

Original Article

No evidence for deception over allocation to brood care in a cooperative bird

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The evolutionary route(s) to cooperative breeding, wherein individuals provide care to the offspring of others, remains contentious. Two hypotheses propose that such helping behavior constitutes a signal, either to remain on the current territory (pay-to-stay) or to advertise quality to potential partners (social prestige). As such, both hypotheses predict that helpers gain from perceived, rather than actual, levels of care provided. Using the chestnut-crowned babbler (*Pomatostomus ruficeps*), we test whether individuals attempt to increase their perceived level of care by visiting the nest without food (nonfeeding [NF]) or with food but fail to deliver it (false-feeding [FF]). We found no evidence that either NF or FF was used as a deceptive tactic, with both being more parsimoniously explained by current levels of brood demand. Most notably, categories of helpers (males, adults, immigrants) expected to be “charged” more for staying or to benefit more from advertising quality, neither nonfed nor false-fed more than other categories (females, yearlings, natal). In addition, there was no evidence that the presence of an audience (the breeding females in their domed nests) influenced the probability of NF or FF in a manner consistent with either hypothesis. Finally, the incidences of both NF and FF were low and insufficient to have significant effects on the perceived levels of care provided, even if they were used in an attempt to deceive other group members over their contributions to rearing young. We conclude that signaling-based hypotheses have, at best, a weak role in selecting for helping behavior in chestnut-crowned babblers. *Key words*: cheating, cooperative breeding, false-feeding, pay-to-stay, policing, signaling, social prestige. [*Behav Ecol*]

INTRODUCTION

Current evolutionary theory proposes that individuals should act in their own selfish interests in order to maximize fitness (Williams 1966; Dawkins, 1976). Cooperative breeding systems, wherein individuals provide care to the offspring of others (hereafter referred to as helpers), represent a challenging case study. Broadly, five adaptive hypotheses are commonly invoked to account for the apparent altruistic behavior of nonbreeding helpers (Emlen 1991; Cockburn 1998; Bergmüller et al. 2007). Kin selection proposes that helpers suffer personal fitness costs, which are offset by the fitness benefits helpers confer on relatives that share genes by descent (Hamilton 1964). The other four propose that helping is selected when any short-term energetic costs (Russell et al. 2003) are offset by future gains to direct fitness mediated through accumulation of breeding experience (Selander 1964), increased group size (Woolfenden 1975; Kokko et al. 2001), increased ability to remain on the natal territory (Gaston 1978), or elevated probability of being chosen as a partner (Zahavi 1995). Testing among these alternatives has proved problematic because they are neither mutually

exclusive nor simultaneously testable within a single study (Cockburn 1998; Clutton-Brock 2002; Bergmüller et al. 2007). A potential solution is to first test among suites of hypotheses that share predictions, before further testing among a more tractable remainder in further investigations. The aim of this study is to test the likely application of signal-based hypotheses for the incidence of helping in a cooperative bird using the seldom quantified behaviors of nonfeeding (NF) and false-feeding (FF), wherein individuals, respectively, either visit the young with no food or do so but fail to deliver it.

Three of the five hypotheses presented above lack a signaling component. In these three, cheating, in terms of deceptively refraining from offspring provisioning, brings no or few fitness benefits. Under kin selection, individuals can only gain indirect fitness if they personally help to increase the productivity of kin (Hamilton 1964; Grafen 1982). Under the experience hypothesis, individuals have to partake in parent-like activities to gain the future benefit of enhanced breeding ability (Komdeur 1996). Finally, under group augmentation, group members are seldom expected to cheat over contributions to brood care because doing so will reduce their own future survival and breeding success (Kokko et al. 2001; Clutton-Brock 2002). By contrast, under signal-based hypotheses, group members are selected to cheat because future benefits of helping are based on perceived, rather than actual, contributions to cooperation. For example, the pay-to-stay hypothesis (Gaston 1978; Kokko et al. 2002) proposes that the persistence of the nonbreeders on the

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territory is dependent on their helping to rear the offspring of the territory owners. Helping is likely to evolve into a signal because failure to advertise investment could lead to eviction (Reyer 1986; Emlen 1991; Mulder and Langmore 1993). Similarly, the social prestige hypothesis proposes that nonbreeders advertise their quality by helping, allowing other group members to make informed decisions about future dispersal or breeding partners (Reyer 1986; Zahavi 1995).

Tests of the two signaling-based hypotheses for the evolution of cooperative breeding are still comparatively rare (Carlisle and Zahavi 1986; Reyner 1986; Mulder and Langmore 1993; Wright 1997; Doutrelant and Covas 2007; McDonald et al. 2008a, 2008b; Koenig et al. 2011); one approach is to use patterns of NF or FF to do so. In white-winged chough (*Corcorax melanorhamphos*), for example, helpers have been observed to visit the nest with food, invariably wait until the current nest attendant departs, and then consume the prey item themselves (11% of nest visits; Boland et al. 1997). Such behavior, when detected by other group members ($n = 3$ occasions), led to apparent retribution. The interpretation of these observations was that the false-feeders deceive other group members as to their actual provisioning rate, thereby broadly supporting signal-based hypotheses (Boland et al. 1997). By contrast, observed patterns of NF and/or FF appear to be inconsistent with signaling-based hypotheses in most other studies conducted. For example, in meerkats (*Suricata suricatta*), 12% of all food items taken to pups failed to be delivered successfully: in 9% offspring rejected the item and in only 3% did helpers consume the item despite begging by offspring (Clutton-Brock et al. 2005). However, FF behavior was never concealed from view of other group members and never led to obvious retribution. In carrion crows (*Corvus corone*), patterns of NF (~7% of nest visits) and FF (~9% of nest visits) were unaffected by an apparent audience and seldom resulted in aggression (~3% of false-feeds) (Canestrari 2004). Finally, in bell miners (*Manorina melanophrys*), NF (~3% of nest visits) and FF (~5% of nest visits) were unaffected by provisioner relatedness, largely unaffected by an apparent audience and never led to retribution (McDonald et al. 2007). The interpretation of these latter studies was that NF was used to gauge offspring need without the costs of unnecessarily bringing food and that FF occurred when potential provisioners brought food but gauged their own needs to exceed those of the offspring.

Although these interpretations might be correct, it does not necessarily follow that signal-based hypotheses have no bearing on the evolution or maintenance of cooperative breeding (but see McDonald et al. 2008a, 2008b for further evidence against signal-based hypotheses in bell miner). For example, if FF occurs for the latter reasons suggested, it is not deceptive; hence would not be expected to lead to retribution (Semple and McComb 1996). In addition, low levels of aggression need not be at odds with signaling-based hypotheses, if threats are sufficient to police potential defectors (Cant 2011). It is noteworthy that in all FF studies presented above, deception has the potential to be detected because offspring are reared in open cup nests (avian species) or while travelling with the group (meerkats). Cheating is known to be most prevalent when policing defectors is costly or difficult (Pellmyr and Huth 1994; Bshary and Grutter 2002; Kiers et al. 2003; Edwards et al. 2006, 2009; Mills and Côté 2010). As a consequence, NF or FF might be a more appropriate indicator of the importance of signal-based hypotheses for the maintenance of cooperation in species where detection of cheating events is difficult and where potential defectors have 100% certainty of whether or not they are being policed. This is because one can make very precise predictions about when potential defectors should nonfeed/false-feed.

The overall aim of this study is to test signaling-based ideas for selection on cooperative breeding in the chestnut-crowned babbler (*Pomatostomus ruficeps*), a species in which helpers know with certainty whether or not their behavior is being monitored. Chestnut-crowned babblers are a 50g cooperatively breeding bird endemic to semi-arid and arid zones of south-eastern Australia. This species breeds in units of 2–15 (mean = 6), a single female in each unit lays a clutch of 3–5 eggs, up to two successful attempts are possible within a season and unit size is positively related to group breeding success (Russell et al. 2010; Browning et al. 2012). Babblers provision offspring exclusively with a single prey item at a time, most commonly spiders and insect larvae of variable sizes and to a lesser extent with adult insects and small reptiles. The aspect of their breeding ecology, however, that makes them unique in the context of earlier FF studies is that they breed exclusively in enclosed domed nests. Consequently, nest visitors have certainty whether or not their behavior has the potential to be observed: if another individual is in the nest on their arrival (almost always the breeding female), then they can be monitored, if not, they cannot. Individuals thus commonly have the opportunity to visit the nest with food, ostensibly to feed the chicks, but instead consume this food undetected inside the nest. If helping behavior represents an effort to signal contributions to care deceptively, we would expect significant and predictable NF and/or FF in this system.

We present five broad aims pertinent to the hypothesis that helping represents a costly signal. First, we describe the extent of NF and analyze whether helper characteristics and/or brood demand best explains its prevalence. Second, we investigate whether nonfeeds are associated with other forms of cooperative behavior (nestling preening or nest maintenance). Third, we describe patterns of FF and again analyze the relevance of helper characteristics versus brood demand in this context. In each of the above three cases, we examine audience effects in the form of breeding female presence (other carers are rarely present). Fourth, we quantify brood begging and helper “provisioning” behavior during successive occasions of feeding and FF by the same helpers. Finally, we examine correlations between rates of both NF and FF with actual rates of nestling feeding and determine whether levels of either are sufficient to alter perceived rates of nestling “provisioning” significantly. Broadly, we predict that if NF and/or FF serve to deceive other group members over contributions to brood care, they should be explained more by individual characteristics and audience effects than by variation in brood demand, and that its prevalence should be sufficient to alter perceived provisioning rates (Gaston 1978; Zahavi 1995; Kokko et al. 2002; Table 1).

MATERIALS AND METHODS

Study site and population

Our study was conducted during the 2007 and 2008 breeding seasons at the University of New South Wales field station at Fowlers Gap in far western New South Wales, Australia (141°42'E, 31°06'S). Details of climate and habitat have been presented elsewhere (Portelli et al. 2009). Briefly, the field site is located in the arid zone of south-eastern Australia, with annual rainfall generally 200–250 mm (Mabbutt et al. 1973). The habitat is dominated by open chenopod shrublands, with tall shrubs and trees generally restricted to small linear stands along dry drainage lines (Portelli et al. 2009). Babblers build their domed nests in this vegetation, have several nests per territory and use them for both communal roosting and breeding. Like all Pomatostomidae babblers, nests are large and obvious dome-shaped structures, constructed of dead twigs (Higgins and Peters 2002). In chestnut-crowned

Table 1
Predictions arising from pay-to-stay and social prestige hypotheses regarding levels of NF/FF expected in chestnut-crowned babblers

Main effect	Effect	Reason
Sex	Males > females	Males more common (1.7: 1) than females and so would be expected to pay more for staying and compete more to be chosen as partners; hence be under selection to increase perceived contribution
Age	Adults > yearlings	Adults more of a threat to current reproductives, so expected to pay more for staying and compete more to be attractive partners (hence see above)
Relatedness	Immigrants > natal	Immigrants less related to group members than natal: only nonrelatives need to pay rent and nonrelatives are expected to gain more from signaling quality to potential mates (hence see above)
In presence of breeding female	Males < females	Prediction unclear because unknown if female helpers pay female breeders to stay, but males should be less inclined to “cheat” in presence of breeding female
	Adults < yearlings	Adults less related to group members and more attractive sexual partners than yearlings; hence would be expected to “cheat” less with an audience
	Immigrants < natal	Immigrants need to pay to stay and will benefit more from advertising quality to unrelated group members; hence would be expected to “cheat” less with an audience
NF/FF	Positive effect on perceived contribution	Those that are perceived to contribute highly are less likely to be evicted and more likely to be chosen as partners

Effect denotes whether levels of NF/FF should be greater (>) or lesser (<) between helpers differing in their sex, age, and immigrant status; how these effects should be influenced by the presence of an audience (the breeding female); as well as the effects of NF/FF rates on perceived provisioning rates. Partners include sexual partners only because dispersal coalitions are rare in chestnut-crowned babblers (Rollins et al. 2012). All predictions based on established theory (Gaston 1978; Noë and Hammerstein 1995; Zahavi 1995; Kokko et al. 2002; Noë 2007); see DISCUSSION for further details.

babbler breeding nests, the entrance hole is ~20 cm from the nest cup and is well-insulated with at least 2 cm of soil, herbivore droppings, and soft lining, such as feathers, wool, and vegetation (unpublished data). Crucially, the contents of the nest are not visible to any of those outside of the nest irrespective of their position, and nestlings do not have specific vocalizations that indicate successful feeding.

The study population was set up in 2004 and covers the groups living within an area of 8 × 7 km. This area has held up to 53 social groups (3–21 individuals ≥6 months old/group) and 88 breeding units (2–15 individuals ≥6 months old/unit) of babblers; the reason for the greater number of the latter is that social groups often disband into up to four (mode = 2) smaller subunits for breeding (Russell et al. 2010). This study was conducted on a total of 22 breeding attempts by 18 breeding units in which more than 90% (mean = 98%) of all non-breeding helpers were known and uniquely tagged ($n = 76$, mean = 3.3 per unit, range = 1–8). All babblers were uniquely identifiable through a numbered metal leg-band (Australian Bird and Band Banding Scheme issued), a combination of three wrap-around color leg-bands and a small (2 × 12 mm) passive-integrated transponder (PIT tag; TROVAN™ Ltd, UK) inserted subcutaneously in the flank. The age (yearling or adult) and immigrant status (immigrant or natal) of helpers were known from the 3 years of previous study, whereas sex was determined molecularly from blood samples collected at the time of banding (Rollins et al. 2012). Yearlings were individuals born during the previous breeding season, whereas immigrants were defined as birds that were not natal to the social group. Whether or not the breeding attempt was the first or second was known with precision, and brood ages and sizes were known through close monitoring of nesting attempts every 3–5 days (Russell et al. 2010).

Recording behavior at the nest

The identity and frequency of birds visiting the nest were determined using PIT-tag technology (Gibbons and Andrews 2004). The unique alphanumeric code of any PIT-tagged bird passing through the nest entrance was detected by a copper coil fitted to the mouth of the nest. This code, along with date

and time, was recorded on a LID650 decoder (TROVAN™ Ltd) connected to the coil. The structure of babbler nests ensures that all birds visiting the nest have to pass through the coil to access the nest contents. For the purposes of this study, we also fitted a 10 × 50 mm-pen camera positioned at the back of the nest, which recorded both visually and acoustically for 1 min each time a bird passed through the coil: the mean nest visit duration of helpers was 17.6 s (range = 1–117 s, with 96% ≤ 1 min). With the exception of the breeding female who was often present inside the nest (27% of nest visits), helpers rarely entered the nest prior to the departure of the preceding bird (<4% of nest visits) and presented too few cases for meaningful analysis. We have no evidence to suggest that our equipment acted as any kind of deterrent to group members. In fact, babblers usually incorporated the equipment into the nest and re-used nests for breeding and roosting both within and between seasons despite the presence of the coil.

Overall, we recorded 1476 nest visits by 54 helpers in the 18 breeding units. For each nest visit, we recorded the date, time of day, and identity of the visiting bird; whether or not the visitor entered with food, the size of the food if it did so, and whether or not it attempted to feed it to the nestlings; as well as whether or not the breeding female was present in the nest. The size of food items was estimated relative to babbler bill sizes and categorized at 25% intervals from a quarter of the size of a babbler bill (the smallest items) to six times larger (the largest items) (median = 1). Prey size was fitted as a linear term, although the final size represented a category containing those prey twice as long as a babbler bill or greater. Where possible, brood begging intensity was measured and categorized into none, low (nestlings make some effort to change their posture or make begging calls), medium (nestlings make begging calls and raise their heads but make no other movements toward the feeding adult), and high (nestlings beg intensely and visibly move toward the feeding adult). We also extracted and quantified a subset of begging data across three successive nest visits by a given helper, with the middle visit in each case being associated with a false-feed ($n = 39$ nest visits, by 13 helpers selected at random from different groups but known to have false-fed). In these cases, brood begging

calls associated with a given nest visit were filtered to remove any noise at background frequencies lower than the begging vocalizations. The amplitude of both the first and second begging calls uttered by nestlings following the entrance of a helper into the nest was measured using the root mean-square algorithm in Raven to provide a measure of begging intensity (Charif et al. 2004; McDonald et al. 2007). In addition, for each of these specific nest visits, we recorded the time between first and second begging calls, the number of “prompt” calls uttered by the helpers, and the time helpers spent in the nest. Prompt calls are specific vocalizations that babblers utter in association with nestling provisioning, occurring inside the nest in 61% of nest visits (this study). Finally, we also recorded whether or not the helpers preened the brood or contributed to nest maintenance. The work conducted conformed to the use of animals in research and was authorized by the University of New South Wales Animal Care and Ethics Committee (Project number: 04-63A) and the Australian Bird and Bat Banding Scheme (Project number 422). All statistical analyses were conducted in Genstat Release 14 (Rothamsted Experimental Station, Harpenden, UK).

Specific questions and statistical analyses

Nonfeeds (visiting the nest without food)

The potential explanatory terms associated with the probability of arriving at the nest without food were investigated using a generalized linear mixed model (GLMM) in which the response term (visit the nest with food [0] or without food [1]) was fitted to a binomial error structure with logit link function, and both the binomial denominator and dispersion parameter were fixed at 1 (see Table 2 for specific sample sizes). Explanatory terms included those pertaining to timing (time of day, breeding attempt, year of study); helper number; the brood (age, size); helper characteristics (sex, age, immigrant status); and audience effects (presence of breeding female). Individual, brood, and group identities were fitted as random intercepts. Quadratic terms were fitted for variables to test for nonlinear effects. For specific predictions regarding the hypotheses under investigation, see Table 1 and DISCUSSION.

Table 2

Factors affecting the probability that carers visit the nest without food (nonfeed)

Term	Estimate \pm SE	Statistic (χ^2)	DF	P value
Constant	-2.1 \pm 0.2			
Time of day	15.0 \pm 5.4	7.6	1	0.006
Time of day ²	-16.4 \pm 5.5	9.0	1	0.003
Breeding Attempt (first > second)	-0.3 \pm 0.3	0.9	1	0.4
Year (2007 < 2008)	0.07 \pm 0.3	0.06	1	0.8
Helper number	0.06 \pm 0.06	1.2	1	0.3
Brood size	-0.3 \pm 0.1	5.2	1	0.02
Brood age	-0.006 \pm 0.03	0.04	1	0.8
Helper sex (male < female)	-0.8 \pm 0.4	3.6	1	0.05
Helper age (yearling < adult)	-1.0 \pm 0.4	6.6	1	0.01
Immigrant status (natal < immigrant)	-0.3 \pm 0.4	0.3	1	0.6
Breeding female present (no > yes)	-0.1 \pm 0.2	0.2	1	0.6
Helper sex * helper age	Figure 1d	4.0	1	0.04
Helper sex * BF present	Figure 1e	4.3	1	0.04
Immigrant status * BF present	Figure 1f	5.2	1	0.02

Analysis was conducted using a GLMM with binomial error structure and logit link function on 1476 nest visits by 53 helpers (measures/individual = 2–178, mean = 27, SD = 31), rearing 22 broods (measures/brood = 8–274, mean = 67, SD = 68) in 18 units (measures/unit = 10–334, mean = 82, SD = 90). Individual, brood, and unit identities were fitted as random intercepts, but only individual was retained (variance component = 0.9 \pm 0.3 SE) because the other two showed equivalent within- versus between-subject variation (components = 0). Terms were retained in the final model when $P < 0.1$; effect sizes and statistics are provided for such terms in the model together and for all others when added to this final model individually. The direction of effects within categories is denoted by < and > signs, irrespective of significance, BF = breeding female. Quadratic terms and interactions are presented when $P < 0.1$.

Nonfeeds and contributions to other cooperative activities

We measured the association between NF and contributions to two other cooperative behaviors that were frequently enough observed to permit statistical analysis. Using the same data and statistical methods outlined above, we investigated the association between the probability of NF and the incidence of both nestling preening and nest maintenance. In both GLMM analyses, we fitted the same explanatory (with the exception of breeding attempt and year) and random terms as indicated above, in addition to whether or not a nest visit occurred with a food item.

False-feeding (visiting with food but failing to deliver it)

Overall, we recorded 1316 nest visits with food by the 53 helpers in the 18 breeding units (see Table 3 for specific details). The potential explanatory terms associated with the probability of arriving at the nest with food but failing to deliver it successfully were investigated using a GLMM in which the response term (feeding [0] or FF [1]) was fitted to a binomial error structure with logit link function, and both the binomial denominator and dispersion parameter were fixed at 1. Explanatory and random terms were as for the analysis of NF above, although categorical measures of begging intensity and a continuous measure of the size of the prey items brought were additionally fitted in this analysis.

FF: brood begging and helper persistence

Two aspects of both brood begging and of helper behavior were considered further when in-association with FF. The two brood measures included the quantitative measures of acoustic begging intensities during both first and second begging calls and the time between the two, whereas the two helper measures were the number of prompt calls given and the time spent in the nest. In all cases, the brood and helper behavior were determined during three successive nest visits by the same individual, where the first and last visits were associated with feeding and the middle visit involved FF. The average time difference (\pm standard deviation [SD]) to the false-feed following the preceding feed was 81 \pm 79 min and to the subsequent feed following the false-feed was 71 \pm 57 min. Normally distributed residuals and homogeneity of variances

were achieved in three of the four response terms following square-root (begging intensity and time in nest) or logarithm (prompt calls) transformations. In each case, the association with FF was analyzed using one-way repeated measures analysis of variance (ANOVA). The data on the time between successive begging bouts could not be normalized and were analyzed using a Friedman's test, the closest nonparametric equivalent to repeated measures of ANOVA.

Correlations between feeding types and consequences for "perceived" investment

We investigated the associations between rates of both NF and FF with those of actual nestling feeding. The rate at which helpers fed nestlings (feeds/h) was fitted as a response term to a normal error structure (following the addition of 1 and a logarithm transformation to ensure normality) in a residual maximum likelihood model (REML). The rate of NF or of FF was entered as the explanatory terms of interest in two separate analyses, and brood and group identities were fitted as random intercepts in each case. Our rationale for these analyses was to investigate whether individuals that nonfeed or false-feed at a high rate, feed nestlings at a low rate, which might suggest that NF/FF serves to deceive other group members over contributions to nestling provisioning. To investigate further whether NF or FF could function to increase perception of actual feeding rates, we ranked all helpers in terms of their actual feeding rates (1–53 for each helper) and correlated these ranks with those ranks obtained when (1) feeds and nonfeeds were combined and (2) feeds and false-feeds were combined. If either NF or FF has the potential to deceive group members into actual feeding rates, we would expect significant changes to the ranks of actual feeds versus all nest visits or to actual feeds versus all nest visits with food.

RESULTS

Nonfeeds

Of the 1476 nest visits observed, 160 (11%) occurred in the absence of a food item. Nonfeeds were observed at least once in 16 of 18 units, in 19 out of 22 breeding attempts, and by 35 of 53 individuals. Nonfeeds represented 0–50% (mean = 12%, SD = 11%) of all nest-visits at the level of the unit, 0–50% (mean = 11%, SD = 10%) at the level of the brood, and 0–100% (mean = 16%, SD = 21%) at the level of the individual. Individual identity constituted a significant random term in the GLMM analysis, suggesting systematic differences among individuals in their propensity to visit the nest without food, but this was neither the case of brood nor unit identities (Table 2). The probability that individuals visited the nest without food showed a significant quadratic relationship with time of day, with NF being more than twice as likely in the middle of the day (Figure 1a), but showed no systematic differences between first or second breeding attempts or between years. Individuals were ~3% less likely to nonfeed for each additional nestling in the brood (Figure 1b), but the propensity to nonfeed was neither significantly influenced by brood age nor the number of helpers in the group. Overall, females and adults were twice as likely to visit nests without food as were males or yearlings, respectively, but there was no difference between natal and immigrant helpers (Figure 1c). Analyses of interactions revealed that this sex difference was generated by a threefold increase in the propensity for adult females to nonfeed compared with males (or yearling females) (Figure 1d) and a fourfold increase in the propensity of females of both ages to visit the nest without food when the breeding female was present on the nest (Figure 1e). By contrast, there was no suggestion that helpers differing in age

were more or less likely to nonfeed in the presence of the breeding female (age * presence interaction; $\chi^2 = 0.02$, df = 1, $P = 0.9$), although immigrants were twice as likely to visit the nest without food when the breeding female was present than when she was absent (Figure 1f).

Nonfeeds and contributions to other cooperative activities

A total of 20 individuals (38%) were observed to preen chicks, doing so in up to 22% of nest-visits (mean = 3.3% of nest-visits by each individual, SD = 5.8%). Preening showed a non-significant tendency to be more consistently conducted by certain individuals (random variance component = 0.4 ± 0.3 [standard error, SE]), but not in certain broods or units (components = 0). Preening probability was not associated significantly with time of day, brood size, helper number, or helper status (sex, age, immigrant status), but increased as broods aged, presumably in response to feather development (Figure 2a legend). Helpers never preened nestlings in the presence of the breeding female, precluding formal analysis of the effects of breeding female presence on nestling preening behavior. Finally, those arriving with food were three times less likely to preen nestlings than those arriving without food (Figure 2a), but there were no significant interactions between helper status and feeding status on the probability of preening nestlings (Figure 2a legend).

Most individuals (72%) were observed to maintain the nest structure at least once. On average, individuals helped to maintain the nest on 11% of visits (range 0–75%, SD 15%), and some individuals showed a tendency to do so more than others (individual identity component = 0.4 ± 0.2 SE). Nest maintenance behavior was unaffected by time of day, brood age, helper number, or helper status, but increased significantly with increasing brood size (Figure 2b legend). Nest maintenance was substantially more common when helpers arrived at the nest without food, although males were three times less likely to do so when arriving at the nest with food than were females, generating a significant sex by feeding behavior interaction (Figure 2b). By contrast, there were no interactions between age or immigrant status and feeding behavior on nest maintenance (Figure 2b legend). Finally, although nest maintenance was 64% more common in the absence, rather than presence, of the breeding female (Figure 2c), there were no significant interactions between helper status and breeding female presence on propensities to maintain the nest (Figure 2c legend).

False-feeding

FF was observed in 33 (2.5%) occasions when food was brought to the nest ($n = 1312$ nest visits with food). Overall, FF was observed in 13 of the 18 units, 14 of the 22 broods, and by 19 of the 53 helpers. False-feeds represented 0–11% (mean = 3.5%, SD = 3.8%) of all nest visits at the level of the unit, 0–11% (mean = 3.3%, SD = 3.8%) at the level of the brood, and 0–28% (mean = 3.2%, SD = 5.8%) at the level of the individual. Unlike NF above, false-feeds were rarely associated with nestling preening or nest maintenance. For example, of the 33 instances of FF, we recorded only one instance each of preening and maintenance. Part of the reason for this low level of alternative behaviors conducted is that in 79% of false feeds in which the fate of the food item was observed ($n = 14$ instances), the provisioner retained the food item throughout the duration of the visit and left the nest with the food item in its bill, presumably precluding involvement in other forms of care.

There was no evidence from the random terms fitted that variation in FF behavior within subjects differed with those

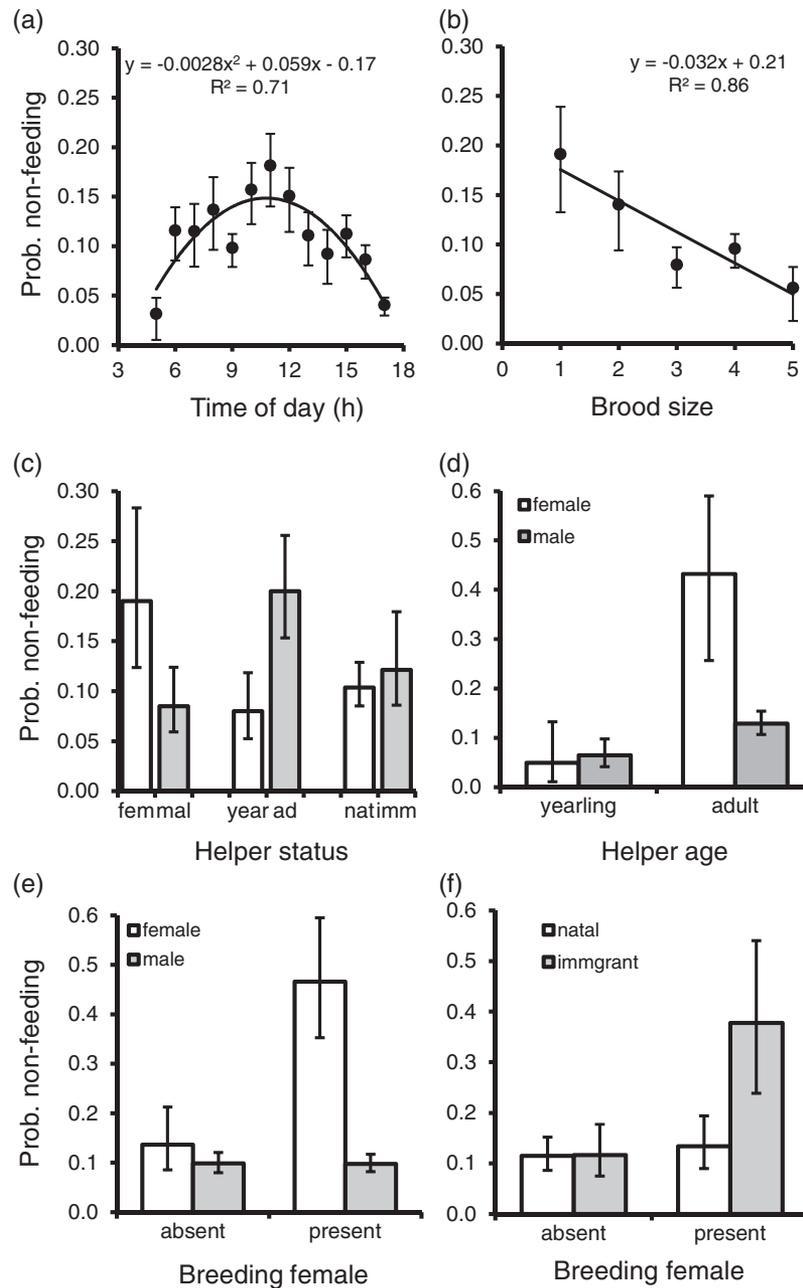


Figure 1

The probability that helpers visit the nest without food (NF). Effects of (a) time of day; (b) the current number of nestlings in the brood; (c) helper sex (fem, female; mal, male), age (year, yearling; ad, adult), and immigrant status (nat, natal; imm, immigrant); (d) helper sex by age; (e) helper sex by whether or not the breeding female was present in the nest; and (f) helper immigrant status by whether or not the breeding female was present in the nest. Figures show predicted means (\pm SE). For details of the model and statistical values, see [Table 2](#).

of between subjects, at any hierarchical level ([Table 3](#)). The probability that helpers false-fed was not influenced by time of day, breeding attempt, or study year, nor was it influenced by the number of helpers in the group. By contrast, FF was two to three times less prevalent in medium-sized broods ([Figure 3a](#)) and increased by 0.15% for every daily increase in brood age ([Figure 3b](#)). FF was substantially more likely to occur when broods failed to beg ([Figure 3c](#)) and showed a nonsignificant tendency to increase with increasing prey size ([Figure 3d](#)). However, there were no differences between the sexes, ages, or immigrant statuses on the probability of FF ([Figure 3e](#)). Similarly, the probability that helpers false-fed was independent of maternal presence in the nest

([Figure 3f](#)), and there were no interactions between helper status and maternal presence on FF propensity (sex * presence: $\chi^2 = 0.01$, $df = 1$, $P = 0.9$; age * presence: $\chi^2 = 0.07$, $df = 1$, $P = 0.8$; immigrant status * presence: $\chi^2 = 0.01$, $df = 1$, $P = 0.9$).

FF: brood begging and helper persistence

Fine-scale analysis of brood demand and helper behavior in association with FF failed to reveal evidence of deceptive behavior. Vocal begging intensity was significantly lower during FF events compared with feeding events ([Figure 4a](#)), and the duration between first and second begging vocalizations

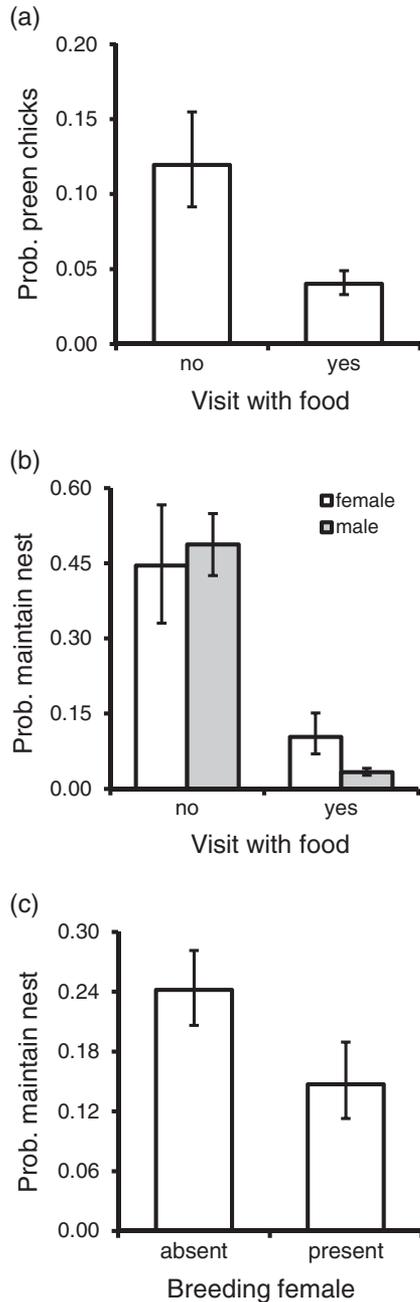


Figure 2
 NF and contributions to other forms of cooperation. (a) The probability that broods would be preened was not associated significantly with time of day (effect = -0.7 ± 1.0 SE; $\chi^2 = 0.5$, df = 1, $P = 0.5$), brood size (effect = -0.1 ± 0.1 SE; $\chi^2 = 0.7$, df = 1, $P = 0.4$), the number of helpers in the group (effect = -0.1 ± 0.06 SE; $\chi^2 = 2.3$, df = 1, $P = 0.1$) or helper status (males < females = -0.6 ± 0.5 SE; $\chi^2 = 1.5$, df = 1, $P = 0.2$; adults < yearlings = -0.3 ± 0.4 SE; $\chi^2 = 0.5$, df = 1, $P = 0.5$; natal < immigrants = -0.6 ± 0.4 SE; $\chi^2 = 2.6$, df = 1, $P = 0.1$). However, nestlings were more likely to be preened as they aged (effect = 0.2 ± 0.04 SE; $\chi^2 = 28.4$, df = 1, $P < 0.001$). After controlling of this effect, we found preening to be more common when helpers arrived without food (GLMM: $\chi^2 = 29.9$, df = 1, $P < 0.001$). None of the interactions between helper status and feeding status on the probability of preening nestlings was significant (sex * feeding status: $\chi^2 = 0.05$, df = 1, $P = 0.8$; age * feeding status: $\chi^2 = 0.4$, df = 1, $P = 0.7$; immigrant status * feeding status: $\chi^2 = 1.9$, df = 1, $P = 0.2$). (b) Nest maintenance was unaffected by time of day (effect = 0.7 ± 0.7 SE; $\chi^2 = 1.0$, df = 1, $P = 0.3$), brood age (effect = -0.001 ± 0.03 SE; $\chi^2 = 0.01$, df = 1, $P = 0.9$), helper number (effect = 0.0009 ± 0.05 SE; $\chi^2 = 0.01$, df = 1, $P = 0.9$), or

Table 3
 Factors affecting the probability of FF

Term	Estimate \pm SE	Statistic (χ^2)	DF	P value
Constant	-3.3 ± 0.2			
Time of day	-0.5 ± 1.2	0.2	1	0.6
Breeding attempt (first > second)	0.6 ± 0.6	1.1	1	0.3
Year (2007 < 2008)	-0.6 ± 0.5	1.3	1	0.2
Helper numbers	-0.07 ± 0.07	0.9	1	0.3
Brood age (days)	0.1 ± 0.04	7.8	1	0.006
Brood size	-2.0 ± 0.8	6.8	1	0.01
Brood size ²	0.3 ± 0.1	5.4	1	0.02
Brood begging intensity	Figure 3c	24.5	3	<0.001
Prey item size	0.5 ± 0.3	3.6	1	0.06
Helper sex (male > female)	0.9 ± 0.7	1.6	1	0.2
Helper age (yearling < adult)	-0.4 ± 0.5	0.6	1	0.4
Immigrant status (natal < immigrant)	-0.2 ± 0.5	0.2	1	0.7
Breeding female present (no > yes)	0.6 ± 0.6	1.1	1	0.3

Analysis was conducted using a GLMM with binomial error structure and logit link function on 1312 nest visits with food by 53 helpers (measures/individual = 1–175, mean = 25), rearing 22 broods (measures/brood = 7–258, mean = 60) in 18 units (measures/unit = 9–318, mean = 73). Individual, brood, and unit identities were fitted as random intercepts, with individual (component = 0.6 ± 0.4 SE) and brood (component = 0.06 ± 0.22 SE) being retained; unit identity being dropped (component = 0). Terms were retained in the final model when $P < 0.1$; effect sizes and statistics are provided for such terms in the model together and for all others when added to this final model individually. The direction of effects within categories is denoted by < and > signs, irrespective of significance. Quadratic effects and interactions are presented when $P < 0.1$.

was also significantly longer during FF events (Figure 4b). These patterns were found despite helpers showing significantly greater numbers of prompt calls (Figure 4c) and spending significantly longer in the nest (Figure 4d) when FF.

Correlations between feeding types and consequences for “perceived” investment

Signaling hypotheses would typically predict negative relationships between helper feeding and NF rates as well as between helper feeding and FF rates. In neither case, did we find

helper status (males < females = -0.6 ± 0.4 SE; $\chi^2 = 2.3$, df = 1, $P = 0.1$; yearlings < adults = 0.4 ± 0.3 SE; $\chi^2 = 1.2$, df = 1, $P = 0.3$; nats < immigrants = -0.3 ± 0.4 SE; $\chi^2 = 0.4$, df = 1, $P = 0.6$). However, it increased with brood size (effect = 0.4 ± 0.1 SE; $\chi^2 = 9.2$, df = 1, $P = 0.002$). After controlling for this effect, we found that nest maintenance was substantially more common when helpers arrived at the nest without food (effect = 3.1 ± 0.2 SE; $\chi^2 = 169.0$, df = 1, $P < 0.001$), although males were three times less likely to do so when arriving at the nest with food than were females, generating a significant sex by feeding behavior interaction (sex * with/without food interaction; $\chi^2 = 5.3$, df = 1, $P = 0.02$). By contrast, there were no interactions between age ($\chi^2 = 0.06$, df = 1, $P = 0.8$) or immigrant status ($\chi^2 = 0.8$, df = 1, $P = 0.3$) and feeding behavior on nest maintenance. (c) Nest maintenance was more common in the absence, rather than presence, of the breeding female (GLMM: $\chi^2 = 5.2$, df = 1, $P = 0.02$), but there were no significant interactions between helper status and breeding female presence on propensities to maintain the nest (sex * presence: $\chi^2 = 0.01$, df = 1, $P = 0.9$; age * presence: $\chi^2 = 0.5$, df = 1, $P = 0.5$; immigrant status * presence; $\chi^2 = 0.01$, df = 1, $P = 0.9$). Figures show predicted means (± 1 SE).

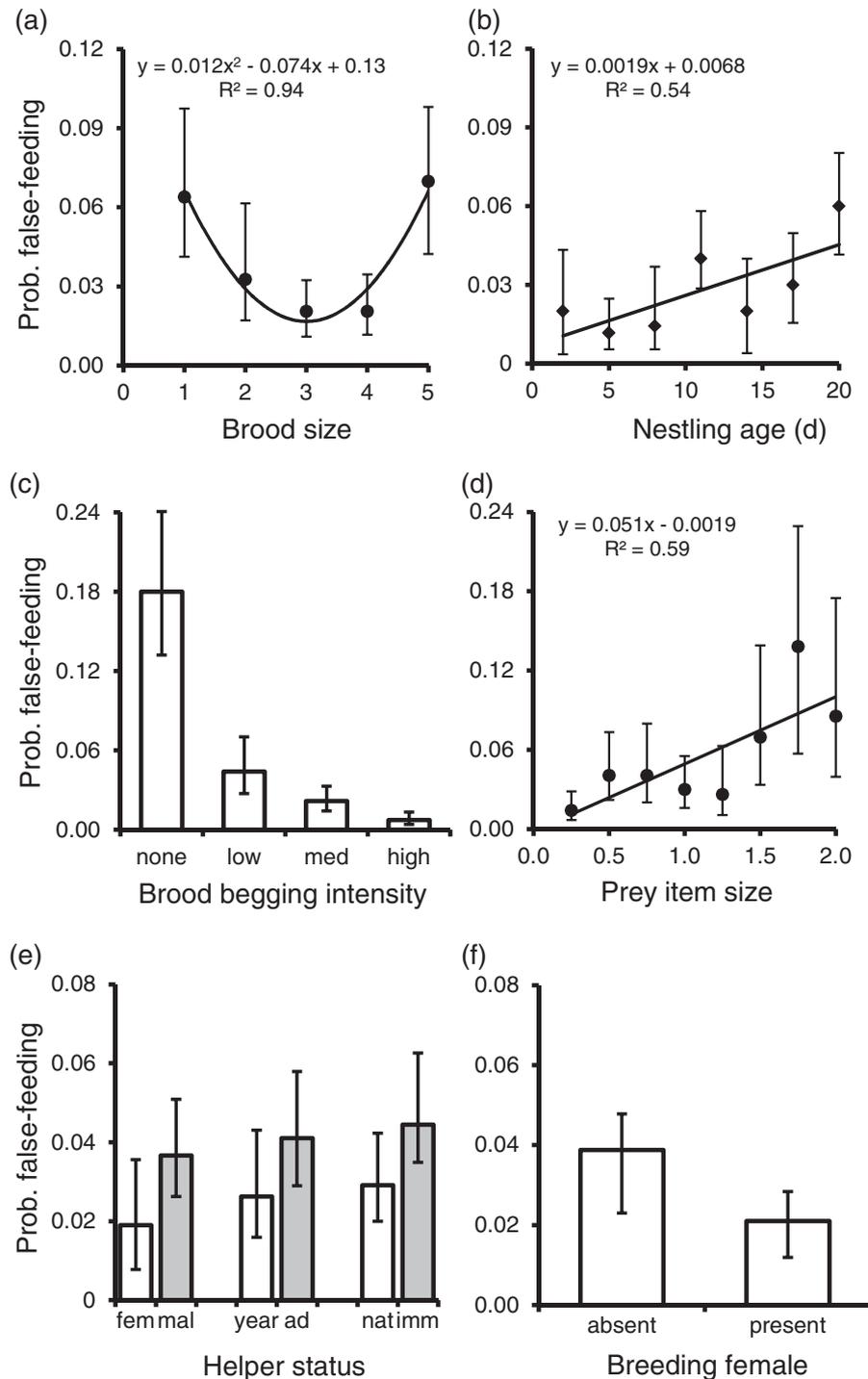
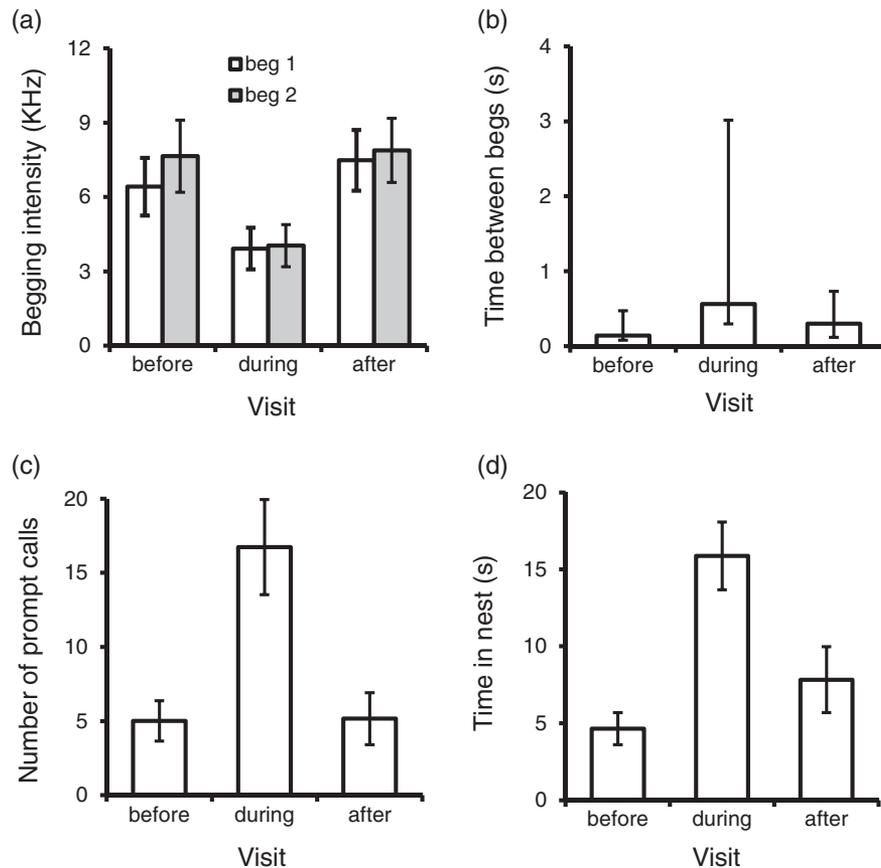


Figure 3

The probability of failing to provision food that was brought to the nest (FF). Effects of (a) brood size; (b) brood age; (c) begging intensity category; (d) prey item size measured relative to the size of a babbler bill; (e) helper sex (fem = female, mal = male), age (year = yearling, ad = adult), and immigrant status (nat = natal, imm = immigrant); and (f) whether or not the breeding female was present in the nest. Figures show predicted means (± 1 SE). For details of the model and statistical values, see [Table 3](#).

evidence of a negative correlation. Individuals that nonfed at a high rate also tended to feed at a high rate ([Figure 5a](#)), whereas there was no significant association between the rates at which helpers fed, versus false-fed, broods ([Figure 5b](#)). In addition, we found no evidence to suggest that relationships between NF and feeding differed between the sexes, ages, or immigrant statuses (REML interaction terms: sex * feeding/NF status, $F_{1,50} = 1.4$, $P = 0.2$; age * feeding/NF

status, $F_{1,46} = 0.05$, $P = 0.8$; immigrant status * feeding/NF status, $F_{1,50} = 0.04$, $P = 0.8$), and the same was true for relationships between FF and feeding (REML interaction terms: sex * feeding/FF status, $F_{1,46} = 1.1$, $P = 0.3$; age * feeding/FF status, $F_{1,50} = 0.7$, $P = 0.4$; immigrant status * feeding/FF status, $F_{1,53} = 3.1$, $P = 0.08$). Indeed, this latter nonsignificant trend was generated only because natal individuals that false-fed offspring at a relatively high level were also likely to feed

**Figure 4**

FF and associating brood and helper behaviors: repeated comparisons. Comparisons are made between FF events and the successful feeding events made immediately preceding and following by the same individuals on the same day. (a) The begging intensity of broods was lower for both first and second begging calls during false feeding than feeding events (one-way repeated measures ANOVAs: $F_{2,24} = 4.8$, $P = 0.02$ (first call); $F_{2,21} = 7.5$, $P = 0.004$ (second call)). (b) Broods took longer to call for the second time during FF, than feeding, events (Friedman's test = 12.5, $df = 2$, $P = 0.002$). (c) Helpers gave significantly more prompt calls during FF events (repeated measures ANOVA: $F_{2,24} = 6.7$, $P = 0.004$). (d) Helpers spent significantly more time in the nest during FF than feeding, despite being the only bird present (repeated measures ANOVA: $F_{2,24} = 14.5$, $P < 0.001$). Figures a, c, and d show means (± 1 SE), whereas figure b shows medians and interquartile ranges.

offspring at a high level. Finally, although the total number of nest visits (those with and without food) and the total number of nest visits with food (including feeds and false-feeds) both exceeded the total number of feeding events by a given individual, the prevalence of NF and FF events were insufficient to have a significant effect on an individual's total rank level of investment (Figure 5c, 5d). In other words, even if group members are deceived by NF and FF, neither is common enough for it to change the "perception" of one helper's provisioning rate relative to another's.

DISCUSSION

We examined the extent of cheating over brood care in chestnut-crowned babblers in order to investigate the role of signal-based hypotheses for the maintenance of cooperative breeding in this system. We found little or no evidence of cheating. Both NF and FF were uncommon and the incidence of each can be explained more parsimoniously by other mechanisms. Most notably, neither NF nor FF was biased toward those individuals most likely to benefit from deception, neither showed consistent evidence of being linked to audience effects, and both were most commonly associated with likely variation in brood requirements. Finally, we found no evidence to suggest that levels of either NF or FF could significantly alter an individual's rank of apparent brood care.

That cheating was not apparent suggests that signal-based hypotheses are unlikely to account for the maintenance of cooperative breeding in this system.

Hypotheses of rent-payment and prestige have a single common prediction regarding the incidence of helping behavior: individuals should be perceived to pass some threshold level of investment or be perceived to invest more than others, respectively (Gaston 1978; Emlen 1991; Zahavi 1995; Kokko et al. 2002). To do so honestly, however, is likely to be energetically costly, at least in the short-term (Russell et al. 2003). The alternative is to be perceived to help more than in reality (Boland et al. 1997). Visiting the nest without food or, perhaps more effectively, with food but then consume that food themselves, constitute the most likely methods of deceiving group members over provisioning effort. Both have been shown to occur, but at a low rate, in cooperative vertebrates (Boland et al. 1997; Canestrari 2004; Clutton-Brock et al. 2005; McDonald et al. 2007). There are two explanations for this relatively low level. First, it would be common, but it is selected against due to actual or potential costly retribution (Cant 2011). Second, it is not selected because the only benefit of provisioning effort is in that delivered rather than that perceived to be delivered, supporting nonsignaling-based hypotheses for the evolution of cooperation (Hamilton 1964; Selander 1964; Woolfenden 1975; Kokko et al. 2001).

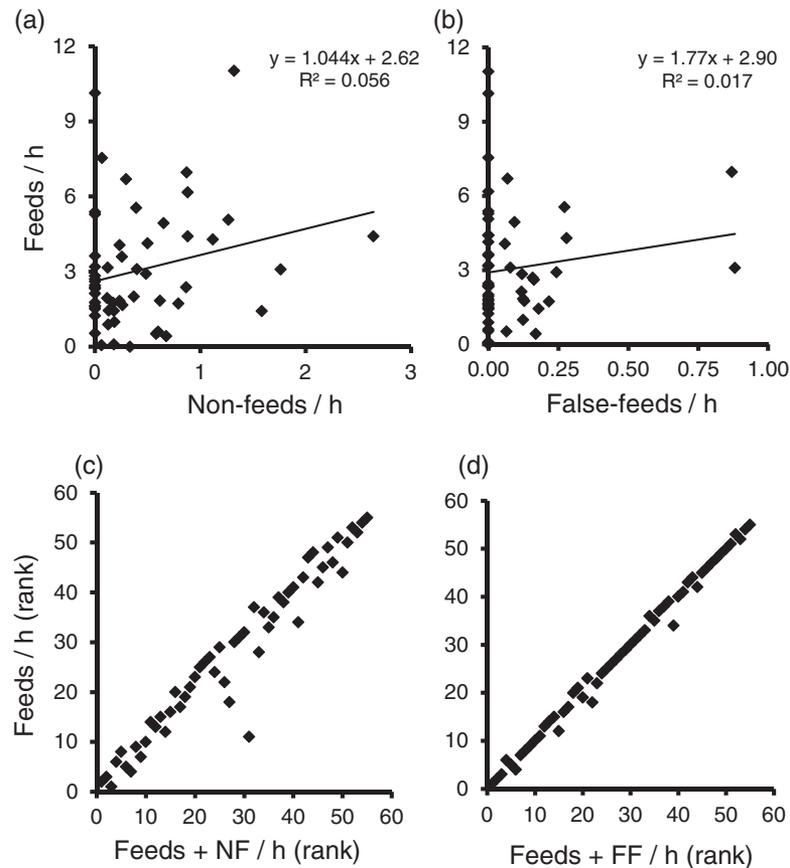


Figure 5

Relationships among feeding, NF, and FF. Rates of NF showed a nonsignificant tendency to be positively associated with rates of feeding (a) (effect = 0.2 ± 0.1 SE; $F_{1,56} = 3.6$, $P = 0.06$), but (b) this was less true of the relationship between FF and offspring feeding (effect = 0.5 ± 0.4 SE; $F_{1,61} = 1.3$, $P = 0.2$). These analyses were conducted using linear mixed effects models with residual maximum likelihoods following logarithm transformation, fitting group identity as a random term. The addition of either NF or FF rates to feeding rates had little effect on changing the rank order of feeding rates (Spearman's rank correlations: NF (c), $r_s = 0.97$, $n = 53$, $P < 0.0001$; FF (d), $r_s = 0.99$, $n = 53$, $P < 0.0001$).

Punishment and policing are known to represent significant ways of reducing the number of cheats from social groups of animals (Ratnieks 1988; Clutton-Brock and Parker 1995; Gardner and West 2004; Cant 2011; Kuemmerli 2011) and levels of cheating are generally high when such tactics are difficult to implement effectively (Pellmyr and Huth 1994; Bshary and Grutter, 2002; Kiers et al. 2003; Edwards et al. 2006, 2009; Mills and Côté 2010). One hypothesis for the low levels of FF measured in other studies (3–11%) is that deceptive behavior can be monitored and punished, either because the offspring are provisioned in visible open-cup nests (Boland et al. 1997; Canestrari 2004; McDonald et al. 2007) or when following the group in view of other members (Clutton-Brock et al. 2005). Although Boland et al. (1997) used this type of explanation to account for low levels of FF in white-winged chough, it is difficult to wholly discount it from other studies, despite the lack of apparent evidence. This is because in the few systems previously studied, a provisioner can never be 100% sure whether or not its behavior is being monitored (see INTRODUCTION). In addition, retribution for deception need not be in the form of direct physical punishment (Raihani and Bshary 2011), especially given the potential costs of such actions (Gardner and West 2004). A more convincing way of examining whether or not FF can represent a deceptive tactic is to do so in a species in which individuals can be fully certain whether they are provisioning offspring in the presence of another or not.

In this study, helpers virtually always entered the domed nest either in the presence of the breeding female or in the absence of all group members, meaning that they could be certain whether or not their behavior could be monitored. Thus, if NF or FF served to deceive other group members over contributions to brood care, we can generate predictions regarding which individuals are likely to benefit most from deception and when. First, male, adult and immigrant helpers are more likely to benefit from deceiving others than females, yearlings or nats. Male helpers are 1.7 times more common in the population than females (Rollins et al. 2012) and so are expected to have to pay more for staying on a territory and compete more to be chosen as mates (Gaston 1978; Zahavi 1995; Noë and Hammerstein 1995; Noë 2007). Yearling helpers are less of a threat to current reproductives than adults and so are expected to pay less for staying (Gaston 1978; Reyer 1986; Kokko et al. 2002), whereas adult helpers, whose future reproductive value is expected to be lower (Hirshfield and Tinkle 1975), are expected to be under greater selection pressure to be perceived attractive (Zahavi 1995). Similarly, immigrant helpers have to pay rent because they are unrelated to breeders, whereas natal helpers do not (Kokko et al. 2002). Second, under both signaling hypotheses, deceptive contributions to brood care should be selected to occur more commonly in the absence of an audience, in this case, the breeding female. Third, under pay-to-stay, apparent deception should be more common among those that contribute little to rearing offspring (Clutton-Brock et al.

2005), and under both hypotheses, it should have a significant bearing on a helper's rank in terms of perceived contribution to brood care.

Despite the opportunity to consume prey items undetected, helpers rarely did so and only on 3% of occasions were helpers observed to consume prey items in the nest, all of them after the brood rejected it. In addition, there was little evidence that male, adult and immigrant helpers were more likely to nonfeed or false-feed than female, yearling and natal helpers, respectively. Although adult helpers were more likely to nonfeed than yearlings, there was a tendency for female helpers to do so more than males, and there were no overall effects of immigrant status on NF propensity. In addition, the adult result above was driven almost entirely by greater NF prevalence by adult females (not males), and both female helpers and immigrants were significantly more likely to nonfeed in the presence (not absence) of the breeding female. Similarly, there were no effects of either sex, age, or immigrant status on the probability of FF, and FF was as likely in the presence, as absence, of the breeding female. Finally, we found no evidence to suggest that either NF or FF was more common amongst those that contributed little to brood provisioning (if anything, the reverse was true) and found little evidence to suggest that helpers would be able to influence significantly another group member's perception of their relative contributions to brood care through either behavior.

By contrast, our results are more supportive of hypotheses proposing that NF functions to evaluate brood demand and that FF occurs when helpers get this demand wrong (Canestrari 2004, 2010; Clutton-Brock et al. 2005; McDonald et al. 2007). For example, NF was most common both during the middle of the day and when brood sizes were small, when brood demand would be expected to be low. In addition, NF was associated with an increased probability of preening nestlings and maintaining the nest, suggesting that nest visits might serve multiple purposes. Accordingly, NF was also more common among females and immigrants in the presence of the breeding female. These are classes of helpers that would be expected to contribute less to cooperation than natal males, on average, suggesting that NF does not only serve to gain information about brood demand, but potentially about breeding success and breeding female state, but testing these possibilities requires further work.

FF showed significant associations with brood size and age: decreasing between broods of one to four nestlings before increasing sharply with broods of five and increasing linearly with increasing brood age. That FF is high in broods of five and increases with brood age might suggest that FF occurs in babblers when personal investment levels are high and helpers sometimes gauge their own demand to be greater than the brood's (Canestrari 2004, 2010; Clutton-Brock et al. 2005). This hypothesis may also explain why helpers are more likely to false-feed large prey items, which yield high returns to helpers (Clutton-Brock et al. 2005). However, an alternative explanation for the above patterns is that as brood demand increases, the costs of encountering a hungry brood without food exceeds those of encountering a satiated brood with food (McDonald et al. 2007). Overall, our results suggest that FF typically occurs in babblers when helpers encounter a disinterested brood with a food item. FF rates were higher when begging levels were low and in small broods where demand is likely to be low. In addition, when helpers encountered disinterested broods, they gave three times as many prompt calls, spent three times longer in the nest and commonly left the nest complete with the food item (79% of occasions). Thus, we suggest that in babblers, FF occurs primarily when satiated broods are encountered and found no evidence to suggest that it served to deceive other group members.

The results of this study have a number of important implications. First, it adds to the growing body of evidence suggesting that neither NF nor FF represent efforts on the part of helpers to deceive others over their contributions to brood care (Canestrari 2004, 2010; Clutton-Brock et al. 2005; McDonald et al. 2007). These studies concluded that FF, for example, occurred when helpers gauged their own requirements to exceed those of the offspring following interaction (Canestrari 2004, 2010; Clutton-Brock et al. 2005) or encountering unexpectedly low brood demand (McDonald et al. 2007). We generally favor the latter interpretation here because, in all cases of FF, helpers attempted to feed the nestlings, often went to great lengths to do so and, following offspring rejection, usually left the nest with the food item. Either way, these conclusions differ markedly from Boland et al. (1997), who favored deception as the likely explanation, based on observations suggesting that false-feeders sometimes waited until the nest-attendant departed, and on three instances were apparently punished for FF. Second, this study revealed that neither breeding females, nor other carers, attempt to police each other's contribution to nestling rearing. This result is informative both because it suggests low rates of FF are not due to potential retribution (Cant 2011) and because it suggests that the maintenance of cooperation is not based on coercion, as has sometimes been suggested (Reeve 1992) but seldom been verified (Cant 2011). Finally, together, our results reduce the possibility that cooperative breeding in this system can be accounted for by signal-based hypotheses, such as pay-to-stay (Gaston 1978) or social prestige (Zahavi 1995). Although it is premature to completely reject these hypotheses, we suggest that kin selection (Hamilton 1964) and group augmentation (Woolfenden 1975; Kokko et al. 2001) represent more likely alternatives, both of which predict helping to be honest because fitness benefits are reaped through actual, rather than perceived, contributions. Of these two latter hypotheses, kin selection currently appears to be the more important (Browning et al. 2012).

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