



PROVISIONING VOCALIZATIONS IN COOPERATIVE BELL MINERS (*MANORINA MELANOPHRYS*): MORE THAN A SIMPLE STIMULUS FOR NESTLING BEGGING?

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ABSTRACT.—Provisioning calls given by nest attendants immediately before or while they feed nestlings have been recorded in many avian species. Although the adaptive significance of these vocalizations has rarely been examined, their most obvious function seems to be to stimulate begging in blind altricial nestlings. Bell Miners (*Manorina melanophrys*), cooperative Australian honeyeaters, give provisioning “mew” vocalizations that are relatively unusual in being individually distinctive and given during both feeding events and as attendants leave the nest. We show that mew calls stimulated begging during playbacks and that more calls were given if the brood initially did not beg, if the prey was of a type that was difficult to transfer, or both. This is consistent with mew calls being aimed at the nestlings to stimulate begging and, thereby, improve the efficacy of food transfer. However, mew calls were given in 52% of visits as attendants left the nest area, and the probability of calling in this context increased if another group member was nearby. Furthermore, mew call rate per visit increased throughout the nestling period as provisioning rates increased, despite nestlings being increasingly able to attend to other (e.g., visual) cues of impending food delivery. Together, these results suggest that mew vocalizations also have a role in communication between nest attendants. By improving the coordination and social cohesion of helpers and parents around a nest, mew calls may facilitate cooperative activities by the same group of birds away from the nest, such as during dangerous predator-mobbing events. Received 16 July 2007, accepted 4 January 2008.

Key words: Bell Miner, cooperative breeding, food calls, *Manorina melanophrys*, nestling provisioning, social behavior.

Vocalizaciones de Aprovisionamiento en *Manorina melanophrys*: ¿Un Simple Estímulo para el Reclamo de los Polluelos?

RESUMEN.—Las llamadas de aprovisionamiento emitidas justo antes o durante la alimentación de los polluelos por parte de los individuos que asisten el nido se han descrito para varias especies de aves. A pesar de que el significado adaptativo de estas vocalizaciones ha sido examinado sólo en escasas ocasiones, su función más obvia parece ser la estimulación de las llamadas de reclamo por parte de los polluelos ciegos altriciales. *Manorina melanophrys*, un mielero con cría cooperativa de Australia, emite vocalizaciones de tipo “miu” durante el aprovisionamiento, las que normalmente no son distinguibles a nivel individual y son emitidas tanto durante los eventos de alimentación como cuando los asistentes dejan el área del nido. Mediante un experimento de emisión de reproducciones de estas llamadas, mostramos que las llamadas “miu” estimularon el reclamo de los polluelos y que se emitieron más llamadas de reclamo si la nidada no había reclamado inicialmente, si la presa era de un tipo difícil de transferir, o en ambos casos. Esto es consistente con la hipótesis de que las llamadas “miu” tienen el propósito de estimular el reclamo por parte de los polluelos, para así aumentar la eficiencia de la transferencia de alimento. Sin embargo, en el 52% de las visitas, las llamadas “miu” fueron emitidas cuando los asistentes dejaban el área del nido, y la probabilidad de emitir un llamado en este contexto fue mayor si otro miembro del grupo se encontraba en las cercanías. Además, la tasa de emisión de las llamadas “miu” por visita aumentó con el avance del periodo de polluelos en el nido junto con el aumento de las tasas de aprovisionamiento, a pesar de que los polluelos eran cada vez más capaces de responder a otros estímulos (e.g., visuales) para recibir el alimento esperado. En conjunto, estos resultados sugieren que las vocalizaciones “miu” también tienen un papel en la comunicación entre los individuos que asisten el nido. Los llamados “miu” mejoran la coordinación y cohesión social entre los ayudantes y padres en el área del nido, lo que facilitaría las actividades cooperativas por parte del mismo grupo de aves fuera del área del nido, como durante los eventos peligrosos de asedio a los depredadores.

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MANY AVIAN SPECIES give context-specific vocalizations when they discover food; examples include the food calls of many gulliforms (Evans and Evans 2007), gulls (Evans 1970, 1975), grebes (Buitron and Nuechterlein 1993), and passerines (Radford and Riley 2006). These calls appear to be used to attract breeding partners, young, or both to the provisioner or food source. In these contexts, the functional advantage of these vocalizations is clear. More puzzling are vocalizations given by attendants of altricial or semi-precocial young confined to a nest, either during or just before the brood is fed. These vocalizations, which we term “provisioning vocalizations” to avoid confusion with the “food calls” described above, have been recorded in a wide variety of birds, including Burrowing Owl (*Athene cunicularia*; Martin 1973) and many passerines, such as Eastern Phoebe (*Sayornis phoebe*; Madden et al. 2005a, b), Black-capped Chickadee (*Poecile atricapillus*; Clemmons 1995a, b), Great Tit (*Parus major*; Bengtsson and Rydén 1981), Red-backed Thrush (*Zoothera erythronota*; Grabowski 1979), Eurasian Blackbird (*Turdus merula*; Bengtsson and Rydén 1981), and several social species, including White-browed Scrub-wren (*Sericornis frontalis*; Maurer et al. 2003, Magrath et al. 2006), European Bee-eater (*Merops apiaster*; Lessells et al. 1995), Cliff Swallow (*Petrochelidon pyrrhonota*; Beecher et al. 1985), Tree Swallow (*Tachycineta bicolor*; Leonard et al. 1997, Leonard and Horn 2001), and several other species (Welty and Baptista 1988; Clemmons 1995a, b).

Despite their apparently widespread occurrence, little attention has been given to the possible functions of provisioning vocalizations. Most authors assume that they stimulate gaping in nestlings; however, this has rarely been demonstrated (cf. Heathcote 1989; Clemmons 1995a, b; Leonard et al. 1997; Maurer et al. 2003). It has been suggested that provisioning vocalizations increase the efficiency of prey transfers, thereby reducing feeding times of attendants and also, possibly, allowing a relatively standardized assessment of total and within-brood hunger levels (Bengtsson and Rydén 1981, Leonard et al. 1997). Further evidence in support of this hypothesis is provided by species in which provisioning vocalizations are given only when nestlings fail to beg or in which the calls become increasingly rare as the brood ages (Bengtsson and Rydén 1981, Buitron and Nuechterlein 1993, Clemmons 1995b, Leonard et al. 1997). The suggestion here is that visual stimuli are more likely to be used by older nestlings when their eyes have opened, along with other cues such as the sounds of attendants landing and approaching the nest. If begging increases nestling mortality by attracting predators (Haskell 1994, 2002; Leech and Leonard 1997; Briskie et al. 1999), it would follow that nest attendants might minimize their vocalizations at the nest when possible, as these too might increase the risk of nest predation.

In cooperatively breeding species, nests are characterized by the presence of multiple nest attendants (or “helpers”) in addition to the breeding pair (Brown 1987, Cockburn 1998). Examining the costs and benefits of provisioning vocalizations in these complex social systems may be particularly fruitful, because nest attendants form complex groups of related and unrelated individuals that likely receive benefits for helping along very different pathways (Cockburn 1998, Koenig and Dickinson 2004). As such, there may be greater conflicts of interest between nest attendants than are evident in biparental species and, thus, selection for signals at the nest to convey greater information than in biparental

species. One particular cooperative species in which provisioning vocalizations have been previously documented is the Bell Miner (*Manorina melanophrys*; Date 1982, Clarke 1987, Heathcote 1989, McDonald et al. 2007a), a cooperatively breeding honeyeater endemic to southeast Australia. Bell Miners live in colonies of between 30 and up to several hundred individuals (Higgins et al. 2001), and nest attendants provision at a subset of nests within the colony. This subset of birds is referred to as a “coterie” (Clarke 1989). Only breeding females maintain territories; the other colony members forage individually in “activity spaces.” Throughout the colony, cooperation also occurs during defensive mobbing of predators and interspecific competitors (Clarke and Fitz-Gerald 1994). Non-breeding helpers and even breeding males attend multiple nests throughout the coterie (Clarke 1989, McDonald et al. 2007b). Helpers are predominantly male in this species, and many are unrelated to the broods they aid (Painter et al. 2000, McDonald et al. 2007b).

Bell Miners produce distinctive vocalizations, termed “mew” calls (Heathcote 1989), both while feeding broods and, unusually for vocalizations at the nest, also frequently while leaving the nest area (see also Grabowski 1979, Leonard et al. 1997). Previous research on a small sample of nests has found that playback of these calls, production of which is confined to the nest area, elicits nestling begging (Heathcote 1989). Thus, one of the main functions of the vocalization seems to be stimulation of nestling begging, which increases the efficacy of food transfer. However, mew calls also contain significant differences in structure among individuals and between the sexes, and these differences are stable over at least two years and in both contexts (i.e., while feeding nestlings and when leaving the nest area; Heathcote 1989, McDonald et al. 2007a). Thus, it is possible that birds in the coterie use these calls to identify provisioners when the latter are out of visual contact of the nest area, as is likely to occur given the dense undergrowth around nests. The ability to identify group members is an important prerequisite for many hypotheses proposed to account for the evolution of cooperative breeding, especially when groups contain a mixture of related and unrelated helpers (Cockburn 1998, Koenig and Dickinson 2004). Given this, provisioning vocalizations in this species could well be directed at receivers other than the brood.

We investigated the context in which mew calls were given by Bell Miners to identify the benefits associated with their use. We first considered that mew calls could be directed at the brood to stimulate increased begging intensity and, thus, aid in the efficacy of food transfer. This is predicted to lead to (1) few mew calls outside of the context of feeding nestlings, (2) few mew calls if nestlings are already begging at the beginning of a visit, (3) a positive relationship between the number of feeding attempts (i.e., dips of an attendant’s bill) required to transfer prey and the number of mew calls produced in a feed, and (4) a positive relationship between the difficulty involved in transferring prey and the number of mew calls (e.g., sticky or large prey are likely to elicit more mew calls). Alternatively, mew calls could be directed toward the brood to signal individual or group–coterie identity, facilitating future reciprocal collaborations or associations (Beecher et al. 1985, Sharp et al. 2005). If this were the case, we might expect to see a negative relationship between feeding rate (and, thus, familiarity to the nestlings) and the number of mew calls given per visit.

Finally, mew calls may be directed to individuals other than the brood. Under this hypothesis, (1) mew calls may function as a wider-ranging signal of brood hunger, predicted to be given more often when begging is louder, when future feeding behavior (e.g., load size on subsequent nest visits) is expected to be positively correlated with the number of mew calls given at the previous feed, or both; (2) the number of calls given, rather than call characteristics *per se*, may indicate social classes such as breeder, related versus unrelated helper, and so on; (3) mew calls may advertise the nest location to recruit additional helpers (Date 1982), with the number of mew calls given expected to cease or be greatly reduced when nestling age reaches the point where additional helpers are rarely recruited to the brood (6 days; L. te Marvelde et al. unpubl. data); and (4) mew calls may be signals to other nest attendants that help facilitate recognition of group membership and coordinate nest-attendant helping behavior, such that more calls would be given in the presence of other nest attendants.

METHODS

Study populations.—The study was conducted between October 2004 and December 2006 on two Bell Miner colonies located northeast of Melbourne, Australia. The first consisted of ~45 individuals at the La Trobe University Wildlife Reserve (37°42'58"S, 145°03'20"E) and ~135 birds situated near Saint Andrews (37°35'09"S, 145°15'41"E). Individuals were captured with mist nets and fitted with unique color bands before release.

Monitoring of provisioning behavior.—We observed 31 nests; 11 were watched in the 2004 breeding season, 9 in 2005, and 11 in 2006. We found nests by weekly searching likely areas within the study site and following females that were building. Multiple nests of the same breeding pair were sampled over different years on five occasions. Exclusion of these observations did not alter the results obtained, so they were retained in analyses. Each nest was watched for 1–4 h day⁻¹ (mean \pm SE = 3.3 \pm 0.9 h), from a hide, beginning when nestlings were \geq 5 days old, until near the end of the nestling period at day 10. Because the assigned social class of attendants varied with each nest they visited, individuals were included in the database as separate individuals for every nest they attended. Nests were observed with a Kowa TS662 spotting scope fitted with a 20–60 \times zoom eyepiece (Kowa, Tokyo) and filmed using either an analog (CCD-TR1100E; Sony, Tokyo) or digital Hi8 camcorder (DCR-TRY265E; Sony). Hides (mean distance from nest: 15.9 m \pm 0.4; n = 56 different hide locations) and equipment (mean distance from nest: 3 m) were placed far enough away from nests to avoid disturbing provisioning behaviors (McDonald et al. 2007b). In all observations, a period of 10 min between the observer entering the hide and observations beginning allowed any disturbance associated with observer presence to dissipate. For each visit to a nest, we recorded the number of mew calls given while attendants fed nestlings and also the number of calls given in flight after leaving the nest area. Using a combination of dictation recorded in the field and perusal of time-stamped video tapes (for accurate assessment of temporal characteristics of visits), arrival and departure times were recorded to the nearest second, which allowed calculation of both the number of visits and the interval intervals (time between leaving the nest area during the focal visit and subsequently returning). The size (in relation to bill volume)

and the proportion of “lerp” (a sugary secretion from phytophagous Psyllidae) was also noted. Lerp is sticky, and higher proportions within loads lead to problems in transferring prey to broods (McDonald et al. 2007b). During visits, we also recorded the identity and number of other individuals in the nest area (within 2 m of the nest), a space that is likely to be the extent of visual contact in the dense vegetative cover surrounding nests.

Begging vocalizations were recorded with a small tie-clip microphone (Sony ECM77B) placed at the same distance (20 cm) below each nest, connected to a Marantz PMD670 solid-state recorder (Marantz, Tokyo). Calls were recorded at 48 kHz in uncompressed PCM format, and spectrograms were constructed with a 512-point fast-Fourier-transform length (3 dB bandwidth, 124 Hz, with smoothing function enabled), with a Hanning window function and overlap set at 90% (grid resolution: 1.16 ms, grid spacing: 86.1 Hz) in RAVEN, version 1.2.1 (Cornell Lab of Ornithology, Ithaca, New York). Calls were high-pass filtered to remove background noise, and the amplitude of the first bout of begging given by nestlings after arrival of an individual at a nest was measured using the root-mean-square (RMS) algorithm within RAVEN (Charif et al. 2004). Recorded begging amplitudes were not influenced by brood size or age (all $P > 0.05$; data not presented, for brevity). Whether or not nestlings began begging vocalizations before the first mew was given was also recorded for each visit after inspection of spectrograms.

Mew-call playback experiments.—To determine the response of the brood to mew-call playback, a speaker (SRS-A27, Sony) was held 10 cm below nests that contained broods at 6 days of age, and a single mew-call exemplar from a known attendant of each nest was played at natural volume. Volume was determined using the sound-level meter within the Marantz recording unit used above. Following playback, the observer noted any changes in the nestlings' behavior.

Molecular analyses.—During capture, a small (~70 μ L) blood sample was collected from the alar vein. This sample was stored in 70% ethanol and then sexed, and six loci were genotyped according to the protocols outlined in Fridolfsson and Ellegren (1999) and Painter et al. (1997), respectively. This allowed the relatedness of helpers to the breeding pair to be calculated and, thus, vocalization behavior to be analyzed in relation to social class, as defined below. Breeding females were identified as the only individuals that participated in nest construction, incubation, and brooding. To identify breeding males, nests were observed, as described above, for a 2-h period within 48 h after nestlings hatched. Helper males rarely feed during this period, which allows the individual that is provisioning at the highest rate to be identified as the breeding male (Poiani 1993). Paternity assigned in this manner closely matches genetic parentage in this species (Conrad et al. 1998), and extrapair offspring are comparatively rare (4%). Relatedness between individuals was then assessed using KINGROUP, version 2 (Konovalov et al. 2004), which calculated the significance of male helpers being either “related” (primary hypothesis $r = 0.5$, null hypothesis $r = 0$; where r = coefficient of pairwise relatedness) or “unrelated” (primary $r = 0$, null of $r = 0.5$) to either the breeding male or female, based on the ratio required to exclude 95% of 1,000 simulated pairwise comparisons. On the basis of these tests, helpers were placed into one of three social classes: “significantly related,” “significantly unrelated,” or,

if neither test reached significance, “unresolved.” Although female helpers are present in this system, they were comparatively rare in the data set and were excluded from analyses. For simplicity, results are presented using relatedness calculated in relation to the breeding male, given that male helpers are more likely to be related to the breeding male (Painter et al. 2000) and interactions between attendants are more likely to be influenced by paternal rather than maternal relatedness (McDonald et al. 2007c). It is important to note that the results presented do not differ markedly if relatedness to the breeding female or a mean of the breeding pair is used instead.

Statistical analyses.—Data were log or square-root transformed, as appropriate, before repeated-measures analyses of variance (ANOVAs) were used to examine the relationship between the number of mew calls given, using mean values for each attendant at a nest, and the within-subject effects of (1) nestling begging before or after the first mew was given during a visit, (2) presence or absence of potential audiences (e.g., breeding female), and (3) differences in the number of mew calls given when a brood’s initial begging bout occurred before or after the first mew call of a visit. Further, the begging response (RMS amplitude) of nestlings to arrival of attendants with and without an accompanying mew call was also compared as a within-subjects effect, as was the number of calls given by breeders when attending their own versus another nest. Throughout, social class was used as a between-subject factor. Simple contrasts were used to compare responses of related male helpers, which have the greatest access to indirect benefits associated with helping broods, versus other social classes. Analyses of covariance (ANCOVAs) were used to assess the effects of the number of mew calls given by individuals according to social class and of the covariates (1) begging response of broods, (2) number of dips of an attendant’s bill into the nestling’s gape during feeding events, (3) interval interval, (4) load size delivered, (5) proportion of lerp within loads, and (6) attendant visit rate. We used ANOVAs and regressions to assess relationships between the number of mews given as attendants fed nestlings and the number given when they left the nest area, as well as the influence of social class alone, with Kruskal-Wallis and Wilcoxon signed-ranks tests used on non-parametric data. Two-tailed tests and an alpha of 0.05 are applied throughout. Analyses were done using SPSS, version 15.0 (SPSS, Chicago, Illinois). Results are presented as means \pm SE.

RESULTS

Are mew calls directed toward the brood?—A total of 185 h of observation yielded 5,964 visits to the 31 nests by 268 nest attendants. Mew calls were more often given as attendants fed nestlings ($84.9 \pm 1.5\%$ of visits) than when they left the nest area ($52.0 \pm 2.0\%$; $n = 268$). On average, birds gave 1.80 ± 0.06 calls while feeding broods and 0.60 ± 0.03 calls per visit as they left the nest area. However, to avoid potential audience effects (addressed explicitly below), we restricted the data set for all bar-the-audience effect analyses to visits where attendants were alone in the nest area: 2,541 visits by 230 nest attendants at 31 nests. Similar patterns in calls given while feeding nestlings were present in this restricted data set (calls given during $88.4 \pm 1.5\%$ of visits; 1.80 ± 0.06 calls

visit⁻¹; $n = 230$), though the number given as attendants left the nest fell slightly (calls given during $41.0 \pm 2.4\%$ of visits; 0.50 ± 0.03 calls per visit).

If mew calls were being used by attendants to stimulate nestling begging, an increase in begging would be expected following playback of a familiar attendant’s mew call. This was indeed the case. In each of five playback experiments, nestlings lifted their heads and began begging. This response was brief (~ 2 s). Given this, fewer mew calls would be expected if nestlings began begging spontaneously upon an attendant’s arrival. This was indeed the case; fewer mew calls (1.80 ± 0.06 ; $n = 146$ individuals) were given if the brood begged before the attendant gave a mew call than during visits where mew calls were given before begging began (1.95 ± 0.07 ; $F = 3.970$, $df = 1$ and 141 , $P = 0.048$). This relationship was not influenced by social class ($F = 2.068$, $df = 4$ and 141 , $P = 0.088$) or by the interaction between class and vocalization order ($F = 0.856$, $df = 4$ and 141 , $P = 0.492$). However, at least one mew call was usually given in a visit, even when only visits in which the brood were already begging were considered (99.4% of visits; $n = 172$). Despite this, there was no difference between the begging amplitude of broods during visits where they begged before a mew was given (RMS amplitude: 1.105 ± 85 ; $n = 145$) and during visits where the attendant gave a mew first (1.073 ± 49 ; $F = 0.187$, $df = 1$ and 140 , $P = 0.666$), again without influence of social class ($F = 0.557$, $df = 4$ and 140 , $P = 0.694$) or a significant interaction term ($F = 0.495$, $df = 4$ and 140 , $P = 0.739$). This may, at first, seem surprising if mew calls function to stimulate greater begging effort and if begging amplitude is consistently related to hunger (as in most species; e.g., Wright et al. 2002). However, nestlings that begged before any mew call was given do not appear to have gone on to beg at any greater level during that visit. Therefore, mew calls were given to alert nestlings that failed to beg immediately, but the reason the nestlings did not immediately detect the nest visit does not seem to have been closely linked to their hunger level.

Mew calls may also assist in the feeding of difficult-to-transfer prey, and consistent with this was a positive relationship between the number of mew calls given during a feeding bout and the number of dips of the attendant’s bill as prey was transferred to the brood ($F = 74.418$, $df = 1$ and 220 , $P < 0.0005$; Fig. 1A). This result is potentially complicated by a significant interaction term involving the number of transfer dips and social class ($F = 5.105$, $df = 4$ and 220 , $P = 0.001$) and by a main effect of social class ($F = 5.053$, $df = 4$ and 220 , $P = 0.001$; Fig. 1A). It is clear from Figure 1A that the interaction is principally driven by breeding females having a flatter, and related male helpers a steeper (though both still positive), slope of mew calls versus dips, compared with other nest attendants. Given that females and related helpers show opposite relationships here despite similarly high relatedness to the brood, especially compared with unrelated helpers, the biological importance of this interaction is unclear.

Following this result, higher rates of mew calls (and, by extension, dips) would be expected to occur during the transfer of larger or more difficult prey items, such as loads of sticky lerp casings. In support of this hypothesis, there was a significant positive effect of the proportion of lerp in a load and the number of mew calls given ($F = 6.893$, $df = 1$ and 209 , $P = 0.009$; Fig. 1B).

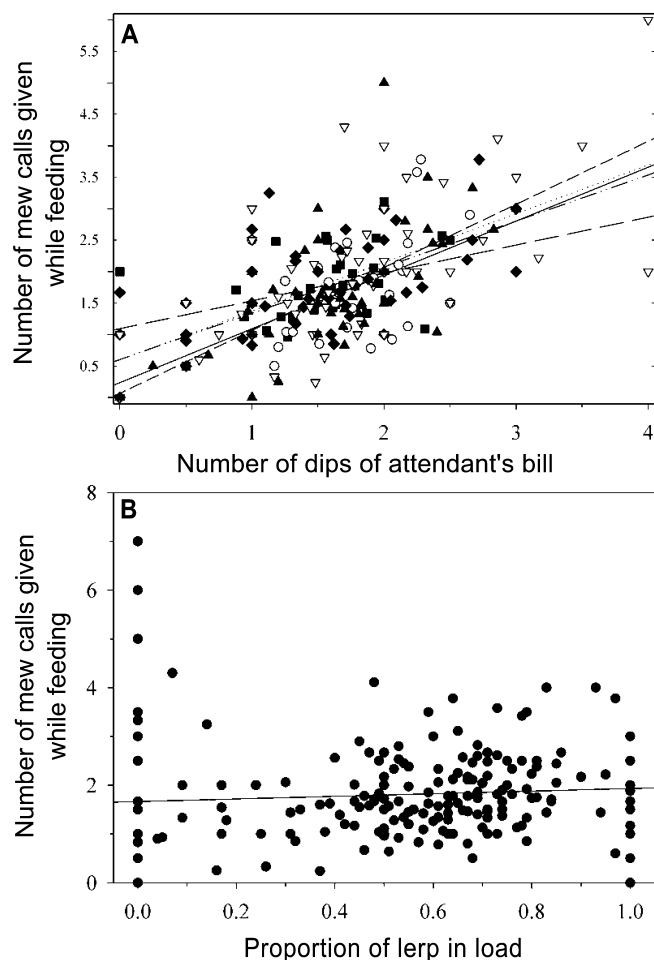


FIG. 1. Number of mew calls given as nest attendants fed nestlings according to (A) the number of times attendants dipped their bills into nestlings' gapes during feeds and (B) the proportion of lerp in loads (number of mews = 0.27 proportion of lerp + 1.66). Lines represent linear-regression results for total effect or (A) per social class: circles and solid line indicate breeding male (number of mews = 0.86 dips + 0.24), squares and line with long dashes indicate breeding female (number of mews = 0.44 dips + 1.09), triangles and line with short dashes indicate related male helpers (number of mews = 1.00 dips + 0.06), inverted triangles and dotted line indicate unresolved male helpers (number of mews = 0.77 dips + 0.60), and diamonds and both broken and dotted line indicate unrelated male helpers (number of mews = 0.73 dips + 0.60).

This was not influenced by social class or by any interaction term ($F = 1.144$, $df = 4$ and 209 , $P = 0.337$; interaction term: $F = 1.029$, $df = 4$ and 209 , $P = 0.393$). This effect held despite the large number of mew calls associated with the few prey loads that contained no lerp at all (Fig. 1B). However, these consisted mainly of invertebrate prey items too large to feed to the nestlings (e.g., orthopterans) and, as with sticky loads of lerp, these data could also be explained by problems of load transfer and the need to restimulate

nestling begging during the extended feeding event. In agreement with this, there was a nonsignificant trend for larger prey loads to be associated with a greater number of mew calls as broods were fed ($F = 3.508$, $df = 1$ and 220 , $P = 0.062$). Neither social class ($F = 2.037$, $df = 4$ and 220 , $P = 0.090$) nor the interaction was significant ($F = 1.785$, $df = 4$ and 220 , $P = 0.133$).

Finally, the mean number of mews given per visit was independent of the mean visit rate of individuals at a given nest ($F = 1.616$, $df = 1$ and 220 , $P = 0.205$), their social class ($F = 1.036$, $df = 4$ and 220 , $P = 0.390$), and the interaction between the two ($F = 0.660$, $df = 4$ and 220 , $P = 0.621$). A negative relationship here might have been expected if relatively unfamiliar brood attendants (to nestlings, using visit rate as a surrogate for familiarity) gave more calls per visit to compensate for their lower visit rate. However, this does not seem to have been the case.

Are mew calls directed to audiences other than the brood?—

If mew calls are directed at receivers other than the brood, one possible function could be to serve as a surrogate for brood demand that reaches a wider audience than brood begging alone. However, contrary to this, begging amplitude was not greater if attendants gave at least one versus no mew calls as they left the nest area (RMS amplitude: called, $1,175 \pm 153$; no call, 946 ± 41 ; $n = 136$; $F = 1.427$, $df = 1$ and 131 , $P = 0.234$). Again, there was no effect of social class ($F = 2.123$, $df = 4$ and 131 , $P = 0.082$) and no interaction between the two factors here ($F = 1.001$, $df = 4$ and 131 , $P = 0.410$). Furthermore, the interval intervals (IVI) of individual nest attendants did not differ according to whether or not they had given at least one mew call when they last left the nest area (IVI [seconds]: called, 427 ± 34 ; no call, 414 ± 26 ; $n = 96$; $F = 0.085$, $df = 1$ and 91 , $P = 0.771$), and again there was no effect of social class ($F = 1.921$, $df = 4$ and 91 , $P = 0.114$) nor any interaction ($F = 1.558$, $df = 4$ and 91 , $P = 0.192$). Likewise, neither the load size (percent bill volume: called, 40 ± 2 ; no call, 42 ± 2 ; $n = 116$; $F = 0.167$, $df = 1$ and 111 , $P = 0.684$) nor proportion of lerp (percent load size lerp: called, 60 ± 3 ; no call, 57 ± 3 ; $n = 116$; $F = 0.745$, $df = 1$ and 111 , $P = 0.390$) differed on the next visit between birds giving mews as they left and those that did not, again without influence of social class (load size: $F = 1.124$, $df = 4$ and 111 , $P = 0.349$; proportion lerp: $F = 1.543$, $df = 4$ and 111 , $P = 0.658$) nor interactions (load size: $F = 1.626$, $df = 4$ and 111 , $P = 0.173$; proportion lerp: $F = 1.543$, $df = 4$ and 111 , $P = 0.658$). Given this, it seems unlikely that mew calls are used by Bell Miners as surrogates for brood demand within the group.

The proportion of visits in which a mew call was given did not differ among the social classes (as feed: Kruskal-Wallis $\chi^2 = 6.193$, $df = 4$, $P = 0.185$; as leave: Kruskal-Wallis $\chi^2 = 7.198$, $df = 4$, $P = 0.126$; Fig. 2A). Likewise, social class also did not influence the number of calls given per visit (as feed: $F = 1.041$, $df = 4$ and 225 , $P = 0.387$; as leave: $F = 1.241$, $df = 4$ and 225 , $P = 0.295$; Fig. 2B). Furthermore, when attending nests other than their own, breeding males did not give a significantly different number of mew calls either when feeding nestlings (calls per visit: own nest, 1.7 ± 0.2 ; other nest, 1.8 ± 0.4 ; $n = 7$; $F = 0.073$, $df = 1$ and 6 , $P = 0.797$) or when leaving the nest area (calls per visit: own nest, 0.20 ± 0.07 ; other nest, 0.4 ± 0.2 ; $n = 7$; $F = 1.970$, $df = 1$ and 6 , $P = 0.210$). Nor was there a difference in the proportion of visits where these males gave a mew call in either context (percent visits with at least one

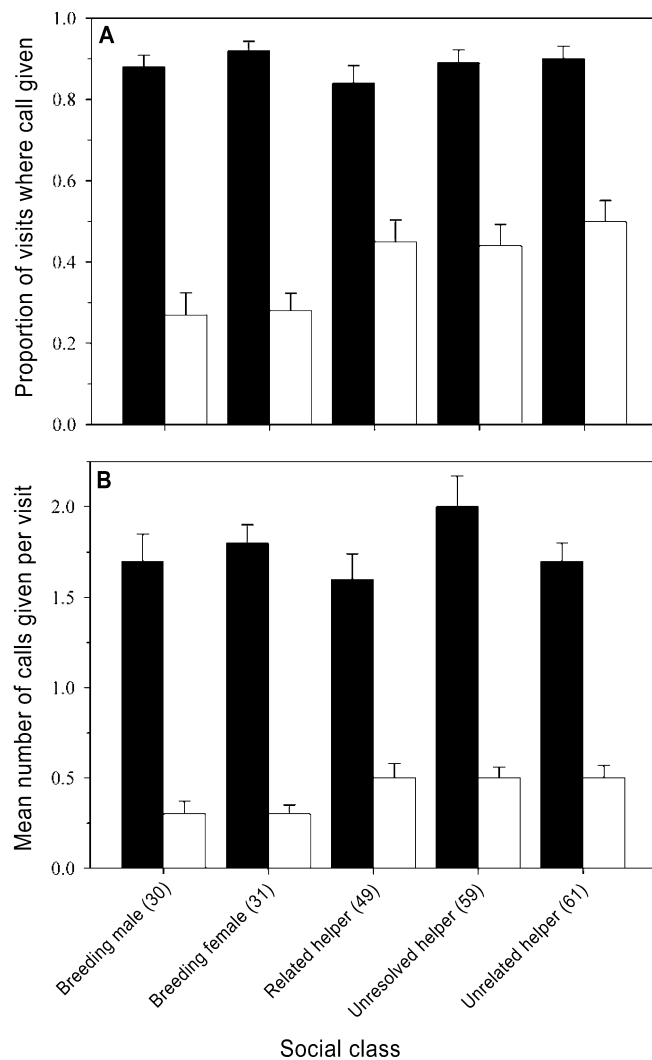


FIG. 2. Mew-call rates per visit: (A) proportion of visits where at least one call was given and (B) mean number of calls given per visit for each social class. Solid bars represent calls given as the nestlings were fed, and open bars represent those given as the bird left the nest area. Error bars represent one standard error, and numbers of individuals sampled from each social class are given in parentheses.

call given as feed: own nest, 91 ± 6 ; other nest, 85 ± 14 ; $n = 7$; percent visits with at least one call given as leave: own nest, 15 ± 6 ; other nest, 31 ± 11 ; $n = 7$; Wilcoxon signed-ranks tests: mew as feed: $Z = -0.405$, $P = 0.686$; mew as leave: $Z = -1.153$, $P = 0.249$. Together, these results suggest that the number or proportion of calls given, *per se*, do not encode social-class identity at a given nest.

Mew calls may function to advertise the nest location to other attendants (Date 1982). Given that the number of helpers attending nests plateaus after six days (L. te Marvelde et al. unpubl. data), a significant reduction or even cessation in mew-call production after this period might be expected. However, nestling

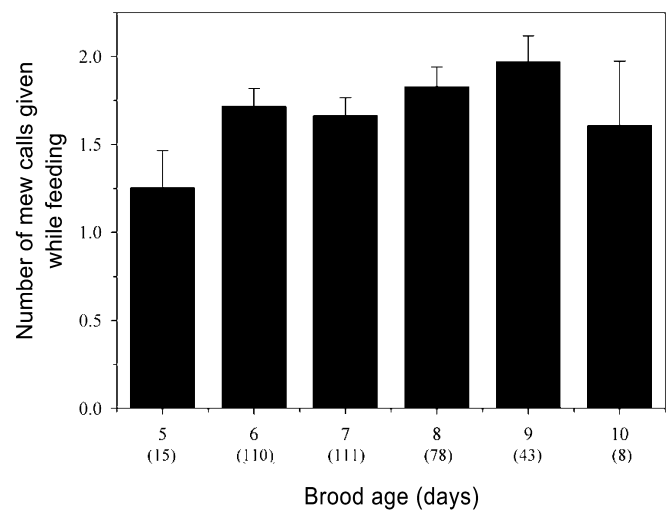


FIG. 3. Mean number of mew calls given as attendants fed nestlings, according to brood age (in days, where 0 is the day of hatching). Error bars represent one standard error, and numbers of visits sampled for each age group are given in parentheses.

age did not significantly affect the number of mew calls given when attendants left the nest area ($F = 3.117$, $df = 1$ and 355 , $P = 0.078$), with no significant effects of social class ($F = 0.332$, $df = 4$ and 355 , $P = 0.856$) or any interaction ($F = 0.441$, $df = 4$ and 315 , $P = 0.779$). We found significant positive effects of nestling age on the proportion of visits where at least one mew call was given either during feeding ($\chi^2 = 17.135$, $df = 5$, $P = 0.004$) or when leaving the nest area ($\chi^2 = 12.276$, $df = 5$, $P = 0.031$) as well as on the number of mew calls given while feeding nestlings ($F = 5.463$, $df = 1$ and 355 , $P = 0.020$; Fig. 3). The number of mews given per visit was, however, not influenced by social class ($F = 0.622$, $df = 4$ and 355 , $P = 0.647$), nor was there any interaction ($F = 0.413$, $df = 4$ and 315 , $P = 0.799$). These relationships were clearly all positive (see Fig. 3) and, thus, in the opposite direction to that predicted if the main function of mew calls is to attract new attendants to nests.

Potential audience effects.—Analyses on the full data set of 5,964 visits identified strong effects of audiences on mew calls (Table 1). More mew calls were given as attendants left the nest area in the presence of either breeding males (calls per visit, present: 0.87 ± 0.05 ; calls per visit, absent: 0.62 ± 0.03 ; $n = 147$) or another helper (present: 0.69 ± 0.03 ; absent: 0.49 ± 0.03 ; $n = 184$), but not in the presence of breeding females (Table 1). When mews given during feeding events were considered, helper presence also had a positive effect (present: 2.14 ± 0.10 ; absent: 1.77 ± 0.06 ; $n = 172$), presence of breeding females a weak negative effect (present: 1.86 ± 0.11 SE; absent: 1.91 ± 0.08 ; $n = 172$), and presence of breeding males no influence on mew-call rate (Table 1). On the two occasions where social class was a significant factor (Table 1), orthogonal simple contrasts revealed that this resulted from breeding males giving fewer calls than related helpers, a result that is difficult to interpret. No interactions between social class and potential audience presence were significant (all $P > 0.05$).

TABLE 1. Results of repeated-measures ANOVAs comparing mew-call production while feeding nestlings and when leaving the nest area, according to the presence of a breeding female, a breeding male, or a helper, with social classes calculated according to relatedness to breeding males. Significant terms are in bold.

	Calls given while feeding			Calls given while leaving		
	F ratio	df	P	F ratio	df	P
Presence of breeding female						
Presence	4.270	1 and 168	0.040	3.392	1 and 168	0.067
Social class	0.043	3 and 168	0.988	4.199	3 and 168	0.007
Presence*class	0.367	3 and 168	0.777	0.551	3 and 168	0.648
Presence of breeding male						
Presence	0.500	1 and 143	0.481	22.063	1 and 143	<0.0005
Social class	0.840	3 and 143	0.474	1.179	3 and 143	0.320
Presence*class	1.881	3 and 143	0.135	0.627	3 and 143	0.599
Presence of helper						
Presence	9.570	1 and 179	0.002	42.874	1 and 179	<0.0005
Social class	0.668	4 and 179	0.615	2.647	4 and 179	0.035
Presence*class	1.654	4 and 179	0.163	1.422	4 and 179	0.228

DISCUSSION

Are mew calls directed solely toward the brood?—The number of mew calls given by Bell Miner attendants during provisioning increased positively with the number of dips of the attendant's bill required to transfer a prey load and with the proportion of loads consisting of lerp, a sticky prey item that is difficult to transfer (McDonald et al. 2007b). Fewer mew calls were given if broods began begging before the attendants arrived at the nest. Together with the evidence that playback of mew calls elicited a begging response (Heathcote 1989, present study), this suggests that one of the main functions of mew calls is to stimulate nestling begging and, thereby, increase the efficacy of food transfer. This is in agreement with previous suggestions regarding provisioning vocalizations in other species (e.g., Bengtsson and Rydén 1981; Clemmons 1995a, b).

Given the possibility of increasing nest predation (Haskell 1994, 2002; Leech and Leonard 1997; Briskie et al. 1999), it is perhaps surprising that Bell Miners gave so many mew calls at nests, with at least one mew call being given during most nest visits (88.4%). This is similar to the percentage of calls given while feeding in Tree Swallows (90%; Leonard et al. 1997) but much higher than that in several other species. For example, Eastern Phoebe give provisioning vocalizations in just 25% of nest visits (Madden et al. 2005a), and Black-capped Chickadees in just 5.9% of visits when the nestlings were already begging (Clemmons 1995a, b), compared with 99.4% of visits in Bell Miners. Furthermore, mew calls were often given as attendants left the nest area (52% of visits), a much higher rate than that in the only other species with a documented rate in this context (Tree Swallows, 10%; Leonard et al. 1997). Moreover, when feeding nestlings, Bell Miners often gave multiple mew calls, averaging 2.4 calls per individual per visit, with a maximum recorded incidence of 28 calls given by an individual during a single visit. Although these calls are not extremely loud (~70 dB SPL at 1 m), they are louder—and audible to human ears

at a greater distance from the nest—than peak nestling begging (mean ~66 dB SPL at 1 m). Therefore, we support the suggestion that mew calls are likely to be highly locatable, at least within the relatively small area in which they are likely to be overheard (Date 1982). However, this potential to attract predators suggests that there must be a clear selective advantage in the use of mew calls.

Despite the evidence that mew calls are aimed at the nestlings to stimulate begging and efficient transfer of food items, mew calls were also frequently given as attendants left the nest area, which suggests other, additional functions. The number of mew calls given during a visit also increased with brood age, even though Bell Miner nestlings are capable of using visual cues to identify incoming feeds by 5–6 days of age (P. G. McDonald pers. obs.). As such, mew calls in the cooperative Bell Miner appear to serve multiple functions beyond their use as a simple stimulus for nestling begging and an aid in prey transfer.

Are mew calls directed to other audiences beyond the brood?—There were few effects of social class on mew-call production, despite the significant differences in individual call structure identified in previous research (Heathcote 1989, McDonald et al. 2007a). This indicates that the number of calls given or the proportion of visits in which individuals call cannot be operating as a simple signal of social class (e.g., “breeder” vs. “helper,” and so on) to other nest attendants or to the brood. It is possible that individual differences in mew-call structure could be learned by other attendants and nestlings and used to identify individuals of different social class. However, this clearly requires greater cognitive abilities. Broods could base their own mew call on those they hear from their nest attendants, thereby providing a cultural pattern of inheritance of mew-call structure within Bell Miner coterie, allowing individuals to classify vocalizations and, thus, attendants on the basis of coterie membership, especially in association with nest attendance (e.g., Beecher et al. 1985, Sharp et al. 2005). Such a need for repeated exposure to train nestlings to the right call structure could explain the continued use of mew calls

beyond the point at which new helpers are recruited to provision broods (~6 days of age). That calling rates per individual increased beyond this age also suggests that mew calls are unlikely to be used simply as a locating beacon for the nest, as previously suggested (Date 1982).

It has also been suggested that provisioning mew calls, and particularly those given when attendants are leaving the nest area, may act as surrogates for temporal variation in brood demand (e.g., McDonald et al. 2007c). This is because a calling bird moving through the coterie is more likely to reach a larger audience and recruit more help than one calling only when at the nest site. However, inter-visit intervals, load sizes, and prey types of individual attendants did not differ according to whether or not they gave a mew call as they left the nest area, which suggests that attendants themselves, at least, did not act as if there were any perceived increase in brood demand. In addition, the experimental playback of increased begging effort has been shown to elicit increased visit rates in different classes of nest attendant in this species; however, changes in visit rates did not correlate positively with changes in the number of mew calls given as these birds left the nest area (P. G. McDonald et al. unpubl. data). Therefore, it seems that there is little evidence to suggest that the function of mew calls in Bell Miners is to broadcast brood demand over a wider area.

It seems unlikely that the mew calls given as birds left the nest area were solely, or even predominantly, directed at the brood. For example, there were the additional calls given by nest attendants when in the presence of another helper or the breeding male (McDonald et al. 2007c, present study), which suggests that mew calls have a social function within coterie. The use of individually distinctive mew calls may increase familiarity between coterie members by transmitting the identity of nest visitors to others out of visual contact with the nest. Such use of vocal communication is likely to be common, given that females nest in thick undergrowth and most birds forage in the (much higher) canopy. Moreover, although the Bell Miner is a social species in that individuals live in colonies, individuals within the colony maintain their own foraging ranges, with only breeding females defending discrete territories (Clarke and Fitz-Gerald 1994). Unlike in many other cooperative species, coterie members do not forage or move through home ranges together and are likely to meet other coterie members only at nest sites and during other cooperative activities, such as predator-mobbing. Individually distinctive calls given at the nest area may increase the ability of a coterie to identify the location and identity of members and, thereby, allow them to work together more efficiently in situations where group cohesion and coordination would be most advantageous, such as during predator-mobbing events. This function would favor strong, repeatable differences among individual calls, as observed previously (Heathcote 1989, McDonald et al. 2007a). The development of coterie-specific calls by coterie members may also be favored, though this has yet to be assessed in this species.

Two additional lines of evidence support this suggestion that cooperative behaviors within coterie are facilitated, at least in part, by acoustic recognition. First, two breeding males that were translocated between colonies were initially tolerated by resident individuals, with instances of resident birds even hopping over

the newly introduced individual to gain access to the same branch without any sign of overt aggression between the two. However, once the newly introduced male vocalized, birds from the resident colony immediately began mobbing the new bird on both occasions (P. G. McDonald pers. obs.). Second, although more mew calls are given in the presence of breeding males and other attendants, this is not the case in the presence of breeding females (McDonald et al. 2007c, present study). This provides further support for a social role of this vocalization, because breeding females maintain distinct breeding territories (Clarke and Fitz-Gerald 1994) and, as such, are unlikely to be part of the wider cooperative behavior of other coterie members away from the immediate nest area. While work continues to demonstrate that Bell Miners pay attention to these differences in very individually distinct mew calls, it seems clear that there is more to the function of these provisioning vocalizations than simply stimulating nestlings to beg upon delivery of food items to the nest.

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