



## Costs of chick provisioning in cooperatively breeding crows: an experimental study

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(Received 27 October 2005; initial acceptance 4 December 2005;

final acceptance 10 April 2006; published online 2 January 2007; MS. number: 8716R)

The costs of providing care to offspring and how these costs influence individual allocation of resources to current and future reproduction are likely to be important in the evolution of cooperative breeding. We reduced the costs of offspring care experimentally in 12 groups of cooperatively breeding carrion crows, *Corvus corone corone*, by providing supplementary food throughout the breeding season. Neither non-breeders nor breeders from supplemented territories significantly increased their levels of provisioning effort. However, unfed crows lost more weight than fed crows and, in contrast to fed crows, lost weight in relation to provisioning effort. Furthermore, breeders decreased their provisioning rates in groups with more than three caregivers, supporting both the idea that provisioning chicks is costly and the conclusion that crows invest in self-maintenance rather than in the current brood when costs are reduced.

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**Keywords:** carrion crow; chick provisioning; *Corvus corone corone*; cooperative breeding; costs of care; food supplementation; helping behaviour

The factors determining individual contributions to offspring care in cooperative societies are not yet fully understood (Cockburn 1998; Heinsohn 2004). Helping behaviour, when young are provisioned by individuals other than their parents, has been the focus of studies on cooperative societies for decades, because it challenges the Darwinian idea that behaviour has evolved to maximize an individual's personal fitness. The traditional approach to test hypotheses on the ultimate function of cooperative behaviour has been to examine how helpers adjust their contribution to provisioning to the magnitude of the potential benefits of helping (Cockburn 1998). For example, a correlation between helping effort and relatedness to the young has revealed the importance of kin selection in some species (Emlen 1991), while higher provisioning effort by the philopatric than the dispersing sex has generated the hypothesis that the benefits of cooperation can

derive from group augmentation, through reduced predation risk and/or better territory defence (Kokko et al. 2001). However, this approach has not always provided compelling results and, in several cases, an adaptive function of helping has not been discovered (Cockburn 1998).

The approach of simply searching for correlates of individual provisioning rates of helpers as a way to test adaptive explanations of cooperative breeding has recently been questioned (Hardling et al. 2003; Heinsohn 2004). In particular, while most studies have concentrated on the benefits of helping, the costs of care of young have been largely neglected (Heinsohn & Legge 1999; Russell et al. 2003b; Russell 2004). Investigating the costs of provisioning is important for two reasons. First, levels of care of young might be influenced not only by the benefits to the current brood, but also by the probability of the parents and helpers breeding successfully in the future. In many animals, reproductive attempts reduce parents' survival or fertility (Clutton-Brock 1991) or weaken the immune system (Alonso-Alvarez & Tella 2001). Therefore, costs of care are likely to be important in influencing decisions on provisioning effort in current broods, as they might reduce the future reproductive potential of individuals (Reyer 1986). Second, cooperative dynamics might

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result from an interaction between the trade-off of costs and benefits of care to helpers and the need for breeders to receive help. This in turn is a function of the costs to breeders of feeding the young, and of the effect of helpers on reproductive success (Heinsohn 2004). Outcomes of such complex interactions might influence levels of help on the one hand, and the response of breeders to help on the other (i.e. whether breeders should maintain their provisioning rate or whether they should reduce their effort if aided by helpers).

In the cooperatively breeding population of carrion crows, *Corvus corone corone*, in northern Spain groups of three to nine individuals form through the association of close relatives (Baglione et al. 2002a, 2003) and up to five group members provide chick care. We examined the costs of chick provisioning for male and female breeders and nonbreeders, in terms of weight loss, and we investigated the individual strategies of allocation of resources to the current brood and to self-maintenance. We collected data on individual feeding rates and changes in weight during the nestling period in unmanipulated groups and in groups that were experimentally supplemented with food. We first examined whether the costs of chick provisioning vary according to breeding status, sex and age. If provisioning affects body mass crows should lose weight in proportion to the amount of care provided during the nestling period. Subsequently, we examined whether such costs influence individual current provisioning effort and how crows vary their provisioning rates in the presence of multiple carers. In particular, we tested (1) whether food-supplemented crows allocate additional resources to the current brood by increasing individual provisioning rates and/or to self-maintenance by reducing weight loss; (2) whether costs of care to the current brood are minimized by adjusting provisioning according to initial body weight; and (3) whether chick provisioning is additive or crows show compensatory reduction to the presence of multiple caregivers to minimize the costs of care, i.e. if helping has a 'load-lightening effect' (Crick 1992).

## METHODS

### Study Area and Population

We have studied a population of carrion crows in a 45-km<sup>2</sup> rural area in northern Spain (42°N, 5°W) since 1995. In this population, 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). Adult immigrants often participate in reproduction within their territory, whereas nondispersing offspring do not, and so avoid incest (Baglione et al. 2002b). The individual contribution to chick feeding is not evenly distributed among group members. Parents of at least one chick in the brood show the highest feeding rates, with no significant difference between the efforts of males and females. Among nonbreeders, males provision the chicks

at higher rates than females, but there is no significant correlation between feeding rates and relatedness to the chicks (Canestrari et al. 2005).

Each year since 1999 we have captured crows using two-compartment walk-in traps and a snap trap specifically developed for this species (Baglione et al. 2002a). The individuals were given a unique combination of colour rings and plastic patagial wing tags (6.5 × 3.5 cm), which did not affect survivorship or social interaction in a study of American crows, *Corvus brachyrhynchos hesperis* (Caffrey 1992, 1999, 2000). Wing tags did not seem to affect survivorship of Spanish carrion crows either. Of 25 crow fledglings tagged with wing tags and 19 fledglings banded with colour rings in 2000, 60% and 63%, respectively, were resighted in spring 2001 (Fisher's exact test: two-tailed  $P = 1$ ). Tagged individuals never showed apparent signs of distress. The birds were aged as 1, 2 and older than 2 years according to the internal colour of the upper mandible (Svensson 1992). The nestlings were banded just before they left the nest (30 days after hatching). We collected 50–200 µl of blood from the brachial vein of each banded individual. The P2/P8 sexing method (Griffiths et al. 1998) provided the sex of the banded birds. All bird manipulations were authorized by Junta de Castilla y León.

### Individual Classification

The mating system in this crow population, where immigrants share reproduction with dominants (Baglione et al. 2002b), complicates the classification of group members. However, in this study we chose groups that showed a simple social structure, where individuals could be classified as breeders or nonbreeders without parentage analyses. Most groups ( $N = 24$ ) were families (Baglione et al. 2002b) or contained sexually immature (yearling) immigrants. We were uncertain about only three birds: two adult males that had been associated on the same territory for 4 years were assumed to be breeders and, in another group, a 2-year-old immigrant male was considered a nonbreeder, because reproduction in crows appears to be rare before the third year (Madge & Burn 1999). The exclusion of these three individuals from the analyses did not influence the results and they were therefore included in the sample. In this study, we used groups where all individuals were recognizable because all, or all but one, group members were banded. In the analyses of variation in weight, we considered only banded individuals because, albeit unlikely, we could not exclude the possibility that unbanded individuals recorded on the weighing scale did not belong to the target groups. In 15 groups, provisioning rates were recorded for 15 unbanded birds ( $N = 4$  male and 11 female breeders), whose breeding status and sex were easily inferred because we knew the composition of the rest of the group. Because we have never observed replacements of breeders during a breeding attempt, or chick provisioning by crows that did not belong to the territorial group, we assumed that these unbanded birds were parents of the brood in their territory. As only one of 44 breeders studied so far in this population has been younger than

3 years, these unbanded breeders were aged as adults. This approximation is unlikely to have affected our results, as age has no significant effect on individual provisioning rates (Canestrari et al. 2005).

### Food Supplementation Experiment

At the beginning of the breeding season in 2003 and 2004, we paired groups where all members were individually recognizable (three to five crows per group) and that were similar in size and composition, and we randomly assigned one group of each pair to the experimental treatment. Different groups were studied in the 2 years. Owing to early nest failures, some of the chosen groups never provisioned the chicks. Eventually, we gathered data on provisioning effort in 14 unfed groups and 12 fed groups. We measured weight changes in 14 unfed groups and 10 fed groups (see below).

We fed the experimental groups with canned dog food every day in the middle of the territory (about 200 m away from the nest) from the beginning of the breeding season (after the first nest was completed but just before egg laying, which typically occurs 6–9 days after the nest is built; J. M. Marcos, unpublished data) until the chicks fledged or the nest failed at the egg or nestling stage. The dog food used (brand DIA, chicken and beef flavour, DIA%, Madrid, Spain) is very palatable for crows (personal observation), and simplified the logistics of fieldwork, being easy to buy, store and dose. Most importantly, this commercial mixture of meat and vegetables (78.8% and 21.2%, respectively) falls within the natural range of variability of the crow's diet in terms of proportions of animal and vegetable components (41.7%–82.6% and 17.4%–58.3%, respectively; Cramp & Perrins 1994). The individual daily amount of food supplemented (about 200 g/crow per day corresponding to ca. 1071 kJ/crow per day), was calculated to provide an energy intake likely to affect the cost of provisioning (Nagy et al. 1999) without exceeding the range of natural variation in food resources in crow territories during the breeding season.

Territory quality is very variable in the study area (Baglione et al. 2005). An estimation of food availability in territories is difficult, because of the crow's wide diet and plastic habitat choice (reviewed in Cramp & Perrins 1994), which makes it hard to identify key resources that can be precisely measured. To circumvent this problem, we assessed territory resources in terms of energy availability. The upper level was calculated by summing the individual daily energy requirements (according to Nagy et al. 1999) of members of the largest group recorded in the study site (seven adults and three fledglings, 7786 kJ/day). The lower limit was estimated as the energetic requirement of an unassisted pair (1621.2 kJ/day), assuming that a pair whose nestlings starved in a particular season had access only to resources that allowed the pair's own survival (crows are not obligate breeders and unassisted pairs can breed successfully in the study population). According to these estimates, territory food resources may vary by at least 6164.8 kJ/day. In our experiment, we provided on average 3070.4 kJ/day per territory.

Although, admittedly, our calculations offer only a rough estimation of resource abundance, they suggest that the experimental treatment was unlikely to create unnatural conditions, at least in terms of food abundance. We tried to reduce the predictability of our visits to the territories by avoiding following a fixed weekly routine.

Video-recording sessions in all experimental groups within the first few days of treatment confirmed that the target crows were actually taking the food and that no group member was denied access. In two experimental territories we also observed that supplementary food was both eaten by group members and given to the nestlings. In all territories, all supplementary food was taken and cached in about 20–30 min.

### Estimates of Provisioning Effort

Throughout the 2 years, we collected information on individual provisioning rates to the broods of 29 breeders (16 males, 13 females) and 28 nonbreeders (18 males, 10 females) in 14 unfed groups, and 23 breeders (12 males, 11 females) and 20 nonbreeders (10 males and 10 females) in 12 fed groups. We videorecorded activity at the nests by placing camouflaged video cameras 2.5 m away. For each nest we collected three to five recording bouts of 4 h each, between day 10 and day 15 from hatching. The crows carry food in their crops and when one arrives on the nest, it puts its beak in a nestling's open gape and regurgitates part of the food, then it extracts the beak and may repeat the act with the same nestling or several others. We measured individual provisioning rate as the number of feeding events/h, where 'feeding event' is defined as every act of delivering food to a chick's open gape. Canestrari et al. (2005) showed that the number of feeds per visit to the nest is correlated with the amount of food carried by a crow in its crop. Because individuals provisioned for different numbers of days (some nests failed during the nestling period) we multiplied individual provisioning rate by the number of days of nestling feeding, and by the number of daily hours of provisioning (determined by daylength as previous observations showed that crows provision their chicks from dawn to dusk). This provided an estimate of the total workload by each group member ('workload' hereafter), which we correlated with the change in weight during the breeding season.

### Measures of Variation in Weight

Throughout the 2 years, we collected complete information (both weight measurements and nest recordings) on 23 breeders (16 males and seven females) and 16 nonbreeders (13 males and three females) belonging to 14 unfed groups, and 13 breeders (10 males, three females) and nine nonbreeders (six males, three females) belonging to 10 fed groups. Members of experimental and control groups were weighed on an Ohaus Champ II digital precision bench scale (capacity  $\times$  readability: 15  $\times$  0.002 kg) made of a rectangular base (30  $\times$  35 cm) with a separate display connected to the base by a cable. We placed the camouflaged scale in an open spot within the chosen crow

territory, and we hid the display near by. We set up two video cameras, one pointing at the scale and the other at the display, and connected them to video-recorders. The two video-recording sets were connected to 12-V batteries and recorded simultaneously for 4 h. The crows were attracted to the scale by a decoy (a crow in a cage) and by bait (one chicken carcass tied to the top of the scale). The decoy crow had been kept in captivity with permission of Junta de Castilla y Leon since 1999, when it was rescued after being wounded by hunters and never recovered its flying ability. When used as a decoy, it was placed in a partially covered cage (120 × 40 cm and 50 cm high), with food and water. Free-flying crows could not reach inside the cage and therefore could not attack the decoy, which did not appear to be distressed by their presence. During the breeding season, a decoy was usually used every 2–3 days for 4–6 h. In especially intensive field seasons, we caught another crow in March and released it in June. Captive crows were kept in aviaries (4 × 4 m and 2.5 m high) when not used as decoys. During weight recording we provided a small amount of food to control groups. However, this occurred a maximum of three times per territory and the chicken carcasses used as bait contained only a small amount of meat. Therefore, it is unlikely that this procedure affected the experiment.

In each territory, we weighed the crows a few days (1–3) before egg hatching and then again when the chicks were close to fledging (30 days old) or as soon as the nest failed ( $\bar{X}$  number of days between weighings  $\pm$  SD = 26.11  $\pm$  7.25). In four territories that never had nestlings (because nests failed at the egg stage) we took the second weight measurement 30 days after the predicted hatching day, and we could hence compare individuals that did not feed chicks with those that did.

To check that the variation in weight recorded throughout the nestling period was not simply due to normal daily variations, we weighed 15 individuals, on 2 consecutive days, and we compared the weights with the variation shown by the same individuals throughout the breeding period. The average  $\pm$  SE variation recorded on 2 consecutive days (3.6  $\pm$  1.5 g) was significantly smaller than that recorded during the nestling period (17.5  $\pm$  3.2 g; Wilcoxon signed-ranks test:  $Z = -2.6$ ,  $N = 15$ ,  $P = 0.009$ ). We calculated the variation in weight as (weight at the end of the nestling period – weight at the beginning of the nestling period)/weight at the beginning of the nestling period. Therefore losses are represented by negative values, while gains are positive.

### Statistical Analyses

For statistical analyses we used Genstat 6.1 (VSN International, Hemel Hempstead, U.K.). All data were first analysed with generalized linear mixed models (GLMM) which allowed us to control for repeated measures within groups by fitting 'territory' as a random factor. In mixed models, a nonsignificant random term (i.e. a random term with a negative component of variance) shows that the variation within groups is not significantly less than the variation between groups, indicating that the analysis is

not affected by inherent properties of that term. Therefore, as territory never gave a significant result, we subsequently fitted general linear models (GLM) to all data, as the most parsimonious model should always be used (Pinheiro & Bates 2000; Crawley 2002). The results of the GLMs were not qualitatively different from the GLMMs where the random factor was nonsignificant. Potential explanatory variables that gave nonsignificant results ( $P > 0.1$ ) were sequentially removed until the model included only 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 from having all significant terms in the model and each nonsignificant term fitted individually (Crawley 2002; Russell et al. 2003a).

To test whether fed and unfed crows differed in their feeding rates, we fitted the following explanatory variables in the model: experimental treatment; breeding status (breeder/nonbreeder); sex; age; number of caregivers; number of chicks; and year. We then tested the effect of treatment, year, individual's breeding status, sex, age and workload on the proportion of weight change during the nestling period. We also included in the model the date of second weighing (calculated as number of days from 1 March) and the number of days between the first and the second weighing, because weight loss during the season might be caused by environmental changes.

## RESULTS

### Weight Variation

At the beginning of the breeding season there was no significant difference in weight between experimental and control crows, when we controlled for sex and age of individuals and included year in the model (unfed crows:  $\bar{X} \pm$  SE = 515  $\pm$  7.2 g,  $N = 39$ ; fed crows: 524  $\pm$  10 g,  $N = 22$ ;  $F_{1,58} = 0.83$ ,  $P = 0.37$ ). In both categories, males were heavier than females ( $F_{1,58} = 17.13$ ,  $P < 0.001$ ) and weight increased with age ( $F_{1,58} = 36.75$ ,  $P < 0.001$ ).

Fed crows lost on average 1.4% of their weight during the breeding season compared to 5.4% for unfed crows, and this difference was significant (Table 1, Fig. 1a). The effect of food supplementation was greater in 2003 than in 2004, as indicated by the interaction between treatment and year. The interaction between treatment and sex showed that, among fed individuals, females benefited from food supplementation more than males. Unfed crows lost weight in proportion to their workload but fed individuals did not, as shown by the interaction between workload and treatment (Table 1, Fig. 1b). Consequently, fed crows were heavier than controls at the end of the breeding period (unfed crows: 484.4  $\pm$  7.7 g,  $N = 39$ ; fed crows: 516.7  $\pm$  9 g,  $N = 22$ ;  $F_{1,58} = 6.06$ ,  $P = 0.02$ ), with a significant effect of sex (males heavier than females;  $F_{1,58} = 20.24$ ,  $P < 0.001$ ) and age ( $F_{1,58} = 28.91$ ,  $P < 0.001$ ).

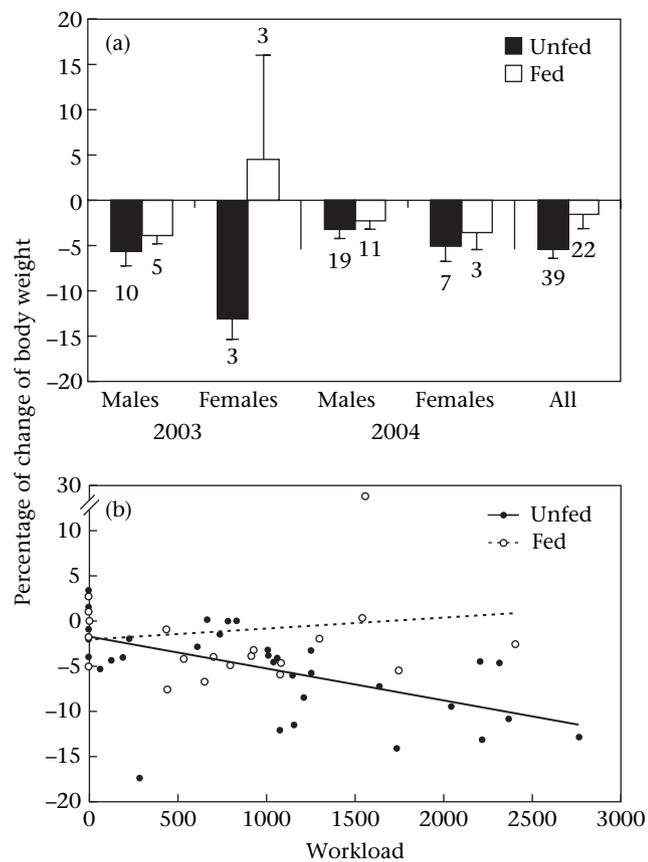
**Table 1.** Factors affecting individual changes in weight throughout the breeding season

Variable	F	df	P
Treatment	6.18	1,54	0.02
Workload	6.67	1,54	0.01
Sex	0.03	1,54	0.89
Breeding status	2.11	1,53	0.15
Age	2.61	1,53	0.11
Year	0.37	1,54	0.55
Date second weighing	0.67	1,53	0.42
No. of days between weighings	2.02	1,53	1.16
Treatment×Workload	4.22	1,54	0.04
Treatment×Sex	4.68	1,54	0.03
Treatment×Year	8.37	1,54	0.01
Treatment×Breeding status	1.22	1,52	0.27

Results of a GLM. See [Methods](#) for definition of terms in the model.

### Individual Provisioning Effort

Food supplementation did not significantly affect the provisioning rates of group members ([Table 2](#), [Fig. 2](#)). Breeders from food-supplemented territories had a slightly



**Figure 1.** (a) Mean  $\pm$  SE percentage of change in body weight during the breeding season of fed and unfed males and females in 2003 and 2004. Sample sizes are given above bars. (b) Percentage of change in body weight plotted against estimate of workload (number of feeds/h  $\times$  hours of chick provisioning per day  $\times$  number of days of provisioning) for unfed and fed crows. Negative values indicate weight loss; positive values indicate weight gain.

**Table 2.** Factors affecting individual feeding rates

Variable	F	df	P
Treatment	0.11	1,93	0.74
Breeding status	44.72	1,94	<0.001
Sex	5.13	1,94	0.03
Age	0.13	1,94	0.71
Year	0.76	1,94	0.38
Group size	0.07	1,94	0.79
No. of chicks	29.52	1,94	<0.001
Group size×Breeding status	7.14	1,94	0.01
Treatment×Breeding status	0.74	1,92	0.39
Treatment×Year	0.48	1,91	0.49
Treatment×Sex	0.04	1,92	0.84

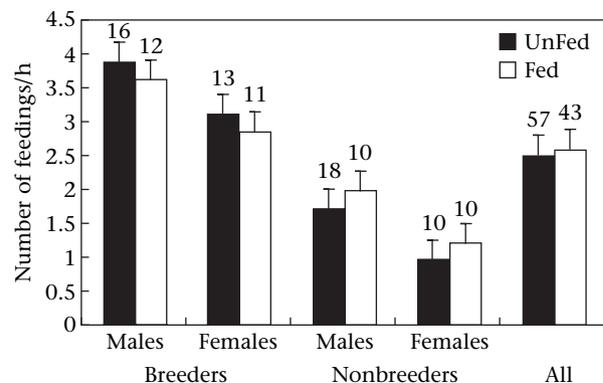
Results of a GLM. See [Methods](#) for definition of terms in the model.

lower provisioning effort than unfed birds, whereas fed nonbreeders slightly increased their feeding rates (by 0.5 feedings/h) compared to controls; [Fig. 2](#). However, these differences were not significant, as indicated by the non-significant interaction between treatment and breeding status ([Table 2](#)). Breeders provisioned chicks at higher rates than nonbreeders, males worked harder than females, and feeding rate was positively correlated with the number of chicks ([Table 2](#)). The significant interaction between breeding status and group size arose because breeders reduced their effort with an increased number of caregivers whereas nonbreeders did not ([Fig. 3](#)).

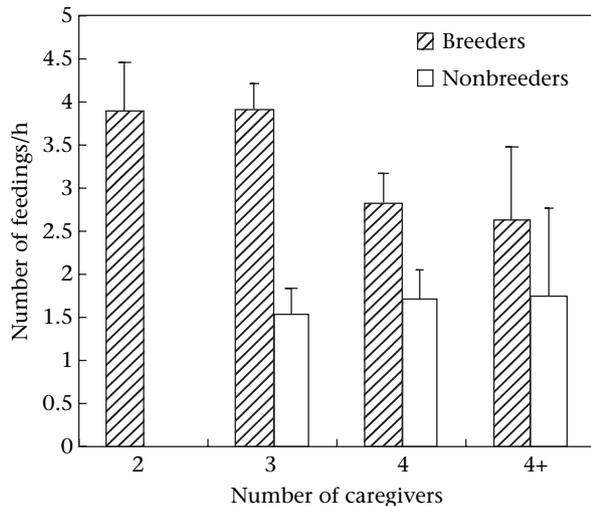
Food supplementation had no effect on the number of fledglings produced (unfed territories:  $\bar{X} \pm \text{SE} = 1.75 \pm 0.39$  g,  $N = 16$ ; fed territories:  $1.85 \pm 0.44$ ,  $N = 14$ ;  $F_{1,26} = 0.04$ ,  $P = 0.84$ , fitting year and group size in the model) or on the average weight of chicks at fledging within broods (unfed territories:  $\bar{X} \pm \text{SE} = 411 \pm 18.39$  g,  $N = 11$ ; fed territories:  $402 \pm 23.89$  g,  $N = 9$ ;  $F_{1,16} = 0.3$ ,  $P = 0.6$ , fitting year and group size in the model).

### Initial Weight and Provisioning Effort

In a subsample of 54 individuals for which initial body weight was known, provisioning effort was not correlated with initial body weight ( $F_{1,46} = 2.6$ ,  $P = 0.14$ ) nor was there any significant effect of the interaction between



**Figure 2.** Model estimates of the mean  $\pm$  SE number of feedings/h by fed and unfed crows. Sample sizes are given above bars.



**Figure 3.** Model estimates of the mean  $\pm$  SE number of feedings/h by breeders and nonbreeders in groups with two, three, four, and more than four caregivers.

body weight and sex ( $F_{1,45} = 2, P = 0.16$ ), or between body weight and breeding status ( $F_{1,44} = 0.22, P = 0.64$ ) on individual provisioning rates. Breeding status, sex, number of chicks and the interaction between breeding status and group size were controlled for, as they are important predictors of individual provisioning rates.

## DISCUSSION

### Costs of Care or Adaptive Weight Loss?

Costs of care are often measured as weight loss, but in birds this may reflect either an energetic cost of nestling care or an adaptive strategy to improve flight abilities during the breeding season, when individuals make frequent flights to the nest (Moreno 1989). According to the latter hypothesis, lighter birds should be able to take on a higher workload because of their superior flying ability. If this was the case in crows, we would expect to find the same patterns of weight loss in relation to increasing workload in unfed and fed crows. In contrast to this prediction, unfed birds lost weight in proportion to workload, whereas fed ones did not, with the consequence that experimental crows were heavier than controls at the end of the nestling period. The observed weight loss in crows is therefore likely to represent a cost of chick provisioning, which affects breeders and nonbreeders in a similar way. However, fed crows also lost weight during the breeding season, although this loss was smaller than that of control birds. This might indicate that part of the change in weight may be explained as an adaptive strategy to improve flight ability. Alternatively, our treatment might not have completely eliminated the costs of chick provisioning. Although the amount of supplementary food provided exceeded group members' daily energetic requirements, individuals probably had to search for other prey items to provision the brood.

### Current Versus Future Reproduction

The costs of rearing offspring influence individual decisions on investment of resources and energy in reproduction. In several biparental bird species, feeding the young represents an activity of high energetic expenditure (Drent & Daan 1980). When offspring care is costly, individuals face a trade-off between the allocation of resources in the current reproductive attempt (reducing their probability of breeding successfully in the future) and self-maintenance to augment the number of reproductive attempts throughout their life (Velando & Alonso-Alvarez 2003). Studying this trade-off has proved to be important for understanding reproductive tactics in biparental systems (Lindén & Møller 1989; Moreno et al. 1999).

If parents suffer costs of care and can adjust their levels of investment to minimize these costs, then helpers are expected to be limited in the same way, and show similar flexibility (Heinsohn 2004). Costs of care are therefore potentially important for understanding the individual contribution to chick provisioning in cooperatively breeding societies. Recent theoretical work on cooperative breeding has incorporated this view, suggesting that helping behaviour, like parental care, must be considered a life history trait with consequences throughout an individual's lifetime, as all current and future benefits of provisioning must be discounted by any reduction in survival or future reproductive success (Heinsohn & Legge 1999; Heinsohn 2004). However, so far, only a few studies have investigated the costs of care to helpers. In white-winged choughs, *Corcorax melanorhamphos*, young helpers lose weight in proportion to the time spent incubating the eggs (Heinsohn & Cockburn 1994), and in meerkats, *Suricata suricatta*, helpers lose weight when they engage in babysitting and pup-feeding activities (Clutton-Brock et al. 1998; Russell et al. 2003b).

Our study on cooperatively breeding carrion crows uncovered the short-term costs of chick provisioning in terms of weight loss, and showed that they are similar for individuals of different breeding status (breeders and helpers), sex and age. When we investigated experimentally the trade-off between current and future reproduction in this population (i.e. allocation of resources to provisioning the current brood or to self-maintenance) by experimentally providing food to the territories, we found that all individuals invested additional resources in self-maintenance by reducing their weight loss and maintaining their weight at a stable level regardless of workload. In this respect, crows differ from other cooperative species for which comparable data are available. White-winged choughs, meerkats and moorhens, *Gallinula chloropus* (Eden 1987; Boland et al. 1997; Clutton-Brock et al. 2002) provisioned at higher rates when the costs of feeding offspring were experimentally reduced.

Exploring such interspecific variation is important for increasing our understanding of cooperative breeding. One possibility is that, in crows, a further augmentation of feeding rates would not improve reproductive success. However, analyses carried out on a 10-year data set where group size and reproductive success on 99 groups have

been monitored every year suggest that the additional workload provided by several caregivers increases fledgling production (Canestrari 2006). According to this scenario, and given that starvation seems to be an important source of chick mortality, it is difficult to believe that an increase in individual provisioning rates would have not positively affected reproductive success in the current brood. Alternatively, the observed interspecific patterns might reflect a different value of 'future' among species, determined by differences in longevity, where the larger the number of potential breeding attempts available to individuals during their lifetime, the higher their investment in self-maintenance. The available data indicate that adult annual survival of crows (0.75; Baglione et al. 2005) is slightly higher than that of meerkats (0.68; Clutton-Brock et al. 1999), but lack of information on the other species does not allow us to explore this hypothesis further. A third possibility is that the crows' strategy of investing in self-maintenance indicates that, in the trade-off between costs and benefits of care, the short-term costs of provisioning are more important for crows than for the other species. In meerkats, the short-term loss of weight has no apparent effect on survival, because it is minimized in the long term through condition-dependent provisioning effort, reduced investment in breeding attempts following a season of high provisioning, and increased foraging effort after the breeding season (Russell et al. 2003b). Crows did not adjust their provisioning rate to their body condition, and they may also lack other mechanisms of cost minimization in the long term. In other words, the shape of the costs/benefits function of offspring provisioning may differ between cooperative species (Crick 1992), determining different patterns of allocation of energy in reproduction. Future research on the effect of provisioning effort on survival rates in crows will allow this hypothesis to be tested.

If self-maintenance constrains investment in current reproduction, it may be predicted that provisioning decisions will vary according to increasing levels of predictability of resources. Given high costs of provisioning, individuals might afford to increase provisioning rates when food is predictable over the long term because the consequences of investing additional resources in the current brood will not affect their own survival. Preliminary support for this prediction comes from a different study on these crows, which focused on the effect of food resources on juvenile philopatry. Seven yearlings from four territories that were food supplemented year round showed higher provisioning rates at the family nest than 11 unmanipulated juveniles (seven territories). This difference was not entirely explained by the fact that food-supplemented yearlings spent more time on the natal territory than controls (Baglione et al. 2006). Because body weight at the beginning of the breeding season does not influence provisioning effort (this study), higher provisioning rates are likely to reflect a response to increased food predictability rather than be a consequence of increased body condition. Although such a limited data set should be interpreted with caution, this result suggests that varying the timing and duration of food supplementation in future experiments in crows and other

cooperative species may shed more light on the complexity of the trade-off between reproduction and self-maintenance.

Our results also showed that weight loss reduction was more noticeable in females than in males, suggesting that the trade-off between current and future reproduction also varies within species. A stronger response to the availability of additional resources may reflect the fact that females are likely to suffer the highest costs of reproduction in the long term. Besides production of eggs, breeding females carry out all incubation and brooding, and have lower survival than males (Baglione et al. 2005). Females are therefore particularly expected to minimize the costs of current breeding to save energy for future attempts. The importance of self-maintenance for breeding females in this species is consistent with a previous study (Canestrari et al. 2004) where we found that, among group members, females were most likely to fine-tune chick provisioning by deciding at the nest whether to deliver the prey item to the chicks or to consume part or all of it themselves ('false-feedings'), probably after assessing the body condition of nestlings in relation to their own.

### Load-Lightening Effect of Helping

In crows, the costs of chick provisioning in terms of weight loss, the importance of self-maintenance and the fact that crow breeders switch from an additive effort to a compensatory reaction when aided by more than one helper suggest a role of 'load lightening' (Crick 1992) in the evolution of cooperative breeding in this species. Although additive care seems to enhance current production of young (Canestrari 2006), our results suggest that securing future reproduction may be an important strategy for breeders to increase their lifetime reproductive success. The aid of helpers seems to allow breeders to reduce their current effort (load-lightening effect) when a threshold of 'workforce' is reached (four carers). From the crow helper's point of view, indirect fitness can therefore be enhanced not only through the increased production of collateral kin in current broods (Canestrari 2006) but also by augmenting the number of reproductive attempts of the parents. The load-lightening effect of helping implies that future indirect fitness should be included in the calculation of helpers' inclusive fitness. Many studies on cooperative species have shown that current inclusive fitness benefits of helpers are very small (Richardson et al. 2002), weakening the idea that kin selection influences the evolution of cooperative breeding (Griffin & West 2002). We believe that estimates of future indirect fitness need to be taken into account before dismissing the view of helping as a kin-selected trait.

We observed a compensatory reaction to the presence of several caregivers only among breeders, whereas non-breeders did not vary their provisioning rates. This pattern may be caused by the different benefits and costs of provisioning strategies in the long term. On the one hand, the efforts of nonbreeders increase fledgling production and therefore their inclusive fitness (Canestrari 2006). On the other hand, nonbreeders generally feed the chicks at

lower rates than breeders (Canestrari et al. 2005), incurring smaller energetic costs during the breeding season. In the trade-off between costs and benefits of feeding the current brood, it may pay nonbreeders to maintain their provisioning effort regardless of the number of caregivers.

## Conclusions

Regardless of sex, age and breeding status, cooperatively breeding crows incur costs of chick provisioning in terms of weight loss that constrain their provisioning effort. If influenced by costs, cooperative contribution to chick care is therefore unlikely to be selectively neutral (Jamieson 1991), and should be considered a life history trait shaped by processes of adaptation, like parental care in biparental species. The fact that the costs are important for cooperatively breeding crows has another evolutionary implication. It suggests that the future component of fitness may be important in shaping the dynamics of cooperation, because breeders may benefit from helpers in terms of increased survival and helpers may augment their indirect fitness by increasing the number of nesting events of their parents. To incorporate the future component into estimates of the benefits of cooperation, we need to explore the long-term consequences of chick care on survival. Meanwhile, we hope that more studies will focus on the costs of chick provisioning in social species to enhance our understanding of the interspecific variability of cooperative behaviour among vertebrates.

## Acknowledgments

Thanks to Nick Davies, Andy Russell, Claire Spottiswoode and Juan Moreno for comments on the manuscript, and to Gloria Robles, Elisa Chiarati, Jesus García and José Navarro for help in the field. This study was financially supported by the Gates Cambridge Trust, Emmanuel College, the Weis-Fogh fund (to D.C.), the Spanish Ministry of Education and Science, project CGL2005-02083/BOS and 'Ramón y Cajal' program (FEDER-FSE), and Junta of Castilla y León, project VA001A05 (to V.B.).

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