THE FUNCTION OF NEST-CALLS IN THE CHESTNUT-CROWNED

BABBLER (*POMATOSTOMUS RUFICEPS*).

Submitted by Helen Kate Mylne, to the University of Exeter as a thesis for the degree of Masters by Research in Biological Sciences, January 2021.

This thesis is available for Library use on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

(Signature) …………………

ACKNOWLEDGEMENTS

ABSTRACT

Despite the predation risk, many birds emit conspicuous vocalisations at the nest. Five general hypotheses can explain nest-calling: stimulating nestling begging, conditioning offspring for fledging, signalling individual investment, coordinating provisioning events and broadcasting brood needs to other carers. Each have their own predictions for the timing of call emission and receiver response, but studies of call function rarely test them all together. I have investigated nest-call function in the chestnut-crowned babbler (*Pomatostomus ruficeps*), a cooperative passerine whose nest visits are commonly accompanied by 'prompt' calls and the structurally related flight call. Using videos from inside babbler nests, I generated a series of statistical models to determine the function of babbler nest-calls, including the specific function of prompt calls. Nest-calls were emitted in 66% of visits, with prompt calls in 45%. I first used binomial generalised linear mixed effects models to predict if carers would nest-call during a visit, and found them most likely in mid-length visits when the carer brings food for chicks that are already begging when the adult enters. Of visits that contained nest-calls, I found carers emitted prompt calls in medium-sized groups and when the offspring were silent. During long visits, helpers and birds with food were more likely to prompt call than breeders and unladen birds. Considering the response of other birds to visits containing nest-calls, nestlings were more likely to beg during visits with nest-calls than without but showed no preference for the prompt call. In contrast, carers reduced their provisioning rate in response to prompt calls but not flight calls. Together with the observations of reduced prompt calling as correlates of brood hunger increase, I propose that chestnut-crowned babblers use prompt calls to inform co-carers of nestling satiation. More generally, nest-calling appears to play a role in stimulating brood begging and coordinating provisioning events.

CONTENTS

CONTENTS OF TABLES AND FIGURES

INTRODUCTION

Offspring predation represents one of the greatest impediments to breeder fitness. While most species have evolved to invest their reproductive resources in large numbers of low-quality offspring, relying on some reaching adulthood by chance, others invest more heavily in the protection and development of just a few high-quality young (Lack 1947). For the latter, which comprise mostly birds and mammals, we would expect considerable selection for camouflage and cryptic behaviour to disguise the presence of young from predators. Many birds and mammals breed underground or in concealed or inaccessible 'nests' (Nice 1957; Ricklefs 1969; Fontaine and Martin 2006a). Further, species with parental care often evolve alarm calls to alert offspring to nearby predators, encouraging them to remain quiet and motionless (Greig-Smith 1980; Platzen and Magrath 2004; Madden et al. 2005; for a review see Magrath et al. 2010) or seek protection (for example Hollén and Manser 2006). They may also synchronise their nest visits (Raihani et al. 2010), visit less frequently in general (Fontaine and Martin 2006b) and avoid vocalisations that could advertise nest location to nearby predators (Yasukawa 1989). Finally, offspring can quickly learn to recognise characteristic cues of adult arrival at the nest or burrow, such as vibrations and changes in local light levels, avoiding the need for more conspicuous parental signals (Khayutin 1985; Madden et al. 2005). Despite all this, avian nest visits across a wide range of taxa are accompanied by overt displays or vocalisations (Magrath et al. 2010; Haff et al. 2015). Given the apparent predation risk to both adults and chicks associated with calling at the nest, these vocalisations must serve a purpose in order to evolve. Broadly, five hypotheses have been proposed to explain nest-calls: two that suggest offspring to be the targets; and three in which other carers are the intended receivers.

The most frequently invoked explanation of nest vocalisations is to stimulate offspring to beg for food, henceforth the 'begging-stimulation' hypothesis (Table 1). This posits that nest-calls can increase the efficiency of nestling provisioning while simultaneously reducing the need for generalised begging (Kuhlmann 1909; Bengtsson and Rydén 1981). Accelerated begging can increase the rate of information transfer to the adult about brood needs (Kilner and Johnstone 1997; Young et al. 2013), allowing carers to make faster decisions

regarding food allocation to individual chicks based on their immediate need and probability of long-term survival (Clemmons 1995b; Bengtsson and Rydén 1981). While the underlying assumption that begging is costly has not been verified for species with nest-calls, it is widely acknowledged that begging inappropriately in the absence of carers can be energetically demanding (Godfray 1991; Kilner and Johnstone 1997; Kilner 2001; Garay et al. 2018) and can advertise nest location to acoustically sensitive predators (Leech and Leonard 1997; Briskie et al. 1999; Haff and Magrath 2011). Begging-stimulation calls therefore enable the chicks to restrict these costs to only the period when food is immediately available. Three main predictions surround begging-stimulation. Firstly, offspring should become increasingly capable of recognising other cues of provisioner arrival at the nest, such as the nest vibrating as the adult lands, so the use of begging-stimulation calls should decline as the chicks age. Linked to this, nest-calls should not be given when offspring are already begging on carer arrival and no further calls should be given once a call successfully initiates begging. Third, a begging-stimulation call must display a significantly greater power to induce offspring gaping and vocalisations than other conspecific adult calls. Begging-stimulation calls may also be more prevalent when adults are carrying food, although carers may potentially stimulate begging to assess brood needs, regardless of their current ability to satisfy those needs. These predictions are individually supported by observations of nest-calling from a variety of species (for example Bengtsson and Rydén 1981; Grieco 2001; Madden et al. 2005; Table 1), though for few have all three been tested. Clemmons (1995a, b) observed that black-capped chickadee (*Parus atricapillus*) 'squawks' were less common with older and/or gaping nestlings and used playbacks to confirm that nestlings begged preferentially to the squawk even when chick preference for a different call had been reinforced during feeding experiments. Similarly, evidence from both white-browed scrubwrens (*Sericornis frontalis*; Platzen 2004; Magrath et al. 2007) and tree swallows (*Tachycineta bicolor*; Leonard et al. 1997) display greater nest-calling with food and around young chicks, and adult calls stimulate begging and cease once begging is initiated. Despite much literary support for the begging-stimulation hypothesis, when the predictions are not fulfilled, alternative explanations must be considered.

A second, somewhat linked hypothesis, is that adults call to nestlings to prepare them for fledging. Under 'offspring-conditioning', as in begging-stimulation, adults may train nestlings to associate a certain vocalisation with food, but now with the purpose to facilitate fledging (Clarke 1988; Reyer and Schmidl 1988) and/or post-fledging care (Strong 1914; Raihani and Ridley 2007). The greatest difference in predictions from begging-stimulation is that calling should increase with brood age to peak around fledging, then continue through post-fledging care. Adult pied babblers (*Turdoides bicolor*) use a 'purr' call in the nest to which chicks preferentially beg and, at least initially, is more common when the adult is carrying food (Raihani and Ridley 2007), suggesting a begging-stimulation function. However, they are very rarely recorded earlier than 12 days post-hatch and peak on the day of fledging (Raihani and Ridley 2007). These calls are prominent during the fledging process and subsequently in post-fledging care to improve fledgling foraging intake and lead vulnerable fledglings away from danger (Radford and Ridley 2006; Raihani and Ridley 2007). A truncated version of the call is also used to maintain group cohesion (Engesser et al. 2017). Further, Rapaport (2006) and Raihani and Ridley (2008) for the pied babbler purr call, and Clarke (2010) for the white-tailed ptarmigan (*Lagopus leucurus*) maternal food call, suggest that these calls are actively teaching optimal foraging behaviours – a phenomenon rarely proven outside of humans. Offspring-conditioning may also be extended to include facilitating carer recognition and family cohesion, particularly in colonial species, preventing fledglings from getting lost or attempting to solicit food from non-relatives (Beecher et al. 1985; Sieber 1985; Lessells et al. 1995). Sharp et al. (2005) demonstrated that long-tailed tits (*Aegithalos caudatus*) preferentially approach speakers playing the 'churr' calls of kin than non-kin and that cross-fostered chicks develop acoustic signatures more similar to foster parents than genetic kin, indicating a role of vocal learning in call production. Offspring can therefore use nest-calls to learn carer identity and adults can recognise one another at the nest. While for some species this may be the entire function of a nest-call (for example, the post-feeding shiver display of the common babbler, *Turdoides caudatus,* in which adults from larger groups call and display to nestlings after feeding; Gaston 1978a), generally it is

unclear whether kin recognition is a cause or consequence of nest-calling and does not necessarily preclude other functions.

Similarly, signature nest-calls targeted towards adults may enable group recognition, even if it is not their primary function. Adults may use nest-call signatures to identify group members for additional purposes such as signalling their provisioning effort to other carers or increasing provisioning efficiency by improving carer coordination or broadcasting offspring nutritional requirements. The first of these, signalling-investment, poses that individuals may advertise their caring behaviour to co-carers, either to gain future breeding opportunities by elevating their social prestige (Zahavi 1995) or avoid eviction from their natal territory by providing sufficient help to counter their own resource consumption costs (pay-to-stay hypothesis; Gaston 1978b; Kokko et al. 2002). The key prediction of this hypothesis is that carers should target their nest-calling towards breeders and should call at every opportunity, regardless of current brood demand and whether or not they are carrying food. While some evidence is available for signalling-investment by timing nest visits to maximise the probability of having an audience (for example, Mulder and Langmore 1993; Doutrelant and Covas 2007), for vocal signalling it remains scant and circumstantial. Further, it is unclear why calling is required to accompany nest visits in the presence of an audience or verifies investment in their absence. Despite suggestions by Carlisle and Zahavi (1986) that the piercing cries of Arabian babblers (*Turdoides squamiceps*) may inform absent group members of individual provisioning effort, Wright (1997) rejected a role of signalling-investment in this species, as call type, volume and prevalence were independent of provisioner social status or having an audience. Bell miners (*Manorina melanophrys*) also lack evidence for signalling-investment: McDonald et al. (2008) found no evidence of aggression towards subordinates to indicate pay-to-stay behaviour, nor of birds timing their visits for maximum audience. Further, presence of the breeding female, who does not participate in communal activity away from the nest, did not affect 'mew' calling by other birds, whereas helper or breeding male presence increased call rate (McDonald and Wright 2008).

Instead of signalling-investment, these results appear more consistent with coordination-of-care. This hypothesises that nest-calling amongst adults

may improve group cooperation (McDonald and Wright 2008; see also McDonald et al. 2008) and provisioning efficiency, thereby increasing chick nutritional intake and reducing predation. Coordination-of-care may be of particular interest for species whose nest-calls are given partially or entirely upon exit such as bell miners, which call during 52% of nest exits (McDonald and Wright 2008), since these calls cannot be communicating with the brood. The first description of coordination calls is given by Nolan (1978) who suggested that male prairie warbler (*Dendroica discolor*) song given from just outside the nest informs the brooding female of his arrival, encouraging her to exit so that he may enter to feed the chicks. Haff et al. (2015) also invoked the coordination-of-care hypothesis to account for their observations of white-browed scrubwren 'chip-zz' calls, which provide specific details of caller location and activity: calls are more common when moving and in the absence of predators so potentially enable adults to exit the nest unobserved by predators, while the proportion of 'chip' elements increases as they approach. Importantly, chip-zz calls are unrelated to the intensity of brood begging. Although potential further support for the coordination-of-care hypothesis has been cited (for example Breitwisch et al. 1989; Grieco 2001; Neudorf et al. 2013), caution is needed to differentiate it from the related 'offspring-demand' hypothesis. By broadcasting the hunger levels of the brood to other carers, individuals may increase chick nutritional intake or limit energy wasted through unnecessary nest visits. This hypothesis predicts that both group and caller provisioning rate should change following calling visits, and adults should not call prior to nest entry. I have found few examples of this particular behaviour in the literature, the closest being in the vocal communications between male and female northern cardinals (*Cardinalis cardinalis*): the male will arrive at the nest and sing to the brooding female inside, and then elect whether or not to enter and feed the chicks based on how she sings back to him (Halkin 1997).

Although nest-calling is widespread across taxa, with a variety of proposed hypotheses for their intended receiver and function, several uncertainties remain (Table 1). First, it is often unclear whether specific calls 'function' as nest-calls or if any non-alarm conspecific call suffices to perform the intended function (but see Raihani and Ridley 2007). For example, Clemmons (1995b) showed that

black-capped chickadees possess two common nest-calls, of which the squawk was given most to young and/or silent nestlings, which responded with begging. Playbacks showed that nestlings were more responsive to the squawk call over the second most-common nest-call, but as that may be above the audible frequency range for young chicks (Clemmons 1995a) chick preference for the squawk cannot be confirmed. Often, playback experiments only compare a single nest-call with an alarm call, a heterospecific call and/or white noise (for example, Leonard et al. 1997; McDonald and Wright 2008). Further, Magrath et al. (2007) found that nestling white-browed scrubwrens begged comparatively in response to playbacks of conspecific nest-calls and superb fairy-wren (*Malurus cyaneus*) songs. A second source of uncertainty is that few studies have attempted to simultaneously test the competing predictions of each hypothesis: of 25 studies that I found investigating nest-call function, ~50% considered a single hypothesis (primarily begging-stimulation), but typically concluded that at least one other hypothesis showed circumstantial support. For example, bell miner mew calls have been suggested to stimulate offspring begging (Heathcote 1989), reinforce individual recognition (McDonald et al. 2007; McDonald and Wright 2008) and coordinate care and communal activities away from the nest (McDonald et al. 2008; McDonald and Wright 2008), but the competing hypothesis predictions were not explicitly tested. It therefore remains unclear if nest-calls can have multiple functions and the relative support for each one in a given system.

In this study, I have tested the competing predictions of the above five hypotheses (Table 2) to identify the function or functions of nest-calling in the chestnut-crowned babbler (*Pomatostomus ruficeps*). I consider the two most common calls emitted during provisioning events (the 'prompt' call and structurally related flight call), first together, then comparing them against one another. Chestnut-crowned babblers are a 50 g cooperative passerine with sexually monomorphic plumage (Higgins and Peter 2002; Figure 1a) endemic to the semi-arid regions of south-eastern Australia. This largely insectivorous bird breeds in a large, dome-shaped nest (Figure 1b and c) where the breeding female incubates alone for up to three weeks. Following hatching, all related members of the breeding unit, which may comprise up to 17 adults, help provision the offspring until fledging at 21-25 days old (Russell et al. 2010). These helpers are

predominantly philopatric males related to the breeding pair, while females disperse and provide little auxiliary care in their new group (Browning et al. 2012a; Nomano et al. 2019). Helping is driven by kin selection: with only 6% of breeding attempts comprising only a pair without helpers (Browning et al. 2012a) and 79% of males never breeding (Russell 2016), most individuals will only gain reproductive fitness indirectly.

Babbler hatchlings are altricial so require significant maternal brooding for at least the first half of post-hatching development. The breeding female is therefore often in the nest when other carers arrive, and she provisions relatively infrequently compared to the breeding male and helpers (Browning et al. 2012b). Prey, predominantly insect larvae (Lepidoptera and Coleoptera, 61%) and spiders (Araneae, 25%), are brought to the nest singly and are delivered directly to the nestlings or via the breeding female (Browning et al. 2012b). Carers average just over three nest visits per hour (range = 0.1 to 13 visits/h), with faster provisioning to older and larger broods (Browning et al. 2012a; Nomano et al. 2019). They arrive at the nest area as a group but do not all visit the nest every time and seldom enter together (Nomano et al. 2014) or twice in a row (Savage et al. 2017). Given that starvation is the greatest threat to nestlings (Russell et al. 2010) it is unsurprising that male feeding effort is fully additive (Liebl et al. 2016b). In contrast, breeding females reduce their provisioning rate by 15% with each additional carer in the group (Browning et al. 2012b). Helper contributions vary with kinship, brood demand (Browning et al. 2012a; Liebl et al. 2016a) and dominant male provisioning rate, but there is currently no evidence from visit timings to suggest helping is a signal of investment (Nomano et al. 2013, 2015). Instead, helpers improve both the survival and reproductive output of breeders, elevating offspring production in both current and future breeding attempts (Russell et al. 2010).

Chestnut-crowned babblers produce at least 18 distinct calls, categorised into threat calls to alert the group to danger, contact calls to maintain group cohesion and social calls used in aggression and play (Crane et al. 2016). Two structurally similar soft calls often accompany nest visits. Bi-element flight calls of form AB (Figure 1d) are emitted during ~64% of babbler flights to and from the nest and are produced exclusively during or immediately prior to aerial movement

(Crane et al. 2016). In contrast, prompt calls, comprised of the same two phonemic elements (Engesser et al. 2015) but arranged BAB, currently have a less defined function. With 90% of prompt calls emitted inside breeding nests (Crane et al. 2016) and aviary playbacks causing adults to look at a nest (Engesser et al. 2015), the call has been previously suggested to stimulate nestling begging (although comparative chick response to flight calls was not tested; Young et al. 2013).

Here, I will investigate the function of nest-calling using acoustic recordings at the nest for up to 1004 visits by 58 birds in 11 breeding events. At each stage, I compare visits containing nest-calls (flight and/or prompt) with silent visits, then repeat the process considering only visits with nest-calls to compare those with only flight calls against those including prompt calls. I first quantify the proportion of visits with each call type during different phases of nest visitation (at entrance, inside and on exit). Second, I evaluate the level of repeatability of carer nest-calling and prompt calling in particular. Third, I investigate the factors affecting nest-calling and prompt calling inside the nest. Finally, I investigate the effects of nest-calling and call type on brood begging, carer coordination, the interval to the next visit and subsequent provisioning rates. In all models, I attempt to control for the potential confounding influences of time of day, visit duration and female presence on the nest. This study represents amongst the first to my knowledge to test all of the main hypotheses for nest-calling simultaneously (Table 2).

Table 1: Tests and functions of nest-calling. This non-exhaustive table summarises the key hypotheses tested, the approaches used and the findings of studies whose specific aim was to test the function of nest-calling. Note that most studies test a single hypothesis, but there is evidence to suggest that multiple hypotheses account for nest-calling within and among species. I generally use the term nest-calls, unless specific other names are provided. Unclear sample sizes are indicated with a question mark. All species listed are bi-parental or cooperative breeders, with the latter denoted with *. Sample sizes must exceed 5 nests to be included.

Species	Hypothesis	Approach	Findings	Reference
Black-capped chickadee (*Parus atricapillus*)	begging stimulation	• Observations (n=620 nest visits, 7 nests). • Playbacks of squawk call + 2-3 other conspecific and 1 heterospecific throughout development on >35 nestlings.	Squawk call most common nest-call (68% visits to young chicks, declining to 20% for old). Squawks are rare without food or if chicks are already begging. Begging responses to this call increase with age relative to others and most heterospecifics.	Clemmons 1995a, b.
Tree swallow (*Tachycineta bicolor*)	begging stimulation	• Observations (n=658 visits to 11 nests, 620 with food). • Playbacks nest-calls vs white noise/silence (n=16 nests 3-5 days old, 13 at 14-17 days).	Call more with food and before feeding; decrease from >60% of visits to <25% with increasing chick age. Chicks begged in response to nest-call playbacks but not white noise or silence.	Leonard et al. 1997.
White-browed scrubwren (*Sericornis frontalis*)*	begging stimulation	• Observations (n=456 visits, 45 nests). • Playbacks 6 stimuli (18 broods): 3 conspecific, 2 heterospecific, 1 predator.	Nest-call in 83% of visits, declining from 100% to ~40% as broods age. Less calls when chicks already begging. Chicks beg more to conspecific nest-calls than contact calls, but also to fairy-wren song (similar to nest-calls but not contact calls); do not beg for alarm calls.	Platzen 2004. Magrath et al. 2007.

The function of nest-calls in the chestnut-crowned babbler (*Pomatostomus ruficeps*). *HK Mylne, MSc by Research 2020.*

Species	Hypothesis	Approach	Findings	Reference
Black-headed grosbeak (*Pheucticus melanocephalus*)	begging stimulation and parent-offspring recognition	• Nest observations (n=21 broods?) • Playbacks: parents vs. stranger songs to 10-17-day old broods (n=5); and maternal songs to fledglings (n=6 broods?).	Chip calls routinely given during visits. Start in incubation and continue post-fledging. Nest singing increases as broods age. Nestlings emit more contact and hunger-distress calls during the stimulus than before, especially to parents. Fledglings show significant tendency to approach the speaker, nestlings do not.	Ritchison 1983.
Cliff swallow (*Hirundo pyrrhonota*)	parent-offspring recognition	• Observations (n=? nests) • Parent vs stranger playbacks (n=6 broods 9-days old, 11 broods 18-days old).	Nest-calling more common with young nestlings (~100% in first week). By fledging, offspring respond more by antiphonic calling to playbacks of parents than strangers.	Beecher et al. 1985.
Bell miner (*Manorina melanophrys*)	begging stimulation and coordination of natal care	• Nest observations (n=5964 visits, 268 birds, 31 nests). • Playback mew call to 5 broods of nestlings, no control call.	Mew calls in >99% of visits (85% during feeding, 52% on exit). Increased with food, brood age and when other carers nearby. Chick hunger reduced calling during feeding but not on exit. No effect on time to next visit. Chicks beg in response to playbacks if silent, but do not increase intensity if already begging.	McDonald and Wright 2008. (see also McDonald et al. 2008).
Northern mockingbird (*Mimus polyglottos*)	coordination of natal care	• Observations (n=1005 visits to 14 nests).	Males peep call to signal arrival at the nest to the female brooding inside; upon which the female typically vacated the nest allowing the male to enter.	Breitwisch et al. 1989.
Carolina wren (*Thryothorus ludovicianus*)	coordination of natal care	• Observations (n=15 pairs, 18 nests, 193 male visits).	34% of male visit entries included song. Males sang more on exit when female absent (55%) than when present (33%). No brood age effect.	Neudorf et al. 2013.

Species	Hypothesis	Approach	Findings	Reference
Northern cardinal (*Cardinalis cardinalis*)	coordinate natal care and inform of offspring demand	• Observations (n=25 broods, 22 birds in 13 pairs, total 491 h).	Male nest entry depends on female vocalisations from inside the nest and vocal responses to his calls.	Halkin 1997.
Arabian babbler (*Turdoides squamiceps*)*	signalling investment	• Nest observations (n=7990 visits, 27 broods, 139 birds, 17 groups).	Nest-calling not influenced by carer sex or status; not influenced by presence of others.	Wright 1997.
Pied babbler (*Turdoides bicolor*)	begging stimulation, facilitation of fledging and post-fledging care	• Observations pre- and post-fledging (n=30 broods, 9 groups). • Playback experiment of purr calls & contact calls (n=12 broods). • Supplemental feeding with divisible vs indivisible food sources (n=10 experimental pairs).	Purr calls during nest visits increase with chick age and continue post-fledging. After fledging, non-feeding purrs more frequent before moving foraging patch and after alarm calls, and fledglings highly responsive. Older chicks beg in response to playbacks of purr but not contact calls. Feeding purr calls more common when divisible supplemental food provided in presence of fledglings.	Raihani and Ridley 2007. Radford and Ridley 2006.
Bank swallow (*Riparia riparia*)	fledging facilitation and parent-offspring recognition	• Observations (n=16 nests, every 3-6 days, total 200 h). • Acoustic analyses (n=6 calls from 20 adults). • Playbacks of parent vs stranger calls to offspring of 20-24 days (n=17 broods).	Highly variable nest-calls most commonly accompany visits to young chicks ~100%, declining to ~25-30% for old chicks; used during fledging. Adult calls show potential for individual signature. Chicks respond with antiphonic calling more to playbacks of own parents than strangers.	Sieber 1985.

Table 2: Key predictions of hypotheses for nest-call function and rationale.
Begging-stimulation proposes that nest-calling serves to improve the efficiency
of food transfer. Over time, offspring learn mechanical signals of carer arrival and
make nest-calls redundant, causing their use to decline. Offspring-conditioning,
including carer-offspring recognition, proposes that nest-calls serve to improve
the coordination and efficiency of post-fledging care; so all else being equal,
calling should increase towards fledging when signals need to be learned and
will result in measurable impacts on post-fledging care and/or parent-offspring
recognition. The signalling-investment hypothesis requires that carers signal
their contribution to remain in the group or guide partner choice. Coordination-
of-care proposes that nest-calling informs other carers of nest arrival, which can
serve to synchronise or stagger nest arrival, and/or departure from the nest area.
Finally, under the offspring-demand hypothesis, carers inform each other of the
hunger level of nestlings, and serves to alter visit intervals or rates.

Hypothesis	Predicted effect with nest-calling				
	chick age	**chick hunger**	**with food**	**presence of others**	**main response**
begging-stimulation	negative	negative	positive	no effect	increase begging
offspring-conditioning	positive	no effect	no effect	no effect	improved post-fledging care
signalling-investment	no effect	no effect	no effect	positive	partner choice
coordination-of-care	no effect	no effect	no effect	positive	influences co-carer nest arrival/ departure
offspring-demand	no effect	positive/ negative	positive	positive	changes co-carer nest visitation intervals/rates
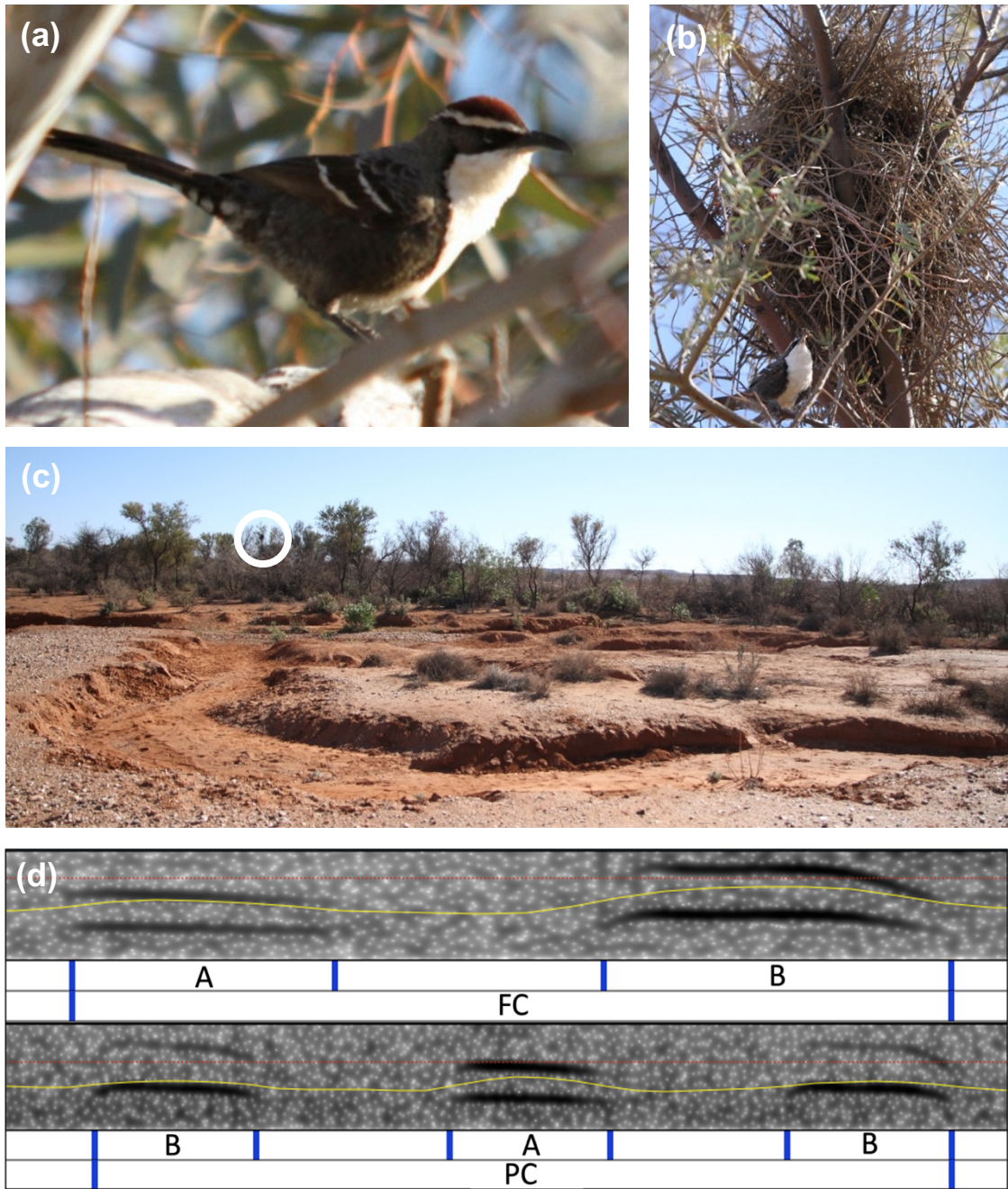
Figure 1: Chestnut-crowned babbler behaviour. (a) Adult chestnut-crowned babbler. **(b)** Nests are dome shaped, with a tight entrance hole near the top, typically positioned in **(c)** a tall shrub or tree. **(d)** Nest-calls include flight calls of form AB and prompt calls of form BAB; A elements have a fundamental frequency of ~1450 Hz and duration of 0.090 s) while B elements have a fundamental frequency of ~1800 Hz and duration of 0.10 s).

METHODS

STUDY SPECIES AND SITE

With a population spread across a large geographic area (10^6 km^2; Higgins and Peter 2002), mostly in New South Wales (Barrett et al. 2003), chestnut-crowned babblers are classed as Least Concern on the IUCN Red List of Threatened Species (BirdLife International 2016). They display fission-fusion sociality, living in large social groups of 3-23 adults (average 12), which fraction into 1-4 smaller breeding units (70% form two) comprising 2-17 adults (average 7.5) during the nesting season (approximately July to December; Russell 2016). Most units will have only one breeding female, and 1-4 (mean 1.3) breeding males. The remaining group will comprise up to 13 non-breeding males (90% of nests have ≤8) and six non-breeding females (Russell 2016). Between 2007 and 2008, breeding unit composition showed 89% repeatability in membership (excluding deaths; Browning et al. 2012a), but close familial ties within social groups facilitate some annual member turnover (Russell 2016).

The field site is located at the Fowlers Gap Arid Zone Research Station (Figure 1c): a 64km^2 area of open bluebush and saltbush chenopod shrubland in New South Wales (141°43'E, 31°05'S). The area receives <250 mm of rainfall in 63% of years and has a breeding season temperature range of 0-45 °C (Russell 2016). Chestnut-crowned babblers prefer areas of low open shrubland with relatively large amounts of vegetative cover from predators, and some tall trees for nesting (Portelli et al. 2009). In 2016, the study site was inhabited by approximately 600 adult babblers in 35-85 breeding units (0.5-1.5 km^{-2}) from 25-55 social groups (Russell 2016), grouped around runoff channels where the scant vegetation is thickest. They are mildly territorial with high plasticity in response to rival groups, with those in territories of low predation risk displaying greatest aggression (Sorato et al. 2015).

RECORDING OF BEHAVIOUR AND VOCALISATIONS

Nests were identified by their distinctive dome-like shape with an entrance hole near the top (Figure 1b), and those in good condition or displaying signs of recent maintenance (fresh building or lining) were investigated further. We determined if nests were currently in use for breeding through physical examination and the

presence of eggs or nestlings. When none was present, we monitored potential roost nests at dawn and dusk to observe whether birds entered or exited. Once we had identified potentially active nests, we set up passive integrated transponder (PIT) decoders to identify specific individuals entering and leaving (demonstrated to be an effective monitoring technique for this species by Nomano et al. 2014). Each bird is microchipped at 10 days old with a PIT-tag, enabling their activity and location to be monitored whenever they pass through the nest entrance for remote identification of individuals and classification of age, sex and dominance status.

Provisioning behaviour was recorded in 2007 and 2008 using 10 mm diameter MO-S408 pen cameras (Misumi Electronics Corporation, New Taipei City, Taiwan) positioned inside the nest, set by Russell and Browning. These cameras were set up to either run continuously, or discontinuously for 60 s at a time following a bird registering as having passed through the nest entrance on the PIT-tag decoder. Notably, this means that during discontinuous videos, if an interval of more than 60 s passed between adults leaving and entering, any vocalisations given on nest approach were not recorded.

Additional field observations and playbacks were performed during the 2019 breeding season. Details for these protocols are available in Appendix 1 but the results will not be analysed here.

VIDEO ANALYSIS

To assess whether variation in calling behaviour reflects the context of emission, I examined the physical and vocal behaviour of both adults and nestlings to determine the response of each to the behaviour of the other, using the 2007 and 2008 video evidence described above. This included all flight and prompt calls made within the nest, and where possible any produced in the two seconds prior to entry and following nest exit. We extracted data from a total of 17 videos from 11 breeding attempts by 10 groups, totalling 24 hours and 38 minutes of footage. This covered 962 nest entries by 51 PIT-tagged birds, and an additional 42 entries by unidentified birds in seven groups. I excluded all untagged birds from my statistical models due to additional uncertainty in their timings and identity. For 16 of the 17 videos coded, I also extracted all begging calls in the 2 s prior

to, and 5 s following, adult entry. I used the begging times to determine first whether a beg was recorded within 1 s before or after the nest entry, and then whether begging was recorded in response to adult calls.

To code the videos, I first played them in VLC media player (Version 3.0.8 Vetinari, Intel 64bit) to identify any faults in the PIT-tag data, and to record physical behaviour and contextual information such as the prey item being brought, which I crosschecked against observations from Browning (2012b). I then converted the video MP3 audio into WAV format and loaded them into Praat (Version 5.3.55) for acoustic analysis. We used both visual and auditory inspection to identify any calls comprising A and/or B elements and recorded the temporal boundaries of each element and call. While recording directly in WAV would have produced higher quality recordings, for this thesis I was only interested in the timings of call emission, which should not have been affected by recording quality, and comparisons by Doyle and Russell (unpublished 2020) indicated no difference in measured frequency parameters between WAV and MP3-WAV converted recordings.

Having identified all calls, I then extracted the start and end times from the recordings (using a Praat script produced by Crosswhite [date unknown] and modified by Antoniou in 2013 and Coye in 2019). I constructed all of my data frames in Excel (version 16.39). I counted the number of calls per nest visit and converted them to binomial data indicating whether or not a call was produced in each of three visit phases: entry, inside and exit, respectively referring to the two seconds prior to nest entry, the time while the bird was inside the nest, and the two seconds after the bird left the nest. To avoid double counting calls produced while multiple birds were in the nest simultaneously, I assigned all calls to the most recently entering bird, apart from when one bird was inside the nest and another was leaving, in which case the calls were assigned to the exit phase of the leaving bird. Full details of this process are provided in Appendix 2. It should be noted that while call times were measured to 0.000001 s of precision, entry and exit times could only be determined to the nearest second.

A total of 1004 visits were recorded from 51 tagged birds (96%) and one or more untagged birds in each of seven groups (4%). Of these, the two seconds prior to entry was visible and audible for 650 visits. The number of visits per bird

ranged from 1 to 59 (mean ± standard error 17.31 ± 0.60, median 14.0, IQR 15.0). Visits by adult male birds were the most frequent, with dominant males and adult male helpers making up 27% (11 birds caring for 10 broods) and 26% (14 birds caring for 7 broods) of recorded visits respectively. Dominant females contributed a further 19% of nest visits (11 birds caring for 11 broods). Yearling helpers contributed a total of 24% of the visits, split evenly amongst males and females (males 9% made up of 8 birds helping at 6 nests, females 9% made up of 3 birds each with a separate brood, and 3 yearling helpers of unknown sex caring for 2 broods contributing to 6% of visits). Adult female helpers contributed the least with only 3 visits recorded from a single bird in one group, while untagged birds made up the remainder of the visits. The dominant female was already present in the nest when another bird arrived for 31% of visits (n = 251, out of 816 visits by birds other than the dominant female). Proportions of visits per bird with nest-calls in each phase are available in Table 11 in Appendix 3.

Of the 1004 total visits recorded, food was brought in 78% (785, plus 30 visits where video quality was insufficient to be sure), with caterpillars the most common (255), followed by spiders (135), beetle larvae (133), adult insects (80) and reptiles (10). Unidentified food items were brought on 172 occasions. Prey item size estimates (data from Browning et al. 2012b) ranged from 0.25 to 6 beak volumes (median 1, mean ± standard error 0.90 ± 0.022). When food was available, for over half of the recorded visits the chick ate the food directly (72%), followed by the dominant female taking the food from the provisioning bird and then passing it to the chicks (19%), so in total the chicks ate the food brought on the vast majority of occasions (91%). The remaining visits comprised 22 (3%) false feeds in which the adult enters with food but then consumes it, 17 (2%) in which the dominant female ate the food herself, and 34 (4%) for which the video quality was insufficient to determine the method of prey transfer. Full details of proportions of visits with each call type in each visit phase depending on the prey item or brooding female presence are available in Table 12 in Appendix 3.

For the statistical models I restricted these data to include only visits by tagged birds which were not adult female helpers, and which had complete data regarding visit timings and whether or not the bird had food (n = 938).

STATISTICAL ANALYSIS

I performed all statistical analyses in *R*, version 3.5.3 and *R* studio, version 1.1.463 (R Core Team 2020). All figures were produced in *ggplot2* (Wickham 2016). All linear and generalised linear mixed effects models (LMMs and GLMMs) I performed in the package *lme4*, version 1.1.23 (Bates et al. 2015).

FREQUENCY OF FLIGHT AND PROMPT CALLS AT THE NEST

To compare the frequency with which nest-calls are emitted, I calculated proportions of visits per bird in which flight and prompt calls were produced in each of the three phases. This produced one value per bird (n = 58) for each visit phase indicating the proportion of visits in which they emitted no call, only flight calls without prompt calls, or prompt calls either with or without flight calls. I subsequently compared the proportion of visits containing each call type across the entry, inside and exit phases. For all comparisons I restricted these data to include only birds for which more than three visits had been recorded (n = 51), and further restricted it when considering the entry phase or entire visit to only birds for which more than three of their entries had been captured on camera (n = 49). For comparing the distribution of call types across visit phases, I used Kruskal-Wallis tests with Tukey post-hoc comparisons in *R* package *PMCMR,* version 4.3 (Pohlert 2014). I then performed a Mann-Whitney *U* test to compare flight calling only against all visits containing prompt calls at each phase of the visit.

INTER-INDIVIDUAL VARIATION

To test the consistency of flight and prompt calling by individuals during nest visits I ran a repeatability analysis, which partitions variance into within- versus among-individual variation (Stoffel et al. 2017). This analysis was run using *rptR*, version 0.9.22 (Stoffel et al. 2017) with 1000 repeats of parametric bootstrapping and 1000 model permutations to generate confidence intervals and standard errors. I included brood age and whether or not the bird was carrying food as fixed effects in all analyses. For each of the entry, inside and exit phases of the visit, and for the visit as a whole, I generated two estimates of repeatability: one for if birds would nest-call or not and one for if they would emit a prompt call specifically

within visits containing nest-calls. When considering the entry phase or entire visit I restricted the data to include only visits for which the video ran continuously (n = 629), whereas for the inside and exit phases I used all visits for which information was available about whether or not the bird had food (n = 974). These sample sizes were reduced by excluding visits lacking calls in the relevant phase when testing the repeatability of prompt calling against flight calling (entire visit = 442, entry = 211, inside = 441, exit = 214). I repeated all analyses excluding the dominant female and adding her presence in the nest as an additional fixed effect to ensure that repeatability was unaffected by an audience.

FACTORS AFFECTING THE PROBABILITY OF NEST-CALLING

To determine how visit variation might affect whether a flight and/or prompt call was produced, I generated a minimal adequate binomial GLMM fitting whether or not a call was emitted as the response variable. I investigated fixed effects of: carer sex, age and status; the age and size of the brood; the number of carers in the group; if the adult brought food; the presence of the dominant female in the nest; the frequency with which birds had recently entered the nest and time since the chicks were last fed; and whether or not the chicks were already begging when the adult entered. I also tested any interactions with the potential to provide a biologically relevant explanation of behaviour. I used adult identity, brood identity and the date as random effects. Date was fitted as a random effect because babbler groups do not breed synchronously and therefore on any given date there could be a multitude of groups raising offspring of varying ages. There would therefore be no predicted consistent effect of date on nest provisioning, but it may still account for some of the variation, due to differing weather conditions for example. Random effects were crossed due to some exchange of birds amongst groups between years. I used basic model simplification to exclude non-significant variables based on Chi-squared tests.

Of the 1004 nest visits recorded, I excluded all visits by untagged birds (42) and by adult female helpers (three visits, all by the same bird) to avoid confounding of sex, age and status variables. I also excluded any visit for which a decoder error prevented calculation of the visit duration, or it was unclear if the adult brought food. Having determined the variables predicting general nest-

calling, I repeated the process excluding any visits with no flight or prompt call recorded to determine which variables predicted whether nest-calls would include a prompt. In total this left sample sizes of 938 visits by 50 individuals to test the probability of general nest-calling, and 464 visits by 47 individuals for prompt calling.

To predict whether a call would be emitted in each visit, I tested main effects of variation at the group, individual and visit levels. Group level variables included the number of birds that were recorded provisioning the brood during the time of the video (carer number); the number of nestlings present (brood size); and the number of chicks per carer (brood size:carer number ratio). At the individual level, I tested the effects of provisioner sex, age and breeding status, determined using plumage and molecular analyses from blood samples (see Rollins et al. 2012). At the visit level I considered whether or not the focal bird was bringing food to the nest; the estimated age of the chicks based on the average number of days since each egg hatched (brood age); the time of day and duration of the visit (visits exceeding 60 s were set to a maximum value of 60); and whether or not the dominant female was present in the nest, for which I excluded all visits by dominant females. To consider the role of chick hunger levels in adult calling behaviour, I tested the role of begging calls in the second before and after nest entry, the time since the chicks were last fed (inter-visit interval) and the number of visits per minute in the past 30 minutes of the day (provisioning rate). To account for the ability of larger groups to provision faster, both inter-visit interval and provisioning rate were mean centred by brood identity, such that the mean value is zero for each group in each year.

EFFECTS OF NEST-CALLING ON BEGGING BEHAVIOUR

Having determined which variables predict calling and call type, I tested the effects of nest-calls on adult and offspring behaviour. If the prompt call aims to solicit chick begging, then we would expect begging to increase for prompt calls but not flight calls. Due to camera positioning, I could only consider vocal begging rather than visual, but visible chicks never gaped silently so vocalisations alone should be sufficient to determine brood response. For all of the response analyses I used individual identity nested within group identity as random

intercepts. These random effects were now nested as only two of 51 identified birds exchanged groups, but this had no qualitative impact on model output. As when testing the predictors of calling, I also tested those interactions for which there was a potential biologically relevant explanation of their impact.

Before looking for differences in begging stimulation between call types, I first tested for predictors of whether chicks would already be begging when the adult entered. I performed a binomial GLMM with a response of whether the chicks would beg or not within the one second on either side of adult nest entry, testing variables predicted to be correlated with brood hunger.

Next, using only visits in which chicks were silent on adult entry, I compared the probability of nestlings begging during the visit depending on whether the adult gave no call, a flight call only, or prompt called inside the nest. I also tested the effects of brood size, carer number, brood size:carer number ratio, brood age, time of day, visit duration, inter-visit interval, provisioning rate and if the adult brought food to examine whether they affected chick response either alone or in interaction with call type.

To further test whether begging differed between call types, I used LMMs to compare the speed of chick response, testing all of the same fixed and random effects as in the binomial GLMM above. Again only using the visits in which the chicks did not beg during the second on either side of nest entry, I compared the time between starting the first flight or prompt call of a visit (which had to occur within 2 s of nest entry) and starting the first beg (within 5 s of entry). Further, to test for a difference in begging duration after flight and prompt calls, I calculated the proportion of time spent begging between the start of the call and the time 5 s after adult entry. I limited recordings of chick begging to 5 s due to the randomness of young chick vocalisations and the inherent link between brood hunger and visit duration (shorter visits when food brought to the nest: Mann-Whitney *U* test W = 38594, p < 0.001, n = 938 visits, no qualitative change when excluding visits exceeding 60 s duration). Results for entry begging and begging speed are presented in Appendix 5.

EFFECTS OF NEST-CALLING ON GROUP PROVISIONING BEHAVIOUR

Finally, I tested whether adult behaviour changed following visits with prompt calls. I first used binomial GLMMs to determine whether calling affected the probability of visits overlapping with one another or if the next bird would bring food (Table 15, Appendix 5). I then used LMMs to compare the role of calling, and the interaction of calling with variables predicted to be correlated with brood hunger, in the time until the next bird entered the nest and the provisioning rate of the group in the following 10 minutes. When considering the response to nest-calling, provisioning rate counted only visits in which an adult brought food to the nest. Inter-visit interval and provisioning rate were mean centred by brood identity and I excluded any visits which were the last of the day.

Within all models, I elected not to adjust *P*-values to correct for the effects of multiple testing in order to avoid increasing the risk of type II error. When investigating a large number of variables and exploring data, *P*-value adjustments would risk missing any weakly significant effects that add to the overall picture (Nakagawa 2004). Further, the level of adjustment would differ between the sections depending on the arbitrary number of analyses contained in each, so the level of significance would be affected by the section of analysis. For a discussion of the use of *P*-value adjustment when testing a variety of related measures, see Feise (2002).

RESULTS

FREQUENCY OF FLIGHT AND PROMPT CALLS AT THE NEST

Overall, 66% of nest visits were accompanied by at least one call, with 21% containing a flight call only, 14% a prompt call only and 31% both. On average, individuals called at the nest entrance, inside the nest and on leaving the nest during 35% (± 24% SD), 51% (± 27% SD) and 27% (18% SD) of nest visits, respectively (Table 3a, Figure 2). Calling was most common inside the nest, which might be due to the longer time period or reflect a response to the social situation. That the frequency distribution of flight versus prompt calling varied across the phases of nest visitation suggests that the social situation has at least some bearing on nest-calling. Notably, flight calls were given with similar probability on entry and exit as well as inside and exit, whereas prompt calls were given at a comparable frequency on entry and inside, but more rarely on exit. These contrasts led prompt calls to be more commonly given than only flight calls at nest entrance and inside the nest (Table 3b).

INTER-INDIVIDUAL VARIATION

Further supporting the suggestion that nest-calling is modified by social environment, repeatability analyses suggest that variation in individual propensities to nest-call was generated mainly by within- rather than among-individual variation (Table 4). Most notably, although significant repeatability was detected, individual identity explained only ~7% of the variation in nest-calling generally and 9% of the variation in prompt calling specifically across the visit. Separating the analyses to consider each visit phase individually suggested that carer identity was a better predictor of general calling during nest entrance and inside (repeatability estimates = ~14-16%) than on exit (estimate = 7%). In contrast, the prompt call repeatability was least inside the nest (~11%) compared to entry and exit (17-21%). These results suggest that although calling is more common inside the nest and that some of this variation is explained by individual differences, there is significant scope for plastic response to the social environment.

FACTORS AFFECTING THE PROBABILITY OF NEST-CALLING

Carer emission of flight or prompt calls while inside the nest was significantly influenced by a combination of social and abiotic environmental factors (Table 5; Figure 3; Figure 11, Appendix 4a). Nest-calling was most common in visits of intermediate duration (Figure 3a), increased fivefold when the carer entered with food (Figure 3b), and was relatively uncommon when the female was brooding (Figure 3c). When present, the dominant female will generally take the food directly from the provisioner (Young et al. 2013). The dominant male and helpers showed a threefold increase in the probability of nest-calling throughout the nestling period, although the breeding female showed a trend for the reverse pattern, generating a significant carer status by brood age interaction (Figure 3d). In addition, there was a tendency for nest-calling to increase throughout the day and when the brood was silent within 1 s of carer entry, but with no additional effects of brood size or carer number (Table 5).

Comparing directly the probability of prompt versus flight calling had a marked impact on the predictors (Table 6; Figure 4; Appendix 4b). Firstly, there was no longer a main effect of food, although birds were more likely to prompt call with food during long visits (Figure 4a). Similarly, individual status no longer significantly interacted with brood age, but instead with visit duration: helpers are more likely to prompt call inside the nest during longer visits, whereas dominants prompt call more during short visits (Figure 4b). Secondly, carer number had no effect on general calling but was a highly significant predictor of prompt calling specifically, with calls least likely to include prompts in medium-sized groups (Figure 4c). The effect of brood begging also becomes significant with prompt calls ~30% more common when chicks were silent on carer entry (Figure 4d). The effect of female presence in the nest is retained but reversed, such that when the female is present adults are less likely to emit any call, but if they do call then there is a greater probability that at least one will be a prompt. Finally, there was no effect of time of day, brood age or brood size on the probability of prompt versus flight calling in the nest (Table 6).

EFFECTS OF NEST-CALLING ON BEGGING BEHAVIOUR

The results above provide ambiguous support for the begging-stimulation hypothesis, but the key prediction is that nest-calling induces a begging response in nestlings (Table 7). Begging inside the nest was more common when carers arrived with food, presumably because carers provision broods more often when nestlings are hungry (Figure 5a), and when there were relatively few carers per chick (Figure 5b). After controlling for these effects, we found that although nest-calling during the inside phase almost doubled the probability of nestling begging, prompt calls were not more likely to induce begging over flight calls (Figure 5c). I also found no effect of call type on speed or duration of brood response (Appendix 5). Together, these results support the begging-stimulation and offspring-conditioning hypotheses with regard to response to nest-calling in general, but do not explain when flight versus prompt calls are given so cannot explain the function of prompt calls specifically.

EFFECTS OF NEST-CALLING ON GROUP PROVISIONING BEHAVIOUR

The potential remaining adaptive explanations for prompt calling in the nest are the coordination-of-care and offspring-demand hypotheses (Table 2). Although related, the former predicts that prompt calling reduces nest visit overlap and/or the interval to the subsequent provisioner to facilitate provisioning efficiency, while the latter predicts that it informs co-carers of brood needs and so changes the rates of subsequent group provisioning. In all analyses I controlled for visit duration, time of day and presence of the breeding female, as proxies for offspring demand, to avoid confounding effects of adults responding to hungry chicks rather than calling. Their inclusion had no qualitative impact on model output regarding the effects of nest-calling.

First, I found a significant interaction between call type and carer number on the probability that the subsequent provisioner entered the nest before the focal bird had exited (Table 8; Figure 6). This interaction arose because nest visitation overlaps increased as an increasing function of group size when either no call was given or a flight call only, while the reverse relationship was evident when prompt calls were given. Why this should be the case is not clear, and it should be noted that overlaps only occurred in ~10% of nest visits.

Consequently, nest-calling generally contradicts evidence for coordination of nest entry in the smallest groups but becomes increasingly supportive for prompt call function as carer number increases.

Second, I found that nest-calling in general tended to reduce the time interval to the subsequent provisioner (Table 9). However, there was no difference in the time interval between the entry of the focal bird and that of the subsequent bird as a function of whether a prompt call or flight call was given inside the nest (Figure 7). Thus, whilst nest-calling might play some role in the coordination of care, the prompt call does not appear to play a specific role.

Finally, by contrast, prompt calling was associated with a significant reduction in the group provisioning rate in the 10 min after a visit containing a prompt call versus a flight call (Table 10; Figure 8). Although this reduction led provisioning rates to be comparable following prompt calls and no calls, calls are presumably more often given in social contexts. We therefore suggest silent visits to be associated with generally low provisioning rates rather than active reductions in feeding. Either way, together my results suggest that prompt calls play a significant role in informing co-carers that the current brood demand is relatively low.

Table 3: Calling propensity and call type during each phase of nest visits.
(a) Shows comparisons of the proportions of individuals calling (or not) and of flight versus prompt calling across nest visit phases (entry, inside, exit). Entry is defined as the 2 s prior to entry and exit as the 2 s period following exit; time in the nest varied from 1-60 s (median = 15). In (a) "any call" compares whether any nest-calling is more likely during entry, inside and exit phases of nest visits. "Flight only" compares the proportion of visits with flights calls but no prompt calls during entry, inside and exit phases. "Prompt calls" compares the propensity for any prompt calling to occur during the three phases, whether or not flight calls were also emitted. These analyses were based on a total of 639 nest visits by 49 individuals attending 11 broods, with analyses conducted on overall proportions per individual. I only included birds for which all phases were visible for at least four visits. In **(b)** the proportion of visits with flight only versus prompt calls during each phase is compared. This analysis is based on 639 visits during the entry phase and 991 (51 individuals) during the other two phases. The differences in sample size arise because at 9 out of 11 nests, our recordings at entry were only possible when a preceding individual had triggered the apparatus within 1 minute of the following individual (see Methods).

(a)	Proportion of calls across phases					
	Kruskal-Wallis Test			**Tukey Post-Hoc *P*-values**		
Call Type	**Statistic**	***df***	***P*-value**	**entry vs inside**	**entry vs exit**	**inside vs exit**
any calls	24.63	2	<0.001	0.0092	0.11	<0.001
flight only	12.01	2	0.0025	0.0017	0.19	0.20
prompt calls	29.00	2	<0.001	0.15	0.0018	<0.001
(b)	**Proportion of prompt vs flight within phases**					
	Mann-Whitney *U*	**n**	***P*-value**	**effect**		
entry	754	49	0.0013	prompt > flight		
inside	954	51	0.020	prompt > flight		
exit	1540	51	0.11	prompt = flight		
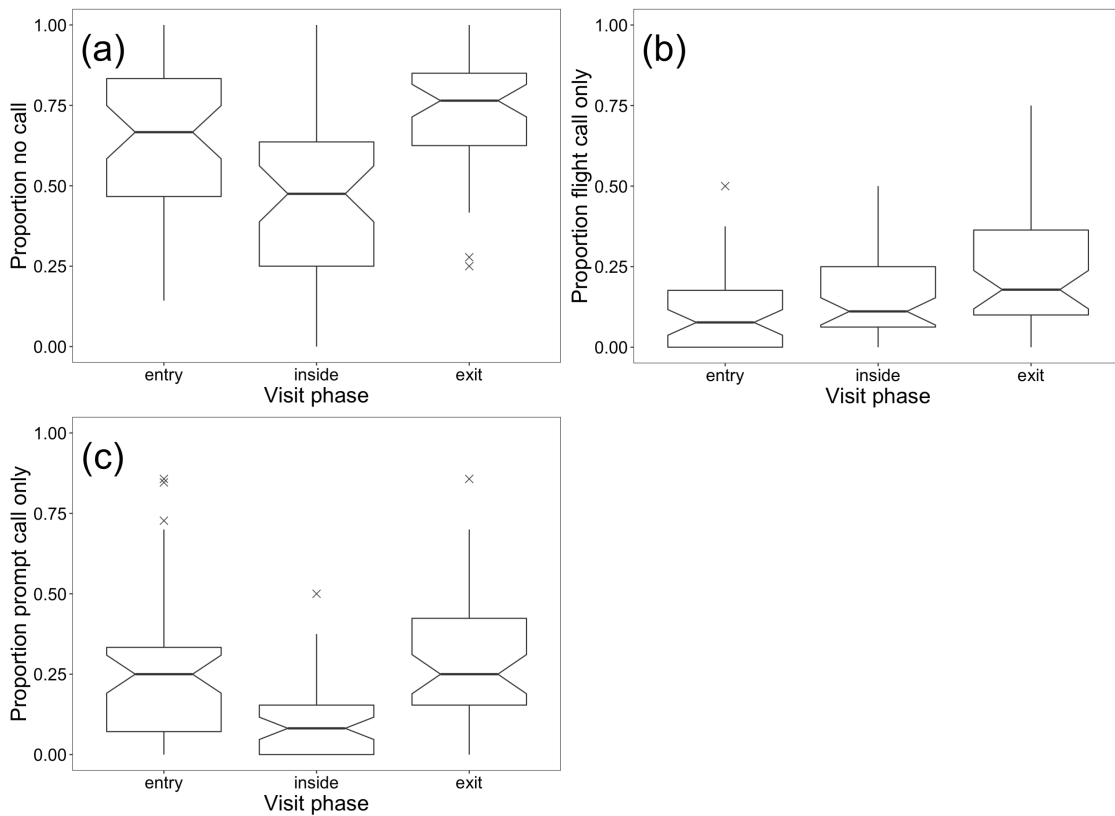
Figure 2: Calling propensity and call type during each phase of nest visits.
Box plots show **(a)** no calls, **(b)** flight call only, **(c)** prompt calls (irrespectively of whether or not flight calls also given) across each phase (entry, inside, exit). Figures show median proportion of nest visits by 49 carers with calls (dark horizontal line), notched at ±1.58 IQR/√n (*grDevices*, version 4.0.2, *R* Core Team 2020), with upper and lower inter-quartile ranges (IQR) shown as the top and bottom of each box, 1.5 x IQR shown as the bars and outliers as individual points. Non-overlapping notches approximate statistical significance (see Table 3). Figures based on 639 visits for which data were available across all phases for at least 4 visits by each bird (n = 49). See Table 3 and Table 11 in Appendix 1 for further details.

Table 4: Repeatability of nest-calling. (a) Shows individual-level repeatability of nest-calling (or not), while **(b)** shows the individual-level repeatability of prompt calling over flight calling only. In both, the repeatability during the entire nest visit, as well as during each phase is compared (see Table 3 legend for definitions of each phase). Sample sizes during the entire visit and entry phase are reduced owing to reduced sampling on-entry (see Methods) and are based on 629 visits, by 54 individuals in 10 groups versus 974 entries by 56 individuals in analyses of inside and exit. In (b), only visits with a call recorded were included to determine the repeatability of prompt calling specifically. In this case the sample sizes were as follows: 222 calling entries by 45 individuals, 480 calling inside phases by 52 individuals, 253 calling exits by 47 individuals, and 442 total visits in which a call was emitted at some point by 54 individuals. Excluding the dominant female, who typically broods the nestlings, had no qualitative impact on the results.

(a)	Repeatability of nest-calling						
	R	SE	2.5%	97.5%	*D*	*df*	*P* (*LRT*)
entire visit	0.07	0.01	0.03	0.08	40.0	1	<0.001
entry	0.16	0.03	0.08	0.21	55.6	1	<0.001
inside	0.14	0.02	0.08	0.17	80.3	1	<0.001
exit	0.07	0.02	0.02	0.11	26.8	1	<0.001
(b)	Repeatability of prompt calling						
entire visit	0.09	0.03	0.02	0.16	13.9	1	<0.001
entry	0.18	0.10	0.006	0.40	6.8	1	0.0047
inside	0.11	0.05	0.02	0.20	25.3	1	<0.001
exit	0.23	0.09	0.05	0.38	21.3	1	<0.001

Table 5: Probability of calling (flight or prompt) inside the nest. GLMM with 938 nest visits by 50 individuals tending 11 broods. All estimates and standard errors are reported on the logit scale. Only terms with predicted or potentially confounding impacts were included; with terms dropped from the minimal model if they failed to improve the explanatory power of the overall model as judged by a likelihood ratio test (*LRT*). The sample was reduced to 758 visits when fitting the effect of female brooding on the nest, since she cannot visit if she is brooding the young, and to 544 when begging (within 1 s) on entry was fitted because one nest lacked such data and I excluded times when other individuals were in the nest. Estimates and statistics for main effects as part of significant interactions are presented outside of their interaction (i.e., brood age and carer status). Combined refers to the overall effect of a term, linear refers to the linear effect without higher order polynomials, while quadratic effect refers to the added impact on the linear. The breeding female is the intercept for carer status. Random terms were individual and brood identity and the date.

TERM	ESTIMATE	SE	*LRT*	*df*	*P*-value
Intercept	-2.62	0.77	-	-	-
Visit duration (combined)	-	-	56.41	2	<0.001
linear effect	0.027	0.0057	23.00	1	<0.001
quadratic effect	-15.53	2.72	33.41	1	<0.001
Visit with food (yes)	2.11	0.27	71.44	1	<0.001
Brood age	0.094	0.042	4.33	1	0.038
Carer status	-	-	21.67	2	<0.001
dominant male	1.53	0.45	-	-	-
helpers	2.047	0.42	-	-	-
Brood age × carer status	Figure 3		12.55	2	0.0019
Female brooding	-0.63	0.25	6.35	1	0.012
NON-SIGNIFICANT VARIABLES EXCLUDED					
Time of day	0.054	0.030	3.13	1	0.077
Brood size	-0.046	0.14	0.10	1	0.75
Carer number	0.084	0.081	1.04	1	0.31
Begging on entry	-0.57	0.31	3.34	1	0.067
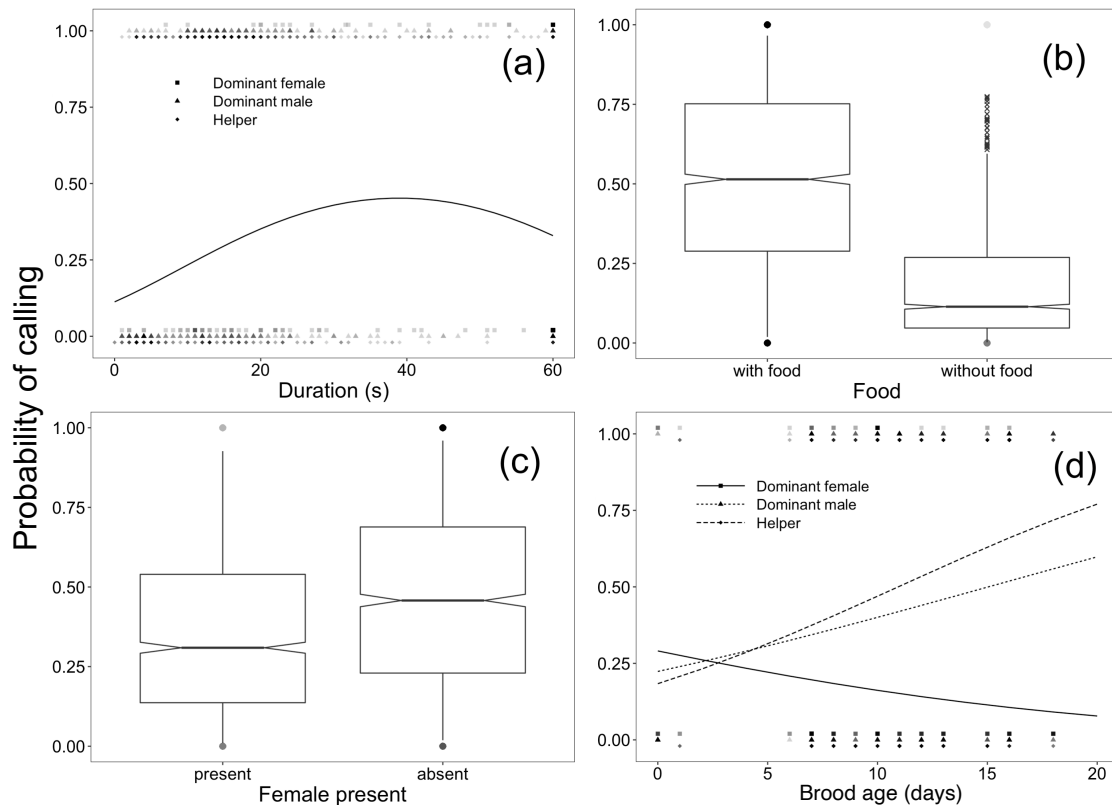
Figure 3: Probability of calling (flight or prompt) inside the nest. Main effects of binomial GLMM predicting the probability that a bird will call (flight or prompt) inside the nest. **(a)** All carers are most likely to call during medium-length visits; **(b)** when visiting with food rather than without; and **(c)** when the breeding female is absent from the nest (breeding males and helpers only). **(d)** Breeding males (dotted) and helpers (dashed) increased calling as broods aged, whereas breeding females (solid line) showed a non-significant trend for the opposite pattern. Points indicate the recorded values, with darker points showing higher sample sizes, where 0 = no call and 1 = call recorded during a visit. Circular points display visits by all birds (n = 938 visits by 50 birds), whereas square, triangular and diamond-shaped points indicate visits by dominant females, dominant males and helpers respectively. Dominant females and helpers are shifted on the y-axis for visual clarity only. See Table 5 and Figure 11 in Appendix 4a for further details.

Table 6: Probability of prompt versus flight calling inside the nest. GLMM with 464 nest visits with calls while the bird was inside by 47 individuals tending 11 broods. All estimates and standard errors are reported on the logit scale. Only terms with predicted or potentially confounding impacts were included; with terms dropped from the minimal model if they failed to improve the explanatory power of the overall model based on *LRT*. The sample size was reduced to 426 visits when fitting the effect of female brooding on the nest and reduced to 272 for begging (within 1 s) of entry (see Table 5). Estimates and statistics for main effects as part of significant interactions are presented outside of their interaction (i.e., with food, visit duration, carer status). For definitions of combined, linear and quadratic effects see Table 5. Carer status is breeder versus helper, with the former set as the intercept. Random terms were bird and brood identity, and date.

TERM	ESTIMATE	SE	*LRT*	*df*	*P-value*
Intercept	1.28	0.84	-	-	-
Visit duration	0.026	0.0073	13.86	1	<0.001
Visit with food (yes)	0.60	0.43	1.94	1	0.16
With food × visit duration	0.044	0.022	3.88	1	0.049
Carer status (helper)	-0.49	0.32	2.43	1	0.12
Carer status × visit duration	0.046	0.015	9.66	1	0.0019
Carer number (combined)	-	-	10.81	2	0.0049
linear effect	0.032	0.083	0.15	1	0.70
quadratic effect	10.86	3.026	10.66	1	0.0011
Female brooding	0.88	0.32	8.07	1	0.0045
Begging on entry	-0.94	0.38	5.60	1	0.014
NON-SIGNIFICANT VARIABLES EXCLUDED					
Time of day	-0.036	0.032	1.30	1	0.26
Brood age	0.035	0.037	0.90	1	0.34
Brood size	-0.019	0.10	0.034	1	0.85
Brood age × carer status	0.10	0.073	2.078	1	0.15
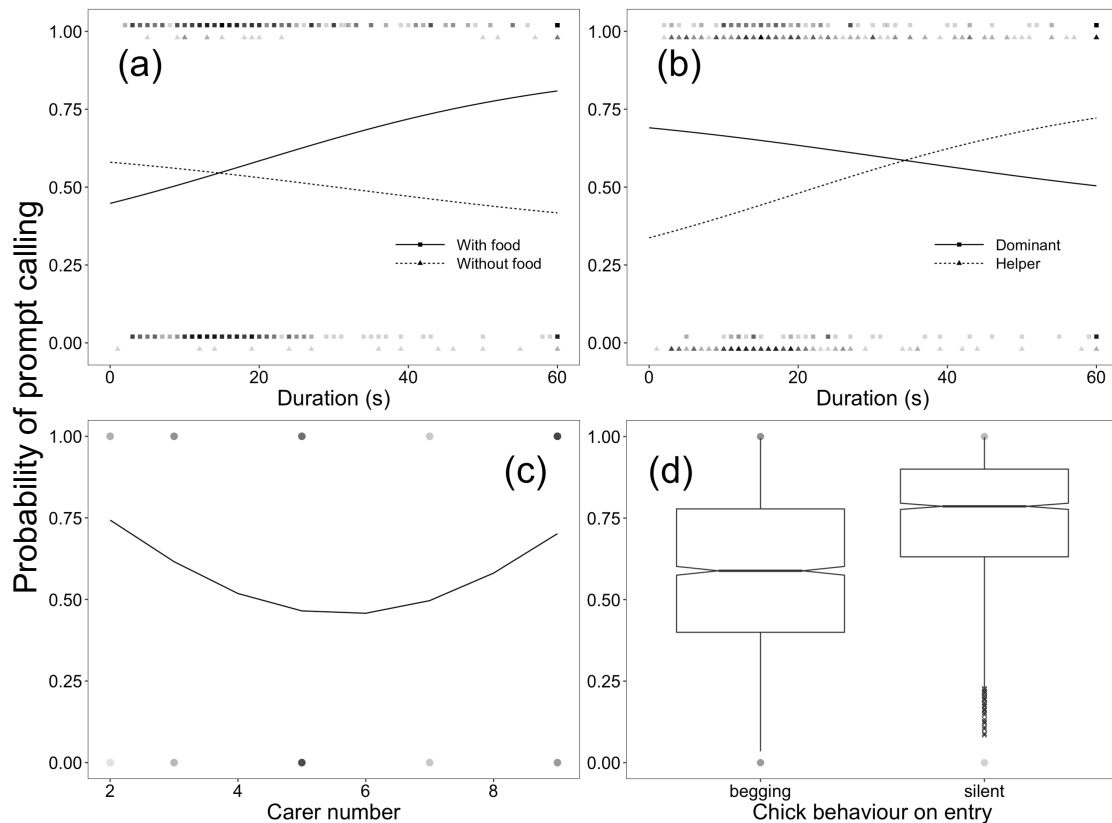
Figure 4: Probability of prompt versus flight calling inside the nest. Prompt calling becomes increasing likely: **(a)** as visits lengthen with food and **(b)** especially by helpers, as well as in **(c)** groups of extreme size and **(d)** when the chicks are silent upon carer entry. Figures (a-c) show predicted lines, with points indicating recorded visits with (probability = 1) or without (probability = 0) prompt calls. Circular points indicate all visits, whereas squares and triangles show visits with and without food or breeders and helpers respectively. Shading of these points shows the sample size of recordings. Figure (d) shows boxplots with median and quartile values, and any outliers (crosses) (see Figure 2 legend for further details). Analyses based on 464 visits by 47 birds, with the exception of begging on entry (defined as begging within 1 s before or after the time of carer entry), which was based on a reduced sample of 272 visits by 37 individuals. See Table 6 and Figures 12 and 13 in Appendix 4b for further details.

Table 7: Effects of nest-calls on brood begging. Analysis based on GLMM with 221 nest visits by 37 individuals at 10 nests of 9 groups. Data were excluded if an individual was already present in the nest or if the chicks were already begging on carer entry. All estimates and standard errors are reported on the logit scale. Only terms with predicted or potentially confounding impacts were included; with terms dropped from the minimal model if they failed to improve the explanatory power of the overall model based on *LRT*. Prompt call is set to the intercept for call type given while the adult is inside the nest. Brood size:carer number is the ratio of the former to the latter. Inter-visit interval represents the time in seconds since last visit entry, while provisioning rate is the average number of visits per minute received in the past 30 min. Due to the inherent ability of larger groups to visit the nest more frequently, and of larger broods to require faster provisioning, both inter-visit interval and provisioning rate were mean centred by brood prior to analysis. Individual identity nested within group identity was fitted as random intercepts.

TERM	ESTIMATE	SE	*LRT*	*df*	*P-value*
Intercept	-1.95	0.61	-	-	-
With food (yes)	3.049	0.48	50.85	1	<0.001
Call type	-	-	11.76	2	0.0028
no call	-1.52	0.47	-	-	-
flight call only	-0.27	0.59	-	-	-
Brood size:carer number	1.21	0.38	10.31	1	0.0013
NON-SIGNIFICANT VARIABLES EXCLUDED					
Visit duration	0.0039	0.010	0.15	1	0.70
Time of day	0.064	0.054	1.37	1	0.24
Brood age	-0.010	0.055	0.035	1	0.85
Brood size	0.21	0.25	0.70	1	0.40
Carer number	0.010	0.11	0.0088	1	0.93
Inter-visit interval	0.0026	0.0016	2.83	1	0.092
Provisioning rate	0.79	0.68	1.33	1	0.25
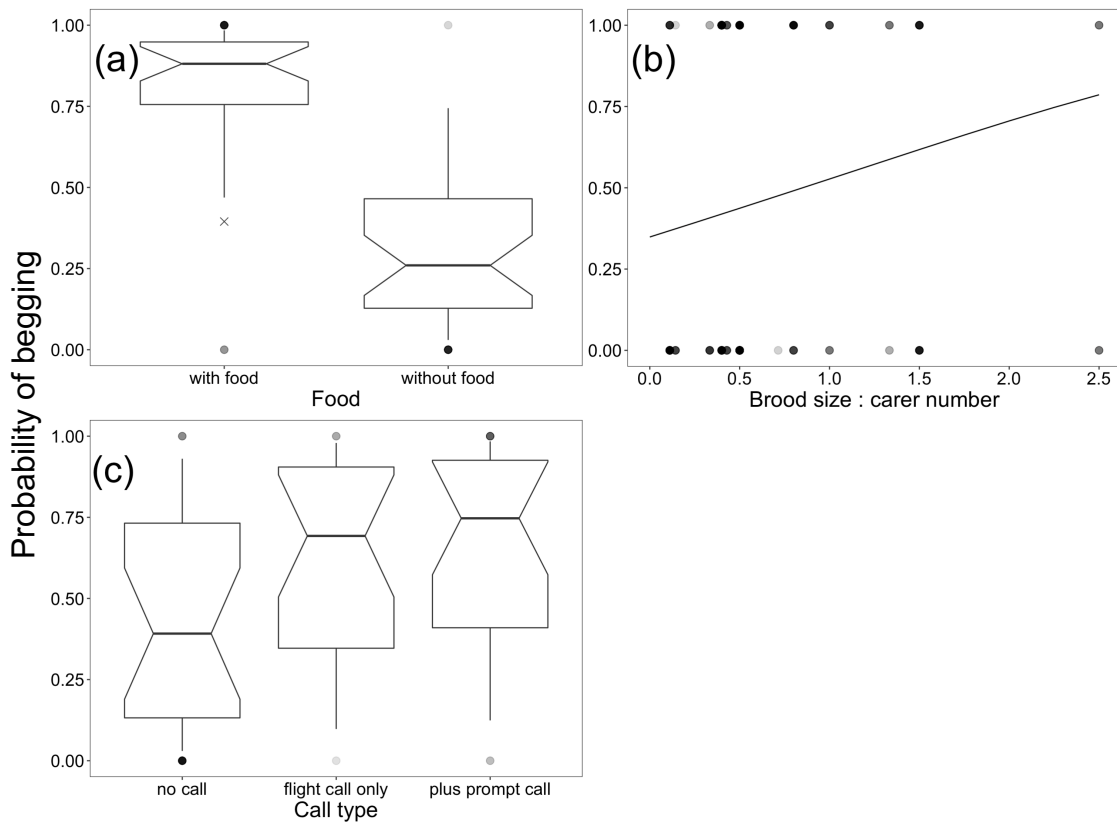
Figure 5: Effects of nest-calls on brood begging. Broods were more likely to beg in the 5 s following nest entry when: **(a)** the carer was carrying food; **(b)** the number of nestlings relative to the number of carers was high; and **(c)** nest-calls were given, but with no difference between flight and prompt calls. Boxplot prediction outliers are displayed as crosses, recorded visits are shown as circular points whose shade indicates the sample size. For details on boxplots see Figure 2 and for line plots see Figure 3. Note that this analysis excludes nest visits with broods begging within 1 s of nest entry (n = 221 visits by 37 carers, with 10 broods). For further details see Table 7.

Table 8: Effects of nest-calls on nest entry overlap. The probability that an individual entered the nest before the focal bird exited was analysed using a binomial GLMM on 782 nest visits by 49 individuals at 11 nests. All visits exceeding 60 s duration were excluded from the model. Sample size dropped to 711 visits for testing the effects of female brooding. Estimates and errors are reported on the logit scale. For description of estimates of linear and quadratic effects see Table 5. The prompt call was fitted as the intercept in call type. Individual identity nested within group identity was fitted as random effects.

TERM	ESTIMATE	SE	X^2	df	P-value
Intercept	-2.32	0.91	-	-	-
Visit duration	-	-	14.55	2	<0.001
linear effect	0.038	0.014	6.42	1	0.011
quadratic effect	13.70	4.78	8.13	1	0.0044
Time of day	-	-	9.58	2	0.0083
linear effect	0.047	0.062	0.59	1	0.44
quadratic effect	-22.51	8.28	8.99	1	0.0027
Call type	-	-	0.29	2	0.87
no call	0.049	0.49	-	-	-
flight call only	0.25	0.50	-	-	-
Carer number	0.11	0.10	1.082	1	0.30
Call type × carer number	-	-	16.14	2	<0.001
no call	0.79	0.22	-	-	-
flight call only	0.46	0.24	-	-	-
NON-SIGNIFICANT VARIABLES EXCLUDED					
Brood age	0.021	0.063	0.11	1	0.74
Brood size	0.18	0.19	0.91	1	0.34
Brood size:carer number	0.70	0.66	1.16	1	0.28
Female brooding	0.0093	0.54	0.0057	1	0.94
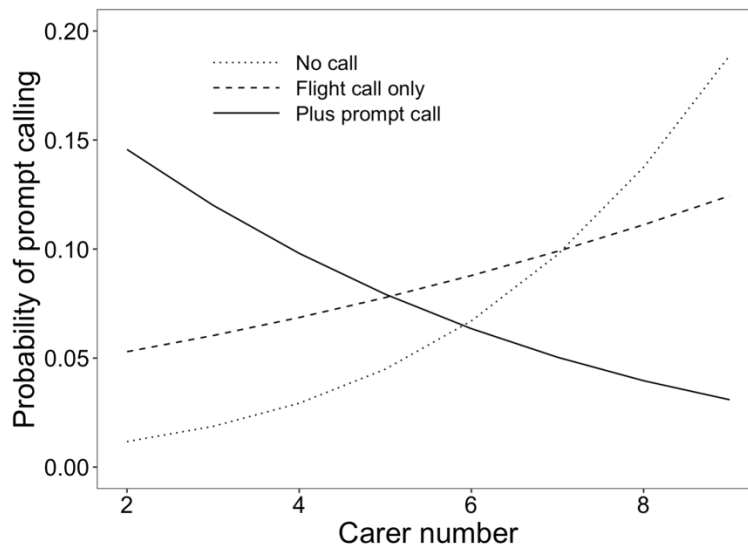
Figure 6: Effects of nest-calls on nest entry overlap. Prompt calling by the bird inside the nest reduced the probability that the next bird would enter before the focal exited as group size increased relative to no calling or flight calls only. Note that the probability of overlap is low generally, and that the recorded visit data are not shown for clarity. Analysis based on 782 visits by 49 birds feeding 11 broods. Visits over 60 s were excluded from the data. For further details, see Table 8.

Table 9: Effects of nest-calls on subsequent visit interval. Inter-visit interval is defined here as the time between the entrance of the focal bird and the entrance of the following bird and was log-transformed and mean centred by brood identity. Analysis was performed using linear mixed effects models on 928 visit intervals, by 50 birds. See Table 5 for description of estimate generation for linear and quadratic effects. All visits exceeding 60 s duration were assigned a maximum value of 60. Prompt call is set as the intercept in call type. Individual identity nested within group identity was fitted as random intercepts.

TERM	ESTIMATE	SE	X^2	df	P-value
Intercept	-0.36	0.14	-	-	-
Visit duration	-	-	21.93	2	<0.001
linear effect	0.0077	0.0021	13.85	1	<0.001
quadratic effect	3.51	1.23	8.08	1	0.0044
Time of day	0.022	0.010	4.74	1	0.030
Call type	-	-	5.20	2	0.074
no call	0.17	0.095	-	-	-
flight call only	-0.038	0.11	-	-	-
Female brooding	0.34	0.11	9.26	1	0.0023
NON-SIGNIFICANT VARIABLES EXCLUDED					
Brood age	0.0020	0.011	0.042	1	0.84
Carer number	0.012	0.019	0.43	1	0.51
Brood size	-0.0020	0.034	0.0012	1	0.97
Brood size:carer number	-0.084	0.10	0.67	1	0.41
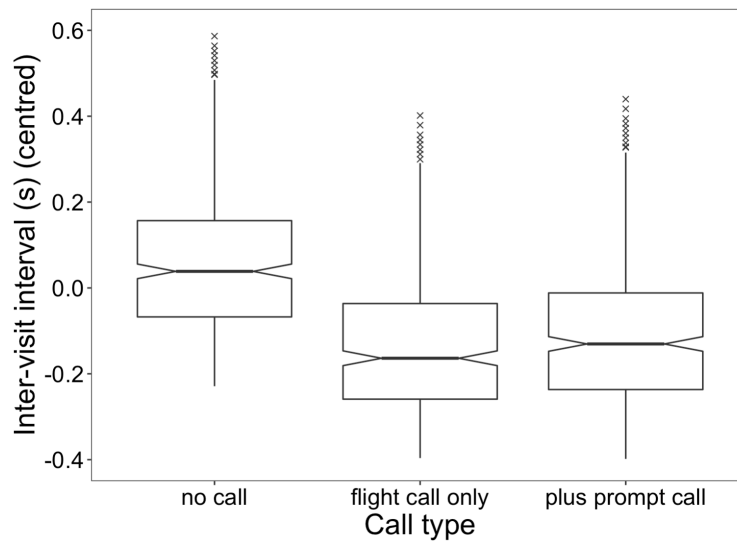
Figure 7: Effects of nest-calls on subsequent visit interval. The time to next visit was longest if no call was given and least if only flight calls were given inside the nest, with visit interval increasing non-significantly following a prompt call relative to only a flight call. Predictions of LMM analysis based on 928 visits by 50 individuals. Outlier predictions are displayed as crosses. For further details see Table 9.

Table 10: Effects of nest-calls on subsequent provisioning rate. Provisioning rate is measured as the average number of feeds per minute in the subsequent 10 min following a focal bird's visit. The analysis was performed using a linear mixed effects model with 935 visits by 50 individuals at 11 nests. Provisioning rate was mean centred by brood prior to analysis, so a negative value indicates fewer feeds per minute than the mean per nest. Descriptions of estimates for linear and quadratic effects are provided in Table 5. Prompt calls are set as the intercept for call type. Random terms were individual identity nested within group identity.

TERM	ESTIMATE	SE	X^2	df	P-value
Intercept	-0.0093	0.020	-	-	-
Visit duration	-	-	11.61	2	0.0030
linear effect	-0.0014	0.00054	5.64	1	0.018
quadratic effect	-0.80	0.33	5.97	1	0.015
Time of day	-	-	16.90	2	<0.001
linear effect	-0.0071	0.0027	6.67	1	0.0098
quadratic effect	1.036	0.32	10.23	1	0.0014
Call type	-	-	10.29	2	0.0058
no call	-0.0044	0.025	-	-	-
flight call only	0.080	0.030	-	-	-
Female brooding	-0.091	0.031	8.63	1	0.0033
NON-SIGNIFICANT VARIABLES EXCLUDED					
Brood age	-0.0021	0.0028	0.56	1	0.45
Brood size	0.011	0.0091	1.16	1	0.28
Carer number	-0.0013	0.0049	0.058	1	0.81
Brood size:carer number	0.035	0.027	1.46	1	0.23
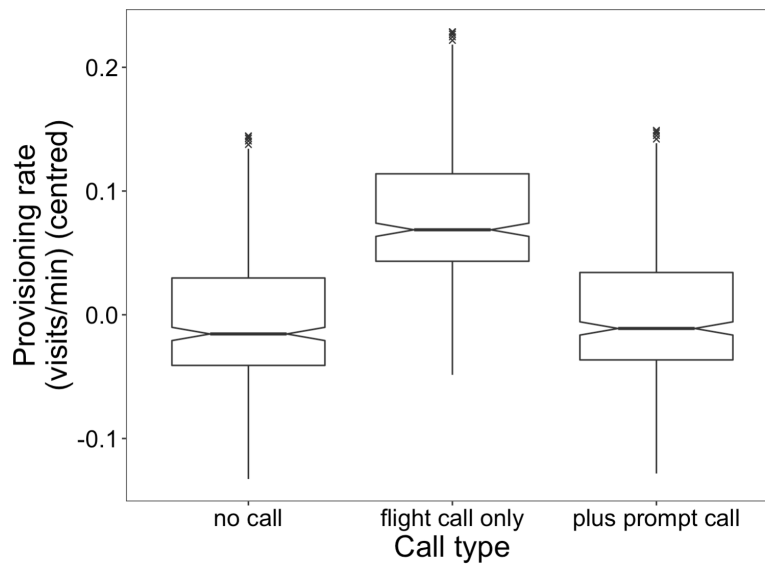
Figure 8: Effects of nest-calls on subsequent provisioning rate.
Provisioning rate (visits with food per minute) over the subsequent 10 min was significantly reduced following visits with prompt calls or no call compared with only flight calls. Low provisioning rates following silent visits are expected to correlate with times when other birds are not nearby. Predictions of LMM analysis based on 935 visits by 50 individuals attending 11 broods. Outlier predictions are displayed as crosses.

DISCUSSION

In this study, 66% of chestnut-crowned babbler nest visits were accompanied by flight and/or prompt calls (collectively nest-calls). Visits containing prompt calls are significantly more common than those with only flight calls, particularly at the nest entrance and inside, but overall a higher proportion of visits contained flight calls than prompt calls. Although carers showed modest repeatability in their propensity to nest-call, breeders and helpers displayed limited systematic differences and both flight and prompt calls were predicted by a range of social stimuli. Nest-calling was generally associated negatively with brood hunger correlates and positively with attempted food delivery. For example, nest-calls, particularly prompt calls, were less common when nestlings were begging on nest entry, and more common when arriving with food and when visits were long, with long feeding durations strongly associated with sated nestlings (Young et al. 2013). Nestlings typically begged in response to nest-calls but showed no preference for prompt calls over flight calls. Carer response to nest-calling displayed contradictory impacts on the probability of nest visit overlap, although calls were associated with reduced visit intervals. In contrast, nest-calls differed in their effect on group provisioning rate, with prompt calling in the nest associated with a reduction in subsequent feeding. That call type affected the average provisioning rate of the whole group suggests that birds are altering their behaviour in response to the calls of others, rather than their own observations of offspring demand. To determine if individuals also respond to their own observations, future research should investigate the effect of offspring demand on the time until the same individual next visits the nest. Carer behaviour was also affected by correlates of brood demand, indicating that adults provision faster when visits are short, early in the day, and the female is present, but controlling for these did not qualitatively alter the impact of nest-calling. Adult response to prompt calling is therefore not dependent on other contextual variation. Together, these results suggest that nest-calling serves multiple functions, but that prompt calling is specifically used to inform co-carers that the current demand of the brood is relatively low.

Two previous studies have been conducted on chestnut-crowned babbler nest-calls. First, when investigating flight and prompt call acoustic similarity,

Engesser et al. (2015) reported that prompt calling occurred exclusively inside the nest and flight calls outside. In contrast, I found that flight calls were overall more common than prompt calls inside the nest and I recorded both call types in all visit phases. One explanation is that the previous study overrepresented prompt calls inside the nest because they did not use acoustic software to distinguish between the two. Differentiating these calls can be hard by auditory methods alone, especially as isolated B notes commonly emitted inside the nest can make the bi-element flight call sound even more like the tri-element prompt call. Second, Young et al. (2013), who coined the term prompt call, found they induced nestling begging. While I also found that this was the case, I found that flight calls do so equally. My study therefore demonstrates the importance of comparing the effects of specific nest-calls against more generic calls given at the nest when investigating nest-call function, but these controls have not always been implemented into previous studies (Table 1).

At least five adaptive explanations might account for nest-calling (Table 2), but two appear unlikely candidates for chestnut-crowned babblers. Offspring-conditioning to facilitate post-fledging care, either through carer-offspring recognition or associative learning of calls and food is supported in other species by both observational and experimental evidence (Table 1). For example, in several swallow species, adult nest-calls are individually distinctive and fledglings respond more to parental nest-calls than strangers (Beecher et al. 1985; Sieber 1985). In addition, purr calling accompanies most pied babbler nest visits, particularly around fledging, and playback experiments confirm their utility in post-fledging care (Radford and Ridley 2006; Raihani and Ridley 2007). However, conditioning through either mechanism appears unlikely to apply in chestnut-crowned babblers. Firstly, brood age has no effect on prompt calling over flight calling, and females decline their nest-calls over time (Table 6; Figure 3; Appendix 4). There is also no evidence for adults luring the chicks from the nest on the day of fledging (Appendix 1) or prompt calling when encouraging threatened nestlings to fledge early (Russell unpublished observation). Secondly, current evidence suggests that neither of the A or B acoustic elements carries reliable information about caller or group identity (Doyle and Russell unpublished 2020). As elements are shared between flight and prompt calls, kin

recognition alone would be insufficient to explain the need for both calls. The lack of identity coding in acoustic parameters also makes it unlikely that calling is a signal of individual investment to be used in future decisions of partner choice (see also Wright 1997) or paying to stay in the natal territory. Signalling would be expected at every possible opportunity by helpers, but there is an overall relatively low frequency of calling and very limited difference between dominants and helpers. Given that chestnut-crowned babblers also lack evidence of individuals attempting to advertise their provisioning contributions in other ways, such as coinciding nest visits with potential partners (Nomano et al. 2013; Young et al. 2013), the signalling-investment hypothesis can be ruled out. Thus, more likely explanations for nest-calling in this species include begging-stimulation, coordination-of-care and broadcasting offspring-demand.

Begging-stimulation is amongst the most common explanations for nest-calling (Table 1). The key predictions of this hypothesis are that nest-calling should: decline with brood age, as nestlings increasingly learn to recognise mechanical signals of nest arrival; increase with food and correlates of brood satiation; and stimulate chick begging to a greater extent than other calls (Table 2). I found significant support for the latter two predictions but no reduction in nest-calls with brood age. First, nest-calling was more common when carers entered the nest with food, when chicks were silent on entry, and during long visits. While long visits might increase the probability of nest-calling by chance, they are also more likely when nestlings are satiated (Young et al. 2013). Second, initiation of begging was more likely following carer entry when a nest-call was given than not given. However, I found no evidence to suggest that prompt calls were used specifically to induce begging or that they increased the efficiency of the begging response. Thus, while my results for general nest-calling are consistent with the predictions of begging-stimulation, this need not be the only explanation, and an alternative hypothesis is required to account for prompt calling.

One possibility is provided by the here-named coordination-of-care hypothesis (McDonald et al. 2008; McDonald and Wright 2008), though testing this is challenging as coordination parameters can be difficult to measure. Although bell miner mew calls show no association with inter-visit interval, they

are more common in the presence of co-carers with whom they forage and defend the territory (McDonald et al. 2008; McDonald and Wright 2008). I did not find a clear association between nest-calling and visit overlap, but calling was associated with reduced time to the arrival of the next bird. I hypothesised that overlapping nest visits might reduce the efficiency of provisioning because the tight entrance hole only allows one bird to pass through at a time, but it might be that the speed with which they do so coupled with the spacious nest interior and the rarity of overlapping by chance minimises the cost of overlap. Overlaps were generally rare so developing a specific coordination call to reduce them further may have been unnecessary. Using nest-calls to influence the timing of the subsequent bird's arrival at the nest can make more sense because entering in quick succession can help to avoid monopolisation of feeding by a single nestling (Shen et al. 2010), reduce the predation risk created by spending time around the nest (Raihani et al. 2010), and maximise foraging time. It remains unclear if nest-calling influences group cohesion and subsequent coordination of provisioning but it is noteworthy that flight calls, which improve group cohesion during flight, constitute a key nest-call in all visit phases. Thus, while nest-calling, particularly flight calls, probably plays some role in group coordination, I found only very limited difference in the impact of flight and prompt calling on the measures of coordination tested.

Finally, I proposed and tested the hypothesis that nest-calling, and specifically prompt calling, might function to inform co-carers of brood demand. Chestnut-crowned babblers live in a highly challenging environment in the Australian outback, and broadcasting brood hunger levels might mitigate provisioning costs. The most successful groups will be those that are able to provide the highest nutritional intake to their offspring while also consuming enough themselves to survive. Halkin (1997) found that female Northern cardinals can inform the males whether or not to bring food. Offspring-demand may therefore consist of either encouraging group members to accelerate provisioning and maximise brood nutritional intake or calling to indicate chick satiation to limit the time wasted on unnecessary nest visits. That prompt calls are more common during long visits with food and when nestlings are not begging suggests that, in this case, they would serve to reduce group

provisioning rate. In support, I found that prompt calling inside the nest by a focal bird reduced feeding in the subsequent 10 min compared with flight calling. Although the reduced provisioning rate following prompt calls did not differ from that following silent visits, this is likely because an absence of nest-calls is associated with provisioning by lone birds in the absence of others. This is consistent with the observations of faster nest entry following nest-calls than silence, though further work is required to test this hypothesis. Thus, I suggest that prompt calls function to inform other provisioners of brood satiation. There still lies some uncertainty around this conclusion: 35% of nest visits contained prompt calls in the entry phase before the carer has observed the brood, and only 10% on exit once they are returning to the group. While further investigation is still needed to explain these observations, evidence from inside the nest strongly supports an offspring-demand hypothesis.

In order to test my conclusions further, I would recommend performing playback experiments at the nest to quantify the impact of prompt and flight calls on adult behaviour. In Appendix 1, I describe a preliminary experiment I carried out in the 2019 breeding season to test whether there is an effect of call type on chick begging. I would recommend a similar protocol to test adult response, observing whether adults delay their entry to the nest based on the nest-calls played. Confirmation that chicks do not respond differentially with call type would be given simultaneously. Further detail of the stimuli of and responses to nest-calls may also be examined by comparing the number of calls given per visit, and their timing within the visit relative to chick feeding. My study has been limited to only considering if a call was emitted or not, but visits contained up to 40 nest-calls. Further, there are other calls made at the nest less frequently, of which some are also comprised of A and B elements, including reverse flight calls (BA) and single elements. The functions of these calls are similarly undefined, so should be looked into in future. They were outside the scope of this study, as to compare these to the similarly undefined flight and prompt call would have required too many variables for comparison using the sample size available. However, their exclusion may have also meant I lacked some of the details regarding responses to nest-calls if a "silent" visit actually contained another nest-call. Finally, future studies should check the impact of nested

versus crossed random effects. In this study, I initially used crossed random effects to develop the models predicting calling behaviour due to the crossover of two birds amongst groups between years. Later, when examining the impact of calling on other birds, we tested the impact of nesting the random effects as the vast majority of the birds did not move between groups. As this had no qualitative impact, we assumed it would be similar for both models, and did not retest the calling models with nested random effects, but this should be checked in the future.

My study has several important implications. First, it reveals that nest-calling can serve several functions. Specifically for chestnut-crowned babblers, nest-calling in general serves to initiate nestling begging and likely has some function in coordinating carers, while prompt calling specifically appears to inform potential provisioners of current brood demand. Despite this, many studies test a single hypothesis, which might generate an incomplete picture of nest-call function (Table 1). Second, it shows the importance of comparing responses to other calls in a species' repertoire, since the precise function of a nest-call can be difficult to detect. For example, prompt calls have previously been suggested to stimulate nestling begging (Young et al. 2013), but this study shows that it does not do so any more than a flight call. Nevertheless, several previous studies in other systems have compared nestling responses to a single call against heterospecific calls, white noise or silence (for example, Heathcote 1989; Leonard et al. 1997; Grieco 2001; Madden et al. 2005; McDonald and Wright 2008). Finally, it suggests that prompt calls are formed from rearranged flight call elements possibly because they have been co-opted to perform a new function; that of informing group members of brood hunger.

APPENDIX 1: OBSERVATIONAL EVIDENCE AND FIELD EXPERIMENTS

During the 2019 field season, I watched two nests from 18 days old to fledging (Figure 9a-b), filming adult physical and vocal behaviour outside the nest during provisioning events and foraging. I recorded the fledging of three chicks from two nests, including the full half hour prior to nest exit for two. Following this study, playback experiments will be required to confirm the nest-call functions. Engesser et al. (2015) previously attempted this in an aviary setting but it has never been performed in the birds' own habitat. I ran a short pilot study to test chick responses at varying stages of development to different call types, testing protocols for future studies. Only two groups successfully fledged a brood in the 2019 season so my sample size was too small to analyse statistically in this project.

I used six stimuli per experimental trial in a semi-randomised order, played at natural volume (40-50 dB; Mine unpublished observation 2019). I separated my stimuli by time slots appropriate to the development stage under study: hatchlings required rapid return to the incubator so were separated by only 3 minutes; nestling and fledgling stimuli were separated by 5 minutes, or longer if parents returned between stimuli. Wherever possible, hatchlings had not been fed prior to the experiment. For nestlings (setup pictured in Figure 9c) a 40-minute break was allowed between the third and fourth stimuli to allow adults time to enter the nest and feed the chicks undisturbed. Fledglings have never been followed or used in playbacks before, so I attempted multiple methods to find the most reliable method for future work. The most reliable was to contain the birds in an aviary, but this created severe stress and therefore likely limited how representative the results were of natural behaviour. Similarly, in the field our most successful attempts involved surrounding the fledglings and chasing the adults away when they tried to approach, but again this is unlikely to have yielded natural responses.

My stimuli were designed to allow for pairwise comparisons between flight and prompt calls, natural and altered calls, nest-calls and controls, and conspecific versus heterospecific calls. Each stimulus, generated by Coye using recordings from Engesser, had three sets of three calls, with the sets separated by 3 s intervals, and 1 s between each call within a set. The first three stimuli

always contained one control, one disyllabic call, and one trisyllabic call, and the second half again one of each. The order within each half was randomised, as was which of each pairing was played in each half of the experiment. Controls were a zebra finch (*Taeniopygia guttata*) contact call and a chestnut-crowned babbler aerial alarm call, both of which the chicks may hear frequently but do not mean food is available. The disyllabic and trisyllabic calls were flight and prompt calls played naturally and inverted (BA and ABA). For the inverted flight call, I used natural reverse flight calls; inverted prompt calls were artificially generated. I carried out one additional playback to older nestlings at one nest using recordings of own-group adults to test whether the nestlings preferred familiar calls, after the first playbacks saw no response to the stimuli but strong responses to adult calls from around the nest.
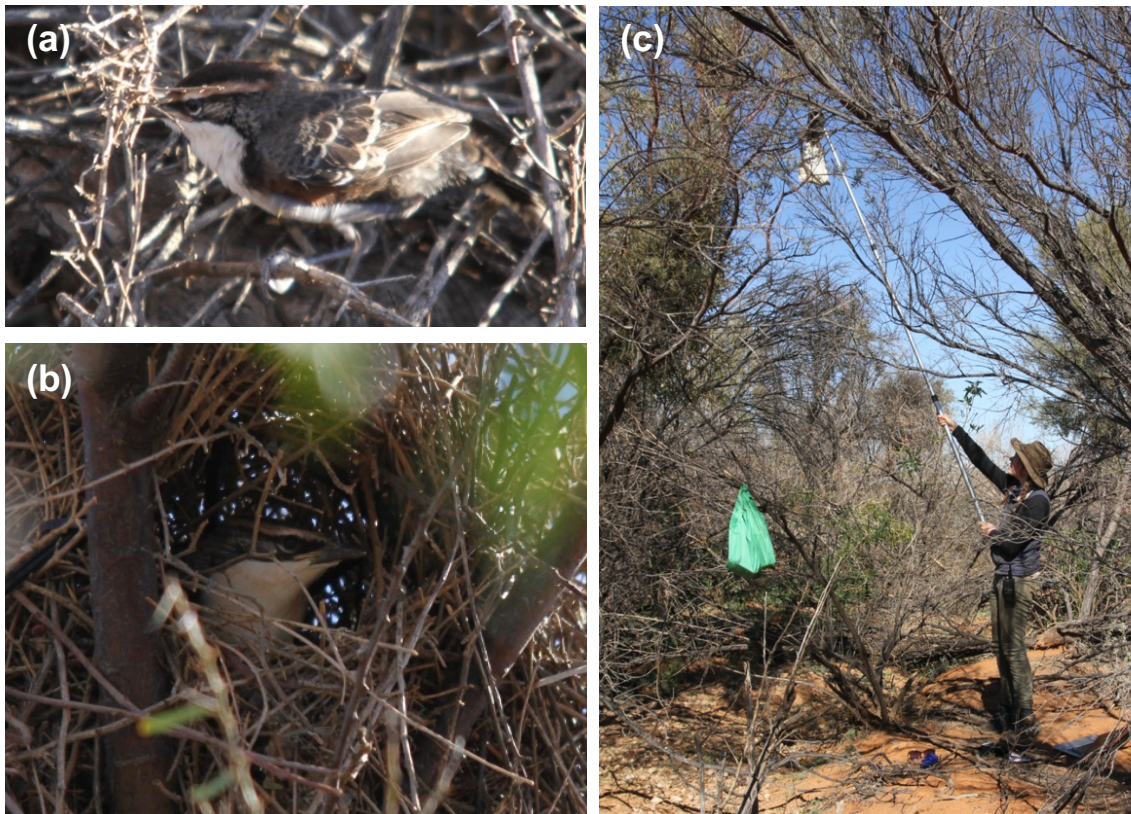
Figure 9: Field observations and experiments. (a) Chestnut-crowned babbler fledgling. Juveniles display less distinct eye markings and shorter tails and are generally more vocal than the adults once out of the nest. **(b)** Late stage nestling looking out of the nest entrance on the day before fledging. **(c)** Experimental setup for nestling playbacks – I stood underneath the nest with the speaker and one microphone attached to the end of a 3 m pole which I held as close to the nest as possible. A second microphone was positioned inside the nest to record the chicks' vocal response.

APPENDIX 2: METHODS OF CALL ASSIGNMENT

To identify calling in each visit phase but avoiding false positives due to overlapping visits, I developed a matrix of overlap types considering the level of overlap with other birds at the start and end of each visit, or if a bird entered and left while another was present (Figure 10). This I performed for all birds other than the dominant female, considering their overlap with any other bird besides her. Female visit duration is extremely variable (n = 188, σ^2 = 413.46; others n = 816, σ^2 = 258.68) and each brooding bout may overlap with several other birds. I therefore only counted calls within 5 s of breeding female entry on the assumption no other birds would be present in that time and that she will call immediately for her own provisioning event. This should not have affected the results because older chicks require less brooding so visits exceeding 5 s are more likely when young. I should therefore be most likely to miss her calls immediately post-hatch, yet I recorded a decline in female nest-calling over time (Table 5; Figure 3d).

For the entry phase, I assigned all calls to the entering bird, discounting any calls within these 2 s from another bird overlapping with the entry. For the exit phase, all calls were assigned to the leaving bird unless the exit of one overlapped with the entry of another, in which case the calls were assigned to the entering bird. For the inside phase, I assigned calls to the most recent bird to enter the nest but discounted any that overlapped with the entry or exit phase of another visit. Type A overlaps occurred when a bird entered while the previous bird was still inside the nest. Type B is when the entry or exit phase overlaps with another visit. Type C indicates no overlap between phases. Some visits were very short and occurred entirely within the inside phase of the previous bird. This I classed as type D. On these occasions, the start and end overlaps consider not the short visit, but the ones on either side of it.
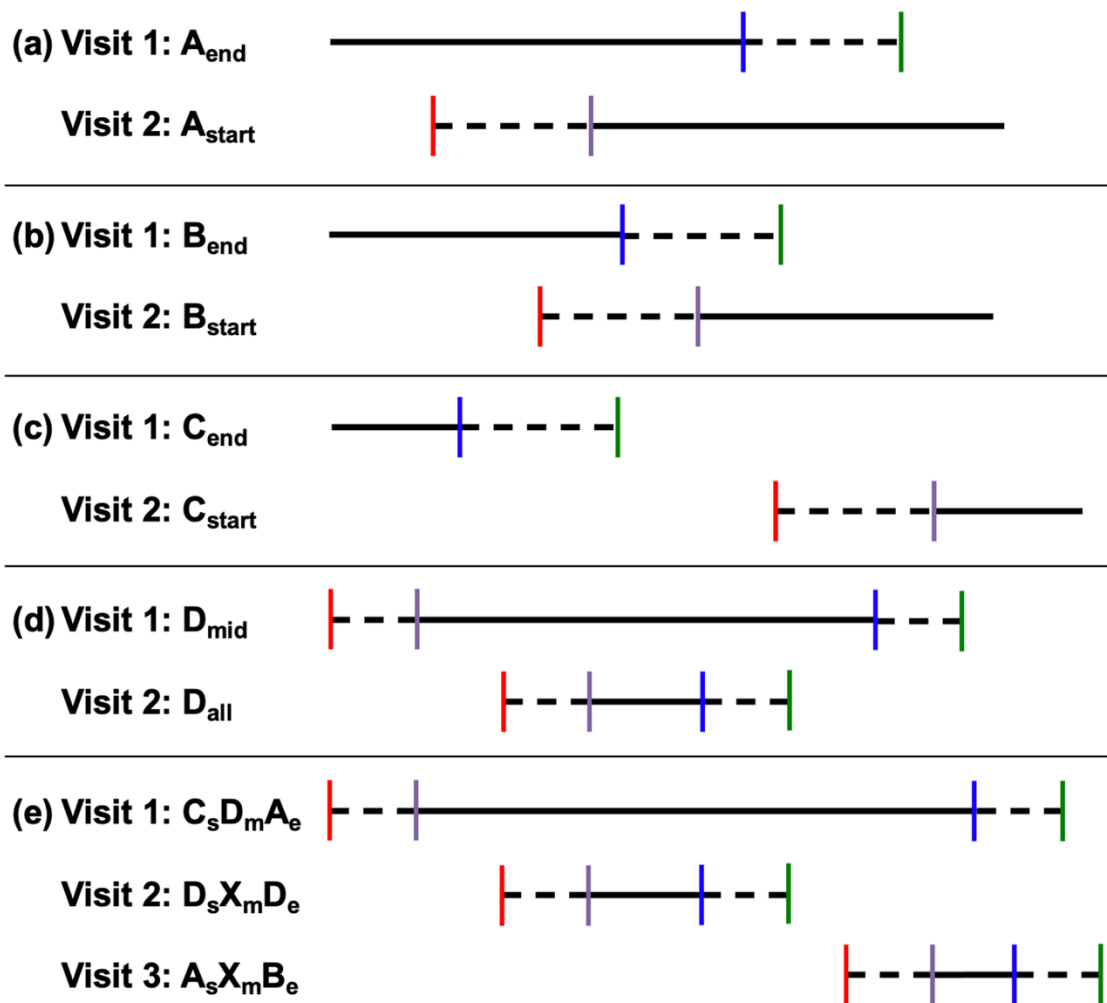
Figure 10: Visit overlaps for call assignment. A diagrammatic explanation of the different overlap types, as bars showing the progression of each nest visit from left to right, and the following nest visit underneath. Solid lines indicate the time that the bird is inside the nest, while dotted lines are outside. Coloured markers show the times of entry and exit (purple and blue) and 2 s before and after (red and green). **(a-d)** show the respective overlap types: A is overlapping inside phases, B is overlapping entry/exit phases, C is no overlap, and D is complete overlap of an entire visit. For type D, the visit 1 end overlap will then refer to the start of visit 3 rather than visit 2. **(e)** A hypothetical example of three consecutive visits showing how the above types may fit together.

APPENDIX 3: VIDEO ANALYSIS SUMMARY

Table 11: Proportion of visit phases with nest-calls per bird and group.
Total number of visits recorded per individual and group and the proportion with flight calls (FC) and prompt calls (PC) in each phase of the visit. Entry refers to the 2 s prior to the adult entering the nest cavity, inside is the time between the adult arriving at and leaving the nest, and exit is the 2 s following adult exit. Full details of how calls were assigned to individuals during overlapping visits are available in Appendix 2. Bird identity is indicated as a 5-figure number referring to the unique ring identity of the individual in question, or as a three-letter code which denotes the entire group followed by the number of individuals in brackets. Status uses a three-letter code for sex, age and status classes, such that FAD indicates a Female Adult Dominant whereas UYH is a Yearling Helper of Unknown sex. This information is unavailable for untagged birds (NO TAG). Some have fewer visible entries than total visits due to the discontinuous nature of recording meaning the camera was often switched off until the adult was already inside the nest (see Methods). Birds denoted with * changed groups from CEK to CEJ between 2007 and 2008.

Birds/ Group	Status	Total visits	Visible entries	FC entry	FC inside	FC exit	PC entry	PC inside	PC exit
CEB (4)	-	143	114	0.088	0.26	0.091	0.13	0.25	0.070
49260	FAD	18	6	0.00	0.056	0.11	0.33	0.056	0.056
49258	MAD	49	42	0.12	0.29	0.00	0.071	0.16	0.08
49411	FYH	59	51	0.020	0.25	0.14	0.098	0.42	0.085
NO TAG	-	17	15	0.27	0.41	0.18	0.33	0.12	0.00
CEJ (6)	-	125	43	0.33	0.53	0.16	0.047	0.27	0.0080
13866	FAD	32	4	0.50	0.44	0.062	0.25	0.25	0.00
13680	MAH	3	2	0.00	0.33	0.00	0.00	0.33	0.00
53316	MYH	17	6	0.5	0.41	0.18	0.00	0.059	0.00
NO TAG	-	1	1	1.00	1.00	0.00	0.00	1.00	0.00
13675*	MAD	40	14	0.29	0.48	0.15	0.071	0.38	0.00
49385*	MAH	32	16	0.25	0.75	0.28	0.00	0.25	0.031
CEK (15)	-	257	157	0.35	0.52	0.29	0.27	0.31	0.093
13781	FAD	19	5	0.00	0.11	0.053	0.00	0.00	0.16

Birds/ Group	Status	Total visits	Visible entries	FC entry	FC inside	FC exit	PC entry	PC inside	PC exit
13674	FAD	8	1	0.00	0.13	0.25	0.00	0.13	0.13
13677	MAD	36	20	0.25	0.17	0.14	0.10	0.11	0.028
13671	MAD	10	8	0.38	0.70	0.00	0.38	0.70	0.10
13895	MAH	55	41	0.29	0.55	0.42	0.29	0.42	0.073
49254	MAH	34	22	0.55	0.74	0.29	0.27	0.24	0.029
13673	MAH	20	11	0.00	0.35	0.10	0.18	0.45	0.15
13672	MAH	9	7	0.14	0.89	0.11	0.57	0.56	0.11
53243	FYH	1	0	NA	0.00	0.00	NA	0.00	0.00
49382	MYH	7	7	0.43	1.00	0.43	0.43	0.86	0.29
62333	UYH	34	17	0.53	0.68	0.44	0.29	0.15	0.088
RXRO	UYH	18	14	0.57	0.83	0.61	0.29	0.50	0.22
NO TAG	-	6	4	0.50	0.50	0.33	0.50	0.50	0.00
EFG(8)	-	104	75	0.16	0.35	0.13	0.15	0.20	0.096
49129	FAD	19	7	0.00	0.11	0.16	0.14	0.21	0.11
49134	MAD	20	17	0.24	0.40	0.10	0.12	0.20	0.20
49130	MAH	15	13	0.23	0.33	0.067	0.23	0.20	0.00
49135	MAH	26	18	0.056	0.31	0.12	0.11	0.15	0.077
49136	MAH	4	4	0.00	1.00	0.75	0.25	0.25	0.25
49378	MYH	8	7	0.00	0.13	0.13	0.00	0.13	0.13
49379	UYH	11	8	0.38	0.73	0.091	0.25	0.36	0.00
NO TAG	-	1	1	1.00	0.00	0.00	0.00	0.00	0.00
EFP(10)	-	147	123	0.22	0.50	0.24	0.52	0.40	0.22
13651	FAD	8	6	0.00	0.00	0.25	0.33	0.00	0.50
49491	MAD	16	15	0.13	0.56	0.25	0.47	0.63	0.38
53331	MAD	16	11	0.18	0.31	0.44	0.27	0.38	0.062
49489	FAH	3	3	0.33	0.00	0.00	0.67	0.33	0.00
49494	MAH	16	13	0.15	0.63	0.062	0.85	0.50	0.13
49488	MAH	13	10	0.50	0.77	0.23	0.70	0.23	0.31
13653	MAH	12	11	0.18	0.67	0.42	0.73	0.67	0.25
53385	FYH	28	21	0.14	0.43	0.14	0.52	0.32	0.18
53255	MYH	23	21	0.14	0.61	0.22	0.43	0.52	0.35
53256	MYH	12	12	0.58	0.50	0.33	0.33	0.17	0.00

Birds/ Group	Status	Total visits	Visible entries	FC entry	FC inside	FC exit	PC entry	PC inside	PC exit
HSB (3)	-	93	32	0.13	0.15	0.24	0.34	0.27	0.14
49271	FAD	48	12	0.083	0.00	0.15	0.25	0.13	0.21
49262	MAD	32	13	0.15	0.22	0.34	0.15	0.44	0.031
49426	MYH	13	7	0.14	0.54	0.31	0.86	0.38	0.15
HSF (4)	-	19	11	0.27	0.11	0.16	0.18	0.11	0.16
49283	FAD	4	0	NA	0.00	0.50	NA	0.00	0.50
49288	MAD	5	5	0.00	0.00	0.20	0.00	0.20	0.00
49346	MYH	7	4	0.50	0.14	0.00	0.25	0.14	0.14
49345	MYH	3	2	0.50	0.33	0.00	0.50	0.00	0.00
OFQ (4)	-	56	35	0.14	0.36	0.21	0.086	0.30	0.071
53141	FAD	17	4	0.25	0.00	0.12	0.00	0.12	0.12
13867	MAD	18	13	0.077	0.44	0.22	0.00	0.33	0.056
13861	MAH	13	12	0.17	0.62	0.23	0.17	0.31	0.077
NO TAG	-	8	6	0.17	0.50	0.38	0.17	0.63	0.00
SFG (3)	-	22	22	0.045	0.41	0.091	0.045	0.32	0.045
49459	FAD	4	4	0.00	0.00	0.00	0.00	0.25	0.00
49143	MAH	10	10	0.00	0.30	0.20	0.00	0.30	0.10
NO TAG	-	8	8	0.13	0.75	0.00	0.13	0.38	0.00
SFN (3)	-	38	38	0.00	0.53	0.53	0.00	0.11	0.00
53023	FAD	11	11	0.00	0.091	0.00	0.00	0.27	0.00
53053	MAD	26	26	0.00	0.038	0.077	0.00	0.038	0.00
NO TAG	-	1	1	0.00	0.00	0.00	0.00	0.00	0.00

Table 12: Proportion of visit phases with nest-calls split by food and female presence. (a) Shows prey item brought to the nest, **(b)** what happens to the prey item once the adult enters the nest, and **(c)** if the breeding female is present in the nest when the adult enters. Column definitions are available in Table 11. "Unknown" values for prey item and feed type include 30 visits for which it was unclear if food was brought to the nest.

(a)	Prey item brought to nest							
Prey Item	**Total Visits**	**Visible Entries**	**FC Entry**	**FC Inside**	**FC Exit**	**PC Entry**	**PC Inside**	**PC Exit**
Caterpillar	255	179	0.21	0.52	0.19	0.26	0.40	0.098
Spider	135	83	0.28	0.42	0.24	0.20	0.37	0.074
Larva	133	98	0.28	0.48	0.30	0.27	0.30	0.083
Insect	80	50	0.20	0.44	0.19	0.38	0.31	0.15
Reptile	10	4	0.25	0.90	0.30	0.50	0.50	0.00
None	189	98	0.071	0.14	0.12	0.061	0.11	0.085
Unknown	202	138	0.19	0.43	0.21	0.27	0.28	0.14
(b)	**What happens to prey item after adult enters**							
Feed Type	**Total Visits**	**Visible Entries**	**FC Entry**	**FC Inside**	**FC Exit**	**PC Entry**	**PC Inside**	**PC Exit**
Feeds chick	565	381	0.26	0.50	0.24	0.32	0.35	0.11
Female feeds chick	151	100	0.070	0.23	0.14	0.080	0.17	0.060
Carer eats	22	15	0.60	0.73	0.23	0.40	0.73	0.18
Female eats	17	11	0.091	0.35	0.24	0.00	0.24	0.18
No food brought	189	98	0.071	0.14	0.13	0.061	0.11	0.085
Unknown	60	45	0.18	0.43	0.15	0.20	0.32	0.083
(c)	**Breeding female presence**							
Female Present	**Total Visits**	**Visible Entries**	**FC Entry**	**FC Inside**	**FC Exit**	**PC Entry**	**PC Inside**	**PC Exit**
Present	251	160	0.088	0.26	0.15	0.088	0.19	0.076
Absent	565	430	0.26	0.55	0.24	0.30	0.37	0.097

APPENDIX 4: EXTENDED MODEL PREDICTION GRAPHS

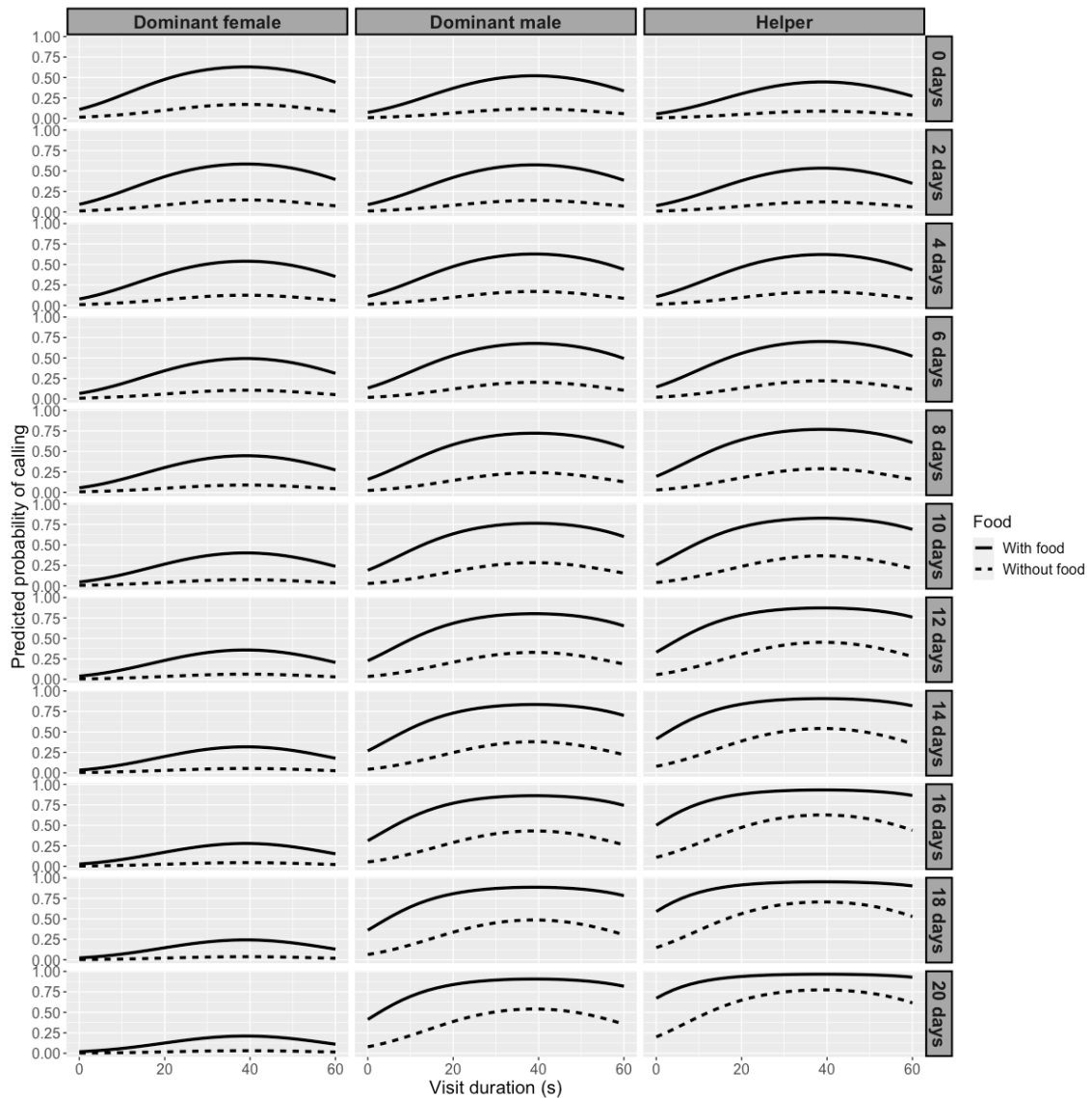**4A: PROBABILITY OF NEST-CALLING INSIDE THE NEST**

Figure 11: Probability of calling (flight or prompt) inside the nest. The probability of a bird calling inside the nest depending on status (columns), chick age (rows), visit duration (x-axis) and whether or not the bird is carrying food (solid lines indicate food brought, dotted is no food). In contrast to the dominant female (left), the dominant male and helpers increase flight and prompt calling as the chicks approach fledging. All birds are significantly less likely to call without food at all chick ages. Calling is most common in visits of medium duration. Model based on 938 visits by 50 birds.

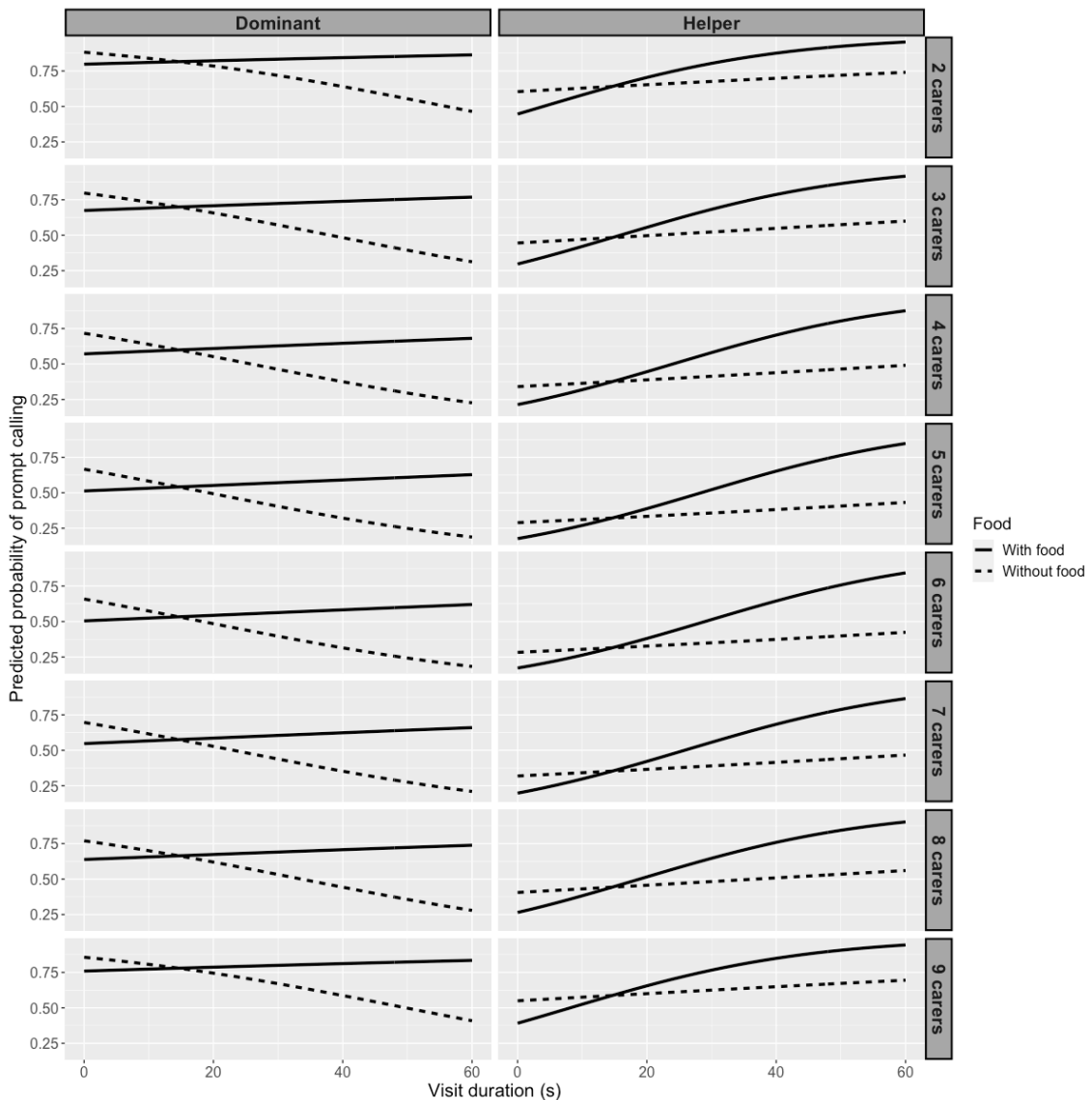## 4B: PROBABILITY NEST-CALLS WILL INCLUDE PROMPT CALLS

Figure 12: Probability of prompt versus flight calling inside the nest. The probability of a bird emitting a prompt call during a visit where they give at least one flight and/or prompt call as a function of focal status (columns), carer number (rows), visit duration (x-axis) and whether or not the bird is carrying food (solid lines indicate birds with food, dotted without). Birds without food only prompt call more than those with food in the shortest visits. Medium-sized groups emit the lowest proportion of prompt calls. Dominants and helpers react differently to brood hunger correlates. Model based on 464 visits by 47 individuals.
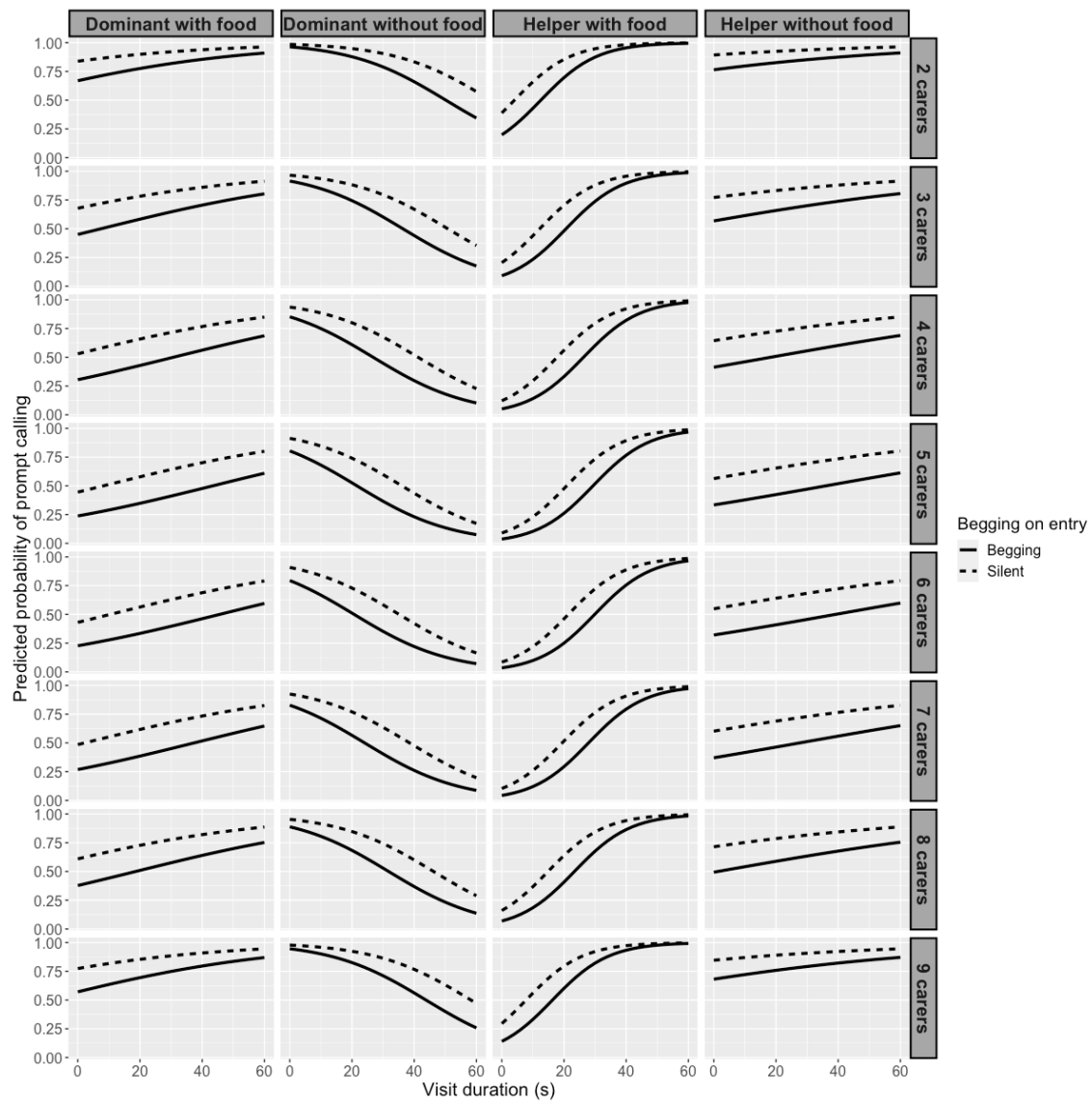
Figure 13: Probability of prompt calling inside the nest with begging. The probability of a bird emitting a prompt call during a visit where they give at least one flight and/or prompt call as a function of focal status and if it is carrying food (columns), carer number (rows), visit duration (x-axis) and if the brood is begging upon carer arrival (solid lines indicate vocalising chicks, dotted show that the brood is silent). Birds prompt call more when the chicks are not begging but the effect size is small. Model based on 272 visits by 37 individuals.

APPENDIX 5: EFFECTS OF NEST-CALLING

Table 13: Probability of brood begging on entry. Begging on entry to the nest is defined as nestlings begging in the 1 s prior to or following carer entry. Analysis based on GLMM with 449 nest visits by 39 individuals attending 10 nests. Data were excluded if another individual was already present in the nest during focal entry. All estimates and standard errors are reported on the logit scale. Only terms with predicted or potentially confounding impacts were included; with terms dropped from the minimal model if they failed to improve the explanatory power of the overall model as judged by *LRT*. Descriptions of estimates for linear and quadratic effects are provided in Table 5. Inter-visit interval represents the time since the last visit by any group member and is scaled by first centring by brood then dividing by the standard deviation for the centred values, while provisioning rate is the average number of visits per minute received in the past 30 min and is mean centred by brood. Calling at entrance refers to the nest visitor, was restricted to only visits in which the 2 s prior to nest entry were visible (see Methods) and is a three-level factor including no-call, flight call only or prompt call (n = 292 visits, by 38 individuals). Individual identity nested within group identity was fitted as random intercepts.

TERM	ESTIMATE	SE	*LRT*	*df*	*P-value*
Intercept	-4.49	0.74	-	-	-
With food (yes)	2.34	0.34	58.50	1	<0.001
Brood age	0.27	0.051	28.66	1	<0.001
Time of day (combined)	-	-	6.83	2	0.033
linear effect	0.051	0.031	2.75	1	0.10
quadratic effect	6.42	3.18	4.08	1	0.044
Inter-visit interval	-0.25	0.13	4.06	1	0.044
NON-SIGNIFICANT VARIABLES EXCLUDED					
Brood size	0.30	0.17	2.85	1	0.092
Carer number	-0.13	0.14	0.80	1	0.37
Brood size: carer number	0.96	0.61	2.13	1	0.14
Calling at entrance	-	-	1.00	2	0.61
Provisioning rate	0.17	0.31	0.31	1	0.58

Table 14: Effects of nest-calls on time to first beg. Begging intensity was defined as the time from the start of the first call after the adult entered (which had to be within 2 s of nest entry) to the start of the first beg (which then had to be within 5 s of entry). This was measured during 47 visits by 20 individuals in 7 groups attending 8 nests. This reduced sample size arose because all visits in which broods were already begging were excluded, and I could only include visits where birds gave a flight or prompt call immediately after entry. No additional variables became significant when excluding a further nine visits in which another bird was present when the adult arrived. Due to the reduced sample size, I only considered carer call type (flight only versus prompt), terms that were shown to be significant in Tables 7 and 8, and potential confounders (i.e., female brooding). Data were analysed using a linear mixed effects model following square root transformation. Random effects were individual identity nested within group identity.

TERM	ESTIMATE	SE	X^2	df	P-value
Intercept	0.94	0.19	-	-	-
Time of day	0.032	0.013	5.92	1	0.015
Brood size:carer number	-0.41	0.15	7.039	1	0.0080
NON-SIGNIFICANT VARIABLES EXCLUDED					
Brood age	-0.00021	0.017	0.010	1	0.92
With food	0.43	0.35	1.70	1	0.19
Call type (flight or prompt)	-	-	0.088	1	0.77
Brood size	-0.011	0.084	0.022	1	0.88
Carer number	0.017	0.036	0.15	1	0.70
Female brooding	-0.048	0.16	0.10	1	0.75
Inter-visit interval	-0.00010	0.00036	0.089	1	0.77

Table 15: Effects of nest-calls on probability of next bird bringing food.
Binomial GLMM to predict whether or not the following bird would bring food to
the nest as a function of calling in the focal visit, based on 923 visits by 50
individuals in 11 groups. Descriptions of estimates for linear and quadratic
effects are provided in Table 5. Only terms with predicted or potentially
confounding impacts were included; with terms dropped from the minimal model
if they failed to improve the explanatory power of the overall model as judged by
LRT. Estimates and standard errors are presented on the logit scale. Random
effects were individual identity nested within group identity.

TERM	ESTIMATE	SE	X^2	df	P-value
Intercept	0.38	0.22	-	-	-
Time of day (combined)	-	-	13.03	2	0.0015
linear effect	0.031	0.024	1.78	1	0.18
quadratic effect	9.60	2.93	11.25	1	<0.001
Brood size	0.42	0.076	16.71	1	<0.001
NON-SIGNIFICANT VARIABLES EXCLUDED					
Visit duration	-0.0050	0.0048	1.076	1	0.30
Brood age	0.045	0.024	3.49	1	0.062
Call type (flight or prompt)	-	-	0.74	2	0.69
Carer number	-0.017	0.040	0.18	1	0.67
Brood size:carer number	-0.23	0.31	0.54	1	0.46
Female brooding	0.25	0.23	1.22	1	0.27
Inter-visit interval	-0.000099	0.00019	0.27	1	0.60

REFERENCES

BARRETT, G., Silcocks, A., Barry, S., Cunningham, R. and Poulter, R., 2003. *The New Atlas of Australian Birds.* Royal Australasian Ornithologists Union: Melbourne.

BATES, D., Maechler, M., Bolker, B. and Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**(1), 1-48.

BEECHER, MD., Stoddard, PK. and Loesche, P., 1985. Recognition of Parents' Voices by Young Cliff Swallows. *The Auk*, **102**(3): 600-605.

BENGTSSON, H. and Rydén, O., 1981. Development of Parent-Young Interaction in Asynchronously Hatched Broods of Altricial Birds. *Ethology*, **56**(3): 255-272.

BIRDLIFE INTERNATIONAL, 2016. *Pomatostomus ruficeps*. The IUCN Red List of Threatened Species 2016: e.T22704992A93994300. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22704992A93994300.en. Downloaded on 10 January 2019.

BREITWISCH, R., Gottlieb, N. and Zaias, J., 1989. Behavioral Differences in Nest Visits between Male and Female Northern Mockingbirds. *The Auk*, **106**(4): 659-665.

BRISKIE, JV., Martin, PR. and Martin, TE., 1999. Nest Predation and the Evolution of Nestling Begging Calls. *Proceedings of the Royal Society of London B: Biological Sciences*, **266**: 2153-2159.

BROWNING, LE., Patrick, SC., Rollins, LA., Griffith, SC. and Russell, AF., 2012a. Kin Selection, Not Group Augmentation, Predicts Helping in an Obligate Cooperatively Breeding Bird. *Proceedings of the Royal Society B: Biological Sciences*, **279**: 3861-3869.

BROWNING, LE., Young, CM., Savage, JL., Russell, DJF., Barclay, H., Griffith, SC. and Russell, AF., 2012b. Carer Provisioning Rules in an Obligate Cooperative Breeder: Prey Type, Size and Delivery Rate. *Behavioral Ecology and Sociobiology*, **66**: 1639-1649.

CARLISLE, TR. and Zahavi, A., 1986. Helping at the Nest, Allofeeding and Social Status in Immature Arabian Babblers. *Behavioral Ecology and Sociobiology,* **18**: 339-351.

CLARKE, JA., 2010. White-Tailed Ptarmigan Food Calls Enhance Chick Diet Choice: Learning Nutritional Wisdom? *Animal Behaviour,* **79**: 25-30.

CLARKE, MF., 1988. The Reproductive Behaviour of the Bell Miner Manorina melanophrys. *Emu*, **88**(2): 88-100.

CLEMMONS, JR., 1995a. Development of a Selective Response to an Adult Vocalization in Nestling Black-Capped Chickadees. *Behaviour*, **132**: 1-20.

CLEMMONS, JR., 1995b. Vocalizations and Other Stimuli That Elicit Gaping in Nestling Black-Capped Chickadees (*Parus atricapillus*). *The Auk*, **112**: 603-612.

CRANE, JMS., Savage, JL. and Russell, AF., 2016. Diversity and Function of Vocalisations in the Cooperatively Breeding Chestnut-Crowned Babbler. *Emu*, **116**(3): 241-253.

CROSSWHITE, K. [Year unknown]. Modified by Antoniou, M. (2013) and Coye, C. (2019). Original script available online from www.ling.upenn.edu/courses/Fall_2013/ling520/DurationLogger.praat.

DOUTRELANT, C. and Covas, R., 2007. Helping Has Signalling Characteristics in a Cooperatively Breeding Bird. *Animal Behaviour*, **74**: 739-747.

DOYLE, M. and Russell, AF., 2020. Flight and Prompt Calls Signal Individual Identity but Weak Kinship Information in a Cooperatively Breeding Bird. *Masters thesis (unpublished)*. University of Exeter, Exeter.

ENGESSER, S., Crane, JMS., Savage, JL., Russell, AF. and Townsend, SW., 2015. Experimental Evidence for Phonemic Contrasts in a Nonhuman Vocal System. *PloS Biology*, **13**(6): e1002171.

ENGESSER, S., Ridley, AR. and Townsend, SW., 2017. Element Repetition Rates Encode Functionally Distinct Information in Pied Babbler 'Clucks' and 'Purrs'. *Animal Cognition*, **20**: 953-960.

FEISE, RJ., 2002. Do Multiple Outcome Measures Require P-value Adjustment? *BMC Medical Research Methodology*, **2**: 8.

FONTAINE, JJ. and Martin, TE., 2006a. Habitat Selection Responses of Parents to Offspring Predation Risk: An Experimental Test. *The American Naturalist*, **168**(6): 811-818.

FONTAINE, JJ. and Martin, TE., 2006b. Parent Birds Assess Nest Predation Risk and Adjust Their Reproductive Strategies. *Ecology Letters*, **9**(4): 428-434.

GARAY, J., Csiszár, V., Móri, TF., Szilágyi, A., Varga, Z. and Számadó, S., 2018. Juvenile Honest Food Solicitation and Parental Investment as a Life History Strategy: A Kin Demographic Selection Model. *PloS ONE*, **13**(3): e0193420.

GASTON, AJ., 1978a. Ecology of the Common Babbler *Turdoides caudatus. Ibis,* **120**: 415- 432.

GASTON, AJ., 1978b. The Evolution of Group Territorial Behavior and Cooperative Breeding. *The American Naturalist*, **112**(988): 1091-1100.

GODFRAY, HCJ., 1991. Signalling of Need by Offspring to Their Parents. *Nature*, **352**: 328-330.

GREIG-SMITH, PW., 1980. Parental Investment in Nest Defence by Stonechats (*Saxicola torquata*)*. Animal Behaviour*, **28**(2): 604-619.

GRIECO, F., 2001. Short-Term Regulation of Food-Provisioning Rate and Effect on Prey Size in Blue Tits, *Parus caeruleus. Animal Behaviour*, **62**: 107-116.

HAFF, TM. and Magrath, RD., 2011. Calling at a Cost: Elevated Nestling Calling Attracts Predators to Active Nests. *Biology Letters*, **7**: 493-495.

HAFF, TM., Horn, AG., Leonard, ML. and Magrath, RD., 2015. Conspicuous Calling Near Cryptic Nests: A Review of Hypotheses and a Field Study on White-Browed Scrubwrens. *Journal of Avian Biology*, **46**: 289-302.

HALKIN, SL., 1997. Nest-Vicinity Song Exchanges May Coordinate Biparental Care of Northern Cardinals. *Animal Behaviour*, **54**: 189-198.

HEATHCOTE, CF., 1989. The Acoustic Repertoire of the Bell Miner, *Manorina melanophrys*. In: *PhD Dissertation*. University of Melbourne, Melbourne.

HIGGINS, PJ. and Peter, JM., 2002. *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 6: Pardalotes to Shrike-thrushes*. Oxford University Press: Melbourne.

HOLLÉN, LI. and Manser, MB., 2006. Ontogeny of Alarm Call Responses in Meerkats, *Suricata suricatta*: The Roles of Age, Sex and Nearby Conspecifics. *Animal Behaviour*, **72**: 1345-1353.

KHAYUTIN, SN., 1985. Sensory Factors in the Behavioural Ontogeny of Altricial Birds. *Advances in the Study of Behavior,* **15**:105–152.

KILNER, RM., 2001. A Growth Cost of Begging in Captive Canary Chicks. *Proceedings of the National Academy of Sciences*, **98**: 11394-11398.

KILNER, R. and Johnstone, RA., 1997. Begging the Question: Are Offspring Solicitation Behaviours Signals of Need? *Trends in Ecology and Evolution*, **12**(1): 11-15.

KOKKO, H., Johnstone, RA. and 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.

KUHLMANN, F., 1909. Some Preliminary Observations on the Development of Instincts and Habits in Young Birds. *Psychological Review,* **11**: 49–85.

LACK, D., 1947. The Significance of Clutch-size. *Ibis*, **89**(2), 302–352.

LEECH, SM. and Leonard, ML., 1997. Begging and the Risk of Predation in Nestling Birds. *Behavioral Ecology*, **8**: 644-646.

LEONARD, ML., Fernandez, N. and Brown, G., 1997. Parental Calls and Nestling Behavior in Tree Swallows. *The Auk*, **114**: 668-672.

LESSELLS, C., Rowe, C. and McGregor, PK., 1995. Individual and Sex Differences in the Provisioning Calls of European Bee-Eaters. *Animal Behaviour*, **49**: 244-247.

LIEBL, AL., Browning, LE. and Russell, AF., 2016a. Manipulating Carer Number Versus Brood Size: Complementary But Not Equivalent Ways of Quantifying Carer Effects on Offspring. *Behavioral Ecology*, **27**(4): 1247-1254.

LIEBL, AL., Nomano, FY., Browning, LE. and Russell, AF., 2016b. Experimental Evidence for Fully Additive Care Among Male Carers in the Cooperatively Breeding Chestnut-Crowned Babbler. *Animal Behaviour*, **115**: 47-53.

MADDEN, JR., Kilner, RM. and Davies, NB., 2005. Nestling Responses to Adult Food and Alarm Calls: 1. Species-Specific Responses in Two Cowbird Hosts. *Animal Behaviour*, **70**(3): 619-627.

MAGRATH, RD., Pitcher, BJ. and Dalziell, AH., 2007. How to be Fed but not Eaten: Nestling Responses to Parental Food Calls and the Sound of a Predator's Footsteps. *Animal Behaviour*, **74**: 1117-1129.

MAGRATH, RD., Haff, TM., Horn, AG. and Leonard, ML., 2010. Calling in the Face of Danger: Predation Risk and Acoustic Communication by Parent Birds and Their Offspring. *Advances in the Study of Animal Behaviour*, **41**: 187-253.

MCDONALD, PG., Heathcote, CF., Clarke, MF., Wright, J. and Kazem, AJ., 2007. Provisioning Calls of The Cooperatively Breeding Bell Miner *Manorina melanophrys* Encode Sufficient Information for Individual Discrimination. *Journal of Avian Biology*, **38**: 113-121.

MCDONALD, PG., Te Marvelde, L., Kazem, AJN. and Wright, J., 2008. Helping as a Signal and the Effect of a Potential Audience During Provisioning Visits in a Cooperative Bird. *Animal Behaviour*, **75**: 1319-1330.

MCDONALD, PG. and Wright, J., 2008. Provisioning Vocalizations in Cooperative Bell Miners (*Manorina melanophrys*): More Than a Simple Stimulus for Nestling Begging. *The Auk*, **125**: 670-678.

MULDER, RA. and Langmore, NE., 1993. Dominant Males Punish Helpers for Temporary Defection in Superb Fairy-Wrens. *Animal Behaviour*, **45**: 830-833.

NAKAGAWA, S., 2004. A Farewell to Bonferroni: The Problems of Low Statistical Power and Publication Bias. *Behavioral Ecology*, **15**(6): 1044-1045.

NEUDORF, DLH., Brodrick, MJ. and Cureton, JC., II., 2013. Parental Provisioning by Carolina Wrens. *The Wilson Journal of Ornithology*, **125**(1): 179-184.

NICE, MM., 1957. Nesting Success in Altricial Birds. *The Auk,* **74**: 305-321.

NOLAN, V., Jr., 1978. The Ecology and Behavior of the Prairie Warbler *Dendroica discolor*. *Ornithological Monographs*, **26**.

NOMANO, FY., Browning, LE., Nakagawa, S., Griffith, SC. and Russell, AF., 2014. Validation of an Automated Data Collection Method for Quantifying Social Networks in Collective Behaviours. *Behavioral Ecology and Sociobiology*, **68**: 1379–1391.

NOMANO, FY., Browning, LE., Rollins, LA., Nakagawa, S., Griffith, SC. and Russell, AF., 2013. Feeding Nestlings Does Not Function as a Signal of Social Prestige in Cooperatively Breeding Chestnut-Crowned Babblers. *Animal Behaviour*, **86**: 277-289.

NOMANO, FY., Browning, LE., Savage, JL., Rollins, LA., Griffith, SC. and Russell, AF., 2015. Unrelated Helpers Neither Signal Contributions nor Suffer Retribution in Chestnut-Crowned Babblers. *Behavioral Ecology*, **26**(4): 986-995.

NOMANO, FY., Savage, JL., Browning, LE., Griffith, SC. and Russell, AF., 2019. Breeding Phenology and Meteorological Conditions Affect Carer Provisioning Rates and Group-Level Coordination in Cooperative Chestnut-Crowned Babblers. *Frontiers in Ecology and Evolution*, **7**: 1-16.

PLATZEN, D., 2004. *Parent-Nestling Vocal Interactions in the White-Browed Scrubwren*. Doctoral Thesis, Australian National University.

PLATZEN, D. and Magrath, RD., 2004. Parental Alarm Calls Suppress Nestling Vocalization. *Proceedings of the Royal Society of London B: Biological Sciences*, **271**: 1271-1276.

POHLERT, T., 2014. *The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR).* https://CRAN.R-project.org/package=PMCMR.

PORTELLI, DJ., Barclay, H., Russell, DJF., Griffith, SC. and Russell, AF., 2009. Social Organisation and Foraging Ecology of the Cooperatively Breeding Chestnut-Crowned Babbler (*Pomatostomus ruficeps*). *Emu*, **109**: 153-162.

RADFORD, AN. and Ridley AR., 2006. Recruitment Calling: A Novel Form of Extended Parental Care in an Altricial Species. *Current Biology*, **16**: 1700-1704.

RAIHANI, NJ., Nelson-Flower, MJ., Moyes, K., Browning, LE. and Ridley, AR., 2010. Synchronous Provisioning Increases Brood Survival in Cooperatively Breeding Pied Babblers. *Journal of Animal Ecology*, **79**: 44-52.

RAIHANI, NJ. and Ridley, AR., 2007. Adult Vocalizations During Provisioning: Offspring Response and Postfledging Benefits in Wild Pied Babblers. *Animal Behaviour*, **74**: 1303-1309.

RAIHANI, NJ. and Ridley, AR., 2008. Experimental Evidence for Teaching in Wild Pied Babblers. *Animal Behaviour*, **75**: 3-11.

RAPAPORT, LG., 2006. Parenting Behaviour: Babbling Bird Teachers? *Current Biology*, **16**: R675-R677.

R CORE TEAM, 2020. *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

REYER, HU. and Schmidl, D., 1988. Helpers Have Little to Laugh About: Group Structure and Vocalisation in the Laughing Kookaburra *Dacelo novaeguineae. Emu*, **88**(3): 150-160.

RICKLEFS, RE., 1969. An Analysis of Nesting Mortality in Birds. *Smithsonian Contributions to Zoology*, **9**: 1-48.

RITCHISON, G., 1983. The Function of Singing in Female Black-Headed Grosbeaks (*Pheucticus melanocephalus*): Family-Group Maintenance. *The Auk*, **100**: 105-116.

ROLLINS, LA., Browning, LE., Holleley, CE., Savage, JL., Russell, AF. and Griffith, SC., 2012. Building Genetic Networks Using Relatedness Information: A Novel Approach for the Estimation of Dispersal and Characterization of Group Structure in Social Animals. *Molecular Ecology*, **21**(7): 1727-1740.

RUSSELL, AF., 2016. *Chestnut-crowned Babblers: Dealing With Climatic Adversity and Uncertainty in the Australian Arid Zone* in W. Koenig, J. Dickinson (Eds.), *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution and Behaviour*. Cambridge University Press, Cambridge, MA.

RUSSELL, AF., Portelli, DJ., Russell, DJF. and Barclay, H., 2010. Breeding Ecology of the Chestnut-Crowned Babbler: A Cooperative Breeder in the Desert. *Emu*, **110**: 324-331.

SAVAGE, JL., Browning, LE., Manica, A., Russell, AF. and Johnstone, RA., 2017. Turn-Taking in Cooperative Offspring Care: By-Product of Individual Provisioning Behavior or Active Response Rule? *Behavioral Ecology and Sociobiology*, **71**: 162.

SHARP, SP., McGowan, A., Wood, MJ. and Hatchwell, BJ., 2005. Learned Kin Recognition Cues in a Social Bird. *Letters to Nature*, **434**: 1127-1130.

SHEN, SF., Chen, HC., Vehrencamp, SL. and Yuan, HW., 2010. Group Provisioning Limits Sharing Conflict Among Nestlings in Joint-Nesting Taiwan Yuhinas. *Biology Letters*, **6**: 318-321.

SIEBER, OJ., 1985. Individual Recognition of Parental Calls by Bank Swallow Chicks (*Riparia riparia*). *Animal Behaviour*, **33**: 107-116.

SORATO, E., Gullett, PR., Creasey, MJS., Griffith, SC. and Russell, AF., 2015. Plastic Territoriality in Group-Living Chestnut-Crowned Babblers: Roles of Resource Value, Holding Potential and Predation Risk. *Animal Behaviour*, **101**: 155-168.

STOFFEL, MA., Nakagawa, S. and Schielzeth, H., 2017. rptR: Repeatability Estimation and Variance Decomposition by Generalized Linear Mixed-Effects Models. *Methods in Ecology and Evolution*, **8**: 1639-1644.

STRONG, RM., 1914. On the Habits and Behavior of the Herring Gull, *Larus Argentatus Pont. The Auk,* **31**(1): 22-49.

WICKHAM, H., 2016. *ggplot2: Elegant Graphics for Data Analysis.* Springer-Verlag New York.

WRIGHT, J., 1997. Helping-at-the-Nest in Arabian Babblers: Signalling Social Status or Sensible Investment in Chicks? *Animal Behaviour*, **54**: 1439-1448.

YASUKAWA, K., 1989. The Costs and Benefits of a Vocal Signal: The Nest-Associated 'Chit' of the Female Red-Winged Blackbird, *Agelaius phoeniceus. Animal Behaviour*, **38**(5): 866-874.

YOUNG, CM., Browning, LE., Savage, JL., Griffith, SC. and Russell, AF., 2013. No Evidence for Deception Over Allocation to Brood Care in a Cooperative Bird. *Behavioral Ecology*, **24**: 70-81.

ZAHAVI, A., 1995. Altruism as a Handicap: The Limitations of Kin Selection and Reciprocity. *Journal of Avian Biology*, **26**(1): 1-3.