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Helping as a signal and the effect of a potential audience during provisioning visits in a cooperative bird

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Research on cooperative breeding has begun to focus on direct fitness benefits gained by helpers, particularly when individuals are unrelated to those they assist. There has been considerable interest in helping possibly operating as a signal, either to show off individual quality to potential mates ('social prestige') or to ensure group membership ('pay to stay'). However, empirical investigation of these phenomena remains sparse. Here we investigate the potential for signalling via provisioning behaviour in the bell miner, *Manorina melanophrys*, an obligate cooperative breeding species in which the predominantly male helpers are commonly unrelated to breeders. Aggression between birds was extremely rare, and there was little to indicate a pay to stay system. The presence versus absence of members of the breeding pair as a potential audience at the nest had little influence on helper behaviour (e.g. load size/composition, visit duration or frequency). Helpers did produce more individually distinctive vocalizations when in the presence of another helper or the breeding male, although presence of the breeding female (a likely target of male signals) surprisingly had no effect. There was also evidence that nest arrival times coincided somewhat. These results are probably best explained by the helpers and breeding males being involved in additional cooperative behaviours when away from the nest, such as mobbing. Overall, there does not appear to be any evidence that bell miner helpers use nestling provisioning to signal their quality and/or work rate to one another or to either member of the breeding pair.

Keywords: bell miner; cooperative breeding; *Manorina melanophrys*; nestling provisioning; pay to stay; signalling hypotheses; social prestige

Research examining the evolution of cooperative breeding has centred on the adaptive basis for provisioning by 'helpers', that is, individuals feeding nestlings that are not their own (Brown 1987). Many reviews have sought to summarize the costs and benefits of such apparently altruistic behaviour (e.g. Brown 1987; Emlen 1991; Clarke 1995; Cockburn 1998, 2006; Heinsohn & Legge 1999). Whereas the indirect benefits associated with helping kin have been recognized as important in many avian systems (Hamilton 1964; Maynard Smith 1964; see reviews above) and indeed other vertebrate taxa (e.g. Russell 2004), the presence of unrelated helpers in many species remains to be explained. Thus recent research has focused on direct fitness benefits that may accrue to helpers (Cockburn 1998; Koenig & Dickinson 2004). For example, direct benefits could be gained through enhancing nestling fitness, because this might lead to future increases in survivorship and/or reproduction for the helper via pseudoreciprocity or augmentation of group size and associated benefits such as territory inheritance and/or acquisition (Woolfenden & Fitzpatrick 1978, 1984; Ligon 1981; Brown 1983, 1987; Connor 1986; Balcombe 1989; Connor & Curry 1995; Kokko et al. 2001).

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An alternative and often-cited possibility is that apparently altruistic acts may instead function as signals to conspecifics. In contrast to most traditional hypotheses, which rely on the help donated increasing the fitness of the brood, under 'signalling' hypotheses helpers gain benefits only if they are *known* to have helped (Wright 1997) irrespective of the effect such help may have on nestling fitness. Under the two main signalling hypotheses, helping is seen either as an indicator of quality which enhances an individual's reputation within the group, hence increasing future breeding or other collaborative opportunities ('social prestige': Zahavi 1977, 1995; Wright 1999), or as simply a means of making oneself useful to dominant group members, thereby securing group membership and its associated benefits ('pay to stay': Gaston 1978; Kokko et al. 2002). Both comprise signalling hypotheses in that third parties must possess some information about helper effort if the helper is to derive any social advantage. Evidence for these hypotheses is sparse in the cooperative breeding literature, although experimental evidence of pay to stay exists in three taxa. Manipulations demonstrated that dominant breeding males would accept help from unrelated males only when conditions were poor and/or workloads high and thus their contribution was needed, with helpers being punished when they failed to contribute sufficiently (Reyer 1990; Mulder & Langmore 1993; Balshine-Earn et al. 1998). Only circumstantial evidence exists for social prestige; for example observations that helpers may competitively 'interfere' with each others' food delivery at the nest (Carlisle & Zahavi 1986; although see Wright 1997, 1998) or 'false-feed' in an apparently deceptive manner (Boland et al. 1997) have been interpreted as evidence that helpers may benefit from being known to have contributed. Moreover, these data derive from systems in which a very high proportion of helpers are related to the broods they provision and kin selection might be sufficient to explain much of the apparently altruistic behaviour of helpers. The most promising systems to explore for clear-cut evidence of helping as a signal would appear to be those in which many individuals are unrelated to the nestlings they provision.

Whereas helpers at the nest perform a variety of activities, the most frequently observed behaviour common to all cooperatively breeding systems is nestling provisioning (e.g. Brown 1987; Cockburn 1998; see other reviews above). We therefore investigated the provisioning behaviour of the bell miner, *Manorina melanophrys*, a honeyeater endemic to southeastern Australia, for evidence of a signalling function. Bell miners form large colonies that often comprise hundreds of individuals, which actively exclude all other insectivorous and nectarivorous birds from the entire colony area. Unlike many other cooperative breeders, bell miners do not forage communally. Breeding females aggressively defend territories from other females, whereas helpers within the colony are observed in discrete 'activity spaces' where they forage independently but apparently allow other helpers to traverse (Clarke & Fitz-Gerald 1994). A colony contains a number of 'coteries', each of which consists of a number of breeding pairs and an attending assemblage of nonbreeding helpers, that forage and help provision at multiple nests that are located within their coterie (Clarke 1989). Young females disperse to breeding positions outside their natal colony, whereas males wait within their natal coterie for a breeding vacancy, which is generally filled by the oldest unrelated helper present during the previous breeding attempt (Clarke 1989). A large number of helpers therefore provision each brood (mean 10.7 ± 0.7 SE helpers per nest; $N = 23$ nests; this study), sometimes at more than one nest simultaneously, with even breeding males helping at nests other than their own. While helpers are often related to the breeding pair they assist, near annual turnover of female breeders (Clarke 1989) means that older attendants (which tend to provision at the highest rates) are often unrelated to the broods they aid (Conrad et al. 1998; Painter et al. 2000). Thus, while some patterns of helping in this species are consistent with kin selection (Clarke 1989), the common and substantial aid giving by unrelated male helpers remains to be explained.

Early indications suggest that the bell miner might be a promising candidate for a signalling function to helping behaviour. For example, immature helpers are reported to be more likely to arrive at the nest empty handed and are likely to be subjected to pecking from their elders on these occasions (Poiani 1993), which might be indicative of a pay to stay system. More importantly, bell miners give 'mew' vocalizations as they arrive at the nest, perhaps to signal a food delivery and stimulate nestling begging. However, mew calls not only are highly individually identifiable and repeatable (M^{C}Donald et al. 2007a) but are also given as birds *exit* the nest area, suggesting that these vocalizations are intended for receivers other than the brood and could allow individuals to advertise their helping effort. Clarke (1989) also documented five instances in which breeding males died or disappeared, and on each occasion the widowed female subsequently paired with the unrelated male helper that had provided the greatest assistance in raising her previous brood. A later study, entailing experimental removal of a larger number of breeding males, revealed similar patterns of mate choice by widowed females (Jones 1998). This suggests that one of the benefits for nonkin helpers may be in showing off to the female to enhance their chance of gaining future breeding opportunities (cf. the social prestige hypothesis). However, provisioning effort may have been confounded with potential differences in age and dominance in helpers at the same nest. Older helpers at the head of the breeding 'queue' might be both more attractive to females and better able to provide high levels of care, without the two necessarily being causally linked.

To explore the possibility that helping constitutes a signal, we conducted a detailed and comprehensive examination of natural provisioning behaviour, recording not only individual visits but also load sizes and prey types delivered, any vocalizations produced at the nest, brood demand, the exact timing of individual presence at the nest and the presence and identity of third parties in the immediate vicinity. One might expect nonrandom arrival times if helpers are attempting to coincide with a potential audience (e.g. the breeding male and/or female) towards whom they are directing their signalling effort. In the absence of an appropriate audience near the nest helping effort might be expected to decline, to reduce costs when there is little likelihood of gaining benefits by signalling. Under a pay to stay system any reduction in care, if detected, might additionally be associated with punishment from dominants. This aggression is most likely to occur from breeders towards helpers of the same sex to whom they are unrelated because breeders gain no indirect benefits from allowing these potential competitors access to group resources. One would also predict clear differences in the behaviour of helpers of differing relatedness and sex because the opportunity to derive any signalling benefits should depend on the need to placate dominant breeders (pay to stay, typically same sex breeder as helper as described above) and/or the possibility of acquiring nonincestuous matings (social prestige, likely opposite sex breeder to helper). For example, in a prestige-based system we may expect male helpers unrelated to the breeding female, and thus the males vying for a future breeding position, to time their visits to when females were near the nest and there was a higher possibility that their signal would be received. In light of these expectations, we examined provisioning behaviour, in terms of both quality and quantity, for evidence of a signalling-based helping system in this species.

METHODS

Study Sites

The study was conducted between June 2004 and December 2005 on two bell miner colonies located northeast of Melbourne, Australia. The first colony consisted of 40–45 individuals at the La Trobe University Wildlife Reserve, 20 km northeast of Melbourne (37°42′58″S, 145°03′20″E), and the second colony consisted of 120–135 birds situated near Saint Andrews, 50 km northeast of Melbourne (37°35′09″S, 145°15′41″E). This research was approved by the La Trobe University Animal Ethics Committee (licence AEC01/19(L)/V2) and the Department of Sustainability and Environment (licence 10002082).

Molecular Analyses

Individuals within colonies were captured with mist nets before being colour banded, and 70-μl blood samples were collected from the alar vein for analysis, a procedure which caused no apparent adverse effects. These samples were stored in 70% ethanol and then transported to The Australian National University, Canberra, Australia, where birds were sexed and six loci genotyped according to the protocols outlined in Fridolfsson & Ellegren (1999) and Painter et al. (1997), respectively. Average number of alleles generated with the six microsatellites ranged three to nine, averaging six per locus. Relatedness between individuals was assessed using KINSHIP v1.2 (Goodnight software, www.gsoftnet.us/Gsoft.html), which calculated the likelihood of male helpers being either related (primary hypothesis: $r = 0.5$, null hypothesis: $r = 0$) or unrelated (primary hypothesis: $r = 0$, null hypothesis: $r = 0.5$) to the breeding female, based on the ratio required to exclude 95% of 1000 simulated pairwise comparisons (Goodnight & Queller 1999). Values of coefficients of pairwise relatedness (r) can range between −1 and +1, with negative values indicating that individuals share fewer alleles than average for the population (Queller & Goodnight 1989). In a randomly mating population r should approximate 0.5 for full siblings and 0.25 for half-sibs and so forth. Values obtained in this manner matched closely those expected when individuals of known putative relatedness were compared (e.g. mother and offspring). Birds were assigned to a ‘social class’ as either a ‘breeding female’ ($N = 23$), a ‘breeding male’ (mean ± SE r to breeding female: 0.15 ± 0.059; $N = 23$) or a helper. Helpers were further divided into three groups based on the outcome of these tests and their relatedness to the breeding female, either being significantly ‘related’ ($r = 0.42 \pm 0.031$, $N = 23$), being significantly ‘unrelated’ ($r = -0.07 \pm 0.020$, $N = 106$) or, if both these tests were nonsignificant ($P > 0.05$), being placed in an ‘unresolved’ category ($r = 0.22 \pm 0.024$, $N = 46$). Female helpers are also present in this system, and these were also grouped as either significantly related ($r = 0.53 \pm 0.041$, $N = 13$), significantly unrelated ($r = -0.17 \pm 0.051$, $N = 19$) or unresolved ($r = 0.16 \pm 0.052$, $N = 9$). Results are presented with relatedness calculated both relative to the breeding female (of most interest when assessing the likelihood of a prestige-based system) and relative to the breeding male (in this system the most relevant for testing the pay to stay hypothesis). However, the results do not differ substantially if relatedness to a mean of the breeding pair is used instead (data not presented).

Monitoring of Nesting Attempts

Nesting activity at each colony was monitored throughout the year because breeding in this species can occur in all months. Once found, nest contents were monitored every second day to determine hatching date (termed day 0). At each nest only one female participated in nest construction, incubation and brooding, allowing the breeding female to be identified in this manner. To identify breeding males, nests were observed remotely via a video camera 4 m from the nest and/or from a hide placed at 20 m, for a 2-h period within 48 h of nestlings hatching. Helper males rarely feed broods during this initial period, allowing the individual provisioning at highest rates to be identified as the putative breeding male (Poiani 1993). Extrapair offspring are rare in this species (4%) and putative parentage assigned in this manner closely matches genetic parentage (Conrad et al. 1998).

Recording of Provisioning Behaviours

The number of helpers present at bell miner nests reaches its maximum when nestlings are 5–6 days old, with attendant number and visit rate remaining constant thereafter until fledging (L. te Marvelde, P. G. M^CDonald, A. J. N. Kazem and J. Wright, unpublished data). Therefore nests were observed from a bird hide from nestling age 6 days through to fledging (day 10 or 11) using a Kowa

TS662 spotting scope with a 20–60× zoom eye piece (Tokyo, Japan) and simultaneously videotaped using either an analogue (CCD-TR1100E; Sony, Tokyo, Japan) or a digital Hi8 Camcorder (DCR-TRY265E; Sony) placed on a tripod. Hides and equipment were placed sufficiently far from nests to avoid potential disturbance effects on provisioning behaviours (see M^{c}Donald et al. 2007b). In all observations data collection did not commence until 10 min after the observer had entered the hide, to allow any disturbance associated with observer presence to dissipate. In most cases individuals resumed provisioning within 2–3 min of an observer entering the hide. The time-stamped videos were later burnt onto DVDs using a DVD recorder (Pioneer DVR-310; Tokyo, Japan) and reviewed using Power DVD v4.0 (LG Electronics) on a laptop computer (Higrade Notino C7000; Essex, U.K.). Using a combination of dictation recorded in the field and perusal of videotapes the number and duration of all individuals' visits to the nest were recorded (to the nearest second). Arrival and departure times were also recorded to the nearest second, allowing calculation of intervisit interval (IVI) and previous intervisit interval. Intervisit interval was defined as the time elapsing between leaving the nest in the focal visit and returning subsequently. Previous intervisit interval was the period between leaving the nest in the visit preceding the focal visit and arriving at the nest for the focal visit. The size (% relative to bill volume) and prey composition (proportion of load made up of 'lerp') brought to the nest area were also noted. Attendants with high-quality prey may have, for example, coordinated visits so that they approached nests only when a desired audience was present. Lerp is a white sugary secretion produced by sap-sucking psyllids (Hemiptera; Psyllidae). While a staple of adult miners, lerp consists entirely of sugars, a food not usually fed to nestlings by species that have a carbohydrate-rich diet (cf. Markman et al. 1999). As such, loads high in lerp content may be relatively low in quality, although recent research suggests that nestlings of this species may unusually be able to digest these simple sugars (L. te Marvelde et al., unpublished data). We also recorded the number of mew calls given by focal individuals, both while provisioning nestlings and as they left the nest area. Finally, the identity of all other birds at the nest (within 2 m radius of the nest cup) while the focal individual was present was recorded. The dense vegetation around most nests meant that while a larger radius was also monitored we could not be sure that we had recorded every conspecific present on every occasion; by the same token, birds present at these greater distances themselves would not necessarily be able to monitor each others' behaviour at the nest.

Statistical Analyses

A one-sample Kolmogorov–Smirnov Z test was used to determine whether the number of individuals present at nests during visits differed significantly from a Poisson distribution. An ANCOVA was used to determine whether visit duration or social class influenced the number of other individuals that a provisioning bird encountered during a visit to the nest area, where social class refers to the eight distinct classes based on their relatedness and sex (see above for details). Finally, separate RM-ANOVAs were used to assess potential differences in an individual's behaviour when in the presence versus absence of either the breeding female, the breeding male or any other helper, regardless of social class. These behavioural comparisons included visit duration, the number of mew calls given during feeds or when leaving the nest area, load size, proportion of lerp in loads, and intervisit and previous intervisit intervals. Simple contrasts were also used to determine significance of differences between specific social classes within RM-ANOVA models (with only significant contrasts being presented for reasons of brevity). This involved a series of orthogonal contrasts where the response of each social class was compared to that of related male helpers; thus the response of, for example, unrelated versus related male helpers could be specifically compared independent of the breeding pair. Given the low numbers of some classes of female helper in some analyses, tests were repeated including only male helpers to confirm the generality of conclusions. A two-tailed Wilcoxon test was used to determine whether an individual that encountered the breeding male during a visit was more or less likely to encounter him again on their subsequent visit compared to visits following those where they had not initially encountered the breeding male, thereby testing whether individuals appeared to change their intervisit interval to coincide with breeding male visits. Variables were arcsine square-root transformed (for proportions) or log transformed (e.g. visit duration) as appropriate to conform to the assumption of normality in ANOVA models. All analyses were carried out using SPSS v.12.0.2 (SPSS Inc.; Chicago, IL, U.S.A.). Data are presented as means ± SE. Two-tailed tests were used and a critical P value of 0.05 applied throughout.

RESULTS

Aggression between Nest Attendants

A total of 7486 visits by 114 individuals were observed in 190 h and 43 min of observation over 23 nesting attempts (mean: 8.4 ± 0.70 h per nest). Of these, a subset of 5832 visits were monitored in greater detail by one observer (P.M.), with all forms of potential aggressive behaviour being described. In 3391 (58.1%) of these visits another bird was present, potentially allowing agonistic interactions to occur. Signs of overt aggression were extremely rare, although during 40 visits (1.18%, $N = 3391$) individuals were seen to flare their crown feathers and open their bills wide while facing in the direction of another bird in the nest area. On six occasions, this behaviour was followed by lunges towards the other bird, pecks at their crown feathers or feet, or taking a prey item from the other bird. These behaviours were most often performed by the breeding female ($N = 27$ incidents), although male helpers unrelated to the breeding female showed such agonistic behaviour on nine occasions, with unresolved male helpers and unrelated female helpers also being observed to open their bills in an aggressive manner to others twice each (Table 1). Similar general results were obtained when relatedness was instead calculated relative to the breeding male (Table 1). The only other behaviour that could be described as aggressive in nature was observed during eight visits, when an individual followed another from the nest area in an apparently agonistic tail-chase, with the follower attempting to bite the retreating bird's rectrices. On four of these occasions the individual that initiated the chase was unknown. On the other four occasions the breeding female was the apparent aggressor, chasing either male helpers unrelated ($N = 3$) or unresolved ($N = 1$) in terms of their social class to the focal breeding female. Thus aggressive interactions were observed only 48 times (1.42%, $N = 3391$). Whereas many involved the breeding female as the aggressor, there was no clear pattern with regard to the recipients or their actions that might have precipitated the exchange, regardless of whether social class was calculated relative to either member of the breeding pair (Table 1).

Temporal Clustering of Provisioning Visits

If provisioning behaviour possesses a signalling function, individuals could maximize its effectiveness if they timed their visits to coincide with the presence of a potential audience in the nest area. The number of other individuals encountered by birds during their visits differed significantly from a Poisson distribution (Kolmogorov−Smirnov test: $Z = 3.580$, $P < 0.0001$). This perhaps indicates that individuals were not arriving at and/or leaving the nest in a strictly random fashion. This result could be due to differences in visit duration, especially because certain types of individual (e.g. breeding females) remain in the nest area for significantly longer periods after provisioning than others (McDonald et al. 2007b; M. L. P. Pacheco, P. G. McDonald, J. Wright, A. J. N. Kazem and M. F. Clarke, unpublished data). We therefore used an ANCOVA to test for effects of both visit duration and social class on the number of conspecifics encountered when at the nest. A significant effect of visit duration was apparent ($F_{1,245} = 34.831$, $P < 0.0005$); unsurprisingly, the longer an individual spent at the nest during a visit, the greater the number of other attendants it encountered. However, there was no significant association between social class and number of conspecifics encountered ($F_{7,245} = 1.726$, $P = 0.104$) nor any significant interaction between the effects of visit duration and those of social class ($F_{7,245} = 1.477$, $P = 0.176$).

Influence of a Potential Audience on Provisioning Behaviours

Breeding female presence/absence

When statistical analyses were conducted using social class categories generated according to relatedness to the breeding female, there was no overall effect of the presence versus absence of the breeding female during visits on the load size, proportion of lerp within load, intervisit interval or previous intervisit interval of other social classes (Table 2). Nor was there any influence on the number of mew calls given by individuals, either prior to provisioning the nestlings or as they left the nest area. There were also no significant interactions between the social class of a nest attendant and the presence/absence of the breeding female during the attendant's visits for any of the above behaviours, as predicted by either signalling hypothesis. Interestingly, individuals visited the nest for longer periods when the breeding female was present (Table 2), with birds averaging 40.8 ± 2.8 s in the presence of the female and 32.5 ± 2.0 s in her absence ($N = 168$ individuals). However, this effect was not influenced by the social class of the individuals involved (i.e. the interaction term was nonsignificant; Table 2), in contrast to the predictions made by the signalling hypotheses. There were significant effects of social class per se on the mean number of calls given as an individual left the nest area, load

Table 1. Frequency of aggressive behaviour according to social class categories calculated relative to the breeding female and the breeding male

Social class of aggressors	Social class of recipient							
	B♀	B♂	Unrel♂	?♂	Rel♂	Unrel♀	?♀	Rel♀
Relatedness calculated according to the breeding female								
Breeding female	—	2 (7)	17 (63)	4 (15)	0 (0)	0 (0)	0 (0)	4 (15)
Unrelated male	1 (11)	—	6 (67)	2 (22)	0 (0)	0 (0)	0 (0)	0 (0)
Unresolved male	0 (0)	1 (50)	1 (50)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Unrelated female	0 (0)	0 (0)	1 (50)	1 (50)	0 (0)	0 (0)	0 (0)	0 (0)
Relatedness calculated according to the breeding male								
Breeding female	—	2 (7)	3 (11)	15 (56)	3 (11)	1 (4)	3 (11)	0 (0)
Unrelated male	0 (0)	—	2 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Unresolved male	0 (0)	1 (50)	0 (0)	0 (0)	1 (50)	0 (0)	0 (0)	0 (0)
Related male	1 (14)	0 (0)	2 (29)	2 (29)	2 (29)	0 (0)	0 (0)	0 (0)
Unrelated female	0 (0)	0 (0)	2 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Social class is defined as breeding female (B♀), breeding male (B♂) and, for male and female helpers, birds that were significantly unrelated (Unrel♂/♀), unresolved (?♂/♀) or related (Rel♂/♀) to the relative member of the breeding pair. Numbers indicate frequency of occurrence, with percentages (of all incidents by that class of aggressor) presented in parentheses.

Table 2. Results of repeated-measures ANOVAs comparing different aspects of provisioning behaviour by the individuals in the presence of different potential audiences, with relatedness calculated relative to the breeding female

		Breeding Female			Breeding Male			Helper		
	Factor	*F* ratio	*df*	*P* value	*F* ratio	*df*	*P* value	*F* ratio	*df*	*P* value
Duration of visit (s)	Presence	**3.918**	**1,161**	**0.049**	0.005	1,147	0.942	**14.096**	**1,189**	**<0.0005**
	Social class	1.377	6,161	0.227	**13.526**	**6,147**	**<0.0005**	**12.208**	**7,189**	**<0.0005**
	Pres.×Soc.	0.884	6,161	0.508	**2.631**	**6,147**	**0.019**	1.097	7,189	0.367
Number of calls given as feed	Presence	0.092	1,162	0.762	**4.043**	**1,148**	**0.046**	**8.659**	**1,190**	**0.004**
	Social class	0.981	6,162	0.440	1.313	6,148	0.255	0.677	7,190	0.691
	Pres.×Soc.	0.486	6,162	0.818	0.827	6,148	0.551	1.481	7,190	0.176
Number of calls given as leave nest	Presence	1.961	1,162	0.163	**9.752**	**1,148**	**0.002**	**12.863**	**1,190**	**<0.0005**
	Social class	**2.477**	**6,162**	**0.026**	1.136	6,148	0.344	**2.342**	**7,190**	**0.026**
	Pres.×Soc.	0.349	6,162	0.910	1.208	6,148	0.305	1.804	7,190	0.088
Load size (% bill volume)	Presence	1.022	1,162	0.314	3.510	1,148	0.063	0.002	1,190	0.961
	Social class	**6.540**	**6,162**	**<0.0005**	**5.676**	**6,148**	**<0.0005**	**6.588**	**7,190**	**<0.0005**
	Pres.×Soc.	0.345	6,162	0.912	1.181	6,148	0.320	0.417	7,190	0.891
Proportion of prey load consisting of lerp	Presence	2.767	1,151	0.098	0.620	1,139	0.432	1.233	1,176	0.268
	Social class	0.876	6,151	0.514	0.803	6,139	0.570	1.217	7,176	0.296
	Pres.×Soc.	1.190	6,151	0.315	**2.547**	**6,139**	**0.023**	0.960	7,176	0.462
Intervisit interval (s)	Presence	0.031	1,139	0.860	**8.654**	**1,132**	**0.004**	0.943	1,171	0.333
	Social class	**4.040**	**6,139**	**0.001**	**9.52**	**6,132**	**<0.0005**	**10.389**	**7,171**	**<0.0005**
	Pres.×Soc.	0.726	6,139	0.630	1.156	6,132	0.334	1.108	7,171	0.360
Previous intervisit interval (s)	Presence	3.520	1,141	0.063	0.724	1,129	0.396	0.649	1,173	0.422
	Social class	**3.582**	**6,141**	**0.002**	**10.955**	**6,129**	**<0.0005**	**11.285**	**7,173**	**<0.0005**
	Pres.×Soc.	1.456	6,141	0.198	1.033	6,129	0.407	1.127	7,173	0.349

Factors assessed included the presence of the potential audience, individual's social class (defined as helper relatedness to the breeding female; Social) and the interaction between the two (Pres. × Soc.). Significant terms are indicated by bold face.

size and intervisit interval (Table 2), indicating differences in these behaviours across classes of individual (irrespective of the presence or absence of potential female audience). These differences were driven principally by breeding males returning to the nest more quickly, delivering larger load sizes and giving fewer calls than related male helpers, with none of the other contrasts being significant (simple contrasts: intervisit interval: $P = 0.002$; previous intervisit interval: $P = 0.026$; load size: $P < 0.0005$; mew calls: $P < 0.0005$).

When these analyses were repeated using categories of social class, generated according to relatedness to the breeding male, virtually identical results were obtained (Table 3). The effect of social class on the number of mew calls, however, became a trend ($P = 0.051$) rather than a significant relationship; however, the significant contrasts reported above, again driven by breeding male behaviour differing from that of related male helpers, were also present in these analyses (simple contrasts: intervisit interval: $P = 0.003$; previous intervisit interval: $P = 0.003$; load size: $P < 0.0005$; mew calls: $P = 0.001$). Again, importantly, no interactions between social class and breeding female presence/absence were observed (Table 3), in contrast to the predictions of the signalling hypotheses.

Breeding male presence/absence

In statistical analyses with categories of social class calculated with reference to the breeding female, the presence or absence of breeding males influenced the number of mew calls given (both as nestlings were fed and as the focal individual left the nest area), with significantly more calls being given by all classes of bird during visits when breeding males were present at the nest (Table 2, Fig. 1a). Interestingly, all individuals also *returned* to the nest more quickly if they had encountered the breeding male during their previous visit, irrespective of their social class (Table 2, Fig. 1b). However, there was no such effect for the intervisit intervals *prior* to feeds that took place when the breeding male was present, suggesting that the former result was not merely a by-product of general temporal clumping of visits. Shorter intervisit intervals could possibly be used to increase an attendant's probability of re-encountering breeding males in subsequent visits, given that breeding males have higher visit rates than attendants. However, after having encountered the breeding male during one nest visit, individuals were actually significantly *less* likely to encounter him again during their subsequent visit to the nest (proportion of subsequent visits with encounters: mean ± SD $= 0.12 \pm 0.20$) than they were in visits immediately following those in which they had not initially encountered the breeding male (proportion of subsequent visits with encounters: 0.21 ± 0.19; $Z = 6.236$, $P < 0.001$, $N = 243$ individuals).

The presence or absence of breeding males had no significant influence on the load size brought by others (Table 2). There was a significant interaction between the effect of male breeder presence/absence and an individual's social class, for both duration of visit and proportion of lerp per load (Table 2, Fig. 2). However, the data on visit

Table 3. Results of repeated-measures ANOVAs comparing different aspects of provisioning behaviour by the individuals in the presence of different potential audiences, with relatedness calculated relative to the breeding male

		Breeding female			Breeding male			Helper		
	Factor	*F* ratio	*df*	*P* value	*F* ratio	*df*	*P* value	*F* ratio	*df*	*P* value
Duration of visit (s)	Presence	**4.599**	**1,161**	**0.033**	0.022	1,146	0.882	**13.719**	**1,189**	**<0.0005**
	Social class	1.575	6,161	0.158	**12.231**	**6,146**	**<0.0005**	**11.941**	**7,189**	**<0.0005**
	Pres.×Soc.	0.362	6,161	0.902	1.637	6,146	0.141	2.497	7,189	0.018
Number of calls given as feed	Presence	0.068	1,162	0.794	1.485	1,148	0.225	**5.748**	**1,190**	**0.017**
	Social class	0.669	6,162	0.675	1.112	6,148	0.358	0.696	7,190	0.675
	Pres.×Soc.	0.639	6,162	0.699	1.937	6,148	0.079	0.959	7,190	0.462
Number of calls given as leave nest	Presence	0.816	1,162	0.368	**14.509**	**1,148**	**<0.0005**	**20.099**	**1,190**	**<0.0005**
	Social class	2.147	6,162	0.051	0.671	6,148	0.674	**2.513**	**7,190**	**0.017**
	Pres.×Soc.	0.956	6,162	0.457	0.748	6,148	0.612	**2.367**	**7,190**	**0.024**
Load size (% bill volume)	Presence	0.677	1,162	0.412	1.699	1,148	0.194	0.043	1,190	0.836
	Social class	**5.795**	**6,162**	**<0.0005**	**4.169**	**6,148**	**0.001**	**6.389**	**7,190**	**<0.0005**
	Pres.×Soc.	0.421	6,162	0.864	1.302	6,148	0.260	1.077	7,190	0.380
Proportion of prey load consisting of lerp	Presence	2.628	1,151	0.107	2.129	1,139	0.147	0.268	1,176	0.605
	Social class	0.913	6,151	0.487	**2.525**	**6,139**	**0.024**	1.228	7,176	0.289
	Pres.×Soc.	1.608	6,151	0.149	**2.791**	**6,139**	**0.014**	1.125	7,176	0.350
Intervisit interval (s)	Presence	0.078	1,139	0.780	**7.267**	**1,132**	**0.008**	0.502	1,171	0.480
	Social class	**4.662**	**6,139**	**<0.0005**	**9.712**	**6,132**	**<0.0005**	**11.118**	**7,171**	**<0.0005**
	Pres.×Soc.	0.633	6,139	0.704	0.654	6,132	0.687	1.517	7,171	0.164
Previous intervisit interval (s)	Presence	1.196	1,141	0.276	0.564	1,129	0.454	1.474	1,173	0.226
	Social class	**4.144**	**6,141**	**0.001**	**10.811**	**6,129**	**<0.0005**	**11.318**	**7,173**	**<0.0005**
	Pres.×Soc.	0.131	6,141	0.060	1.670	6,129	0.133	1.895	7,173	0.073

Factors assessed included the presence of the potential audience, individual's social class (defined as helper relatedness to the breeding male) and the interaction between the two (Pres. × Soc.). Significant terms are indicated by bold.

duration appear to show little meaningful pattern, with any differences being marginal at best (Fig. 2a). Indeed this relationship disappeared when helper relatedness was calculated relative to the breeding male (Table 3) or breeding pair (results not presented). The proportion of lerp was substantially higher for unresolved male helpers when breeding males were present but showed a concurrent decrease for unresolved and related female helpers, which is also not expected under the predictions of any signalling hypothesis (Fig. 2b). Finally, several variables showed significant overall effects of social class per se (namely visit duration, load size and both types of intervisit interval), consistent with patterns of provisioning found in this system, for example breeding females visit nests more frequently, for longer periods each visit, and tend to bring larger load sizes than other social classes (simple contrasts between breeding females and related helpers: $P < 0.0005$ for load size and both intervisit interval and previous intervisit interval; see M$^{\text{c}}$Donald et al. 2007b, P. G. M$^{\text{c}}$Donald, A. J. N. Kazem, M. F. Clarke and J. Wright, unpublished data; L. te Marvelde et al., unpublished data; J. Wright, P. G. M$^{\text{c}}$Donald, L. te Marvelde and A. J. N. Kazem, unpublished data).

Results obtained when potential effects of a breeding male audience were instead assessed using social class calculated with respect to breeding males were again very similar to those generated using relatedness to breeding females (Table 3). Exceptions to this were the number of mew calls given as broods were fed, with breeding male presence/absence no longer influencing call production during feeding (Table 3). Moreover, a weak effect of social class on the proportion of lerp delivered was found, with related male helpers bringing a greater proportion of lerp in loads than did unresolved female helpers (simple contrast: $P = 0.040$). For all other variables the results did not differ between the two methods of calculating relatedness.

Presence/absence of another helper

When a helper of any type was present at the nest, all classes of birds showed significantly longer visit durations and gave more mew calls, both during feeding and when leaving the nest area (Table 2, Fig. 3). It is hard to explain why all classes of birds remained longer at the nest on occasions when there was a helper present (or, conversely, why helpers might be more likely to arrive or remain at nests if the focal individual was already there), but this does match the result (above) for female breeder presence and perhaps indicates that some additional social interaction occurs between nest attendants (beyond mere provisioning of nestlings). Similarly, the result for mew calls neatly mirrors that for the presence/absence of breeding males (above) but not breeding females. This suggests that mew calls are being used in communication at the nest between helpers and breeding males, individuals who, unlike breeding females, are frequently involved in joint activities *away* from the nest area, such as mobbing and provisioning elsewhere within the coterie. There was no influence of helper presence/absence on the load size, proportion of lerp within load or intervisit intervals

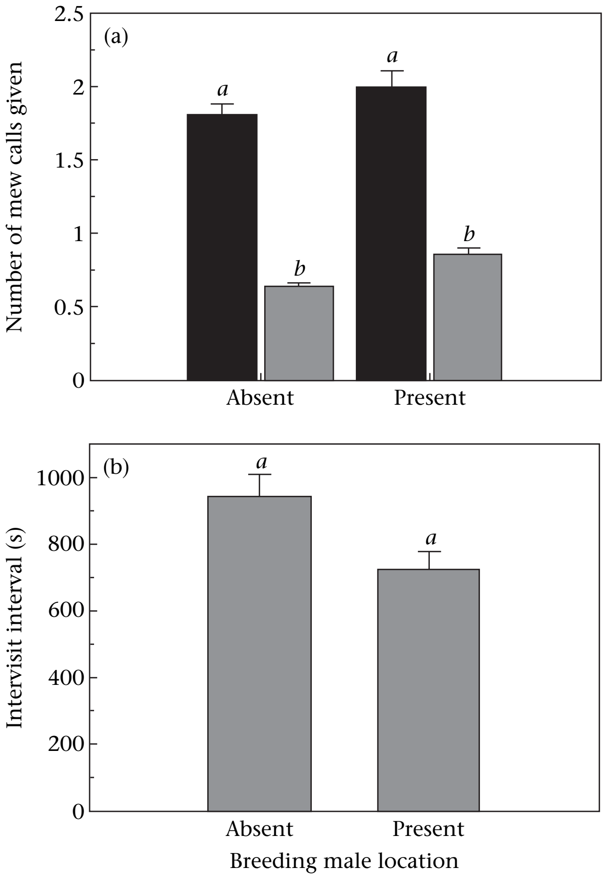

Figure 1. Effect of the presence/absence of the breeding male at the nest on (a) number of mew calls given (either prior to and during the feed, black bars, or as leaving the nest area, shaded bars), $N = 155$ birds, and (b) intervisit interval, $N = 135$ birds. Data are displayed as mean ± SE for all social classes combined. Bars marked with the same italicized letter differ significantly ($P < 0.05$).

of any class of bird (Table 2). As in the preceding analyses, there were significant overall effects of social class for several behavioural variables. The details of these differences are addressed elsewhere (McDonald et al. 2007b, unpublished data; L. te Marvelde et al., unpublished data; J. Wright et al., unpublished data), because these do not provide any evidence that is particularly relevant to the signalling hypotheses.

Again, when analyses were repeated using social classes calculated relative to breeding males, the same set of results were generated (Table 3). The one exception was an interaction between social class and presence/absence of another helper in the number of calls given as attendants left the nest area (Fig. 4). As in the equivalent analysis using social class relative to breeding females, the main effects of social class and importantly helper presence were present in the same direction when relatedness was calculated according to breeding males (Table 3). However, this weak interaction ($P = 0.024$) does not appear to provide support for the signalling hypotheses and may have little biological relevance given the more robust main effect of an increase in mew call production by all birds in the presence of a helper (Table 3, Fig. 4).

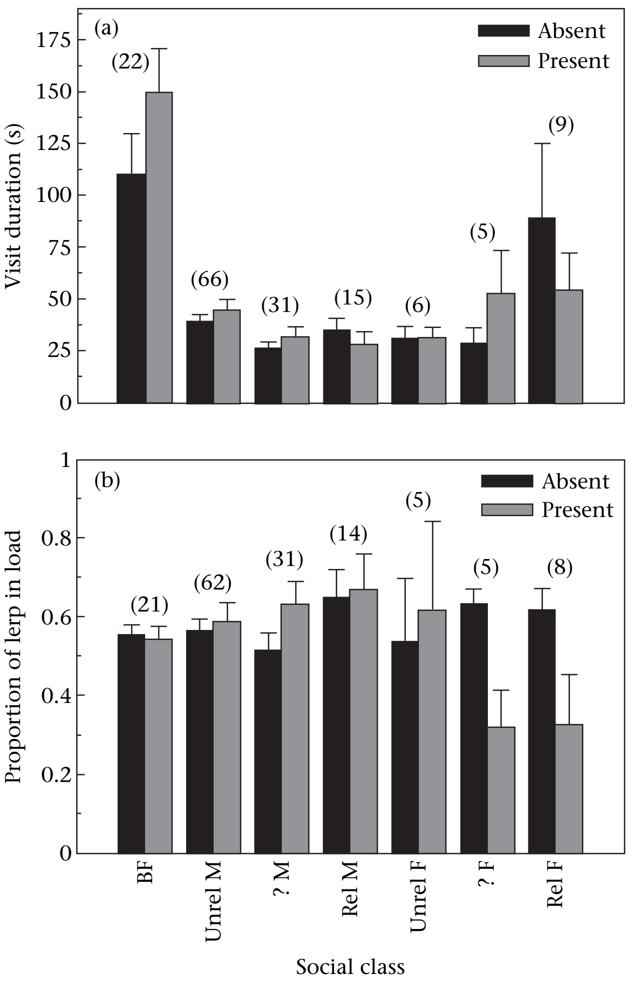

Figure 2. Effect of the presence/absence of the breeding male at the nest on (a) duration of visits to the nest and (b) proportion of lerp in loads delivered. Data are shown with social class calculated relative to breeding females (similar results are obtained when breeding males are used instead; see Results). BF: breeding female; Unrel M: unrelated male helper; ? M: unresolved male helper; Rel M: related male helper; Unrel F: unrelated female helper; ? F: unresolved female helper; Rel F: related female helper. Data are displayed as mean ± SE; numbers in parentheses indicate sample sizes. Both interactions are significant ($P < 0.05$).

DISCUSSION

Bell miners would at first glance appear a promising candidate for a signalling-based system of helping at the nest (see Introduction). However, the details of provisioning behaviour do not seem consistent with the interpretation that helping is either a signal of individual quality or a payment of rent. Aggression at the nest was extremely rare, and there was no indication that these incidents were aimed more often at specific social classes that possess a correspondingly low helper effort. Thus these acts appear unlikely to be either 'punishment' for lack of effort or pre-emptive harassment. The presence of a potential conspecific audience near the nest had little effect on critical provisioning behaviour, especially in those classes of helper most likely to benefit from signalling (e.g. unrelated

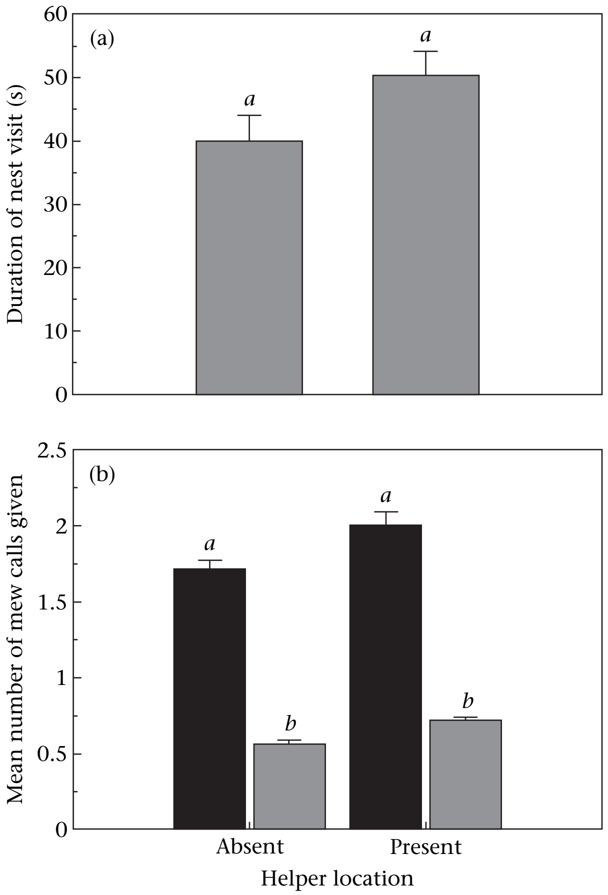

Figure 3. Effect of the presence/absence of another helper at the nest on (a) duration of nest visit, $N = 197$ birds, and (b) the number of mew calls given either prior to and during the feed (black bars) or as leaving the nest area (shaded bars), $N = 198$ birds. Data are displayed as mean ± SE for all social classes combined. Bars marked with the same italicized letter differ significantly ($P < 0.05$).

male helpers). However, the pattern of mew calls produced did suggest that some form of social interaction was occurring between coterie members during nest visits. Furthermore, temporal clustering of nest visits indicated some coordination in the behaviour of successive birds attending the nest, if only as a by-product of other activities away from the nest in question (e.g. cooperative mobbing, colony defence). Despite these interesting social insights, these observations do not match expectations from the signalling hypotheses. This overall null result is consistent with recent work examining other aspects of helping at the nest in this species, for example the occurrence of and reasons underlying false feeding behaviour (M^{c}Donald et al. 2007b).

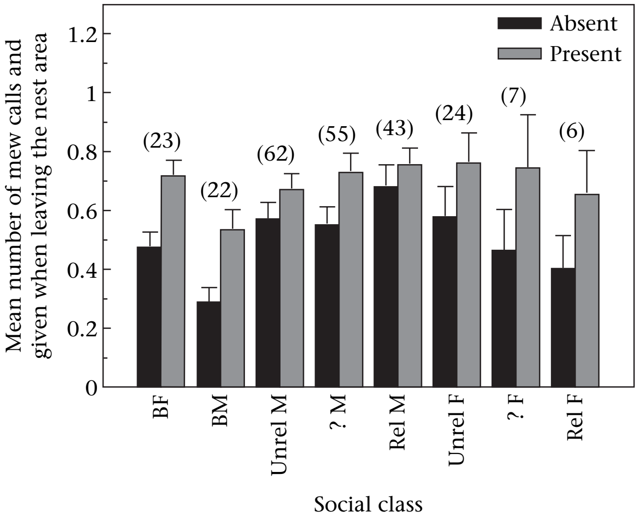

Figure 4. Effect of the presence/absence of another helper at the nest on the number of mew calls given as attendants left the nest area. Data are shown according to social class within the group calculated relative to breeding males. Data are displayed as mean ± SE and numbers in parentheses indicate sample sizes in each case. BM: breeding male; see Fig. 2 legend for other social class abbreviations.

Intraspecific Aggression during Provisioning

Surprisingly few observations of aggression between nest attendants (less than 1.5% of visits) were made, especially considering the generally aggressive nature of this species, towards both heterospecific competitors and predators (Smith & Robertson 1978; Clarke 1984; Poiani 1993) and between breeding females within a colony (Clarke & Fitz-Gerald 1994). There was little indication that this aggression might be in response to low provisioning effort by others, the usual hallmark of a pay to stay system. Whereas in principle a pay to stay system might be maintained without this observable temporal link, in that case one would expect to see high levels of 'pre-emptive' aggression by breeders within a context of clearly differentiated dominance relationships between group members and/or conspicuous appeasement displays by helpers on occasions when they have failed to provision (cf. Bergmüller et al. 2007), neither of which are observed in bell miners. Furthermore, the aggression recorded in the nest area was principally by breeding females towards male helpers and occasionally even towards the breeding male. In any rent-payment system, breeders are expected to demand effort primarily from (and direct any harassment towards) unrelated same-sex helpers, whose presence constitutes a reproductive threat. In bell miners the vast majority of helpers are male, which would suggest that the male breeder should be most involved in any policing of others' effort. However on no occasion, in over 190 h of observation, was a breeding male seen being aggressive at or around the nest area. This clearly contrasts with documented pay to stay systems (e.g. Reyer 1990; Mulder & Langmore 1993). Whereas it is possible that breeding males were more aggressive when away from the nest setting, this appears unlikely; whereas aggression between neighbouring female nest-holders is common, it is very rare between male members of bell miner coteries (Clarke & Fitz-Gerald 1994). Given the amount of time that various researchers, including ourselves, have spent observing marked individuals and the conspicuous nature of aggression between female members of this species, it seems very unlikely that aggression away from the nest area regularly occurs between other social classes of bell miners.

In the only other published case of aggression at the nest in bell miners, Poiani (1993) reported aggression predominantly from breeding females towards younger nest attendants, which was interpreted as punishment and training to induce appropriate provisioning behaviour. However, mortality is known to be greatest in this species shortly after fledging (Clarke 1989), and aggression from breeding females towards these helpers (which are likely to be their young from previous broods) may be an occasional tactic to prevent young from expending much-needed resources during a crucial stage of their life. In addition, in a larger data set we have shown that atypical provisioning, such as failure to transfer food to nestlings during a visit, is most often associated with experiencing low levels of brood demand (rather than being a function of helper age or relatedness) and thus should not be interpreted as 'lack of effort' (M^{C}Donald et al. 2007b).

Influence of the Presence of a Potential Audience on Provisioning Behaviour

There was a general tendency for different individuals' nest visits to be temporally clustered (although clustering of arrival times is not necessarily obvious when watching nests). Bell miner helpers and breeding males (but not breeding females) spend a lot of their time away from the nest vicinity in cooperatively mobbing both predators and heterospecific competitors within the colony area (Smith & Robertson 1978; Clarke 1984; Poiani 1993). Whereas we do not have data on the timing of specific mobbing by individuals relative to our nest observations, it seems likely that birds taking part in joint activity elsewhere, and therefore subsequently returning in quick succession to provision nestlings, is sufficient to explain the modest temporal clustering of nest visits found.

We did detect one clear effect of the presence/absence of breeding males, in that all classes of bird showed a shorter intervisit interval immediately after having encountered the latter at the nest, regardless of whether social classes were determined according to relatedness to the breeding male or to the breeding female. This relationship was not a straightforward by-product of the general clustering of visits, which should apply to all classes of bystander rather than only to male breeders, and an equivalent effect was not apparent for those IVIs which *preceded* the same individual's encounters with the breeding male. The result could be interpreted as consistent with both signalling hypotheses, for example if encountering the breeding male in some way encouraged individuals to increase their work rate for a period of time. Presumably any such increase in effort would be most effective if witnessed by the breeding male; however, attendants that coincided with the breeding male during one visit were actually *less* likely to encounter him near the nest on their subsequent visit than they were in visits where the two had not previously coincided with one another. Furthermore, nonsignalling explanations may also account for an asymmetric effect on IVI versus previous IVI. Following the frequent periods in which helpers and breeding males engage in joint activity away from a given nest (both cooperative defence and provisioning other nests within the coterie), it is likely to be the breeding male (who typically shows higher visit rates) that returns first. Thus a returning helper is likely to encounter the breeding male near the beginning of a period in which it repeatedly provisions a particular nest (i.e. shorter than average IVIs), before its activity shifts to elsewhere in the coterie. Given the lack of consistent evidence in other aspects of behaviour (below), signalling of individual effort does not seem the most plausible explanation for the pattern found.

Visit duration was one of the few variables influenced by the presence of all types of potential audience. When the breeding male was the conspecific concerned, the interaction with social class (calculated relative to the breeding female) makes the result a little less clear, and the P value of only 0.019 (Table 2) suggests that the effect may not be biologically significant given the number of such tests conducted. At first glance the result that visit durations were extended when in the presence of the breeding female or a helper could be construed as an attempt to signal one's contribution (although we cannot distinguish this possibility from the alternative that these other individuals simply have a greater chance of arriving during those visits by a focal individual which lasted longer, particularly where breeding females are the focal individual concerned). However a more parsimonious explanation is that birds coming to the nest at the same time have to form a 'queue', with only one or two birds being able to provision the nestlings at any one time because of the relatively small nest cups that bell miners build containing in most cases just two nestlings. As such, the presence of another bird, be it a member of the breeding pair or even a helper, would lead to a longer wait for any and all classes of bird until they are able to feed. The fact that this effect appeared to apply equally to all classes of bird would seem to support the queuing explanation, rather than one based on signalling.

Of more interest in terms of signalling hypotheses is the intriguing influence of conspecific presence on the production of mew calls at the nest. More mew calls were given by all classes of bird (including breeding females) when the breeding male or any class of helper was also present. The rate of mew call production was not related to nestling begging effort; thus mew calls are unlikely to be simply an additional means of broadcasting brood need used to incite greater provisioning effort by other coterie members (P. G. M^{C}Donald et al., unpublished data). Therefore mew calls, especially when leaving the nest area, appear to constitute a behaviour at the nest that is unconnected with nestling provisioning. Mew vocalizations are individually distinctive (M^{C}Donald et al. 2007a), and, while this may have evolved for many reasons, individuals may have been using these calls to reinforce their identity and association with an active nest within the coterie. Use of acoustic signals would clearly be advantageous because nests are usually situated in dense undergrowth and intruding individuals from other colonies are expelled by residents (P. G. M^{C}Donald, personal observation).

Individually distinctive calls could also offer a way of drawing attention to an individual's provisioning effort. In this system, the social prestige hypothesis might predict that male helpers should advertise their presence and work rate, particularly to breeding females. However, the breeding female was the one category of potential audience whose presence/absence did *not* exert any significant effect on calling by any class of individual. Mew calls directed towards breeding males could be consistent with predictions of the pay to stay hypothesis, but there was little direct evidence for operation of such a system (see above). Moreover, the increase in mew calls was produced by all classes of bird, including breeding females, and occurred in response to the presence of all helper classes as well as breeding males, which the pay to stay hypothesis would not predict. The lack of mew calls in association with the breeding female audience may be linked to the different social position with respect to all other coterie members that these individuals occupy because they maintain and defend exclusive territories (Clarke & Fitz-Gerald 1994). Breeding females are likely to travel shorter distances to mob predators or heterospecifics and likewise do not provision at other nests, unlike breeding males and helpers (Clarke 1989; Poiani 1993). Therefore helpers and breeding males generally interact and cooperate with one another, but not the breeding female, when away from a given nest. Mew calls may be involved in coordination of behaviour between these (predominantly male) individuals at a wider colony or coterie level. Further research is currently underway to investigate this and other possible functions of mew calls.

No Evidence for a Signal-based Helping System

Overall, there is a distinct lack of consistent and compelling evidence for helping being used as a signal in this system. There were no consistent changes in provisioning behaviour when in the presence of a potential audience and, notably, such effects were particularly lacking when the breeding female was the bystander concerned. Given the large sample size of individuals used, the main analyses being performed within-subjects, and other effects (e.g. the influence of social class) being easily detected, we feel confident that our analyses possessed sufficient statistical power to detect an audience effect had one been present. Experimental evidence from the same colonies, in which either the breeding female or the breeding male was temporarily removed (for periods long enough that other coterie members were likely to be aware of their absence), also did not produce alterations in helper behaviour (P. G. M^CDonald et al., unpublished data). The absence of such effects could conceivably indicate that there is a very high penalty for individuals that do not consistently work hard, that provisioners might be monitored by conspecifics from greater distances than those considered here or that the probability of a potential audience being present near the nest is typically very high. Under those conditions an evolved response (e.g. higher levels of provisioning effort), rather than a facultative response to perceived audience presence, might be used. However, the lack of any evidence for punishment and the placement of nests in dense undergrowth argue against the above possibilities.

Thus, despite possessing many characters suggestive of a system where helping could be operating as a signal, bell miner behaviour around the nest contains little that is consistent with either the social prestige or the pay to stay hypotheses. This is regardless of whether female helpers were included in analyses and whether social class was calculated relative to the breeding female, breeding male or a mean of both pair members. Whereas two avian examples of pay to stay systems have been documented (Reyer 1990; Mulder & Langmore 1993), the evidence for prestige-based signalling in cooperative breeding birds remains largely circumstantial, and studies of other aspects of the bell miner system do not provide any support for this notion (M^CDonald et al. 2007b, unpublished data; M. L. P. Pacheco et al., unpublished data). Exactly why helpers, and especially so many clearly unrelated individuals, are assisting with the care of nestlings in bell miners remains unclear. Kin selection can explain only some of the helping behaviour in this system, and alternative adaptive explanations for investment in nestlings should now be investigated in more detail, such as the direct fitness benefits of pseudo-reciprocity or augmenting group size (see J. Wright et al., unpublished data).

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References

Balcombe, J. P. 1989. Non-breeder asymmetry in Florida Scrub Jays. *Evolutionary Ecology*, **3**, 77–79.

Balshine-Earn, S., Neat, F. C., Reid, H. & Taborsky, M. 1998. Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behavioral Ecology*, **9**, 432–438.

Bergmüller, R., Johnstone, R. A., Russell, A. F. & Bshary, R. 2007. Integrating cooperative breeding into theoretical concepts of cooperation. *Behavioural Processes*, **76**, 61–72.

Boland, C. R. J., Heinsohn, R. & Cockburn, A. 1997. Deception by helpers in cooperatively breeding white-winged choughs and its experimental manipulation. *Behavioral Ecology and Sociobiology*, **41**, 251–256.

Brown, J. L. 1983. Cooperation: a biologist's dilemma. *Advances in the Study of Behavior*, **13**, 1–37.

Brown, J. L. 1987. *Helping and Communal Breeding in Birds*. Princeton, New Jersey: Princeton University Press.

Carlisle, T. R. & Zahavi, A. 1986. Helping at the nest, allofeeding and social status in immature Arabian babblers. *Behavioral Ecology and Sociobiology*, **18**, 339–351.

Clarke, M. F. 1984. Interspecific aggression within the genus *Manorina*. *Emu*, **84**, 113–115.

Clarke, M. F. 1989. The pattern of helping in the bell miner (*Manorina melanophrys*). *Ethology*, **80**, 292–306.

Clarke, M. F. 1995. Cooperative breeding in Australasian birds: a review of hypotheses and evidence. *Corella*, **19**, 73–90.

Clarke, M. F. & Fitz-Gerald, G. F. 1994. Spatial organisation of the cooperatively breeding bell miner *Manorina melanophrys*. *Emu*, **94**, 96–105.

Cockburn, A. 1998. Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, **29**, 141–177.

Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society of London, Series B*, **273**, 1375–1383.

Connor, R. C. 1986. Pseudo-reciprocity: investing in mutualism. *Animal Behaviour*, **34**, 1562–1584.

Connor, R. C. & Curry, R. L. 1995. Helping non-relatives: a role for deceit? *Animal Behaviour*, **49**, 389–393.

Conrad, K. F., Clarke, M. F., Robertson, R. J. & Boag, P. T. 1998. Paternity and the relatedness of helpers in the cooperatively breeding bell miner (*Manorina melanophrys*). *Condor*, **100**, 343–349.

Emlen, S. T. 1991. Evolution of cooperative breeding in birds and mammals. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 301–337. Oxford: Blackwell Scientific.

Fridolfsson, A. K. & Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology*, **30**, 116–121.

Gaston, A. J. 1978. Ecology of the common babbler *Turdoides caudatus*. *Ibis*, **120**, 415–432.

Goodnight, K. F. & Queller, D. C. 1999. Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Molecular Ecology*, **8**, 1231–1234.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. *Journal of Theoretical Biology*, **7**, 1–52.

Heinsohn, R. & Legge, S. 1999. The cost of helping. *Trends in Ecology & Evolution*, **14**, 53–57.

Jones, D. A. 1998. Parentage, Mate Removal Experiments and Sex Allocation in the Cooperatively Breeding Bell Miner, *Manorina melanophrys*. M.Sc thesis, Queen's University, Kingston, Canada.

Koenig, W. D. & Dickinson, J. L. (Eds) 2004. *Ecology and Evolution of Cooperative Breeding in Birds*Cambridge: Cambridge University Press.

Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001. The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London, Series B*, **268**, 187–196.

Kokko, H., Johnstone, R. A. & Wright, J. 2002. The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? *Behavioral Ecology*, **13**, 291–300.

Ligon, J. D. 1981. Demographic patterns and communal breeding in the green woodhoopoe, *Phoeniculus purpureus*. In: *Natural Selection and Social Behavior: Recent Research and New Theory* (Ed. by R. D. Alexander & D. W. Tinkle), pp. 231–243. New York: Chiron Press.

M^cDonald, P. G., Heathcote, C. F., Clarke, M. F., Wright, J. & Kazem, A. J. N. 2007a. Provisioning calls of the cooperatively breeding bell miner *Manorina melanophrys* encode sufficient information for individual discrimination. *Journal of Avian Biology*, **38**, 113–121.

M^cDonald, P. G., Kazem, A. J. N. & Wright, J. 2007b. A critical analysis of 'false feeding' behaviour in a cooperative bird: disturbance effects, satiated nestlings or deception? *Behavioral Ecology and Sociobiology*, **61**, 1623–1635.

Markman, S., Pinshow, B. & Wright, J. 1999. Orange-tufted sunbirds do not feed nectar to their chicks. *Auk*, **116**, 257–259.

Maynard Smith, J. 1964. Group selection and kin selection. *Nature*, **201**, 1145–1147.

Mulder, R. A. & Langmore, N. E. 1993. Dominant males punish helpers for temporary defection in superb fairy-wrens. *Animal Behaviour*, **45**, 830–833.

Painter, J. N., Crozier, R. H., Crozier, Y. C. & Clarke, M. F. 1997. Characterization of microsatellite loci for a cooperatively breeding honeyeater. *Molecular Ecology*, **6**, 1103–1105.

Painter, J. N., Crozier, R. H., Poiani, A., Robertson, R. J. & Clarke, M. F. 2000. Complex social organization reflects genetic structure and relatedness in the cooperatively breeding bell miner, *Manorina melanophrys*. *Molecular Ecology*, **9**, 1339–1347.

Poiani, A. 1993. Social structure and the development of helping behaviour in the bell miner (*Manorina melanophrys*, Meliphagidae). *Ethology*, **93**, 62–80.

Queller, D. C. & Goodnight, K. F. 1989. Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.

Reyer, H.-U. 1990. Pied kingfishers: ecological causes and reproductive consequences of cooperative breeding. In: *Cooperative Breeding in Birds: Long Term Studies of Ecology and Behavior* (Ed. by A. B. Stacey & W. D. Koenig), pp. 527–557. Cambridge: Cambridge University Press.

Russell, A. F. 2004. Mammals: comparisons and contrasts. In: *Ecology and Evolution of Cooperative Breeding in Birds* (Ed. by W. D. Koenig & J. L. Dickinson), pp. 210–227. Cambridge: Cambridge University Press.

Smith, A. J. & Robertson, B. I. 1978. Social organization of bell miners. *Emu*, **78**, 169–178.

Woolfenden, G. E. & Fitzpatrick, J. W. 1978. The inheritance of territory in group-breeding birds. *Bioscience*, **28**, 104–108.

Woolfenden, G. E. & Fitzpatrick, J. W. 1984. *The Florida Scrub-Jay: Demography of a Cooperatively Breeding Bird*. Princeton, New Jersey: Princeton University Press.

Wright, J. 1997. Helping-at-the-nest in Arabian babblers: signalling social status or sensible investment in chicks? *Animal Behaviour*, **54**, 1439–1448.

Wright, J. 1998. Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. *Behavioral Ecology and Sociobiology*, **42**, 423–429.

Wright, J. 1999. Altruism as a signal: Zahavi's alternative to kin selection and reciprocity. *Journal of Avian Biology*, **30**, 108–115.

Zahavi, A. 1977. Reliability in communication systems and the evolution of altruism. In: *Evolutionary Ecology* (Ed. by B. Stonehouse & C. Perrins), pp. 253–259. Baltimore: University Park Press.

Zahavi, A. 1995. Altruism as a handicap: limitations of kin selection and reciprocity. *Journal of Avian Biology*, **26**, 1–3.