

False feedings at the nests of carrion crows *Corvus corone corone*

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Abstract

False feedings, when individuals visit the nest but refrain from feeding the chicks, occur in some cooperative species and have been interpreted in the white-winged chough (*Corcorax melanorhamphos*) as active deception by helpers towards the rest of the group. In a cooperatively breeding population of carrion crows (*Corvus corone corone*) 81.5% of the individuals that provided nestling care showed various kinds of false feedings: arriving at the nest with no food, consuming part or all the food brought to the nest, or taking back from a chick's gape the food that had just been delivered. False feedings occurred on average during 16.3% of nest visits, with some individuals performing them at very high rates (up to 64% of nest visits). False feedings occurred at similar rates in unassisted pairs and groups with helpers, and breeding females showed false feeding at significantly higher rates than other group members. Furthermore, individuals showed false feedings regardless of whether they were alone on the nest or in the presence of other group members, and false feedings did not provoke aggression by the rest of the group. False feedings are not likely to represent deceptive help in the carrion crow. We suggest that crows evaluate the chicks' condition during nest visits and that false feedings occur as result of a trade-off between their own hunger and the chicks' needs.

Key words: deception, false feedings, cooperative breeding, carrion crow

Introduction

In some cooperative bird species group members occasionally refrain from feeding the nestlings during nest visits. Australian bell miners (*Manorina melanophrys*) sometimes visit the nest carrying no food (Clarke 1984; Poiani 1993), and in the laughing kookaburra (*Dacelo novaeguineae*), young female helpers occasionally fail to deliver food to the nestlings (Legge 2000). “False feedings” have been specifically studied only in white-winged choughs (*Corcorax melanorhamphos*), where some individuals consumed the food they carried to the nestlings in up to 30% of visits (Boland et al. 1997). Such behaviour has been interpreted as active deception by the helpers towards the other group members. In support of this view, two choughs are usually present at the nest when chick feeding occurs, but individuals show false feedings only when they are alone on the nest. Moreover, the rest of the group punishes deceptive individuals when they are detected.

“Honesty” of helping can be informative on the evolution of cooperative breeding. The occurrence of deception suggests direct fitness benefits to the helper independent of any benefits to the nestlings (Boland et al. 1997). For example, helpers might feed the chicks in order to signal their parental skills to potential mates (Cockburn 1998; Putland 2001) or to “pay a rent” to the dominants in order to have access to their territory’s resources (Kokko et al. 2002). Correct interpretation of false feedings is therefore important to understanding the evolution of cooperative behaviour.

False feedings might be common among cooperative species, but in many species they can only be detected by techniques that allow detailed observation of behaviour at the nest. When we observed nestling care activities in cooperatively breeding carrion crows (*Corvus corone corone*) by placing video cameras close to the nests, we detected five different types of false feedings. In this paper we describe false feeding behaviour in carrion crows and

we address the following questions: 1) do false feedings occur more frequently in cooperative groups than in unassisted pairs? 2) within a cooperative group, who is more likely to show false feedings? 3) are false feedings more frequent when individuals are alone on the nest? and 4) are false feedings punished when detected by the other group members?

Methods

Study population

Unlike other European populations, carrion crows in northern Spain breed cooperatively. In a 45 km² rural area near León (42° N, 5° W), about 75% of the territories are held by cohesive cooperatively breeding groups of up to 9 birds (mode = 3 birds). Groups form by delayed natal dispersal of offspring, which remain on the natal territory for up to 2 years, and by immigration of individuals from other territories (Baglione et al. 2002a). Groups can be families (a pair with non-dispersing offspring), mixed groups (a pair with non-dispersing offspring and immigrant extra-birds) and pairs with immigrants. Reproduction can be shared among group members of both sexes, but non-dispersing offspring do not reproduce within their natal group (Baglione et al. 2002b). Both non-dispersing offspring and non-breeding immigrants can help at the nest. Within a group, up to five individuals feed the nestlings and contribute to nest building and nest sanitation.

Data collection

Since 1995 we have banded all crow nestlings reared in the study area with colour rings just before they left the nest (30 days old). In spring 1999 and 2000 we captured 61 free-flying

crows using two-compartment walk-in traps and a “snap trap” specifically developed for this species (for details on catching methods see Baglione et al. 2002a). We banded these crows with colour rings and wing tags. The birds were aged as one, two, or more than two years old according to the internal colour of the upper mandible (Svensson 1992). We collected between 50 and 200 microlitres of blood from the alar vein of each banded individual. A microsatellites-based parentage analysis provided information on the breeding status of group members (Baglione et al. 2002b), while the P2/P8 sexing method revealed the sex of the birds (Griffiths et al. 1998). In a previous analysis, eight microsatellite loci (5.1 alleles on average, range = 2-8) were used to determine parentage in the groups (for details see Baglione et al. 2002b). We classify as a “breeder” every individual that generated nestlings in the brood on its territory ($n = 36$) and we define as a “helper” every non-breeding individual that contributed to nestling feeding ($n = 18$). In such a classification of breeding status based on parentage, unsuccessful breeders that obtained copulations but generated no nestlings might be incorrectly classified as non-breeders. Copulations are very difficult to observe in carrion crows, and therefore field observations could not complement our genetic data. However, other criteria indicated that our classification of breeding status is reliable for at least 86% of non-breeders. As *a*) non-dispersing offspring do not participate in reproduction (Baglione et al. 2002b), *b*) sexual maturity in crows is delayed until the second year and reproduction is rare until the third year (Cramp and Perrins 1994; Madge and Burn 1999), and *c*) supernumerary breeding females are easily detected because they enlarge the brood, only three individuals in our sample could have been incorrectly regarded as non breeders. However, this fact did not affect the conclusions of this study. When we excluded those three individuals from the analyses, the results did not change qualitatively.

We placed camouflaged micro video cameras (size: 4x2x2 cm) 2-2.5 m away from the nests to record nestling care activities from day 4 after egg hatching to chick fledging at

day 30. Recording bouts (4 hours) were randomly distributed from 5:00 a.m. till 8:00 p.m.

Due to nest failure, not all nests were sampled for the entire nestling period. The overall time of recording per nest varied between 8 and 56 hours (total 558 hours). We collected data on 4 nests belonging to unassisted pairs and 13 nests belonging to cooperative groups ranging in size between three and six members. We obtained information on 2894 trips to the nest made by 36 breeders (18 males and 18 females), 10 non-dispersing offspring (8 males and 2 females), and 8 immigrants (6 males and 2 females).

Results

False feedings

We observed 472 nest visits (16.3% of visits recorded) in which crows did not feed the chicks or only partially delivered the food that they carried to the nest (false feedings). Forty-four banded individuals (81.5% of the banded birds providing nestling care) showed false feedings. Within these individuals, false feedings occurred on average in 17.5% of nest visits, with some exhibiting false feedings at a very high rate (e.g. 18 false feedings in 28 visits, or 64%).

Feedings are conspicuous in the carrion crow and are always unequivocally visible in the video recordings. Crows carry food in their crops and it was possible to determine whether they brought food to the nest by looking at the swelling of the crop. Typically, when an individual arrives at the nest, nestlings beg vehemently and the individual transfers the food into the gape of one or more chicks. We observed five different kinds of false feedings. 1) "Empty visits" (45% of false feedings). Individuals arrived at the nest without food in their crops and consequently did not feed the nestlings. 2) "Partial feedings" (36% of false feedings). Individuals carried food to the nest, but they delivered to the chicks only a part of it

and swallowed the rest. During partial feedings, the swelling of the crop clearly indicated that, after having fed the chicks, the individuals still carried a substantial amount of food in their crop. After a conspicuous swallowing, the crop eventually looked empty. 3) “No feedings” (4% of false feedings). Individuals consumed all the food that they carried to the nest, without feeding the chicks at all. 4) “Recoveries” (10% of false feedings). Individuals delivered food to the chicks but immediately took it back from the chick’s mouth and swallowed it. 5) “Stolen recoveries” (5% of false feedings). Individuals took food delivered by another crow from a chick’s gape. The ability to re-observe a video-recorded sequence in slow motion was extremely useful in unequivocally classifying false feedings.

Unlike empty visits, in all other behaviours (partial feedings, no feedings, recoveries and stolen recoveries) the crows carried food to the nest and then denied it to the chicks. We gathered these behaviours in a single category, “feeding reductions”. Empty visits were instead considered separately to cover the obvious possibility that they were unrelated to feeding chicks. To characterize the individual rate of false feedings we used the proportion of an individual’s visits that were false. Hereafter we call “ P_{ev} ” the proportion of empty visits and “ P_{fr} ” the proportion of feeding reductions. P_{ev} and P_{fr} values were normalized by applying the arcsine transformation (Sokal and Rohlf 1994).

False feedings in unassisted pairs and groups (question 1)

Our data suggest that false feedings are as common in unassisted pairs as in cooperative groups, although the sample size of unassisted pairs is low ($n = 4$). False feedings occurred on average in 16.4% and 16.2% of nest visits in unassisted pairs and groups respectively (Mann-Whitney U Test: $U = 28$, $n_{pairs} = 4$, $n_{groups} = 13$, $p = 0.84$). Within the four unassisted pairs, only females showed empty visits and they also performed feeding reductions at higher

rates than males, although the difference was not statistically significant (mean P_{fr} by males \pm SE = 0.03 ± 0.01 , females = 0.1 ± 0.02 , Paired-Samples T Test: $t = -2.2$, $n = 8$, $p = 0.1$).

Distribution of false feedings among group members (question 2)

We used SPSS general linear model (GLM) type III to determine the effect of breeding status (breeder versus helper, see below), sex, age and tarsus length (which provides an estimate of body size and dominance rank in the carrion crow; Richner 1989) on the occurrence of false feedings among members of cooperative groups. The number of nestlings and number of adults providing care ("group size") were also included in the analyses as they can affect the intensity of the begging stimulus that feeders perceive at the nest, influencing in turn the occurrence of false feedings. An exploratory analysis detected no difference between the false feeding rate of non-dispersing offspring and non-breeding immigrants when controlling for the other variables (mean P_{ev} by non-dispersing offspring \pm SE = 0.024 ± 0.01 , non-breeding immigrants = 0.015 ± 0.008 , $F = 1.3$, $n = 18$, $p = 0.27$; mean P_{fr} of feeding reductions by non-dispersing offspring \pm SE = 0.05 ± 0.02 , non-breeding immigrants = 0.07 ± 0.02 , $F = 0.3$, $n = 18$, $p = 0.6$). We therefore pooled those two categories together as "helpers" in the subsequent analyses. Individuals that were sampled sequentially in 1999 and 2000 were considered only once in the analyses to avoid pseudoreplication. Three video-recorded breeding females could not be captured. Their breeding status and sex could be assessed according to their behaviour at the nest and the composition of the rest of the group, but we lacked information on their age and body measures. They were therefore excluded from this analysis.

Breeding status, sex and the interaction between sex and breeding status influenced the occurrence of empty visits among group members (Table 1). Breeding females showed empty visits at significantly higher rates than any other individual (Fig. 1a). Our data were not

affected by the fact that, at the beginning of the nestling period, females spend substantial time brooding the chicks, and are presumably more constrained in feeding them. For most groups, behavioural data were collected when the breeding female was no longer brooding. In only two groups, did part of the observations include the early nestling period. When we excluded those days from the analysis, the results did not change qualitatively. Feeding reductions were significantly more frequent among breeders than non-breeders. Again, breeding females exhibited feeding reductions more frequently, and the interaction between sex and breeding status was significant (Table 1; Fig. 1b). Age and tarsus length, as well as number of chicks and number of individuals providing chick care, had no significant effect on the occurrence of any kind of false feeding.

Effect of the presence of other individuals at the nest (question 3)

We recorded 785 nest visits in which two or more group members arrived simultaneously to the nest (27.1% of total visits recorded). Forty-three crows were recorded at the nest both alone and simultaneously with one or more group members. For each of these individuals we calculated the proportion of false feedings for nest visits alone or with other group members. Stolen reductions were included in this analysis, as they occurred either when the individual who fed the chicks was still at the nest or when it had already left. Individuals showed empty visits more frequently when they were alone at the nest (Wilcoxon Matched Pair Test: $Z = 3.21$; $p = 0.001$), but the presence of other individuals at the nest did not influence the occurrence of feeding reductions ($Z = 1.14$; $p = 0.25$; Fig. 2).

The identity of the on-looker did not have a primary role in the occurrence of false feedings. In 9 groups containing only one helper, on average 37% of false feedings by the helper were made in the presence of a breeder, and in 4 groups with more than one helper,

helpers showed false feedings both in the presence of a breeder and in the presence of another helper (mean proportion of false feedings in joint visits with a breeder \pm SE = 0.04 ± 0.01 , mean proportion of false feedings in joint visits with a helper \pm SE = 0.03 ± 0.02 , Wilcoxon Matched Pair Test $Z = -0.4$, $n = 9$, $p = 0.7$). Breeders performed false feeding visits at a similar rate in the presence of their mate and in the presence of a helper (mean proportion of false feedings in joint visits with a breeder \pm SE = 0.08 ± 0.02 , mean proportion of false feedings in joint visits with a helper \pm SE = 0.06 ± 0.04 , Wilcoxon Matched Pair Test $Z = -1.4$, $n = 28$, $p = 0.16$).

Evidence of punishment of false feedings (question 4)

We considered “aggression” to be a situation where one individual pecked or intimidated another group member by aiming to peck it. We recorded 14 instances of aggressive behaviour among group members at the nest (1.8% of the visits with two or more crows at the nest). In only three cases was the aggression addressed towards an individual that had just committed false feedings. Crows committing false feedings in presence of other individuals were therefore attacked in only 3.1% of occasions ($n = 97$). The proportion of aggression recorded in joint visits where false feedings occurred did not differ statistically from the proportion of aggression in normal joint visits (Yates Corrected Chi-Square = 0.31, $p = 0.58$).

Most aggressive behaviour occurred in one particular group where the breeders were observed attacking the two non-breeding immigrants twelve times. On only two occasions did aggression occur after the immigrants showed a false feeding (an empty visit and a stolen recovery). In another group, a non-dispersing offspring moved aggressively towards his full sib after they both had fed the nestlings. No false feedings were recorded in this circumstance. In a third group, a non-dispersing offspring pecked his stepmother when she took the food that

he had just delivered from a chick's gape. Overall that false feedings were often ignored or provoked weak reaction within the social groups. Nevertheless, our observations could not account for more subtle or delayed punishment of false feeders.

Discussion

What a cooperatively breeding carrion crow is up to, when it flies to a nest of begging chicks, is not as obvious as might be expected. In this study, most individuals (81.5% in our sample) were observed at times to withhold food from the nestlings. They did so in different ways, which were sometimes as subtle as delivering only part of the contents of their crops. False feedings occurred with remarkable frequency (16.3% of nests visits), and therefore deserve close attention. The occurrence of false feedings would have never been revealed in crows without the use of video cameras at the nest. We encourage the use of this technique in studying other species in which the nests are difficult to observe, and we predict that detailed observations of nestling care activities will reveal that false feedings are common among cooperative species.

Previously, false feeding behaviour has been addressed only once, in cooperative white-winged choughs, where it has been interpreted as deception by helpers towards the rest of the group (Boland et al. 1997). Behavioural deception is defined as an interaction where, as a consequence of the behaviour of the signaller, the receiver perceives a certain situation to be different from reality. As a result of the interaction the signaller benefits, while the receiver pays a cost (Semple and McComb 1996). The occurrence of deceptive behaviour in cooperative species can provide important clues in understanding helping behaviour. Benefits of helping such as increased production of collateral kin (kin selection) and improvement of local conditions through group augmentation require enhancement of the survival of the nestlings (Cockburn 1998). However, helping might confer benefits that require helpers to be

seen provisioning the nest by the other group members, whether or not this benefits the chicks. For example, it has been suggested that male Arabian babblers (*Turdoides squamiceps*) increase their social prestige through helping and that females choose mates according to their prestige (Zahavi 1990). Female pied kingfishers (*Ceryle rudis*) (Reyer 1990) preferentially mate with males that have acted as helpers in previous nesting attempts. Male savannah sparrows (*Passerculus sandwichensis*) acquire a level of paternity in subsequent broods in proportion to their contribution to parental care in previous broods (Freeman-Gallant 1997). Nestling care has high costs in most bird species (Clutton-Brock 1991). Therefore, in all cases where helping has a signalling function, a helper gains the best returns by being seen helping while in reality practicing behavioural deception by retaining the food (Boland et al. 1997).

As false feedings in white-winged choughs seem to be truly deceptive, helping behaviour in this species has been interpreted as a signal of individual quality which may be important to facilitate future coalitions of dispersers (Boland et al. 1997). The idea that white-winged chough helpers fool dominant birds by pretending to feed the chicks therefore strongly supports the idea that helpers benefit in ways other than enhancing the fitness of the young (Cockburn 1998; Griffin and West 2002). Putland (2001) suggested that, since false feedings have been described in other cooperative birds and could be common among cooperative species, the signalling function of helping behaviour might have a general value. It is therefore important to verify whether false feedings invariably imply deception or depend on other causes.

Are false feedings deceptive in the carrion crow?

Our data do not support the hypothesis that false feedings represent deceptive help in carrion crows. First, if false feeding were the result of deception by helpers alone, we would not expect them to occur within unassisted pairs. However, in the carrion crow, false feedings occurred commonly in unassisted pairs. Second, deception should occur more frequently among helpers than among breeders, but carrion crows showed the opposite pattern.

Despite being performed mostly by breeders, false feedings might still be deceptive. If parental care itself has a signalling component, in order to maintain breeding status in subsequent years, deceptive behaviours might evolve even among breeders (Lotem et al. 1999). However, this does not seem to occur in the crows. First, the sex ratio among cooperative crows is skewed toward males (Baglione et al. 2002b). In terms of breeding opportunities, males find themselves in a more competitive environment than females, who have better chances to reach and maintain breeding status. Therefore, males rather than females would need to signal their quality to attract mates, and the best payoff for them would be to show exceptional parental skills without paying the associated costs. Therefore, we would expect false feedings to be more frequent among breeding males, which is not the case. Second, since the aim of a deception is to make the receivers register a situation that is not occurring, we would expect individuals to make false feedings when others cannot detect them (Boland et al. 1997). Crows were more likely to make empty visits when they were alone on the nest but, surprisingly, the presence of other group members at the nest (no matter whether breeders or helpers) did not prevent individuals from showing feeding reductions. One possibility might be that empty visits are deceptive and feeding reductions are not. However, crows are unlikely to fool their group members by visiting the nest with no food for the chicks. Cooperative crows forage in close group, and therefore they are likely to realise if a group member flies to the nest carrying no food in its crop. It is also unlikely that crows fly to the nest carrying food and consume it before arriving at the nest. In 969 hours of

observation with spotting scopes, we sometimes observed crows flying from the ground to the nest with no food, but we never saw a crow consuming food during the trip. Furthermore, empty visits and feeding reductions apparently provoked no reactions at all from other group members.

By lumping together four false feedings in a single category we might have oversimplified the analysis of feeding reductions. This approach was necessary due to the rarity of those behaviours and the consequent small sample sizes. However it seems unlikely that our analysis has masked some relevant pattern. All feeding reduction types showed qualitatively the same distribution among breeders and helpers and did not seem to differ in terms of the social context where they occurred (alone or accompanied at the nest).

Why do carrion crows show false feedings?

In the Bell Miner, young and inexperienced helpers show empty visits at high frequencies (Poiani 1993). Empty visits and feeding reductions in the carrion crow are not likely to represent mistakes. Age had no significant effect on the occurrence of false feedings and young crows were not more likely to show them than older, and presumably more experienced, individuals. We suggest that crows sometimes visit the nest with no food merely to carry out other nestling care activities, for example nest cleaning. This is consistent with the fact that empty visits were shown mainly by breeding females, who perform most of the nest cleaning (out of 612 minutes of observed nest cleaning activities, 79% was carried out by breeding females, which almost invariably spent some minutes cleaning the nest after an empty visit, Canestrari unpublished data).

The question remains, why do carrion crows fly to the nest to eat the food that they might have consumed at the point where it was collected? The hypothesis that nestlings were

so satiated that they refused the food can be dismissed since nestlings begged on all occasions where false feedings occurred. We suggest that crows evaluate the chicks' condition during nest visits and make false feedings as a result of a trade-off between their own hunger and the chicks' needs. This idea is supported by the fact that breeding females showed false feedings at a higher proportion than other group members. All individuals showing the highest false feeding rates (between 40% and 64% of visits, $n = 7$) were breeding females. Breeding females are likely to suffer the highest costs of reproduction in this crow population. First, energetic costs of egg production are substantial in birds (Clutton-Brock 1991) and they are probably very high for female crows. In this population breeding females lay a second and sometimes a third clutch if the nest fails before the chicks are about 10 days old. As one clutch usually consists of 4-6 eggs and nest failure is very common, females often lay 8-12 eggs, occasionally more (up to 17 eggs), every breeding season (Marcos and Baglione unpublished data). Second, only breeding females incubate the eggs and brood the chicks (until about 10 days after egg hatching), and this activity is energetically costly in birds (Clutton-Brock 1991; Heinsohn and Cockburn 1994). As eggs hatch after 19-20 days, breeding females can incubate for long periods (up to 47 days in the most extreme case observed). The fact that breeding females in this population undergo higher mortality than breeding males after the breeding season (Baglione unpublished data) is likely to be a consequence of the costs of reproduction. Therefore, breeding females are expected to finely adjust their effort in current reproduction in order to secure future breeding and to maximise their lifetime reproductive success. Furthermore, our data show that brood reduction is common in this population, and that it can be related to chick starvation in many cases (Marcos unpublished data). Fine mechanisms to monitor the chick's needs and to adjust the feeding level accordingly might therefore be important in this population. It is not yet clear which cues adult crows might use to assess the condition of the chicks. Among the various

possibilities, are begging intensity, begging posture, mouth colour, position in the nest or body mass. Unfortunately our recordings had no sound and were black and white, and the position of the video camera was often inadequate to study begging postures. Further studies will need to address this issue to test more thoroughly the hypothesis that false feedings represent a form of parental control.

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Figure legend

Figure 1. Proportion of all visits to the nest that were empty visits (a) and feeding reductions (b) among male and female breeders and helpers.

Figure 2. Proportion of all visits to the nest that were false feedings when birds were alone or with other group members

Table 1. Factors affecting the individual rate of empty visits and feeding reductions. Results of SPSS General Linear Model type III.

	Empty visits		Feeding Reductions	
	F	P	F	P
Breeding status	5.26	0.03	8.2	<0.01
Sex	4.74	0.04	0.01	0.91
Age	1.12	0.29	0.43	0.52
Tarsus	0.45	0.51	0.19	0.66
Group size	1.21	0.27	1.13	0.29
Num. chicks	0.17	0.68	2.64	0.11
Breeding status * Sex	10.2	<0.01	4.75	0.04

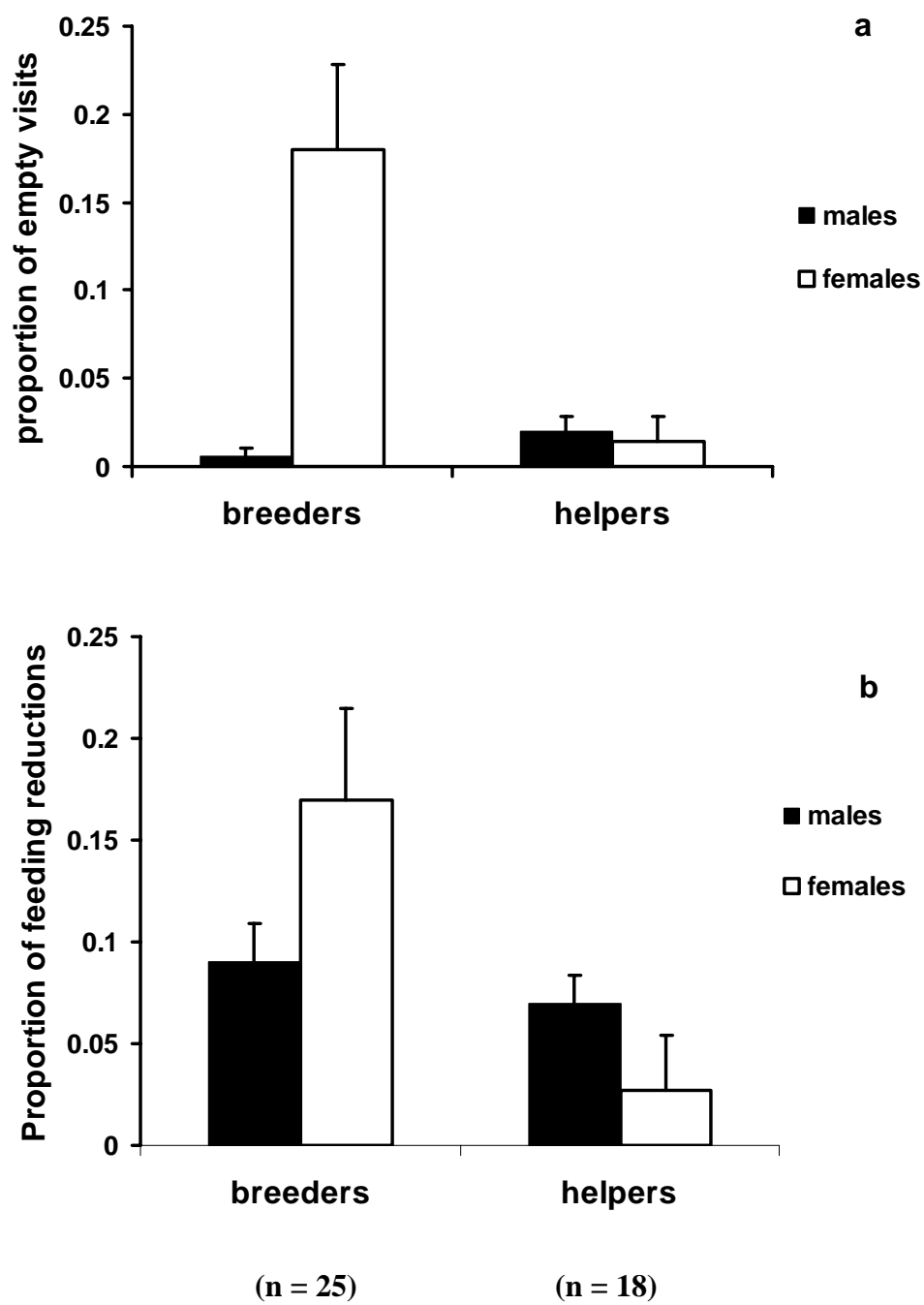


Fig.1. Canestrari D, Marcos JM, Baglione V

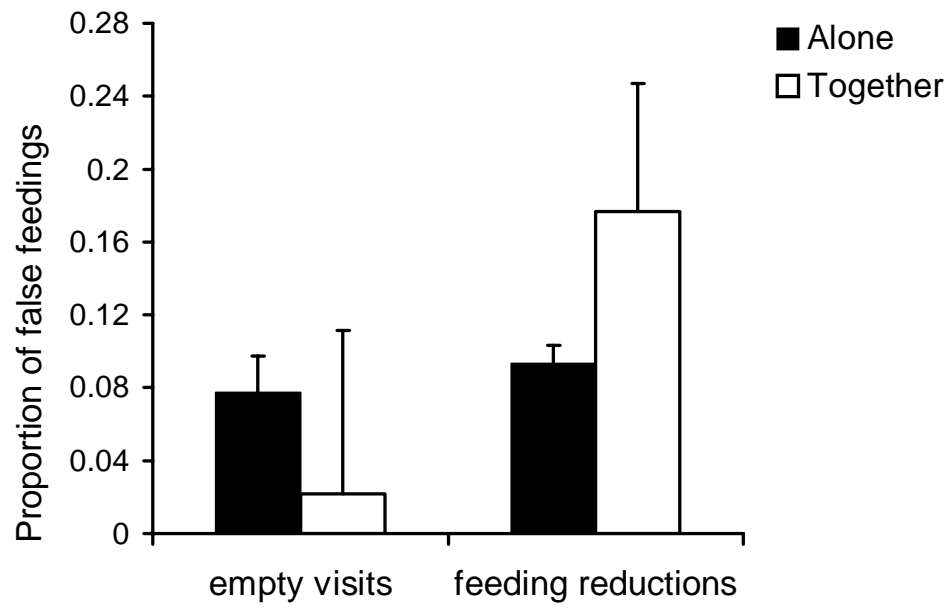


Fig.2. Canestrari D, Marcos JM, Baglione V