Lazy group members are substitute helpers in carrion crows

Vittorio Baglione^{1,2,*}, Daniela Canestrari^{1,3}, Elisa Chiarati¹,
Ruben Vera¹ and Jose M. Marcos¹

¹Department of Agro-forestry, and ²Sustainable Forest Management Research Institute, University of Valladolid, Avenida de Madrid 44, 34004 Palencia, Spain

³Department of Animal Biology and Ecology, University of Granada, Spain

In many cooperatively breeding societies, helping effort varies greatly among group members, raising the question of why dominant individuals tolerate lazy subordinates. In groups of carrion crows *Corvus corone corone*, helpers at the nest increase breeders' reproductive success, but chick provisioning is unevenly distributed among non-breeders, with a gradient that ranges from individuals that work as much as the breeders to others that completely refrain from visiting the nest. Here we show that lazy non-breeders represent an insurance workforce that fully compensates for a reduction in the provisioning effort of another group member, avoiding a decrease in reproductive success. When we temporarily impaired a carer, decreasing its nest attendance, the laziest non-breeders increased their provisioning rate and individuals that initially refrained from visiting the nest started helping. Breeders, in contrast, did not increase chick provisioning. This shows that lazy non-breeders can buffer a sudden unfavourable circumstance and suggests that group stability relies on the potential contribution of group members in addition to their current effort.

Keywords: cooperative breeding; lazy helpers; chick provisioning; parental tolerance; coercion; *Corvus corone*

1. INTRODUCTION

In cooperatively breeding vertebrate species, helpers are typically subordinate group members that postpone their own reproduction and care for the offspring of the dominant breeders. Research on the adaptive explanation of helping based on natural selection has focused on the benefits that helpers gain from their seemingly altruistic behaviour. It is widely accepted that helping can be a kin-selected trait that increases inclusive fitness of helpers (Griffin & West 2003), but it has also been shown that, in many species, direct benefits related to future reproduction, territory inheritance or group augmentation can play an important role in maintaining cooperative breeding in a population (Cockburn 1998; Kokko *et al.* 2001).

In most cooperative species, helping conveys benefits to the dominants, usually in terms of increased reproductive success (Woxvold & Magrath 2005) or better survival owing to workload-lightening in raising the young (Crick 1992; Cockburn 1998). If helpers are beneficial to the dominants, theory suggests that the latter should be choosy, allowing the most helpful subordinates to stay in the group and evicting the lazy ones when (i) the number of potential helpers available in the group is large, (ii) subordinates are costly to dominants, and (iii) subordinates can be easily evicted (Ragsdale 1999; Kokko *et al.* 2002; Mitchell 2003). These conditions apply to most cooperatively breeding birds, where (i) ecological constraints that hinder dispersal are widespread (Ekman *et al.* 2001), allowing the dominants to choose

their helpers among several offspring of different cohorts; (ii) groups typically live year round in all-purpose territories (Arnold & Owens 1999), the resources of which can be depleted if the group is too large, with important negative consequences on the reproductive success of the dominants (also, it has been shown that subordinates can compete with the dominants for reproduction, as in the pied kingfisher *Ceryle rudis*; Reyer & Westerterp 1985); and (iii) dominants are usually older than subordinates and perfectly capable of evicting them (Curry 1989; Faaborg & Bednarz 1990; Zahavi 1990).

Through eviction and/or punishment of lazy group members on the one hand and tolerance towards efficient helpers on the other hand, dominants' choosiness should eventually lead to a (roughly) egalitarian share of workload among subordinates. However, empirical data show the very opposite pattern: a remarkable variability in helpers' contribution and the presence of lazy or uncooperative group members is the rule rather than the exception in cooperative societies, from termites to vertebrates (Cant & Field 2001). Such 'tolerance of laziness' is poorly understood. Kin selection is likely to play a role in family-living societies, as dominants may benefit indirectly from tolerating all group members irrespective of their contribution to cooperative tasks, if this enhances survival and/or future reproduction of relatives (Ekman *et al.* 1999; Griesser *et al.* 2006). This explanation, however, cannot apply to societies where cooperation arises among non-kin. Dominants may also benefit directly from the presence of lazy helpers if individuals survive better in large groups, because of reduced predation or increased foraging efficiency (Kraus & Ruxton 2005).

* Author for correspondence (baglione@agro.uva.es).

Alternatively, dominants may be merely unable to evict or punish subordinates, but this is unlikely in most avian societies because the latter are typically young individuals that have little scope for retaliation against older and more experienced adults. Another non-exclusive explanation is that helpers specialize in different tasks and that subordinates that care less for the young carry out a larger share of other duties (e.g. territory defence). However, work specialization has been described rarely in cooperatively breeding birds (Arnold *et al.* 2005) and does not seem to represent a general pattern in avian societies.

The idea that apparent lazy group members may in reality play a hidden but beneficial active role within the group has not been explored so far. Here we test, in cooperatively breeding carrion crows *Corvus corone corone*, whether lazy non-breeders (i.e. those that contributed less or not at all to feeding the nestlings) are 'insurance' helpers that compensate for a sudden reduction of group provisioning rate, allowing the dominants to maintain their current effort in feeding the nestlings. The carrion crow is a suitable model because helping effort varies greatly within groups, with a gradient that ranges from individuals that work as much as the breeders to others that completely refrain from visiting the nest (Canestrari *et al.* 2005). Also, chick feeding is the prevalent duty of helpers, which do not contribute much to nest sanitation (D. Canestrari 2010, unpublished data) or to active territory/nest defence, being involved in only 8 per cent of territorial fights against intruders (Baglione *et al.* 2002a). Therefore, work specialization is unlikely in this species and differences in contribution to chick feeding truly mirror a large variability in helpfulness. In 17 experimental groups, we temporarily impaired one carer, causing a decrease in its contribution to chick provisioning, and observed who compensated for that reduction. If apparently lazy group members were substitute helpers, we would expect them to take the largest share in compensating for the deficit in provisioning, while breeders maintain their current effort. In particular, we would expect to find among non-breeders a negative correlation between the individual provisioning effort prior to the treatment and the compensatory response to the presence of an impaired carer. We discuss the implications of the results in explaining group stability under conditions of uneven distribution of workload among members of cooperative groups.

2. MATERIAL AND METHODS

(a) Study area and population

We have studied a population of carrion crows in a 45 km² rural area in northern Spain (42° N, 5° W) since 1995. The study area represents a traditional Spanish low-intensity agricultural landscape, with a mosaic of crops, meadows, poplar and pine plantations, scrubs, oak forest patches and uncultivated land.

In this population, carrion crows form cohesive kin groups (average size $\pm$ s.e. = 3.2 ± 0.08 ; range, 2–9) that live year-round in all-purpose territories and that form through delayed dispersal of offspring (which can remain on their natal territory with their parents for up to 4 years) and/or immigration of individuals that are related to the resident breeder of the same sex (Baglione *et al.* 2002a, 2003).

Within the groups, crows form stable linear hierarchies, where resident breeding males are the most dominant (Chiarati *et al.* 2010). Sex ratio in the groups is skewed towards males, but females are found both among non-dispersing offspring and immigrants. Unlike non-dispersing offspring, adult male immigrants often sire offspring within their group, while immigrant females only occasionally lay eggs (Baglione *et al.* 2002b). If nests fail at the eggs or hatching stage, crows may re-nest up to three times, but they raise only one successful brood per year.

Breeders benefit from the presence of helpers, whose main task is that of feeding the nestlings, in two ways. First, helpers significantly increase the production of fledglings, enhancing the numbers of chicks raised per successful attempt and the probability of re-nesting after a nest failure (Canestrari *et al.* 2008a). Second, they lighten the workload of breeders, who reduce their provisioning effort when assisted by more than one helper (Canestrari *et al.* 2007). This is important because crows lose body mass throughout the nesting period in proportion to their provisioning effort (on average 5.4% of initial weight for both breeders and helpers), and reducing this cost has proved to be paramount in this population. If food is abundant during the breeding season, crows invest in self-maintenance, by reducing body mass loss, rather than increasing provisioning of the current brood (Canestrari *et al.* 2007). In addition, it has been shown that carers, particularly the breeders, finely adjust chick provisioning to their own needs, deciding whether to deliver to the young the food brought to the nest or consume it themselves according to a trade-off between their hunger and the conditions of the brood (Canestrari *et al.* 2004, 2010).

Contribution to chick care is unevenly distributed among group members. Parents show the highest provisioning rates while non-breeders vary largely and some individuals refrain from visiting the nest (27% of non-breeders). In general, male helpers work harder than females, while the degree of relatedness to the chicks, which is generally high in this kin-living population (Baglione *et al.* 2003), is not correlated with the provisioning effort (Canestrari *et al.* 2005).

(b) Field methods and wing-clipping experimental treatment

Details on crow catching and banding, as well as group surveying, are given in previous papers (Baglione *et al.* 2002a; Canestrari *et al.* 2005). Briefly, we caught adult birds both with walk-in traps and remote-controlled snap traps, while young were captured in the nest before they fledged. All individuals were banded with a unique combination of colour rings and plastic patagial wing tags that did not affect survivorship (Caffrey 2000; Canestrari *et al.* 2007). The birds were aged as 1, 2 and older than 2 years according to the internal colour of the upper mandible (Svensson 1992) and were sexed with P2/P8 molecular method (Griffiths *et al.* 1998). During the breeding season (March–July), we recorded group size and followed the reproductive attempts, collecting information on laying date, brood size and fledgling success. Data on chick provisioning were obtained from video-recorded observations using camouflaged micro-cameras placed close to the nest (see Canestrari *et al.* 2005 for details).

At the beginning of breeding seasons 2006 and 2007 we chose, respectively, seven and ten groups where all members were individually recognizable. The exceptions were three

Figure 1. Provisioning rate of treated breeders and helpers before and after the wing-clipping manipulation. White bar, before clipping; black bar, after clipping.

groups that contained two unbanded individuals that could not be differentiated in the recordings and that were therefore excluded from the analyses. Overall, we collected data on 33 breeders (17 males and 16 females), 27 non-dispersing offspring (17 males and 10 females) and one 2-year old male immigrant that was classified as non-breeder owing to his young age. No groups were sampled more than once throughout the study period.

Between 11 and 13 days after the first egg hatched, we made a first set of three video-recording sessions (one per day, 4 h each) at each nest and measured individual chick provisioning for all group members, pooling data from the three bouts. We measured individual provisioning rate as the number of feeds per hour, where 'feed' is defined as every act of delivering food to a chick's open gape. We have shown previously that the number of feeds per visit to the nest is correlated with the amount of food carried by a crow in its crop (Canestrari *et al.* 2005), and it is therefore a good measure of provisioning effort. Between days 14 and 16, we captured one carer in each group and clipped its seventh and ninth primary feathers of each wing close to the base. The removal of those feathers, the area of which averaged 41.5 cm² per wing, reduced total wing area (average 399 cm²), causing an 11.6 per cent increase in the wing loading for a crow weighing 500 g (from 12.28 to 13.71 N m⁻²; Pennycuik 1989). By using a selective remote-controlled snap trap, we were able to catch and wing-clip individuals that contributed substantially to chick provisioning (figure 1). We clipped nine breeders (eight males and one female) and eight non-breeders (seven males and one female). Starting the day after the treatment, we made a second set of three video-recording sessions per nest (one per day, 4 h each) and measured again the provisioning rate.

(c) Statistical analyses

Statistical analyses were performed using GENSTAT 10.0. The analyses on the effect of wing clipping on individual provisioning effort were carried out with linear mixed models (LMMs), which allow fitting both fixed factors and random terms in the analyses, using the restricted maximum likelihood method. Potential explanatory variables that gave non-significant results ($p > 0.1$) were sequentially removed until the model only included significant terms. Significant probability values were derived from having all significant terms fitted in the model together, whereas those of non-significant terms were obtained from having all significant terms in the model and each non-significant term fitted

individually (Crawley 2002; Russell *et al.* 2003). In the results, values for non-significant interactions are omitted.

First we analysed the effect of wing clipping on the treated crows to confirm whether they showed the expected reduction in chick provisioning, using the individual frequency of feeds as a dependent variable. We fitted into the LMM 'treatment' (before/after clipping), 'category' (breeder/non-breeder), brood size, total number of carers (i.e. including parents) and the interaction between category and treatment as explanatory variables, and individual identity as a random term. Sex was omitted because only two females were sampled. After this, we analysed the individual provisioning rate of unmanipulated crows to test whether they responded to the decreased effort of the impaired group member. In the model, we added sex and age to the explanatory variables listed above. Year, territory identity and individual identity nested into territory were fitted as random factors. In the next step, we asked whether the change in provisioning rate following manipulation in unclipped non-breeders depended on the intensity of their helping effort prior to the treatment. Specifically, we were interested in testing whether lazy helpers were more likely to compensate for our experimental reduction of chick provisioning than efficient helpers. To do so, we ran a new LMM where we correlated the difference of individual provisioning effort before and after the treatment with the initial provisioning rate, also fitting sex, age and brood size as explanatory variables and territory as a random term.

In our experiment, individual changes in chick provisioning after the treatment could be potentially confounded by an effect of time, because observations necessarily followed a set order, where crows were first measured in unmanipulated conditions and subsequently in the presence of an impaired group member. To control for this, on a different sample of 48 individuals (23 breeders and 25 non-breeders from 14 different territories) that were video-recorded under natural conditions (i.e. in the absence of experimental manipulations), we checked whether individual provisioning rate changed over subsequent observation bouts (4 h each, $n = 169$ bouts) between day 11 and day 19 after the first egg hatched (i.e. within the time frame considered in this study; see above). In the LMM, we fitted year, territory identity and individual identity nested within territory as random factors, while chronological bout order, category (breeder/helper), sex, number of carers and brood size were used as explanatory variables. The results showed that chick provisioning did not change over successive observation bouts within the specified time frame (Wald statistic = 1.22, d.f. = 1, 121.8, $p = 0.27$), suggesting that any observed response to the wing-clipping treatment could not be confounded by the effect of time. A second problem related to the experimental design is that our results might suffer from a regression towards the mean effect (Bland & Altman 1994), where individuals that showed the most extreme values in the first measurement are by chance expected to be closer to the mean on a second measurement. This is especially important in our study, because a key prediction of the insurance function of lazy helpers is that those individuals with the lowest provisioning rates in the first set of observations (days 11–13) would show a larger increase following manipulation (days 16–19). To control for this, we checked in the control sample of naturally breeding groups mentioned above whether the laziest non-breeders changed their provisioning behaviour across two observation periods, which corresponded in time with those of the experimental

Table 1. Effect of impairment of one carer ('treatment') on individual provisioning effort of unmanipulated group members. The average effects of the significant terms and the constant are calculated for the minimal model.

model terms	Wald statistic	d.f.	<i>p</i>	random term estimated variance component $\pm$ s.e.	average effect $\pm$ s.e.
territory identity ^a				0.22 $\pm$ 0.27	
individual identity ^a				0.5 $\pm$ 0.3	
year ^a				0.53 $\pm$ 0.86	
breeding status	27.72	1, 32.2	<0.001		
sex	0.46	1, 34.2	0.49		
age	0.05	1, 39.4	0.83		
treatment	2.23	1, 45	0.14		
brood size	12.18	1, 12.7	0.004		0.62 $\pm$ 0.18
number of carers	0.68	1, 18.8	0.4		
breeding status $\times$ treatment	4.86	1, 43.6	0.03		
constant					3.34 $\pm$ 0.59

^aRandom terms.

sample (i.e. days 11–13 versus 16–19). A lack of difference would imply absence of regression towards the mean. In addition, we checked in the same control sample of non-breeders from unmanipulated groups ($n = 25$) whether the change in provisioning rate between the two observation periods was correlated with the intensity of helping shown in the first period. To do so, we replicated the same LMM run on the experimental sample, fitting sex, age and brood size among the explanatory variables and territory as a random term (see above). Again, if lazy helpers had an insurance function, we would expect to find a significant correlation in the presence of the handicapping manipulation, but not in naturally breeding groups.

To determine whether group members fully compensated for the reduced effort of the handicapped crow, we analysed the effect of the following explanatory variables on the provisioning rate of the whole group (total number of feeds per hour per chick brought to the nest by all members of the group): treatment (before/after impairment of one carer), brood size and number of carers. Territory identity and year were fitted as random factors. Finally, we compared the reproductive success (number of fledglings) of the 17 experimental groups with that of the rest of the territories surveyed in the study area during the 2-year duration of the experiment ($n = 76$ territories). For this, in an LMM, we fitted treatment (presence/absence of wing-clipped individuals in the group), clutch size and group size as explanatory variables, and territory and year as random terms.

(d) *Ethical note*

All bird manipulations were authorized by Junta de Castilla y León and had no visible adverse effect. In particular, wing-clipped individuals did not abandon the territory or the nest. One year after the treatment, all but one clipped individual were observed alive in their territory, and those that were clipped as breeders in the previous year reproduced normally. An alternative method to increase the cost of flying is to attach weights to the bird's legs (Cuthill 1991). However, weights need to be removed at the end of the experiment to avoid permanent effects, and recapture is problematic in crows. Removal of two primary feathers represents a temporary handicap that resembles the natural situation of moult.

3. RESULTS

Clipped crows significantly reduced their provisioning rate by, on average, 29.3 per cent (effect of wing clipping: Wald = 28.71, d.f. = 1, 16.4, $p < 0.001$; figure 1), with no significant difference between breeders and helpers in their response to the treatment (category $\times$ treatment: Wald = 2.01, d.f. = 1, 15.5, $p = 0.17$). In this sample, breeders showed an overall tendency to feed more than helpers (Wald = 3.14, d.f. = 1, 14, $p = 0.09$), confirming previous results (Canestrari *et al.* 2005). Also, chick provisioning tended to increase with brood size (Wald = 3.34, d.f. = 1, 18, $p = 0.08$), but not with the number of carers (Wald = 0.39, d.f. = 1, 28.9, $p = 0.54$).

Among unclipped group members, non-breeders responded to the presence of a handicapped individual by augmenting their provisioning rate, while breeders did not, as shown by the significant effect of the category $\times$ treatment interaction (table 1 and figure 2). Again, chick provisioning increased with brood size (table 1). To further investigate the compensatory reaction of non-breeders, we ran a new LMM on the sample of unmanipulated non-breeders. We found that the individual difference in helping effort before and after the clipping treatment was inversely correlated with the provisioning effort prior to the manipulation (Wald = 6.36, d.f. = 1, 13.6, $p = 0.02$), showing that lazy non-breeders increased their effort more than the efficient ones (figure 3). Remarkably, five out of eight unmanipulated non-breeders that initially refrained from visiting the nest started helping when the clipped group member decreased its nest attendance. In contrast, non-helping subordinates ($n = 6$) sampled in groups breeding in natural conditions (i.e. without handicapping manipulation of one group member) never changed their behaviour between the two corresponding measurement periods (two-tailed Fisher's exact test, $p = 0.03$, $n = 14$). When we enlarged the sample of lazy non-breeders in unmanipulated groups to include the lowest non-zero values needed for computing a Wilcoxon paired matched test, the result confirmed that they did not increase their helping effort in the second measurement ($T = 1.0$, $p = 0.29$, $n = 9$). In addition, the correlation shown in figure 3 for experimental non-breeders was absent in the sample of naturally breeding groups (results of an

Figure 2. Provisioning rate of unmanipulated breeders and helpers before and after one carer of their group was wing-clipped and reduced its contribution to young feeding. White bar, before treatment; black bar, after treatment.

LMM; effect of the initial helping effort on the second measurement of chick provisioning: Wald statistic = 1.0, d.f. = 1, 21.4, $n = 25$, $p = 0.33$). These results exclude a regression towards the mean effect in our experiment and strongly indicate a true response of lazy helpers to the impairment of a group member.

The response of non-breeders fully compensated for the reduced effort of the impaired group member. The provisioning frequency per chick of the whole group did not decrease significantly after the clipping treatment (average $\pm$ s.e.: before treatment = 9.91 ± 1.03 , after treatment = 9.55 ± 1.27 ; Wald = 1.24, d.f. = 1, 17.5, $p = 0.28$), being negatively influenced by brood size (Wald = 4.44, d.f. = 1, 18.2, $p = 0.05$) and positively by the number of carers (Wald = 6.18, d.f. = 1, 27.1, $p = 0.02$). No difference was found in the reproductive success between experimental groups and the rest of the unmanipulated groups ($n = 76$) that were surveyed during the same period in the study area. In an LMM, the number of fledglings produced by a group did not depend on the presence or absence of one handicapped individual (1.35 ± 0.29 versus 0.99 ± 0.13 , respectively; Wald = 0.68, d.f. = 1, 103.7, $p = 0.4$) nor on the clutch size (Wald = 0.31, d.f. = 1, 114.9, $p = 0.56$), but was marginally correlated with group size (Wald = 2.76, d.f. = 1, 103.7, $p = 0.09$).

4. DISCUSSION

(a) Insurance function of lazy helpers and group stability

In this study, we have shown that, in cooperatively breeding groups of crows, non-breeders compensated for a sudden reduction of the overall provisioning of the nestlings, avoiding negative consequences on the reproductive success. Particularly, the lazy non-breeders (i.e. those that initially showed the lowest provisioning rates) were those that mostly increased their effort in response to the impairment of a group member. We suggest that their presence in the group represents an insurance for the dominant breeders, which can maintain their provisioning effort constant in spite of a provisioning failure of another group member, without consequences on the survival of their offspring. In previous studies, we have shown that feeding the chick conveys important costs for crows in terms of loss of body mass and that breeders

Figure 3. Correlation between the initial helping effort of unmanipulated non-breeders and the change in provisioning rate following impairment of one carer.

are especially cautious in the allocation of resources during the breeding season, often deciding to invest in self-maintenance rather than increasing provisioning to the current brood (Canestrari *et al.* 2004, 2010). This was confirmed in this study, where crows responded to an increase in the cost of flying (wing clipping) with an immediate reduction of their nest attendance. As expected, breeders reduced more than helpers, although the difference was only qualitative in this limited sample size. Considering the importance of the costs of provisioning for crows and the fact that a sudden reduction of group provisioning is very likely to occur under natural conditions (for example, because of predation, accident, illness or dispersal of a group member), lazy helpers may be useful to breeders and their insurance function is likely to play an important role in maintaining group stability in spite of an asymmetric distribution of workload. In the crow society, however, other factors may strengthen dominants' tolerance of lazy helpers. First, high relatedness among group members (Baglione *et al.* 2003) is likely to provide indirect fitness benefits to dominants that do not evict non-breeders from the territory. This has been shown, for example, in the Siberian jay *Perisoreus infaustus*, where offspring that stay at home with their parents survive better than those that disperse early in life (Griesser *et al.* 2006). Second, if individuals survive better in large groups than in smaller ones (Kraus & Ruxton 2005), lazy helpers may be valuable because they increase group size.

In cooperatively breeding birds, however, group stability does not depend only on dominant tolerance, but also on the dispersal decisions of non-breeders, which are expected to trade off the benefits of staying at home against those of leaving. We suggest that the 'insurance function' may provide important indirect fitness benefits to non-breeders that refrain from helping under normal conditions but remain associated with their group, as it allows buffering unfavourable circumstances, thus preventing a reduction of the reproductive success of the group. In the sociable weaver *Philetairus socius*, it has been shown that helpers increase the production of fledglings only during bad conditions within breeding seasons, proving that a discontinuous effect on the reproductive success is sufficient to maintain cooperation in this society (Covas & du Plessis 2005; Covas *et al.* 2008). We suggest

that, in crows, the benefits derived from the insurance function of lazy helpers may be important to stabilize the group, promoting dominants' tolerance on the one hand and subordinates' philopatry on the other hand.

(b) *Mechanisms of recruitment of lazy helpers*

Two possible mechanisms may explain the recruitment of lazy non-breeders in our experiment, namely (i) unforced decision of non-breeders or (ii) dominant control. Considering the former mechanism first: in crow kin groups, non-breeders may increase voluntarily their contribution when they perceive a sudden reduction of group chick provisioning (for example, through detection of a decreased nest visit rate of the impaired group member and/or changes in chick begging), because in this circumstance their help is most likely to increase the reproductive success of the group and it is therefore beneficial in terms of personal indirect fitness gain. In this case, a positive correlation between the degree of relatedness with the chicks of lazy workers and their compensatory response to the handicapping manipulation may be found. This could not be specifically tested in this study because the sample included virtually only nuclear families and lacked variability in relatedness. However, we would not expect such a correlation in crows, even though kin selection is known to play a central role in promoting cooperative breeding in our study population (Baglione *et al.* 2003; Canestrari *et al.* 2008b). This is because the degree of relatedness among group members is generally high (Baglione *et al.* 2003) and helpers in natural situations do not adjust their provisioning effort to the degree of relatedness with the chicks, either because they lack a finely tuned mechanism of recognition of relatives or because their indirect fitness benefits are generally high enough to compensate for any contribution to chick rearing (Canestrari *et al.* 2005). Nonetheless, it may be interesting to test this prediction in future studies on cooperatively breeding societies where the degree of relatedness varies largely among group members. An alternative explanation for a voluntary recruitment of lazy helpers to the cooperative workforce may be that crows may respond to the weakness of one group member, taking the chance of increasing their own status through helping (Putland 2001). However, this is unlikely because helping in this population does not seem to convey any signalling function (Canestrari *et al.* 2004, 2010).

The other non-exclusive mechanism may be that dominants enforce helping, either directly, by coercing non-breeders to feed the nestlings, or indirectly, by being intolerant with uncooperative group members and hindering the access to the resources of the territory. Coercion has been shown to be a major cause of workers' contribution to queen's reproduction in social insects (Ratnieks & Wenseleers 2008) and plays a central role in the maintenance of other kinds of cooperative behaviours. In keas *Nestor notabilis*, dominants force subordinates to manipulate an experimental apparatus to obtain food (Tebich *et al.* 1996; but see Werdenich & Huber 2002), and in cleaner fish *Labroides dimidiatus*, coerced cooperation involves a refined form of third party punishment (Raihani *et al.* 2010). In cooperatively breeding vertebrates, however, few studies have proved that helpers are manipulated by the dominants and 'pay a

rent' (Gaston 1978) to be allowed to stay in a group. Compelling evidence found in cichlids *Neolamprologus pulcher* (Bergmuller & Taborsky 2005), naked mole rats *Heterocephalus glaber* (Reeve 1992) and superb fairy-wrens *Malurus cyaneus* (Mulder & Langmore 1993) contrast with data from other species where helping seems to be voluntary, as, for example, in meerkats *Suricata suricatta* (Clutton-Brock *et al.* 2005). More data are urgently needed from cooperatively breeding vertebrates, including crows, to assess the role of dominant manipulation in the evolution and maintenance of helping.

(c) *Flexibility of helping behaviour*

Regardless of the mechanisms behind it, our study uncovered the flexibility of helping behaviour in crows, showing that chick provisioning can be triggered in previously uncooperative group members. One of the fundamental obstacles for the integration of cooperative breeding into the context of the 'general theory of cooperation', which is fundamentally based on the analysis of the response of individuals to each other's behaviour to identify individual strategies (Bergmuller *et al.* 2007a), is that helping may be rather inflexible because of the strong influence of phylogenetic, environmental and phenotypic constraints (Bergmuller *et al.* 2007b; Ekman 2007; Komdeur 2007). Our study, however, shows that a great deal of individual plasticity remains. Individual helping behaviour may, therefore, at least potentially, respond to the behaviour of other group members, suggesting that a game theoretical perspective may improve our understanding of cooperative breeding in birds.

We are grateful to Redouan Bshary and two anonymous referees for useful comments on the manuscript, and to Rudy Valfiorito and Gloria Robles for help in the field. This work was supported by the Spanish Ministry of Science and Innovation through the project grants CGL2005-02083/BOS, CGL2008-01829/BOS and SEJ2007-29836-E in the framework of the COCOR 'Cooperation in Corvids' programme, which forms part of the ESF-EUROCORES TECT 'The Evolution of Cooperation and Trading' programme (to V.B.); and through the 'Ramón y Cajal' programme (FEDER-FSE) and the 'Juan de la Cierva' FSE programme (to V.B. and D.C., respectively).

REFERENCES

- Arnold, K. E. & Owens, I. P. F. 1999 Cooperative breeding in birds: the role of ecology. *Behav. Ecol.* **10**, 465–471. (doi:10.1093/beheco/10.5.465)
- Arnold, K. E., Owens, I. P. F. & Goldizen, A. W. 2005 Division of labour within cooperatively breeding groups. *Behaviour* **142**, 1577–1590. (doi:10.1163/156853905774831927)
- Baglione, V., Marcos, J. M. & Canestrari, D. 2002a Cooperatively breeding groups of Carrion Crow (*Corvus corone corone*) in northern Spain. *Auk* **119**, 790–799. (doi:10.1642/0004-8038(2002)119[0790:CBGOCC]2.0.CO;2)
- Baglione, V., Marcos, J. M., Canestrari, D. & Ekman, J. 2002b Direct fitness benefits of group living in a complex cooperative society of carrion crows, *Corvus corone corone*. *Anim. Behav.* **64**, 887–893. (doi:10.1006/anbe.2002.2007)
- Baglione, V., Canestrari, D., Marcos, J. M. & Ekman, J. 2003 Kin selection in cooperative alliances of carrion crows. *Science* **300**, 1947–1949. (doi:10.1126/science.1082429)
- Bergmuller, R. & Taborsky, M. 2005 Experimental manipulation of helping in a cooperative breeder: helpers 'pay

- to stay' by pre-emptive appeasement. *Anim. Behav.* **69**, 19–28. (doi:10.1016/j.anbehav.2004.05.009)
- Bergmuller, R., Johnstone, R. A., Russell, A. F. & Bshary, R. 2007a Integrating cooperative breeding into theoretical concepts of cooperation. *Behav. Process.* **76**, 61–72. (doi:10.1016/j.beproc.2007.07.001)
- Bergmuller, R., Russell, A. F., Johnstone, R. A. & Bshary, R. 2007b On the further integration of cooperative breeding and cooperation theory. *Behav. Process.* **76**, 170–181. (doi:10.1016/j.beproc.2007.06.013)
- Bland, J. M. & Altman, D. G. 1994 Some examples of regression towards the mean. *Br. Med. J.* **309**, 780–780.
- Caffrey, C. 2000 Marking crows. *North Am. Bird Bander* **26**, 146–148.
- Canestrari, D., Marcos, J. M. & Baglione, V. 2004 False feedings at the nests of carrion crows *Corvus corone corone*. *Behav. Ecol. Sociobiol.* **55**, 477–483. (doi:10.1007/s00265-003-0719-8)
- Canestrari, D., Marcos, J. M. & Baglione, V. 2005 Effect of parentage and relatedness on the individual contribution to cooperative chick care in carrion crows. *Behav. Ecol. Sociobiol.* **52**, 422–428.
- Canestrari, D., Marcos, J. M. & Baglione, V. 2007 Costs of chick provisioning in cooperatively breeding carrion crows: an experimental study. *Anim. Behav.* **73**, 349–357. (doi:10.1016/j.anbehav.2006.04.013)
- Canestrari, D., Chiarati, E., Marcos, J. M., Ekman, J. & Baglione, V. 2008a Helpers but not breeders adjust provisioning effort to year-round territory resource availability in carrion crows. *Anim. Behav.* **76**, 943–949. (doi:10.1016/j.anbehav.2008.05.013)
- Canestrari, D., Marcos, J. M. & Baglione, V. 2008b Reproductive success increases with group size in cooperative carrion crows *Corvus corone corone*. *Anim. Behav.* **75**, 403–416. (doi:10.1016/j.anbehav.2007.05.005)
- Canestrari, D., Vera, R., Chiarati, E., Marcos, J. M., Vila, M. & Baglione, V. 2010 False feeding: the trade-off between chick hunger and care-givers needs in cooperative crows. *Behav. Ecol.* **21**, 233–241. (doi:10.1093/beheco/arp177)
- Cant, M. A. & Field, J. 2001 Helping effort and future fitness in cooperative animal societies. *Proc. R. Soc. Lond. B* **268**, 1959–1964. (doi:10.1098/rspb.2001.1754)
- Chiarati, E., Canestrari, D., Vera, R., Marcos, J. M. & Baglione, V. 2010 Linear and stable dominance hierarchies in cooperative carrion crows. *Ethology* **116**, 346–356. (doi:10.1111/j.1439-0310.2010.01741.x)
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L. & Jordan, N. R. 2005 'False feeding' and aggression in meerkat societies. *Anim. Behav.* **69**, 1273–1284.
- Cockburn, A. 1998 Evolution of helping behavior in cooperatively breeding birds. *Annu. Rev. Ecol. Syst.* **29**, 141–177. (doi:10.1146/annurev.ecolsys.29.1.141)
- Covas, R. & du Plessis, M. A. 2005 The effect of helpers on artificially increased brood size in sociable weavers (*Philetairus socius*). *Behav. Ecol. Sociobiol.* **57**, 631–636. (doi:10.1007/s00265-004-0888-0)
- Covas, R., du Plessis, M. A. & Doutrelant, C. 2008 Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. *Behav. Ecol. Sociobiol.* **63**, 103–112. (doi:10.1007/s00265-008-0640-2)
- Crawley, M. J. 2002 In *Statistical computing*. London, UK: John Wiley.
- Crick, H. Q. P. 1992 Load-lightening in cooperatively breeding birds and the costs of reproduction. *Ibis* **134**, 56–61. (doi:10.1111/j.1474-919X.1992.tb07230.x)
- Curry, R. L. 1989 Geographic variation in social organization of Galapagos mockingbirds—ecological correlates of group territoriality and cooperative breeding. *Behav. Ecol. Sociobiol.* **25**, 147–160. (doi:10.1007/BF00302932)
- Cuthill, I. 1991 Field experiments in animal behavior—methods and ethics. *Anim. Behav.* **42**, 1007–1014. (doi:10.1016/S0003-3472(05)80153-8)
- Ekman, J. 2007 Cooperation—the role of past and present. *Behav. Process.* **76**, 118–119. (doi:10.1016/j.beproc.2006.12.017)
- Ekman, J., Bylin, A. & Tegelstrom, H. 1999 Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. *Proc. R. Soc. Lond. B* **266**, 911–915. (doi:10.1098/rspb.1999.0723)
- Ekman, J., Baglione, V., Eggers, S. & Griesser, M. 2001 Delayed dispersal: living under the reign of nepotistic parents. *Auk* **118**, 1–10. (doi:10.1642/0004-8038(2001)118[0001:DDLUTR]2.0.CO;2)
- Faaborg, J. & Bednarz, J. C. 1990 Galápagos and Harris' hawks: divergent causes of sociality in two raptors. In *Cooperative breeding in birds: long term studies of ecology and behavior* (eds P. B. Stacey & W. D. Koenig). Cambridge, UK: Cambridge University Press.
- Gaston, A. J. 1978 Evolution of group territorial behaviour and cooperative breeding. *Am. Nat.* **112**, 1091–1100.
- Griesser, M., Nystrand, M. & Ekman, J. 2006 Reduced mortality selects for family cohesion in a social species. *Proc. R. Soc. B* **273**, 1881–1886. (doi:10.1098/rspb.2006.3527)
- Griffin, A. S. & West, S. A. 2003 Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science* **302**, 634–636. (doi:10.1126/science.1089402)
- Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. 1998 A DNA test to sex most birds. *Mol. Ecol.* **7**, 1071–1075. (doi:10.1046/j.1365-294x.1998.00389.x)
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001 The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond. B* **268**, 187–196. (doi:10.1098/rspb.2000.1349)
- Kokko, H., Johnstone, R. A. & Wright, J. 2002 The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? *Behav. Ecol.* **13**, 291–300. (doi:10.1093/beheco/13.3.291)
- Komdeur, J. 2007 Constraints on evolutionary shifts in cooperative breeding. *Behav. Process.* **76**, 75–77. (doi:10.1016/j.beproc.2007.01.012)
- Kraus, J. & Ruxton, G. 2005 *Living in groups*. Oxford, UK: Oxford University Press.
- Mitchell, J. S. 2003 Social correlates of reproductive success in false clown anemonefish: subordinate group members do not pay-to-stay. *Evol. Ecol. Res.* **5**, 89–104.
- Mulder, R. A. & Langmore, N. E. 1993 Dominant males punish helpers for temporary defection in superb fairywrens. *Anim. Behav.* **45**, 830–833. (doi:10.1006/anbe.1993.1100)
- Pennycuik 1989 *Bird flight performance: a practical calculation manual*. Oxford, UK: Oxford University Press.
- Putland, D. 2001 Has sexual selection been overlooked in the study of avian helping behaviour? *Anim. Behav.* **62**, 811–814. (doi:10.1006/anbe.2001.1831)
- Ragsdale, J. E. 1999 Reproductive skew theory extended: the effect of resource inheritance on social organization. *Evol. Ecol. Res.* **1**, 859–874.
- Raihani, N. J., Grutter, A. S. & Bshary, R. 2010 Punishers benefit from third-party punishment in fish. *Science* **327**, 171–171. (doi:10.1126/science.1183068)
- Ratnieks, F. L. W. & Wenseleers, T. 2008 Altruism in insect societies and beyond: voluntary or enforced? *Trends Ecol. Evol.* **23**, 45–52. (doi:10.1016/j.tree.2007.09.013)
- Reeve, H. K. 1992 Queen activation of lazy workers in colonies of the eusocial naked mole-rat. *Nature* **358**, 147–149. (doi:10.1038/358147a0)
- Reyer, H. U. & Westerterp, K. 1985 Parental energy expenditure: a proximate cause of helper recruitment in the

- pied kingfisher (*Ceryle rudis*). *Behav. Ecol. Sociobiol.* **17**, 363–369. (doi:10.1007/BF00293214)
- Russell, A. F., Brotherton, P. N. M., McIlrath, G. M., Sharpe, L. L. & Clutton-Brock, T. H. 2003 Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behav. Ecol.* **14**, 486–492. (doi:10.1093/beheco/arg022)
- Svensson, L. 1992 *Identification guide to European passerines*, 4th edn. Stockholm, Sweden: Privately published.
- Tebbich, S., Taborsky, M. & Winkler, H. 1996 Social manipulation causes cooperation in keas. *Anim. Behav.* **52**, 1–10. (doi:10.1006/anbe.1996.0147)
- Werdenich, D. & Huber, L. 2002 Social factors determine cooperation in marmosets. *Anim. Behav.* **64**, 771–781. (doi:10.1006/anbe.2002.9001)
- Woxvold, I. A. & Magrath, M. J. L. 2005 Helping enhances multiple components of reproductive success in the cooperatively breeding apostlebird. *J. Anim. Ecol.* **74**, 1039–1050. (doi:10.1111/j.1365-2656.2005.01001.x)
- Zahavi, A. 1990 Arabian babblers: the quest for social status in a cooperative breeder. In *Cooperative breeding in birds: long-term studies of ecology and behavior* (eds P. B. Stacey & W. Koenig), pp. 103–130. Cambridge, UK: Cambridge University Press.