

Helping effort increases with relatedness in bell miners, but ‘unrelated’ helpers of both sexes still provide substantial care

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Indirect fitness benefits from kin selection can explain why non-breeding individuals help raise the young of relatives. However, the evolution of helping by non-relatives requires direct fitness benefits, for example via group augmentation. Here, we examine nest visit rates, load sizes and prey types delivered by breeding pairs and their helpers in the cooperatively breeding bell miner (*Manorina melanophrys*). In this system, males remain in their natal colony while young females typically disperse, and helpers of both sexes often assist at multiple nests concurrently. We found extremely clear evidence for the expected effect of genetic relatedness on individual helping effort per nest within colonies. This positive incremental effect of kinship was facultative—i.e. largely the result of within-individual variation in helping effort. Surprisingly, no sex differences were detectable in any aspect of helping, and even non-relatives provided substantial aid. Helpers and breeders of both sexes regulated their provisioning effort by responding visit-by-visit to changes in nestling begging. Helping behaviour in bell miners therefore appears consistent with adaptive cooperative investment in the brood, and kin-selected care by relatives. Similar investment by ‘unrelated’ helpers of both sexes argues against direct fitness benefits, but is perhaps explained by kin selection at the colony level.

Keywords: helping-at-the-nest; kinship; nest visit rate; load size; brood demand; natal philopatry

1. INTRODUCTION

The apparent altruism of helping to raise the offspring of other individuals has been explained by kin selection in cooperative breeding birds (Brown 1987; Emlen 1997; Koenig & Dickinson 2004). A recent meta-analysis by Griffin & West (2003) confirmed that individual helping effort tends to be positively associated with genetic relatedness, although the authors were able to include only a small minority of published studies and none of these involved the key within-individual comparison indicating facultative adjustment on the part of helpers. Griffin & West (2003) also tested for an effect of relatedness on the probability of helping, and the results were even clearer (but not significantly so) than for helping effort. This is perhaps to be expected because such effects should be easier to detect than relatedness effects on levels of helper effort, the measurements of which tend to contain more noise owing to temporal and spatial variation in factors such as helper condition, brood need, etc. (Emlen & Wrege 1988).

Despite the utility of kin selection as an explanation, many studies report substantial levels of helping by

non-relatives, which argues against indirect fitness benefits as the only, or even the most important, explanation for helping behaviour (Cockburn 1998; Clutton-Brock 2002). The most likely alternative explanation is that helpers gain future increases in survivorship and/or reproduction from enhancing the number and/or quality of younger group members. Such direct fitness benefits have been variously referred to as group augmentation, pseudo-reciprocity and delayed/cross-generational mutualism/reciprocity (Ligon & Ligon 1978, 1983; Woolfenden & Fitzpatrick 1978, 1984; Brown 1983, 1987; Connor 1986, 1995). The overlapping and non-mutually exclusive nature of these different ideas means that they now tend to be referred to under the single heading of ‘group augmentation’ (Kokko *et al.* 2001; Clutton-Brock 2002; Bergmüller *et al.* 2007; Wright 2007).

The problem for studies of cooperative breeding is that group augmentation provides relatively few critical predictions and tends to be invoked post hoc as a theory of last resort with little explicit testing (Wright 2007). However, sex biases in natal philopatry (Weatherhead & Forbes 1994) can potentially provide predictable sex differences in the benefits that accrue from group augmentation. Thus, in addition to variation in relatedness and therefore indirect fitness benefits, male and female

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helpers should vary consistently in their expected future direct fitness benefits from group augmentation. However, any empirical test requires a cooperative breeding system that includes sufficient numbers of male and female helpers varying in level of relatedness, together with sufficiently extreme sex-biased dispersal.

Bell miners (*Manorina melanophrys*) in southeastern Australia represent just such a system. They form large colonies often comprising hundreds of individuals, which actively exclude all other insectivorous and nectarivorous birds from the colony area. A colony often contains a number of 'coterie', each of which consists of many different breeding pairs and an attending assemblage of non-breeding helpers of both sexes of varying relatedness, each of which provisions at multiple nests within what is their natal coterie (Clarke 1989; Conrad *et al.* 1998; Painter *et al.* 2000). Male offspring always remain within their natal coterie, but females almost always disperse within eight months of fledgling and move to other colonies, where they obtain breeding positions and do not help. Bell miners are therefore obligate cooperative breeders that need large colonies comprising many non-breeding helpers for both individual survival and successful reproduction (Clarke & Heathcote 1990). Non-dispersing individuals, let alone breeding pairs, have never been observed outside of functioning colonies despite many years devoted to their study. Female dispersal results in male-biased colony sex ratios, presumably because dispersal is dangerous and carries a high mortality factor (Clarke & Heathcote 1990). Coterie are thus characterized by small numbers of young, non-breeding females helping prior to their dispersal, and large numbers of males helping while waiting for breeding positions to open up. The large number of breeding pairs per coterie and the relatively rapid turnover of breeding females mean that most helpers are not the direct descendents of the many different adult breeders they aid. Recent work on bell miners has already demonstrated no obvious role of direct fitness benefits for unrelated helping that involve signalling for social prestige or pay-to-stay (McDonald *et al.* 2007a, 2008a,b; Pacheco *et al.* 2008). This system therefore represents an excellent opportunity to distinguish between the only remaining hypotheses, kin selection and group augmentation, for the evolution of helping-at-the-nest in a cooperative bird.

This paper explores in detail within- and between-individual variation in nest visit rates, load sizes and prey types delivered by parents and helpers according to sex and genetic relatedness in bell miners. We also examine visit-by-visit responses of breeders and helpers to nestling begging signals of brood need. This study therefore represents a rare example of a comprehensive test for both direct and indirect fitness effects on helping, as well as an exploration of the behavioural rules of thumb used to regulate individual helping effort within each nest.

2. MATERIAL AND METHODS

(a) *Study population*

Data were collected from June 2004 to December 2006 at two different bell miner colonies northeast of Melbourne, Australia. One consisted of 40–45 individuals at the La Trobe University Wildlife Reserve (37°42'58" S,

145°03'20" E), and the other of 120–135 birds near Saint Andrews (37°35'09" S, 145°15'41" E). All research was approved by La Trobe University Animal Ethics committee (licence AEC01/19(L)/V2), the Department of Sustainability and Environment (licence 10002082) and the Australian Bird and Bat Banding Scheme.

(b) *Molecular analyses*

Individuals within colonies were individually colour banded, and a *ca* 70 μ l blood sample was collected from the alar vein for analysis. This sample was stored in 70 per cent 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. Pair-wise relatedness between individuals was assessed using KINSHIP v. 1.2, by calculating likelihoods of birds being either related (hypothesis $r = 0.5$, null hypothesis of $r = 0$), or unrelated (hypothesis $r = 0$, null hypothesis of $r = 0.5$), based on the ratio required to exclude 95 per cent of 1000 simulated pair-wise comparisons (Queller & Goodnight 1989; Goodnight & Queller 1999). Relationships could thus be assigned using statistical significance to one of three categories: (i) significantly 'unrelated' $r = 0.0$ (i.e. average relatedness between all individuals in all coterie and colonies sampled here); (ii) significantly 'related' $r = 0.5$; or (iii) as 'unresolved' $r = 0.25$ if *p*-values for both tests (i) and (ii) were non-significant.

For each nest, parent birds were initially identified from behaviour: only breeding females build nests and only breeding males join females in feeding the young during the first 48 h in the nest. These classifications were later validated via molecular analyses (Poiani 1993; Conrad *et al.* 1998; McDonald *et al.* 2008a). Estimates of relatedness to both the breeding male and the breeding female combined were calculated for each of the 217 helpers to provide a mean *r* to the brood of either: 0.0 (29.5% of helpers); 0.125 (25.3%); 0.25 (26.7%); 0.375 (12.4%) or 0.5 (6.0%). The variable 'relatedness status' within each sex therefore consisted of these five classes of helper relatedness, plus the category of 'parent'.

(c) *Provisioning observations*

The number of bell miner helpers per nest and individual provisioning effort reaches its maximum when nestlings are 5–6 days old and remains constant thereafter until fledgling at 12 days (te Marvelde *et al.* 2009). Data were therefore collected from nests from day 6 onwards, from a bird hide at >10 m using a telescope (Kowa TS662 20–60x), and video recorded from >1 m (Sony Hi8 camcorders CCD-TR1100E or DCR-TRY265E). Vocalizations at the nest were recorded using a solid-state recorder (Marantz PMD670) and a tie-clip microphone (Sony ECM77B) placed 20 cm below the nest. A settling period of 10 min was used at the start of all observations to allow any disturbance associated with observer arrival to dissipate. Previous work has confirmed that these observation methods cause no measurable disturbance effects in any aspect of provisioning behaviour in bell miners (McDonald *et al.* 2007a).

We observed 27 nests, all containing broods of two nestlings, for an average of 8.5 h per nest (s.d. = 3.1, range 2.0–15.5 h). For each of the 9898 nest visits observed we recorded: individual identity; arrival and departure times (to the nearest second); load size (relative to bill volume)

and prey composition (proportion of arthropod prey to 'lerp'—a white sugary secretion of sap-sucking psyllids, which is the staple food of adult bell miners—see *te Marvelde et al.* (2009)).

(d) Nestling begging

A visual score of brood begging intensity during each provisioning visit was assigned from nest videos. Mean nestling body orientation was used to provide a continuous interval measure of begging intensity comparable with height in the nest: (i) 0° (horizontal resting, no discernible response); (ii) 1–44° (head lift only); (iii) 45–89° (head lift, body upright and resting back on tarsi); and (iv) 90° (standing fully erect on feet).

Acoustic begging intensity during each provisioning visit was recorded using the digital sound (DAT) recorder (record level 7), and stored in uncompressed wav file (PCM) format (48 kHz, 16 bits). Begging calls were analysed in RAVEN 1.2.1 (Cornell, USA) and a high-pass filter used to remove background noise. Spectrograms were used to measure the amplitude of the first bout of begging per visit, using the root-mean-square algorithm within RAVEN (*Charif et al.* 2004).

(e) Statistical analyses

For a small minority of visits, data were not available for either visual begging scores (1.7% of visits) or acoustic begging volume (6.9% of visits). As visual and acoustic measures of begging were highly correlated ($r = 0.45$, d.f. = 6396, $p < 0.001$), we used linear regression equations to estimate substitute values for these few missing data points (i.e. beg posture = $0.0017 \times$ beg volume; beg volume = $331.63 \times$ beg posture). We then used a principal component (PC) analysis to generate a composite (visual + acoustic) PC1 measure of 'begging intensity' (for more detail see *McDonald et al.* 2008a).

Individual provisioning responses to begging cues were assessed on a visit-by-visit basis. Begging intensity experienced by an individual during a visit at time ' t ' was compared with the load size and prey types delivered by that individual during its subsequent visit (at time $t + 1$), and its inter-visit interval (IVI—time between departure from the nest at time t and arrival back at the nest at the start of the subsequent visit at $t + 1$). We also tested for any additional effects of begging that individuals experienced during earlier visits (i.e. at time $t - 1$, $t - 2$ to $t - 5$), but found no measurable effects. Therefore, for reasons of brevity, we present only the effects involving the begging experienced (at time t) immediately prior to the provisioning visit of interest (i.e. the visit at $t + 1$). Note that the calculation of these IVI provisioning responses required the observation of consecutive visits by an individual, which did not always occur for all birds in all observation sessions. Sample sizes therefore vary for different analyses.

Data were analysed using linear mixed models, with individual bird as a random effect. Additional models were used to separate within- versus between-subject effects using the simple technique of individual centring (*Van de Pol & Wright* 2009). In this way, we compared measures of individual provisioning effort according to the fixed effects of relatedness status and sex. We tested visit-by-visit provisioning responses of breeders and helpers to the fixed effect of begging, with any sex or relatedness status differences in the slopes being assessed via the interaction terms with begging. The linearity of the covariates relatedness status and begging was confirmed by entering second-order terms, which were then removed from the model when

non-significant. Backwards sequential elimination of non-significant interaction terms was also used to simplify final models. However, certain non-significant interaction terms of interest were left in and are reported here whenever they did not substantially influence the main effects in the model.

Variables were arcsine square root (proportion lerp) or log-transformed (visit rates, biomass delivered, IVI) as appropriate to conform to assumptions of normality. All analyses were carried out using SPSS v. 16.0, with two-tailed tests and a critical p -value of 0.05 applied throughout.

3. RESULTS

(a) Probability of helping

In addition to the breeding male and female, the average bell miner nest was attended by 8.63 helpers (s.d. = 3.07, range 3–16). We observed a total of 176 male and 25 female helpers, which roughly matched the 7:1 sex ratio of non-breeding individuals seen in these colonies (personal observation, this study). Most non-breeding individuals were seen attending at least one nest, with male helpers attending an average of 2.26 nests (s.d. = 1.37, range 1–7) and female helpers attending an average of 1.19 nests (s.d. = 0.40, range 1–2), which again probably reflects sex differences in time spent in the focal colonies owing to female dispersal at eight months. Female helpers were therefore on average younger than male helpers ($F_{1,147} = 17.18$, $p < 0.001$). However, there was no effect of age on helper relatedness ($F_{1,180} = 0.33$, $p = 0.568$), and so younger helpers (often females) were not more likely to be related to the pairs they assisted.

(b) Provisioning effort

Table 1 shows a significant positive linear effect of relatedness status for breeders and helpers together on visit rates (figure 1a), load size and biomass delivered to the nest (figure 1b), but no significant effect of relatedness status on the proportion of lerp delivered. For visit rates and biomass delivered (table 1), this main effect of relatedness status was the result of significant within- and between-subject effects, the slopes of which did not differ significantly from each other (visit rates: $F_{1,212} = 0.11$, $p = 0.737$; biomass delivered: $F_{1,170} = 0.67$, $p = 0.413$). This suggests that individuals changed their visit rates at different nests according to variation in their genetic relatedness, and that the same effect was present in the relationship between average individual relatedness and visit rate values. However, the weak main effect of relatedness status on load size was the result of a solely between-subjects effect (table 1). Therefore, individuals did not facultatively adjust the load sizes they delivered to different nests according to genetic relatedness, and the positive effect of relatedness on load size was entirely owing to some kind of difference between different classes of individual.

Individual sex had no significant effect on any measure of provisioning, but there were significant interactions between the main effect of relatedness status and sex for visit rates and biomass delivered (table 1). These interactions seem to be the result of between-subjects effects arising from the significantly greater visit rates (and therefore a trend for more biomass to be delivered) by female breeders compared with male breeders (figure 1; visit rate: $F_{1,47} = 6.03$, $p = 0.018$; biomass delivered: $F_{1,48} = 3.27$, $p = 0.077$),

Table 1. The effects of individual relatedness status and sex on: visit rate; load size; proportion of lerp and biomass (visit rate \times load size) delivered. (F -ratios, degrees of freedom (d.f.) and p -values are shown for mixed model results for all group members including the breeding pair. The main effect of relatedness status (and its interaction with sex) is decomposed into its within- and between-subjects components for each measure of provisioning effort (see text for details).)

	relatedness status			sex			relatedness \times sex		
	F	d.f.	p	F	d.f.	p	F	d.f.	p
visit rate									
main effect	70.87	1,251	<0.001	1.80	1,245	0.181	5.91	1,251	0.016
within-subjects	30.26	1,232	<0.001				0.62	1,232	0.689
between-subjects	42.54	1,211	<0.001	1.50	1,223	0.223	5.25	1,211	0.023
load size									
main effect	9.48	1,230	0.002	0.66	1,219	0.417	0.98	1,230	0.322
within-subjects	2.52	1,179	0.135				0.21	1,179	0.650
between-subjects	5.03	1,180	0.026	0.86	1,191	0.354	1.33	1,180	0.250
proportion lerp									
main effect	0.60	1,233	0.439	3.21	1,227	0.075	3.45	1,233	0.064
within-subjects	0.19	1,199	0.660				1.79	1,199	0.182
between-subjects	1.07	1,200	0.303	2.13	1,210	0.146	2.36	1,200	0.126
biomass									
main effect	62.35	1,232	<0.001	3.15	1,226	0.077	5.51	1,232	0.020
within-subjects	9.63	1,191	0.002				0.49	1,191	0.485
between-subjects	43.26	1,193	<0.001	3.84	1,206	0.051	6.42	1,193	0.012

whereas there were no such sex differences for helpers (visit rate: $F_{1,199} = 0.05$, $p = 0.830$; biomass delivered: $F_{1,182} = 0.28$, $p = 0.600$; see also table 2). Therefore, members of the breeding pair differed in their provisioning investment in the brood, but male and female helpers did not.

The strong effect of relatedness status could have been driven by the significantly greater provisioning effort of breeders compared with helpers (figure 1; visit rate: $F_{1,253} = 86.22$, $p < 0.001$; load size: $F_{1,234} = 28.33$, $p < 0.001$; biomass delivered: $F_{1,236} = 72.18$, $p < 0.001$). Therefore, we re-ran the analyses from table 1 excluding both members of the breeding pair and obtained qualitatively similar results using just the data from helpers (table 2). Only in the case of load size did the greater provisioning effort by the breeding pair appear to be responsible for the previously significant effect of relatedness status (table 2). This follows from the results above (table 1), showing that the main effect of relatedness status on load size was owing to a between-subjects effect (i.e. between breeders and helpers). Importantly, when considering just helpers, there were no significant interactions between relatedness status and sex for both visit rate and biomass delivered (table 2; figure 1). This again follows from the results above (table 1) in which these original interactions were owing to between-subjects effects based on the contrasting patterns of sex differences in behaviour between breeders and helpers. So, irrespective of sex, all helpers increased their provisioning effort when feeding more related broods by facultatively increasing their visit rates but not their load sizes, and with no changes in the proportion of lerp delivered.

(c) Visit-by-visit provisioning responses

There was a significant negative linear effect of brood begging on IVI ($F_{1,2902} = 9.90$, $p = 0.002$). Moreover, this effect was entirely owing to a within-subjects effect (figure 2a; $F_{1,2824} = 12.33$, $p < 0.001$), with no between-subjects component ($F_{1,579} = 0.64$, $p = 0.424$).

This within-subjects effect of brood begging on IVI (figure 2a) was unaffected by sex or relatedness status (i.e. $p > 0.292$ for all interaction terms). So, irrespective of their overall provisioning work rates, all classes of individual made the same kind of visit-by-visit adjustment according to brood need.

There was also a significant positive linear effect of brood begging on load size delivered ($F_{1,5278} = 13.46$, $p < 0.001$). This effect was owing to both a within-subjects effect (figure 2b; $F_{1,5169} = 6.16$, $p = 0.013$) and a between-subjects effect ($F_{1,1983} = 21.15$, $p < 0.001$), neither of which differed according to sex or relatedness status ($p > 0.176$ for all interaction terms). However, the between-subjects slope was significantly steeper than the within-subjects slope ($F_{1,2215} = 13.82$, $p < 0.001$), implying two different biological explanations. As with adjustments in IVI, the within-subjects effect seems to have been a general facultative response by bell miners to levels of brood demand—after hearing a hungry brood all individuals returned to the nest with larger load sizes on their next visit. The between-subjects effect seems to have resulted from the significantly higher average levels of brood begging experienced by female breeders compared with male breeders and helpers ($F_{1,106} = 4.92$, $p = 0.029$), while breeding males and helpers experienced similar average levels of brood begging ($F_{1,1543} = 0.24$, $p = 0.626$). Combined with the larger load sizes delivered on average by breeders (see above), this would explain the strong between-subjects effect of begging on load size delivered, because breeding females both delivered larger loads and experienced louder begging on average, as compared with helpers.

4. DISCUSSION

(a) Kin-selected helping

Bell miner helpers of both sexes clearly showed an incremental increase in visit rates, and therefore biomass

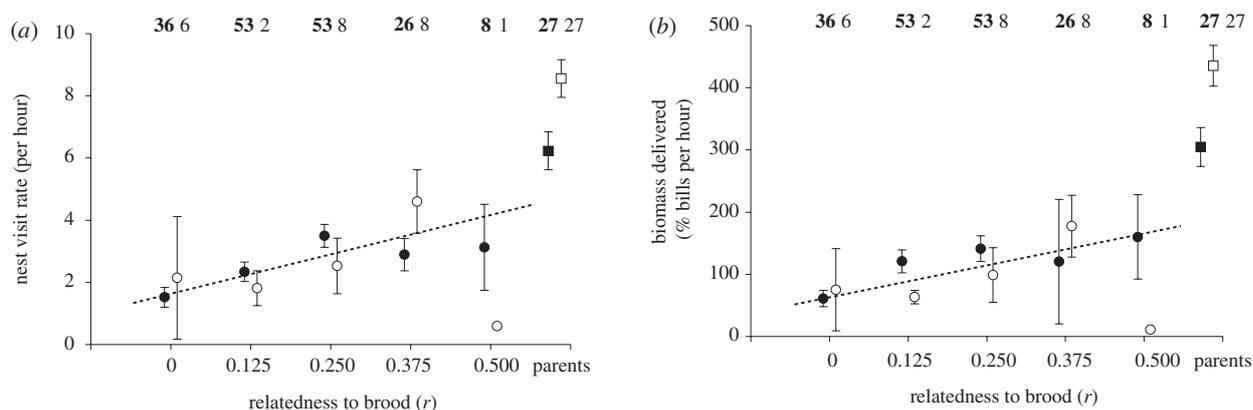


Figure 1. The effects of relatedness status on (a) visit rate (per hour) and (b) biomass delivered to the nest (percentage bill volume equivalents per hour) per individual per nest. The numbers of males (in bold) and females in each relatedness class are displayed at the top of each graph, values shown are means (\pm s.e.). Dashed best-fit lines illustrate the main effect of relatedness for male and female helpers combined (table 2). Filled circles and squares, males; open circles and squares, females.

Table 2. The effects of helper relatedness status and sex on: visit rate; load size; proportion of lerp and biomass (visit rate \times load size) delivered. (F -ratios, degrees of freedom (d.f.) and p -values are shown for mixed model results for only the helpers (i.e. excluding the breeding pair). The main effect of relatedness status (and its interaction with sex) is decomposed into its within- and between-subjects components for each measure of provisioning effort (see text for details).)

	relatedness status			sex			relatedness \times sex		
	F	d.f.	p	F	d.f.	p	F	d.f.	p
visit rate									
main effect	11.93	1,197	0.001	0.89	1,197	0.346	1.14	1,197	0.286
within-subjects	30.26	1,187	<0.001				1.24	1,187	0.267
between-subjects	5.07	1,187	0.026	0.56	1,185	0.454	0.91	1,187	0.342
load size									
main effect	0.76	1,180	0.383	0.01	1,177	0.942	0.79	1,180	0.376
within-subjects	0.35	1,131	0.554				0.08	1,131	0.774
between-subjects	2.46	1,151	0.119	0.06	1,152	0.810	0.90	1,151	0.346
proportion lerp									
main effect	0.02	1,180	0.891	3.70	1,179	0.056	6.36	1,180	0.057
within-subjects	0.11	1,141	0.737				1.92	1,141	0.168
between-subjects	0.16	1,161	0.690	2.59	1,162	0.109	2.62	1,161	0.107
biomass									
main effect	9.55	1,179	0.002	1.32	1,180	0.251	0.63	1,179	0.429
within-subjects	5.25	1,132	0.023				0.34	1,132	0.563
between-subjects	4.90	1,161	0.028	1.61	1,162	0.206	0.91	1,161	0.343

delivered, in response to fine-scale differences in genetic relatedness to the broods they were provisioning. As such, this confirms previous observations on this system (Clarke 1984) and provides perhaps one of the best examples so far for kin-selected helping in a cooperative bird (Brown 1987; Griffin & West 2003; Koenig & Dickinson 2004). Importantly, this main effect of helper relatedness was largely owing to individual facultative adjustments in nest visit rates (i.e. the within-subjects effect). There was a weak between-subjects effect of relatedness, but this had the same slope and so was probably merely a reflection of the strong within-subjects effect. This will have arisen because each individual helper in the dataset happened to attend nests covering only a relatively limited range of relatedness values. Therefore, the between-subjects effect will have reflected these differences in the positions of the individual response curves (each describing one helper's facultative response) along the

line of the main effect describing how relatedness affects helping effort for all individuals combined.

This type of fine-scale facultative adjustment in helping effort per nest must involve a relatively sophisticated mechanism for kin discrimination in order for individuals to assess their relatedness to the many different pairs within the coterie. One possibility is that individually distinct 'mew' calls given by both breeders and helpers at the nest in this species (McDonald *et al.* 2007b; McDonald & Wright 2008) may contain information to facilitate the preferential care of relatives (Beecher *et al.* 1985; Sharp *et al.* 2005). We are currently assessing the effects of kinship, familiarity and within-coterie social structure on the acoustic features of bell miner mew calls, including a comparison of calls adults will themselves have heard as nestlings. However, helpers in this system are in their natal coterie and therefore probably have access to all sorts of additional social information concerning their

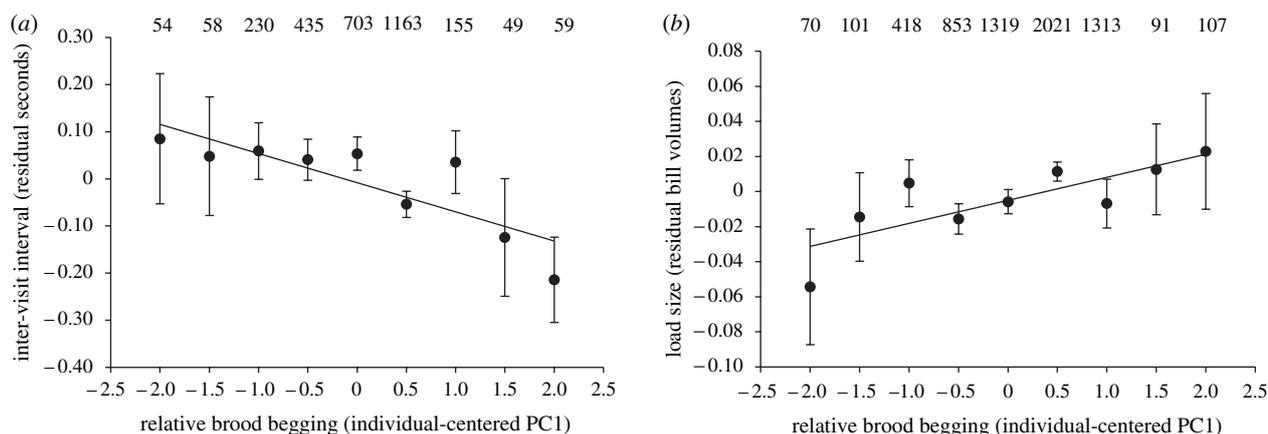


Figure 2. The within-subjects effects of brood begging intensity on visit-by-visit changes in (a) IVI (log seconds) and (b) load size delivered (arcsine square-root proportions of bill volume). For ease of viewing, mean (\pm s.e.) values are shown for standardized residuals of IVI and load size (from mixed models with individual as a random effect) for successive classes of individually centred values for brood begging. Numbers of visits within each class of brood begging are given at the top of each graph. Best-fit lines (from mixed model parameter estimates) show the within-subjects effects of brood begging for all individuals combined (i.e. slopes did not differ with sex and relatedness status—see text for details).

relatedness to each breeding pair. For example, the continued presence of mothers and/or fathers (or siblings from the same brood) within the coterie would provide helpers with a crude estimate of higher relatedness to some broods versus all others associated with presumed non-family members. Geographical and social distances within coterie might also reflect contours of genetic relatedness, such that helpers could use an estimate of linear distance from their natal nest to estimate their relatedness to broods they provision. Unfortunately, we do not have enough years of data involving the natal nest sites or family pedigrees of helpers from these coterie to estimate what types of information may or may not have been available to helpers in this system. Unlike previous studies (e.g. Wright *et al.* 1999), we cannot therefore assess which kin discrimination ‘rules-of-thumb’ bell miner helpers might have been using in terms of their perceived relatedness to broods that they were helping at different rates.

There was no corresponding individual facultative adjustment (i.e. within-subjects effect) of helper relatedness on load sizes or prey types delivered, which is interesting given that variation in these variables can have measurable consequences for nestling growth in this system (te Marvelde *et al.* 2009), and the fact that load size was involved in visit-by-visit responses to nestling begging (see below). Load sizes and prey types delivered per visit have been shown to be important components of parental investment in monogamous birds (Wright *et al.* 1998), but they are rarely considered in cooperative breeding studies estimates of helper investment, despite being shown to be of some importance (Wright 1998). In their meta-analyses of helping and kinship, Griffin & West (2003) do not distinguish between effects owing to variation in visit rates, load sizes or some combination of the two. However, such distinctions might reveal important differences in the nutritional benefits to nestlings (te Marvelde *et al.* 2009), as well as insights into contrasting costs of provisioning for different classes of breeders and helpers. For example, the consistently greater provisioning investment shown here by parent bell miners compared with helpers was the result

of both sexes delivering larger loads, but only female parents visited the nest more than expected from relatedness alone (figure 1). This probably reflects the fact that male breeders move throughout the whole colony, feeding at multiple nests as do helpers, and therefore have to trade-off visits to their own nest against other duties in cooperative provisioning, mobbing and colony defence.

In contrast to other colonial cooperative breeders (Emlen & Wrege 1988; Russell & Hatchwell 2001), there was no evidence that bell miners were more likely to help at the nests of relatives. The youngest helpers did not seem to stay close and preferentially help their parents, although such opportunities might also have just been rare in this system with its rapid turnover of breeding pairs (owing mainly to low breeding female survival). Either way, the effect of relatedness on helping effort shown here was not owing to any confounding effects of helper age—i.e. younger helpers were not more related and did not work harder.

(b) *Direct benefits of helping*

The overall lower numbers of female helpers, and the fewer nests attended per female helper, appear to be simply a consequence of early dispersal by most young females in this species (Clarke & Heathcote 1990; Clarke *et al.* 2002). Therefore, bell miner helpers seemed to attend hungry broods located within their coterie as required, irrespective of helper sex or relatedness to the brood. Consistent with this, helper numbers per nest increased with age-related increases in brood demand, resulting in helpers providing approximately 60 per cent of total food delivery and having substantial positive effects on nestling condition (te Marvelde *et al.* 2009). Although fully related helpers worked at 50 per cent of the rate of parents, ‘unrelated’ helpers still provided food at 25 per cent of the rate of parents (figure 1). This represents substantial investment per helper, especially since helpers often attend more than one nest simultaneously and breeding in this species may occur in all months of the year. So, while

within-colony variation in relatedness may explain a significant proportion of the within-individual variation in helper work rates, there is still a substantial level of help provided by ‘unrelated’ bell miners of both sexes to be explained.

We therefore have to consider the direct fitness benefits to helping arising from ‘group augmentation’ (Woolfenden & Fitzpatrick 1978; Brown 1983; Connor 1986; Kokko *et al.* 2001). Under this hypothesis the extreme sex-biased dispersal in this species (Clarke & Heathcote 1990; Clarke *et al.* 2002) should have produced large sex differences in the future fitness benefits accrued from increasing the number of healthy offspring recruited to the coterie. For example, ‘active’ benefits from group augmentation might arise if the offspring assisted later become helpers themselves and thereby enhance the reproductive success of the individuals that helped raise them. Such a benefit is clearly going to be restricted to male helpers, since female helpers disperse alone to breed. Some ‘passive’ fitness benefits from group augmentation might accrue to female helpers in the short term, owing to improved chances of survival for all individuals in larger bell miner colonies, which should be more effective in defending themselves from attack by predators and foraging competition from other species. However, it is the non-dispersing male helpers that will clearly gain the most from such passive benefits and do so throughout the rest of their lifetime. Hence, even if female helpers rely heavily upon their natal colony as a base from which to disperse in the few months during which they are resident, many of them are likely to have left the colony before most of the offspring they helped raise are mature enough to provide such benefits. Therefore, whichever of the various different and overlapping direct fitness benefits one invokes under group augmentation (§1), they would all seem to predict clear sex differences in helping effort in bell miners, which we did not find.

How then do we explain the apparent substantial and persistent helping by both male and female ‘non-relatives’ (i.e. those of only average relatedness across the coterie and colonies sampled here)? An important issue here might be to distinguish between the effects of kin selection owing to variation in relatedness *within* groups versus *between* groups. Like most other studies in cooperative breeding, ours was designed to test adaptive hypotheses that might explain individual variation in helping effort *within* the immediate social group (McDonald *et al.* 2007a, 2008a,b, 2009; Pacheco *et al.* 2008; te Marvelde *et al.* 2009). Also, like most studies, our genetic sampling was limited to only a small local sub-set of the actual bell miner population, so we effectively quantified mostly *within*-colony variation in relatedness (i.e. zero relatedness here represents the average relatedness between all the birds sampled in our two colonies; Queller & Goodnight 1989; Goodnight & Queller 1999). Future studies should perhaps address this common shortcoming by representatively sampling spatial and temporal variation in kinship structure, within and between social groups, across the wider population in which any adaptive strategies in helping behaviour are thought to have evolved.

For now, we need to recognize that results such as the one shown here demonstrating facultative adjustment of bell miner helping effort according to kinship (i.e. the

slope in figure 1) largely represent kin selection for inclusive fitness benefits *within* these social groups or coterie. And crucially, the substantial helping we still see by ‘non-relatives’ of both sexes (i.e. the intercept in figure 1) could largely be the result of kin selection *between* social groups or coterie. Individual bell miners clearly use the rule-of-thumb of only helping within their natal coterie (i.e. females only help prior to dispersal), and this could well be because average levels of relatedness are much higher within coterie than between them, even within the same colony. Interestingly, male-biased natal philopatry in bell miners results in higher levels of male than female relatedness within coterie (Painter *et al.* 2000), and so we might expect greater between-coterie kin selection on male helping than female helping. However, competition between relatives can completely counteract any effects of kin selection (West *et al.* 2001), and so male–male competition for breeding positions within coterie could explain why sex differences in average relatedness are not manifest as sex differences in between-coterie kin-selected helping in bell miners.

(c) *Visit-by-visit responses to begging*

Despite provisioning at very different rates for apparently contrasting fitness benefits, parents and helpers of both sexes used the same proximate rule involving begging to regulate their effort on a visit-by-visit basis. Both IVI and load size were adjusted according to the begging that individuals experienced during their previous visit to the nest. This result has recently been confirmed using experimental playbacks of begging in this system (McDonald *et al.* 2009) and matches similar effects found in other cooperative (Wright 1998) and monogamous bird species (Wright & Leonard 2002). Therefore, helping in bell miners appears consistent with sensible investment according to the needs of the brood, whether the fitness benefits are direct or indirect.

Interestingly, breeding females experienced higher than average levels of brood begging noise as compared with other classes of individual attending the nest. This may have been the result of nestlings begging more in response to the presence of their mothers, but it seems more likely that this effect arose because breeding females visited nests most often and were therefore more likely to be present when broods were particularly hungry—e.g. during prolonged absences by breeding males and helpers when they were performing other cooperative behaviours elsewhere in the colony, in which breeding females do not participate nor leave the nest area. One consequence of this is that male breeders often arrive back at the nest in the company of helpers (McDonald *et al.* 2007a), and it is only these classes of birds that appear to also use changes in each other’s nest visit rates as an additional indirect measure of brood demand (McDonald *et al.* 2009).

(d) *Conclusions*

The large numbers of male and female helpers of varying relatedness in bell miners provide an excellent test of the effect of kinship on helping effort. Evidence was found for the predicted (but rarely demonstrated) incremental increase in helping effort with genetic relatedness, which

interestingly was driven by individual facultative adjustments in nest visit rates within coterie. However, even ‘unrelated’ helpers within coterie provided substantial investment in broods, which could not be explained by direct fitness benefits, since we detected none of the sex differences in helping predicted by group augmentation in the context of the extreme sex-biased dispersal seen in bell miners. We suggest that high average within-coterie relatedness, even for what we have labelled ‘unrelated’ helpers, might explain these baseline levels of helping as a result of between-coterie kin selection. However, more theoretical and empirical work is clearly needed on the explicit effects of such population structuring in order to confirm this. Nevertheless, all individuals appeared to use the same behavioural rules to regulate their provisioning investment according to brood begging, despite the very different individual fitness benefits accrued by parents and helpers of varying relatedness.

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