1994) and grey-crowned babblers, *Pomatostomus temporalis* (Brown et al. 1982), groups that were experimentally reduced produced fewer fledglings than unmanipulated groups, but this pattern has not been found in moorhens *Gallinula chloropus* (Leonard et al. 1989). However, the value of removal experiments has been questioned, as a decreased reproductive success in experimental groups might be caused by the disruption of the social groups, rather than by a reduced number of helpers (Cockburn 1998; Dickinson & Hatchwell 2004).

A powerful way to assess the effect of helpers on breeding success is to compare the productivity of the same territory over several years with a variable number of helpers, controlling statistically for the possible confounding effect of territory quality in a mixed model (Cockburn 1998; Dickinson & Hatchwell 2004). A shortcoming of this approach is that it requires large data sets from long-term studies. This is why mixed models have been employed only in a few species: white browed scrubwrens, *Sericornis frontalis* (Magrath 2001), meerkats, *Suricata suricatta* (Russell et al. 2003), long-tailed tits, *Aegithalos caudatus* (Hatchwell et al. 2004), apostlebird, *Struthidea cinerea* (Woxvold & Magrath 2005).

In this paper, we used mixed models to investigate the effect of group size on the annual number of fledglings produced in cooperatively breeding carrion crows, based on a 10-year survey (1995–2004) of 99 territories. To investigate the mechanisms behind this relationship, we analysed the effect of group size on various stages of reproduction, that is, clutch size, hatching success, probability of re-nesting after failure, probability of breeding successfully (producing at least one fledgling) and number of nestlings per successful nest. To examine whether provisioning by additional carers has a role in enhancing fledgling production, we investigated whether the labour force at the nest (i.e. the number of care-givers), rather than actual group size, better explained the number of fledglings produced, and whether the number of care-givers enhances the total feeding rate in groups. Finally, we asked whether group size and the number of care-givers also affect the quality of fledglings, that is, their body size and condition.

METHODS

Study Area and Population

We studied a population of carrion crows in a 45-km² rural area in Northern Spain (42°N, 5°W). The study area represents a traditional Spanish low intensity agricultural landscape, with a mosaic of crops, meadows, poplar and pine plantations, scrub, oak forest patches and uncultivated land. Since 1995, all nestlings in the study area have been banded with colour rings and/or wing tags (Caffrey 2000b) just before fledging and, between 1999 and 2004, 79 adult crows were caught with walk-in traps and a snap-trap developed for this species (Baglione et al. 2002a). In this population, about 75% of territories every year are occupied by social groups containing three to nine individuals, while the remaining territories are held by pairs (Baglione et al. 2002a). Sociality arises both through delayed dispersal of offspring that stay on the natal territory, associated with one or both parents, and through immigration into the territories of individuals that are related to the dominant breeder of the same sex (Baglione et al. 2002a, 2003). Delayed dispersal and immigration are skewed towards males, but females can be found in both categories. Yearling group members, which are sexually immature, and nondispersing offspring of all ages do not breed within their group, while adult immigrants often share reproduction with the resident breeders (Baglione et al. 2002b). Both nondispersing offspring and immigrants may contribute to building the nest, feeding the incubating female and the chicks, and defending the territory against intruders and predators (Baglione et al. 2002a). However, not all group members participate equally in nestling feeding, with some individuals refraining from provisioning the chicks. The maximum number of care-givers recorded in a group is five. In general, individuals that generated offspring make the greatest contribution to chick provisioning. Among nonbreeders, nondispersing offspring and nonbreeding immigrants do not significantly differ in their provisioning effort, being females of both categories the least likely to help at the nest (Canestrari et al. 2005).

In this population, crows live in all-purpose nonoverlapping territories (average size \pm SE = 0.13 ± 0.01 km²), which are occupied and defended from conspecific intruders year-round (Baglione et al. 2005). Given the paucity of trees suitable for nesting, crows consistently use a few traditional sites, maintaining territory boundaries that are constant over years. Individual territories are therefore recognizable across years even when crows are unbanded, or when banded groups are replaced by unbanded individuals. Between successive years, on average 19.4% breeding males and 33.3% breeding females (considering only resident breeders, but not immigrants who participated in reproduction) disappear from their territories (Baglione et al. 2005). When only one breeder disappears, nondispersing offspring may remain on the natal territory with the other parent. Because of turnover of breeders, delayed dispersal of new offspring and immigration of crows from other territories, group composition changes gradually across years within territories. Conversely, sudden disappearance of entire groups occurs in 14% of territories every year

(Baglione et al. 2005), and the frequency of whole groups moving to a new territory is negligible (it has been documented twice for 77 group-years throughout the study period; V. Baglione, unpublished data).

Chick mortality is highest within the first 10 days of the 30 days nestling period (on average 75.1% of chicks that disappeared from nests that fledged at least one young did so within the first 10 days; range 56.3–85.5%; number of broods = 139). Both chick starvation and predation are causes of brood reduction in this population, as indicated, respectively, by common observations of small, emaciated nestlings growing weaker and weaker and eventually disappearing and by remains of nestlings eaten inside their nest or on the ground, close to the nest tree (J. M. Marcos, unpublished data), but their relative importance is still unknown. In bird studies, nestling mortality is usually attributed to predation when the whole brood suddenly disappears, while the loss of single chicks is interpreted as starvation (Innes & Johnston 1996; Hatchwell 1999). However, this criterion is not fully applicable in crows, where predation of single chicks occurs (in a video-recorded observation a common buzzard, *Buteo buteo*, took one nestling from a brood of two, and the surviving chick fledged successfully).

Territories and Groups' Survey

During each breeding season (March–July), we monitored group size and composition (presence or absence of banded birds and their identity) on the surveyed territories. In 64–79% of territories every year this was done in March, just before egg laying, by observing the groups from a favourable spot for at least 1 h. Additional censuses were carried out in all territories every time they were visited for routine data collection (egg-laying sequence, nestling growth, fledgling success). Since group members usually form a cohesive group, these short visits to the territories (15–30 min, repeated 5–10 times throughout the breeding season) provided reliable information on group size. When a territory remained vacant during a whole breeding season, or when group size or breeding success of a group was unknown, we excluded the data point from that particular year in the analyses. Complete information on group size and reproductive success was collected on 588 territory-years (99 different territories; mean number of sampled breeding seasons per territory \pm SE = 6 ± 0.28). Fluctuations in group size (± 1 individual) within a breeding season were recorded in 33 group-years. Such events are sometimes because of death of a group member or, more often, to movements to and from the territory of juveniles prospecting neighbouring areas. In those cases, we entered the minimum number recorded in the analyses, because unsettled individuals typically do not contribute much to allofeeding and territory defence (Baglione et al. 2006; V. Baglione, unpublished data). Removal of those groups from the analyses did not change the results' qualitatively.

Breeding Success

At the beginning of each breeding season (end of March), all territories in the study area were surveyed to find the new nests. Afterwards, regular visits allowed the

detection of late nesting attempts. All nests were followed regularly to record the time of egg laying, clutch size and hatching success. When failure occurs at eggs or hatching stage, crows may renest up to two (occasionally three) times in a season (for a maximum of four nesting attempts), and therefore new nests were searched for in territories where early failure was recorded. Renesting does not occur after a successful attempt, and therefore groups have a maximum of one successful attempt per season.

All nestlings were measured and banded just before fledging (28–30 days after hatching of the older chick in the brood) with a unique combination of colour rings and, since 2002, plastic patagial wing tags (6.5×3.5 cm) that did not affect survivorship nor provoked apparent signs of distress (Caffrey 2000b; Canestrari et al. 2007). As hatching is asynchronous in crows, siblings from the same brood could differ in age between 0 and 4 days. The length of the sixth primary feather provided a reliable estimate of chicks' age (J. M. Marcos, unpublished data). From 1998, we collected blood (50–200 μ l) from the brachial vein for DNA extraction and P2/P8 molecular sexing (Griffiths et al. 1998). No chick died or was harmed as a consequence of blood sampling. Complete information on nestling body measures, sex and size of their natal group was collected for 293 chicks in 129 broods from 62 different territories between 1998 and 2003 (mean number of broods per territory \pm SE = 2.17 ± 0.14 ; mean number of chicks per brood = 2.25 ± 0.1). All bird manipulations were authorized by Junta de Castilla y León (permit EP/177/2003).

Number of Care-givers and Feeding Rates

Group members may refrain from feeding the chicks, but when they provision, they do it throughout the breeding attempt. The number of care-givers was assessed in 132 different territory-years (86 territories) either by conducting three observations of 3 h (87 territory-years, 873 h in total) from favourable spots, with binoculars and spotting scopes 300 m away from the nest, or with 3–10 video-recorded observations of 4 h each (45 territory-years, 718 h in total) obtained by placing small video cameras close to the nests (Canestrari et al. 2005). In 18 nests that were observed for more than 20 h, the number of care-givers did not increase after 7 h of observation.

Video-recorded observations also allowed to count the number of feedings that nestlings received. Here 'feedings' are defined as every act of delivering food into a chick's open gape, that is, every visit to the nest may lead to more than one feeding. All groups ($N = 45$) were observed when the chicks were 15–20 days old (three to five bouts of 4 h each) from 0700 hours to 1100 hours, and for 11 of those, two observation bouts of 4 h were carried out also when the chicks were younger than 10 days. We measured groups' provisioning rates to the broods as the average provisioning rate shown by the group during the observation period.

Statistical Analyses

We used mixed models (Genstat 6.0), where both fixed and random terms are fitted into the models, to analyse all

data. Potential explanatory variables that gave nonsignificant results ($P > 0.1$) were sequentially eliminated until the model only included those terms for which elimination would have significantly reduced the explanatory power. Significant probability values were derived from having all significant terms fitted in the model together, whereas those of nonsignificant terms were obtained by individually reintroducing each nonsignificant term to the minimal model (Crawley 2002; Russell et al. 2003). Only interactions that were biologically meaningful were entered in the models (see description of specific analyses). In the results, values for nonsignificant interactions are omitted. For each question listed below, we used in the analyses a data set that contained the relevant information. Sample sizes, with a brief description of the subsample used in each analysis, are given in Table 1.

Data collected in the same territory across years are not independent because of intrinsic characteristics of the territory (e.g. resource abundance, predators' density) and/or the group (e.g. individuals' quality). By fitting 'territory identity' as random term into the GLMMs, we controlled for the effect of territory quality, assuming that territories retain the same relative quality between seasons. This assumption seems realistic, because the traditional low intensity agricultural landscape of our study area virtually does not change across years. Unless stated otherwise, territory identity is fitted as random factor in all analyses. Ideally, our analyses should have also included 'group identity' and/or 'breeders' identity' to account for individual variability in reproductive quality. Unfortunately, determining a biologically relevant criterion to define 'group identity' within the same territory is difficult, because changes in group composition across years are gradual and occur by many different routes. In addition to this, the data set poses limitations, because the number of territories where the turnover of identifiable groups or breeders could be followed throughout the study period is small. Restricting our sample only to groups where changes in composition or breeders turnover could be documented would have dramatically reduced the power of the analyses and masked the typically elusive effect of group size on reproductive success.

Group Size and Reproductive Success

To analyse the effect of group size on reproductive success, measured as number of fledglings produced per year, we fitted year, group size and their interaction as explanatory variables in an REML model. To detect whether group size affects particular stages of reproduction, we analysed the factors influencing: (1) clutch size; (2) the success in reaching hatching stage; (3) the number of eggs hatched in nests that reached hatching stage; (4) the probability of re-nesting after failure; (5) the probability of completing the nesting attempt successfully (at least one nestling fledged in nests that reached the hatching stage); and (6) the number of fledglings produced in successful nests. In all analyses, we fitted as explanatory variables: group size, nesting attempt (first, second, third, fourth) as covariates, year as fixed factor, interactions between group

size and year and between group size and nesting attempt. We included clutch size in analyses 2–4, and the number of eggs hatched in analyses 5 and 6. We used REML in analyses 1, 3 and 6 and GLMM with binomial distribution and logit link function in analyses 2, 4 and 5.

Number of Care-givers and Fledgling Production

In a subsample of 86 different territories (132 territory-years; Table 1) where the number of individuals provisioning the chicks was known, we fitted group size and number of care-givers into separate models to test their effect on: (1) the probability of breeding successfully (at least one fledgling produced after reaching hatching stage) analysed with a GLMM with binomial distribution and a logit link function; and (2) on the number of fledglings produced in successful breeding attempts, analysed with an REML, and we compared the results. The models were constructed with the same random factor and dependent variables in the previous analyses.

Number of Care-givers and Chick Provisioning

To test the effect of the number of care-givers on: (1) the total number of feedings per hour to the whole brood showed by groups; and (2) the number of feedings per hour per chick showed by groups, we ran four different GLMs for two different brood age classes (<10 days, 15–20 days) because nestling mortality is highest for chicks younger than 10 days, and therefore an effect of multiple care-givers is more likely to occur for this age class. Number of care-givers, brood size, reproductive attempt, year and interactions between year and number of care-givers, and between number of care-givers and brood size were entered as explanatory variables. In these analyses, each group was measured only once and therefore represents an independent data point.

Nestlings' Body Measurements

We used REML mixed models to test the effect of: (1) group size; (2) number of care-givers; and (3) average number of feedings per chick per hour on fledglings' tarsus length and body mass, including brood size, nestling sex, length of the sixth primary feather to provide an estimate of chick age, year, and interaction between group size (or number of care-givers) and year as explanatory variables. When examining the effect on body mass, we included tarsus length (cubed) in the model as covariate. To account for repeated measures, we fitted territory identity and brood identity as random factors. In these analyses, we used data from 1998 to 2003.

RESULTS

Effect of Group Size on Reproductive Success

Over 10 years of the study, the average annual fledgling production per territory varied between 0.65 and 1.24,

Table 1. Sample sizes in the analyses

Question	Number of different territories (territory-years)	Number of data points	Description of the sample
Effect of group size on the annual number of fledglings produced	99 (588)	588 Territory-years	All territory-years across the study period
Effect of group size on Clutch size	99 (588)	932 Attempts	All territory-years across the study period. For each, all reproductive attempts were considered
Probability of hatching	99 (588)	779 Attempts	As above
Hatching success	99 (394)	442 Attempts	As above
Probability of renesting	99 (412)	466 Failed attempts	As above
Probability of breeding successfully	97 (398)	637 Attempts	As above
Number of fledglings per successful attempt	84 (180)	336 Attempts	As above
Effect of the number of care-givers versus group size on reproductive success (models comparison)	86 (132)	453 Attempts	Territory-years where the number of care-givers was known through direct or video-recorded observations at the nests
Effect of the number of care-givers on the number of feedings per chick per hour	11 With broods <10 days	11 With broods <10 days	Groups where video-recorded observations at the nest were carried out. Each group was sampled only once
	45 With broods 15–20 days	45 With broods 15–20 days	
Effect of group size on nestlings' body measures	62 (129 broods)	293 Chicks	Chicks close to fledging (about 30 days old)
Effect of number of care-givers on nestlings' body measures	24 (33 broods)	66 Chicks	As above, for groups of known number of care-givers
Effect of the number of feedings per chick per hour on nestling body measures	20 (20 broods)	59 Chicks	As above, for groups where feeding rates were known

while the proportion of successful territories varied between 26.5% and 55%. Group size showed a highly significant positive effect on the number of fledglings produced in a territory (Wald statistic = 15.63, $df = 1$, $P < 0.001$; Fig. 1). Trios produced on average 0.10 fledglings (18.07%) more than pairs, and groups of four birds fledged 0.20 chicks (31.74%) more than trios. Groups larger than four were slightly more successful than groups of four (0.03 chicks of difference, 3.61%). The number of fledglings produced varied significantly across years (Wald statistic = 22.14, $df = 9$, $P = 0.008$), while the interaction between year and group size was not statistically significant (Wald statistic = 7.11, $df = 9$, $P = 0.64$).

Effect of Group Size on Different Stages of Reproduction

The results of these analyses are summarized in Table 2.

Clutch size

On average (\pm SE), crows laid 4.6 ± 0.05 eggs on their first attempt (range 1–7, $N = 588$). When nests failed with eggs or small chicks, crows renested up to two, occasionally three times (for a total of four nesting attempts), laying on average 3.6 ± 0.12 eggs on their second attempt (range 1–6, $N = 200$) and 4 ± 0.24 on their following attempts (range 1–6, $N = 144$). Clutch size at each nesting attempt decreased significantly after the first attempt,

but was not influenced by group size, year or by interactions between factors.

Success in reaching hatching stage

The success in reaching hatching was positively correlated with clutch size (the percentage of nests that reached hatching stage increased steadily from 15% of nests with

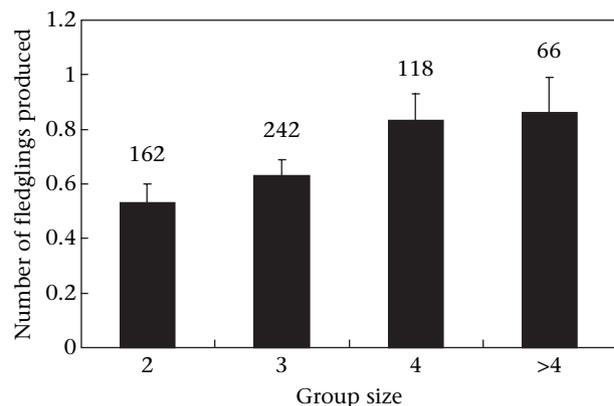


Figure 1. Average number \pm SE of fledglings produced per year by groups of two, three, four and more than four members in 1995–2004. Groups larger than four are uncommon and therefore are pooled together in the figure for simplicity, although group size was entered as a continuous variable in the models. Sample sizes are given above bars.

Table 2. Model summaries of the factors affecting: (a) clutch size in each nesting attempt; (b) success in reaching hatching stage; (c) number of eggs hatched; (d) probability of reneest after failure; (e) probability of breeding successfully (at least one young fledged); (f) number of fledglings per successful nest

Model terms	Wald statistic	df	P	Random term estimated variance component±SE	Average effect±SE
Clutch size					
Territory identity*				0.19±0.007	
Group size	0.14	1	0.71		
Year	15.27	9	0.09		
Nesting attempt	25.98	1	<0.001		
Minimal model					
Constant					4.57±0.16
Nesting attempt					-0.61±0.09
Success in reaching hatching stage					
Territory identity*				0.54±0.19	
Group size	0.26	1	0.61		
Year	12.72	9	0.15		
Nesting attempt	0.27	1	0.6		
Clutch size	41.27	1	<0.001		
Minimal model					
Constant					1.24±0.35
Clutch size					0.43±0.07
Number of eggs hatched					
Territory identity*				0.03±0.04	
Group size	1.33	1	0.25		
Year	12.02	9	0.21		
Nesting attempt	4.41	1	0.04		
Clutch size	206.77	1	<0.001		
Minimal model					
Constant					3.78±0.06
Nesting attempt					-0.23±0.11
Clutch size					0.69±0.05
Probability of reneesting after failure					
Territory identity*				0.6±0.2	
Group size	7.25	1	0.007		
Year	9.51	9	0.48		
Nesting attempt	105.04	1	<0.001		
Clutch size	0.88	1	0.35		
Minimal model					
Constant					-0.04±0.12
Group size					0.24±0.09
Nesting attempt					-1.7±0.16
Probability of breeding successfully					
Territory identity*				0.18±0.12	
Group size	4.01	1	0.04		
Year	25.43	9	0.003		
Nesting attempt	1.47	1	0.22		
Number of eggs hatched	1.76	1	0.18		
Minimal model					
Constant					0.2±0.29
Group size					0.15±0.07
Year					
1995					0
1996					-0.89±0.45
1997					-0.15
1998					-1.14
1999					0.26
2000					-0.84
2001					-0.79
2002					-0.81
2003					-0.74
2004					-0.59

Table 2. (continued)

Model terms	Wald statistic	df	P	Random term estimated variance component \pm SE	Average effect \pm SE
Number of fledglings produced per successful nest					
Territory identity*				-0.02 \pm 0.04	
Group size	11.93	1	<0.001		
Year	4.56	9	0.87		
Nesting attempt	22.23	1	<0.001		
Number of eggs hatched	94.76	1	<0.001		
Minimal model					
Constant					2.43 \pm 0.05
Group size					0.15 \pm 0.004
Nesting attempt					-0.49 \pm 0.1
Number of eggs hatched					0.36 \pm 0.04

*Random factors.

only one egg to 86% of nests with seven eggs). Group size, year, nesting attempt within the season and the interactions between variables showed no significant effect, although there was a marginally nonsignificant interaction between group size and year.

Number of eggs hatched

In nests that reached the hatching stage, on average \pm SE 79.9% \pm 0.01 of eggs hatched (range 17–83%, $N = 442$). The number of eggs hatched was positively correlated with clutch size, while the other variables showed no significant effect.

Probability of renesting after failure

When nests failed, larger groups were more likely to renest, but the probability of renesting decreased after the first failed attempt (Fig. 2).

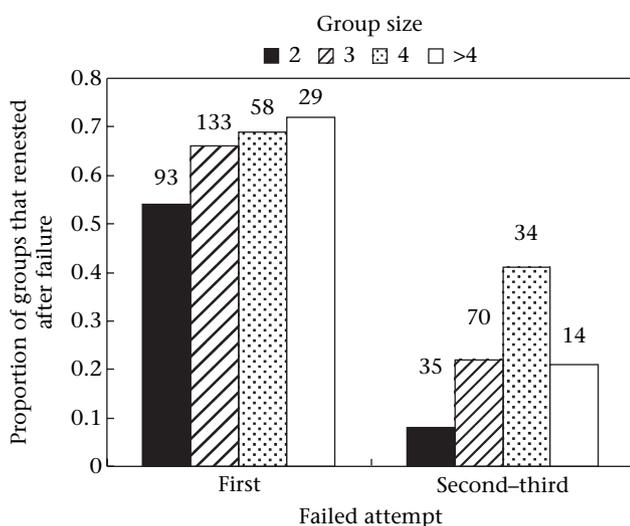


Figure 2. Proportion of groups with two, three, four and more than four members that renested after failure in the first, and second-third attempts. Groups larger than four are uncommon and therefore are pooled together in the figure for simplicity, although group size was entered as a continuous variable in the models. Sample sizes are given above bars.

Probability of breeding successfully

Once the hatching stage was reached, the probability of breeding successfully (at least one chick fledged) varied across years and it was positively influenced by group size, as larger groups were more likely to produce at least one chick (Fig. 3).

Number of fledglings per successful nest

Among successful territories, larger groups produced more fledglings (Fig. 4). The number of fledglings was positively correlated with the number of eggs hatched and depended on the nesting attempt, as later attempts were less successful than early ones.

Effect of the Number of Care-givers on Reproductive Success

Group size and number of care-givers were strongly correlated (Spearman rank correlation: $r_s = 0.95$, $N = 86$, $P < 0.001$) and were entered in separate models ('group

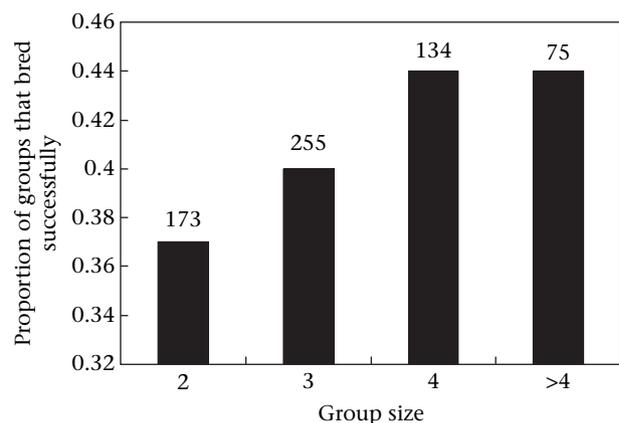


Figure 3. Proportion of successful attempts (those fledging at least one young from those that reached hatching stage) by groups with two, three, four and more than four individuals. Groups larger than four are uncommon and therefore are pooled together in the figure for simplicity, although group size was entered as a continuous variable in the models. Sample sizes are given above bars.

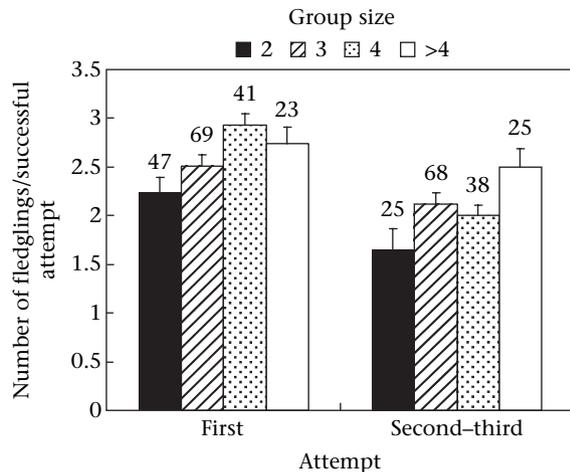


Figure 4. Mean number \pm SE of fledglings produced by successful groups with two, three, four and more than four individuals in the first and second–third attempts. Groups larger than four are uncommon and therefore are pooled together in the figure for simplicity, although group size was entered as a continuous variable in the models. Sample sizes are given above bars.

size models' and 'care-givers models'). Table 3 summarizes the results of these analyses.

Group size was more strongly correlated with the probability of breeding successfully than the number of care-givers, but the models had similar explanatory powers (deviance of group size model = 1200.6, $df = 452$; care-givers model = 1191.83, $df = 452$).

Conversely, the productivity of successful nests seemed to be more strongly correlated with the number of care-givers, but again the models showed similar explanatory powers (deviance of care-givers model = 69.41, $df = 62$; group size model = 67.25, $df = 62$).

Effect of the Number of Care-givers on the Feeding Effort of a Group

In 11 broods where chicks were less than 10 days old, the number of feedings per hour to the brood increased with the number of care-givers and with the size of the brood (Table 4). Consequently, individual nestlings received significantly more food as the number of care-givers increased (Table 4, Fig. 5), while the feeding frequency per chick was negatively correlated with brood size. In older broods (15–20 days), the number of feedings per hour to the whole brood was positively correlated with brood size but not with the number of care-givers (Table 4). As a consequence, the total frequency of feedings per chick did not increase with the number of care-givers after controlling for the negative significant effect of brood size (Table 4, Fig. 5).

Effect of Group Size on Body Measures of Fledglings

Table 5 summarizes the results described here.

Group size was not significantly correlated with nestling body mass or tarsus length (Table 5). Males had

significantly longer tarsi than females, and tarsus length was positively correlated with the length of the sixth primary feather (age). Fledgling mass was strongly influenced by sex (males were relatively heavier than females), by the length of the sixth primary feather (age), and by tarsus length³. When we restricted the analyses to 66 fledglings in 24 different territories where the number of care-givers was known we found no statistically significant effect of the number of care-givers or its interaction with year on nestling body measures. The average number of feedings per chick per hour did not significantly affect nestling body measures, either.

DISCUSSION

How does Group Size Increase Reproductive Success?

In our study population, there was a significant positive influence of group size on annual fledgling production, and this effect occurred at several reproductive stages. Group size did not significantly influence clutch size, the success in reaching hatching stage, or the number of eggs hatched. Within a breeding season, clutch size decreased in subsequent attempts, suggesting a cost of producing eggs and/or a response to changing environmental conditions. However, group size was positively correlated with the probability of re-nesting after failure, the probability of breeding successfully at each attempt and the number of fledglings produced in successful nests. We suggest three nonexclusive mechanisms to explain these patterns: (1) reduced nestling starvation due to the presence of multiple care-givers; (2) reduced nest predation; and (3) load lightening of breeders.

In our analyses, both the number of care-givers and group size were robust predictors of the probability of breeding successfully and the fledgling production per successful nest. Because 'group size models' and 'care-givers models' showed similar explanatory powers, we cannot tell apart statistically the effect of group size per se from that of the number of care-givers. However, further data suggest a role for allofeeding in augmenting the production of fledglings. Chick starvation certainly occurs in the study population. Brood reduction typically takes place at the beginning of the nestling period and, at this stage, provisioning from multiple care-givers is therefore likely to prevent starvation of nestlings. Consistent with this idea, chicks younger than 10 days received more food per capita the larger the number of care-givers, while such relationship was not found later in the nestling period. This suggests that larger groups are able to feed a larger number of chicks and that brood size is adjusted to the number of care-givers at an early stage, after which investment in individual chicks does not vary among groups. This is consistent with the fact that group size and number of care-givers were positively correlated with the number of fledglings produced but not with their body measures. In other words, helpers apparently influence the number, but not the quality of the chicks. A positive effect of helpers on fledglings' number, but not body

Table 3. Model summaries of the effect of group size and number of helpers on reproductive success

Model terms	Wald statistic	df	P	Random term estimated variance component±SE	Average effect±SE
Probability of breeding successfully					
Group size model					
Territory identity*				0.44±0.21	
Group size	12.48	1	<0.001		
Year	22.19	9	0.008		
Nesting attempt	2.31	1	0.13		
Number of eggs hatched	0.10	1	0.75		
Minimal model					
Constant					0.26±0.32
Group size					0.51±0.14
Year					
1995					0
1996					-1.19±0.45
1997					-0.23
1998					-1.27
1999					0.29
2000					-0.89
2001					-0.78
2002					-0.58
2003					-0.44
2004					-0.48
Care-givers model					
Territory identity*				0.42±0.2	
Number of care-givers	6.45	1	0.01		
Year	22.51	9	0.007		
Nesting attempt	2.27	1	0.13		
Number of eggs hatched	0.09	1	0.76		
Minimal model					
Constant					0.27±0.31
Number of care-givers					0.45±0.18
Year					
1995					0
1996					-1.25±0.45
1997					-0.28
1998					-1.24
1999					0.28
2000					-0.92
2001					-0.82
2002					-0.63
2003					-0.45
2004					-0.42
Number of fledglings produced per successful nest					
Group size model					
Territory identity*				-0.11±0.11	
Group size	5.32	1	0.02		
Year	4.39	8	0.82		
Nesting attempt	10.07	1	0.002		
Number of eggs hatched	26.30	1	<0.001		
Minimal model					
Constant					2.82±0.1
Group size					0.22±0.09
Nesting attempt					-0.58±0.18
Number of eggs hatched					0.39±0.08
Care-givers model					
Territory identity*				-0.07±0.12	
Number of care-givers	6.85	1	0.009		
Year	4.68	8	0.79		
Nesting attempt	10.74	1	0.001		
Number of eggs hatched	24.93	1	<0.001		
Minimal model					
Constant					2.31±0.27
Number of care-givers					0.39±0.14
Nesting attempt					-0.55±0.19
Number of eggs hatched					0.39±0.08

*Random factor.

Table 4. Factors affecting the total provisioning rate (number of feedings per hour) of groups

Dependent variable	Model terms	F	df	P
Feeds per hour to broods <10 days	Number of care-givers	8.04	1,8	0.02
	Brood size	18.76	1,8	0.003
	Year	0.04	1,6	0.65
	Attempt	0.19	1,7	0.68
Feeds per hour per chick (broods <10 days)	Number of care-givers	25.38	1,9	0.001
	Brood size	5.34	1,8	0.054
	Year	0.64	1,8	0.45
	Attempt	0.12	1,8	0.74
Feeds per hour to broods >10 days	Number of care-givers	1.16	1,42	0.29
	Brood size	48.2	1,44	<0.001
	Year	0.19	3,42	0.9
	Attempt	0.18	1,42	0.67
Feeds per hour per chick (broods >10 days)	Number of care-givers	0.04	1,42	0.85
	Brood size	8.62	1,43	0.005
	Year	0.03	1,42	0.99
	Attempt	0.09	1,42	0.76

Results of GLMs.

condition, was also detected in the sociable weaver, *Philetairus socius* (Covas & du Plessis 2005), while in meerkats and long-tailed tits the body mass of the young increases with the number of helpers (Clutton-Brock et al. 2001; Hatchwell et al. 2004). However, an effect of helpers on offspring quality may not emerge by looking at body measures alone. In azure-winged magpie, *Cyanopica cyanus*, fledglings raised in large groups are fed more frequently and show better immune response than those provisioned by fewer helpers, even though they do not differ in body mass or tarsus length (Valencia et al. 2006). Such a subtle

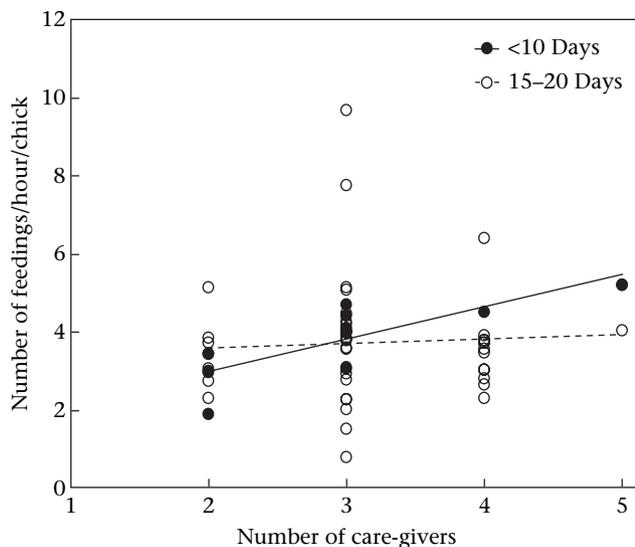


Figure 5. Correlation between the number of feedings per chick per hour and number of care-givers for broods younger than 10 days and between 15 and 20 days old.

effect on offspring quality cannot be discarded in crows, although it is unlikely, because crow nestlings after the first 10 days of life did not receive more food per capita in larger groups.

In crow cooperative society, breeding group members make the largest contribution to chick provisioning, while subordinate females often refrain to feed the nestlings (Canestrari et al. 2005). The variability in provisioning effort in groups of different composition is therefore expected to affect reproductive success at a fine scale. Unfortunately, our data set does not allow investigating the relationship between group composition and reproductive success, as the analyses based on the limited number of groups for which such information is available do not reach sufficient power.

Besides starvation, nestling predation is also likely to be reduced by increasing group size. Crows commonly attack avian nest predators (ravens, *Corvus corax*, buzzards, goshawks *Accipiter gentilis*) that intrude on their territories (Baglione et al. 2002a) and can mob carnivores as well (fox *Vulpes vulpes* and genet *Genetta genetta*; V. Baglione, unpublished data). Larger groups are likely to perform better against predators, as observed in cooperative groups of Florida scrub jays (Francis et al. 1989), and this might explain why crows that do not provision the chicks are tolerated in the territories. Furthermore, care-givers may also have an antipredator role because the detection of predators may increase with the number of individuals visiting the nest. Further research is needed to investigate the relative importance of reduced starvation and predation as mechanisms of cooperative enhancement of reproductive success.

The relationship between group size and the probability of renesting after failure suggests a load-lightening effect (Crick 1992; Heinsohn 2004) on breeders, as occurs in the apostlebird (Woxvold & Magrath 2005). In a previous study, we showed that breeders aided by two or more additional care-givers reduce their individual contribution to chick provisioning (Canestrari et al. 2006), but this is unlikely to facilitate a new reproductive attempt in case of nest failure. Renesting typically occurs when nest loss happens at the egg or hatching stage, when breeders have provisioned little, or not at all. Besides nestling care, additional group-members participate in territory defence and nest building, and feed the incubating female. A higher frequency of feedings to the incubating female and a load lightening in other activities may improve her physiological conditions and facilitate the production of a new clutch. Alternatively, breeders that have lost the nest may decide whether to invest resources in a new clutch after evaluating the probability of receiving help. Because the number of care-givers augments with group size, breeders in larger groups may afford to renest because they perceive higher chances to be load lightened in their provisioning duties.

Reproductive Success and Benefits of Cooperation

In group living animals where helping is directed towards relatives, indirect fitness benefits through

Table 5. Factors affecting nestling body mass and tarsus length

Model terms	Wald statistic	df	P	Random term estimated variance component±SE	Average effect±SE
Nestling body mass					
Group size model					
Territory identity*				149.7±118.4	
Brood identity*				606.8±144.3	
Tarsus length ³	161.52	1	<0.001		
Sex	15.60	1	<0.001		
Sixth primary feather (age)	16.96	1	<0.001		
Brood size	1.41	1	0.24		
Group size	1.39	1	0.24		
Year	8.42	5	0.13		
Minimal model					
Constant					422.2±3.54
Tarsus length ³					0.001±0.00009
Sex					
Males					0
Females					-15.51±3.9
Sixth primary feather (age)					5.15±1.25
Care-givers model					
Territory identity*				149.7±118.4	
Brood identity*				606.8±144.3	
Tarsus length ³	16.41	1	<0.001		
Sex	88.72	1	<0.001		
Sixth primary feather (age)	16.46	1	<0.001		
Brood size	0.02	1	0.89		
Number of care-givers	2.16	1	0.14		
Year	4.64	5	0.46		
Minimal model					
Constant					422.2±3.54
Tarsus length ³					0.0012±0.00009
Sex					
Males					0
Females					-15.51±3.93
Sixth primary feather (age)					5.15±1.25
Feeding rates model					
Territory identity*				1262.4±583.1	
Tarsus length ³	10.76	1	0.001		
Sex	7.28	1	0.007		
Sixth primary feather (age)	3.93	1	0.047		
Brood size	0.76	1	0.38		
Feedings per hour per chick	0.10	1	0.75		
Year	7.49	3	0.06		
Minimal model					
Constant					424.7±9.66
Tarsus length ³					0.0007±0.0002
Sex					
Males					0
Females					-28.01±12.5
Sixth primary feather (age)					7.05±3.69
Nestling tarsus length					
Group size model					
Territory identity*				0.941±0.319	
Brood identity*				0.249±0.319	
Sex	181.34	1	<0.001		
Sixth primary feather (age)	181.34	1	<0.001		
Brood size	1.71	1	0.19		
Group size	1.39	1	0.24		
Year	9.15	5	0.1		
Minimal model					
Constant					60.24±0.19
Sex					
Males					0
Females					-2.53±0.19
Sixth primary feather (age)					0.52±0.06

(continued on next page)

Table 5. (continued)

Model terms	Wald statistic	df	P	Random term estimated variance component \pm SE	Average effect \pm SE
Care-givers model					
Territory identity*				0.941 \pm 0.319	
Brood identity*				0.249 \pm 0.228	
Sex	117.59	1	<0.001		
Sixth primary feather (age)	75.43	1	<0.001		
Brood size	0.12	1	0.73		
Number of care-givers	0.68	1	0.4		
Year	8.42	5	0.13		
Minimal model					
Constant					60.24 \pm 0.19
Sex					0
Males					-2.53 \pm 0.19
Females					0.52 \pm 0.06
Sixth primary feather (age)					
Feeding rates model					
Territory identity*				2.11 \pm 1.17	
Sex	29.39	1	<0.001		
Sixth primary feather (age)	8.22	1	0.004		
Brood size	0.4	1	0.52		
Feedings per hour per chick	0.38	1	0.54		
Year	5.02	3	0.17		
Minimal model					
Constant					60.23 \pm 0.46
Sex					0
Males					-2.98 \pm 0.55
Females					0.45 \pm 0.19
Sixth primary feather (age)					

Results of REMLs.

*Random factors.

increased production of related young are believed to be one of the most likely explanations of kin sociality and cooperative breeding (Cockburn 1998), although controversy has recently arisen over this view (Griffin & West 2002). A central issue in this dispute is to ascertain whether additional group members increase the production of young, because in the absence of such relationship any kin selected function can be firmly dismissed. Unfortunately, this relationship is elusive, and some studies are difficult to interpret because of the pitfalls of the methods used (see Introduction). Furthermore, where uncovered, the effect of helpers on the production of young is typically small, that is, 0.31 fledglings per helper per year in the apostlebird, with an average group production of 4.2 (Woxvold 2004; Woxvold & Magrath 2005), 0.18 (16%) in Seychelles warblers (Richardson et al. 2002), and on average 0.11 fledglings (18%) per additional group member in crows (this study). Analyses should therefore be based on large data sets to ensure the appropriate statistical power. Our long-term data showed that in cooperative carion crows the annual number of fledglings produced was correlated with group size after controlling for the possible confounding effect of territory quality. It is interesting to note that besides our study on crows, the few others that applied mixed models to long-term studies on a large number of groups consistently found an effect of group size and/or allofeeding on reproduction. In white browed scrubwrens, group size increased the success of yearling

females (Magrath 2001); in meerkats, helpers positively affected the number of litters produced every year (Russell et al. 2003); in long-tailed tits, helpers enhanced the probability of fledglings to be recruited as breeders in the following year (Hatchwell et al. 2004); in the apostlebird, fledgling production was positively and linearly correlated with the number of helpers (Woxvold & Magrath 2005). We suggest that the effect of helpers on reproductive success may be more ubiquitous than previously thought and that direct and indirect benefits deriving from increased production of young are important to explain the maintenance of cooperative breeding in a large variety of systems.

We believe that a combination of indirect and direct benefits is likely to explain cooperative breeding in crows. We have previously shown that: (1) immigrant males can sire some nestlings within their group, gaining immediate direct fitness benefits from aiding at the nest (Baglione et al. 2002b); and (2) immigrants are related to the resident breeder of the same sex (Baglione et al. 2003) and therefore also contribute to raise nondescendant kin by provisioning the brood. On the contrary, nondispersing offspring do not breed within their natal group and help raising full or half siblings (Baglione et al. 2002b; Canestrari et al. 2005). For both categories of helpers, that is, immigrants and nondispersing offspring, the two central predictions of kin selection theory are fulfilled, as help-at-the-nest is directed towards relatives and enhances

reproductive success (this study). In addition, group augmentation from increased production of young may also confer benefits through, for example, reduced per capita risk of predation, improved foraging efficiency, or maintenance of the breeding territory for a longer time (Kokko et al. 2001). Future investigation will explore these hypotheses to address all possible benefits of group living in crows.

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