Experimental evidence for fully additive care among male carers in the cooperatively breeding chestnut-crowned babbler

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Although theory developed to understand carer response rules in cooperative breeders typically predicts partial compensation, where additional investment by one carer is optimally met by incomplete reductions by the other, fully additive care is a viable alternative under particular conditions. Primary among these conditions is an opportunity for both existing and additional carers to gain comparable fitness from contributing to rearing offspring. That, in a number of cooperative birds, at least one parent often maintains its level of contribution to offspring rearing independent of carer numbers is supportive, but experimental evidence is lacking. Here, in naturally occurring groups of the cooperatively breeding chestnut-crowned babbler, *Pomatostomus ruficeps*, we found that provisioning rates of male carers were insensitive to the number of other males present; this resulted in an increase in total brood and per capita nestling provisioning rates across the range of total carer numbers tested (i.e. two − seven). Further, remaining male carers failed to change their provisioning rates following the temporary removal of one to three other males for up to 36 h, leading to significant decreases in total brood and per capita nestling provisioning. We found no obvious evidence to suggest that carer removals were otherwise disruptive and confounded the opportunity for remaining carers to respond. Our results confirm the existence of strongly additive care in cooperative breeders, and corroborate recent theory predicting that such response rules will arise when all carers in a group have the potential to contribute similarly to offspring success.
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An understanding of how individual contributions to rearing offspring are influenced by the contributions of co-carers is central to understanding the evolutionary stability and functional significance of cooperative care systems. With increasing contributions by co-carers, individuals face a hypothetical choice: reduce contributions by an equivalent amount (full compensation), reduce contributions partially (incomplete compensation), maintain contributions (no compensation) or increase contributions (positive matching) (Johnstone & Hinde, 2006). The choice adopted has downstream consequences for the levels of care received by offspring, with no change for chicks reared under full compensation rules and partially additive, fully additive and super-additive care for chicks reared under partial compensation, no compensation and matching, respectively (Savage, Russell, & Johnstone, 2013a). Theory developed to understand carer response rules in

biparental care systems typically predicts the stable solution to be for each parent to respond incompletely in the opposite direction to any changes made by the other (i.e. partial compensation; Houston & Davies, 1985; Lessells & McNamara, 2012; McNamara, Gasson, & Houston, 1999), and results from manipulative experiments are generally supportive (Harrison, Barta, Cuthill, & Szekely, 2009). Although partial compensation is also a theoretical expectation in more cooperative systems, wherein offspring are reared by individuals in addition to the breeding pair, no change in response to other carers, and thus fully additive care can also be a stable solution under certain circumstances (Johnstone, 2011; Savage et al., 2013a; Savage, Russell, & Johnstone, 2013b).

Correlative evidence suggesting that carers can be insensitive to the contributions of others in cooperative breeders has been documented. For example, of 27 cooperatively breeding birds, 37% and 44% of species showed breeding females and males (respectively) maintained levels of nestling provisioning across the range of group sizes observed, while both sexes did so in 26% of species (Hatchwell, 1999). Further, this study suggested and provided

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significant support for the hypothesis that additive, rather than compensatory, care is selected when nestling starvation is the primary mode of offspring mortality. Formal game-theoretic modelling has confirmed that a lack of compensation among carers in response to a change in care is stable under two scenarios in cooperative breeders. Johnstone (2011) showed that it could be stable when the costs of increasing investment accelerate sharply while the benefits of reducing investment are marginal. Subsequently, Savage et al. (2013a,b) showed that although incomplete compensation was generally expected, fully additive care could be stable when mothers increased offspring productivity in response to increasing carer numbers. Nevertheless, correlative evidence for additive care might be confounded by variation in territory quality, as high-quality territories might simultaneously support more carers and high investment (Dickinson & Hatchwell, 2004). Despite several manipulative studies addressing carer provisioning rules in cooperative breeders (Hatchwell & Russell, 1996; MacGregor & Cockburn, 2002; McDonald, Kazem, & Wright, 2009; Peters, Cockburn, & Cunningham, 2002; Russell, Langmore, Gardner, & Kilner, 2008; Wright & Dingemanse, 1999), no study has yet shown evidence for fully additive care.

Here we tested responses among male carers to variation in male carer numbers in chestnut-crowned babblers, *Pomatostomus ruficeps*, a cooperative breeder in which additive care might be expected because starvation is the primary form of offspring mortality (Browning, Young, et al., 2012). Endemic to the arid and semiarid zone of southeastern Australia, this 50 g passerine bird breeds in units consisting of a single breeding female, one to four breeding males (mode = 1) and 0–13 nonbreeding helpers (mean = 4) (Russell, 2016). All breeders and most natal nonbreeders contribute to provisioning offspring (Browning, Patrick, Rollins, Griffith, & Russell, 2012; Browning, Young, et al., 2012; Nomano et al., 2015). Over 90% of nonbreeding helpers are male, because females chiefly disperse to new groups in their first year and all have done so by their second (Rollins et al., 2012); immigrant females are not known to help. Brood sizes vary from two to six, and clutch size increases with carer numbers (Liebl, Russell, Nomano, Browning, & Russell, n.d.). Correlative evidence suggests breeding females show load lightening (i.e. reduced provisioning with increasing carer numbers), but that males maintain biomass delivery rates to offspring across the range of carer numbers observed here (Browning, Young, et al., 2012). Finally, carers have significant effects on offspring productivity, and kin selection appears to be the primary mechanism accounting for helpers in this system (Browning, Patrick, et al., 2012; Russell, 2016).

Providing evidence for fully additive care requires demonstrating that carers are unresponsive to changes in the investment by co-carers. Therefore, any experimental test needs to be sufficiently extreme to ensure that a lack of response is not generated by an overly subtle experimental design, and yet not so invasive that a spurious response is generated. In this regard, handicapping experiments, such as feather clipping or tail weighting, might not lead to sufficient reductions in the contributions to generate confidence that a lack of response by unmanipulated carers is not due to type II error. Consequently, we measured carer provisioning during a control period and during the removal of one to three male carers and conducted specific analyses designed to test for disruptive effects of experimental manipulation on provisioning (Cockburn, 1998). During control days, the removed male carers combined contributed ca. 25% of the brood's feeds by male carers (SD = 10%, range 7–44%).

First, we used data collected on control days to determine individual provisioning rates in relation to natural variation in carer numbers and the consequences for brood and per capita nestling provisioning rates. Under the no compensation−additive care hypothesis, individual provisioning rates should be independent of carer numbers, leading to positive relationships between carer numbers and both brood and per capita nestling provisioning rates. Second, we determined the consequences of temporary male carer removals on the provisioning rates of each remaining male carer, and again analysed the consequences for both brood and nestling level rates of food acquisition. The no compensation−additive care hypothesis predicts remaining carers to be unresponsive to removals, resulting in broods and nestlings acquiring food at a significantly reduced rate relative to control days. Finally, to test whether our results might be confounded by disruptive effects of removals (e.g. by reducing foraging efficiency or changing dominance hierarchies among remaining group members; Cockburn, 1998), we tested whether or not removing group members impacted the synchrony of provisioning visits to the brood. We surmised brood-provisioning synchrony to be particularly informative because maintaining premanipulation levels of synchrony will be difficult if group members become less efficient foragers or engage in renewed conflict over dominance following removals (Cockburn, 1998). In this regard, we predicted that if helper removals were disruptive, the synchrony of visits to the nest would change between control and experimental days.

METHODS

The study was conducted at the University of New South Wales Arid Zone Research Station, Fowlers Gap (141°43′E, 31°05′S), New South Wales, Australia, in four breeding seasons (2007, 2008, 2013 and 2014). Details of the harsh, arid habitat and study population are provided elsewhere (Portelli, Barclay, Russell, Griffith, & Russell, 2009; Sorato, Gullett, Griffith, & Russell, 2012).

Study Design and Group Composition

We used a balanced within-subject study design using all male carers from 14 breeding units (one additional group was excluded as it included natal female carers). Contributions to offspring provisioning were determined during control and experimental days in each unit, with control periods always within 2 days before or after experimental days. In addition to the breeding female (identified by her brood patch), groups averaged 3.7 male carers (SD = 1.1, range 2–6); as there were no natal females in any of the units included, no female helpers contributed to brood provisioning. For logistical reasons, the provisioning rates of the breeding female could not be determined (see below), so we only report effects on male responses here. There are no known confounding influences of this omission (see Discussion). For the purposes of the current study, male carers are defined, irrespective of breeding status, as those provisioning broods ≥0.25 items/h during either the control or experimental period (mean provisioning rate of carers = 3.5 items/ h, SD = 1.8, range 0.25–8.8). This cutoff ensures we minimize the probability of providing supporting evidence for fully additive care by including noncarers in the analysis. We are unable to investigate effects of breeding status or relatedness on responses because molecular analyses of the relevant groups have not yet been performed. Nevertheless, we do not foresee this to be confounding because: (1) the distinction between male breeders and helpers is obscured in this system by high levels of polyandry (ca. 30% of broods; Nomano et al., 2015); (2) the provisioning behaviour of male helpers is not affected by their relatedness to the breeding female (Nomano et al., 2013) or the breeding male (Nomano et al., 2015); and (3) we excluded noncaring group members from our measures of carer numbers and provisioning rates.

Provisioning Data

Babblers are single prey loaders, with insect larvae and spiders comprising the majority of food items (Browning, Young, et al., 2012). Additionally, provisioning rates explain three times more variance in biomass delivery than prey size (Browning, Young, et al., 2012). Thus, provisioning rates capture most of the variation in food acquisition by offspring. Provisioning rates of male carers were determined remotely and continuously for an average of 17 h per breeding unit during the control period (range 9—25 h) and 6 h during the subsequent experimental day (range 2—14 h), with times in excess of 13 h resulting from data collected over 2 consecutive days. There was no effect of observation duration in any analysis (results not presented). To avoid the potentially confounding impact of measuring provisioning on the day of capture, and to give groups and broods time to become accustomed to their size and provisioning rate, provisioning responses of nonremoved male carers were recorded the day following capture and removal. Provisioning was determined from sunrise the day following capture until removed individuals were released (typically before sunset the day following capture, except one group which was released the subsequent morning).

The extensive recording periods were made possible by the use of remote census techniques. For these purposes, all individuals captured in the population (including nestlings) are injected in the flank with a small (2×12 mm) Trovan passive integrated transponder (PIT) tag. These tags contain a unique alphanumeric code which is recorded along with date and time when birds pass through a copper coil antenna linked to a LID-650 PIT-tag reader (Trovan Ltd, U.K., http://www.trovan.com/). The antenna is fitted to the entrance of the babblers' enclosed, dome-shaped nest, ensuring that all birds must pass through it to access the nest. The antenna and decoder are concealed and we have no evidence to suggest that this equipment impacts behaviour as groups commonly integrate the antenna into their nests and reuse nests with the antenna in place (for further details see Young, Browning, Savage, Griffith, & Russell, 2013).

One drawback with the decoder system is that it cannot distinguish nest entrances from exits. Previous research combining the decoder system with internal nest cameras indicates independent nest visits for the breeding female cannot be discerned because she spends highly variable amounts of time in the nest during each visit (Nomano, Browning, Nakagawa, Griffith, & Russell, 2014). However, these cameras also indicate that females provision at a rate of only 1.3—2.7 prey items/h in groups of three to seven (Browning, Young, et al., 2012); this rate is too low to confound our results. By contrast, male carers are highly consistent in their durations of nest visits (ca. 5—15 s), allowing a simple algorithm to predict independent nest visits with 99% accuracy using just the decoders (Nomano et al., 2014). Additionally, as male carers seldom enter the nest without food (on only ca. 5% of occasions) and rarely fail to deliver food (only ca. 2.5% of the time, i.e. false feed), we know that visits equate well with provisioning events (Young et al., 2013) and biomass delivered (Browning, Young, et al., 2012).

Manipulation of Male Carer Numbers

We temporarily removed a total of 22 male carers from 14 breeding units for up to 36 h when broods were 10—19 days old and provisioning rates had reached their asymptote (mean fledging date = 23 days; Russell, Portelli, Russell, & Barclay, 2010). Units were captured using mist nets and one to three males known to be provisioning were removed at random. Those removed provisioned at an equivalent rate to those remaining on control days

($F_{1,38} = 0.76$, $P = 0.39$; determined using a general linear mixed model (see below) with rate during the control day as the response variable, whether or not the individual was removed as the fixed factor, and group as the random term). More carers were removed from larger units, and no unit was left with fewer than two carers, including the breeding female. Because multiple breeding males can exist in each unit and these cannot be identified without molecular analysis, male carers were removed without regard for breeding status. This does not pose a problem for the key aims of this study which are to determine the response of male carers to carer removal and their consequences for rates of nestling food acquisition. Following manipulation, units comprised one to four male carers (mean = 2.1, SD = 0.7), leading to average reductions in numbers of male carers of 44% (range 33—60%) and in overall carer numbers (i.e. including the breeding females) of 35% (range 25—50%).

Following capture, removed birds were transported immediately in bird bags by vehicle to on-site aviaries where they were housed in compartments (2×2.5 m and 2 m high) containing natural substrate and perches, as well as ad libitum access to water and mealworms. Full details of the aviary and housing conditions are provided elsewhere (Engesser, Crane, Savage, Russell, & Townsend, 2015). Groups show no signs of retribution following the release of removed birds (Nomano et al., 2015).

Ethical Note

All methods were conducted in concordance with ASAB/ABS's Guidelines for ethical treatment and were approved by Macquarie University's Animal Care and Ethics Committee (licence no. 06/40A), the NSW National Parks and Wildlife Service and the Australian Bat and Bird Banding Scheme.

Statistical Analyses

Our three key aims were to determine: (1) the relationship between individual male carer provisioning rates and natural male carer numbers, as well as its consequences for brood and per capita nestling provisioning rates; (2) the effects of male carer removal on the provisioning rates of those males remaining, and its consequences (as for aim 1); and (3) whether carer removals are disruptive, as has been suggested but not formally tested (Cockburn, 1998).

Aims (1) and (2) comprised three analyses each, pertaining to individual provisioning rates (mean rate for each individual per h of observation), as well as their consequences for the rates at which broods (total feeds per h) and nestlings (total feeds per nestling per h) received food. First, individual provisioning rates were analysed using linear mixed models (LMM) with normal errors performed in the nlme package in R version 2.15.3 (R Core Development Team, 2013). In analysis of control data, brood size and male carer numbers were fitted as explanatory terms, and group identity was fitted as the random term to account for repeated measures of individuals from the same breeding unit. In analysis of carer responses, treatment was added as a further explanatory term, whereas the random term was set as individual nested within group. Second, on control days, brood and per capita nestling provisioning rates were analysed using general linear models (GLM) with normal errors in the R package lm, with brood size and carer numbers fitted as explanatory terms. Finally, comparisons of brood and nestling provisioning rates on control versus experimental days were analysed using an LMM, with treatment added as a further explanatory term, and group identity fitted as a random term to block the analyses by data collected from the same units on control and experimental days. In all analyses quadratic and

logarithmic relationships between carer numbers and response terms were tested, but neither added significantly to the explanatory power of the model over linear estimates and are not included in the results.

Aim (3) was tested by investigating the effects of helper removal on nest visit synchrony using a generalized linear mixed model (GLMM) using lme4 package in R. Our rationale is that the synchrony of individual nest visits would change during experimental days if removals influenced intragroup dynamics. For example, if, following helper removal, foraging efficiency declines or disputes over dominance increase, we would expect reduced provisioning synchrony among individuals on experimental days. Alternatively, if foraging efficiency increases, due to reductions in interference competition, we would expect increased synchrony. Finally, in some systems, synchrony might be maintained without any active regulatory mechanism, if, for instance, group members start foraging at the same time in a dense and clumped area of prey, allowing all members to return repeatedly to the same patch at similar rates. This, however, is unlikely in babblers given the dispersed (and often mobile) distribution of prey. The number of synchronous visits was obtained for all combinations of individuals within each unit. We defined synchronous visits as successive nest visits separated by less than 1 min (entry—entry time; Nomano et al., 2014). We assumed all individuals visiting the nest within 1 min synchronized once with each other ('gambit of the group'; Whitehead & Dufault, 1999). Here, 142 synchronous visits by 78 dyads from the 14 breeding units were included. The effect of manipulation on the level of synchrony was examined using a GLMM with Poisson distribution and logarithm link function. The number of synchronous visits was included as a response term and the natural log-transformed monitoring duration (h) was set as an exposure (also called offset term). Individual visit rate was accounted for by including the logarithm of the product of the feeding rates (visits/h) of two individuals in the dyad, and absolute difference in individual visit rates within the dyad as a fixed effect. The number of male carers, treatment (control versus removal) and their interaction were also included as fixed effects, and group was included as a random effect. All the nontransformed fixed effects were centred by subtracting the mean (Schielzeth, 2010).

RESULTS

Male Carer Provisioning Rates on Control Days

On control days, male carers provisioned at a mean rate of 3.1 items/h (SD = 2, range 0—6.2, N = 61 male carers). There was no obvious tendency for male carers to provision larger broods more frequently (LMM: $F_{1,12} = 1.93$, $P = 0.19$; estimate = 0.29 ± 0.21 SE) or for larger broods to be provisioned more overall (GLM: $F_{1,11} = 1.26$, $P = 0.23$; estimate = 1.16 ± 0.92 SE), and brood size was negatively associated with the rate at which each nestling received prey (GLM: $F_{1,11} = 2.73$, $P = 0.02$; estimate = -0.78 ± 0.29 SE). Male carers also provisioned broods at comparable rates across the range of unit sizes analysed (LMM: $F_{1,11} = 0.73$, $P = 0.41$; Fig 1a). Here, the slope of the best fit line ($y = -0.16x + 3.79$) does not differ significantly from zero ($r^2 = 0.014$; 95% confidence interval, CI = -0.55 to 0.22). Consequently, an incremental increase in the number of male carers was associated with a significant linear increase in both the rate at which broods received food (i.e. 2.3 feeds/h; GLM: $F_{1,11} = 8.11$, $P = 0.016$; Fig. 1b) and the rate at which each nestling received food (i.e. 0.7 feeds/h; GLM: $F_{1,11} = 5.07$, $P = 0.05$; Fig. 1c). Taken together, these results suggest that in chestnut-crowned babblers, the provisioning rates of male carers were insensitive to variation in carer numbers, at least across the range considered, and consequently contributions by such individuals were fully

additive. However, the validity of these conclusions pends the outcome of experimental manipulation of male carer number.
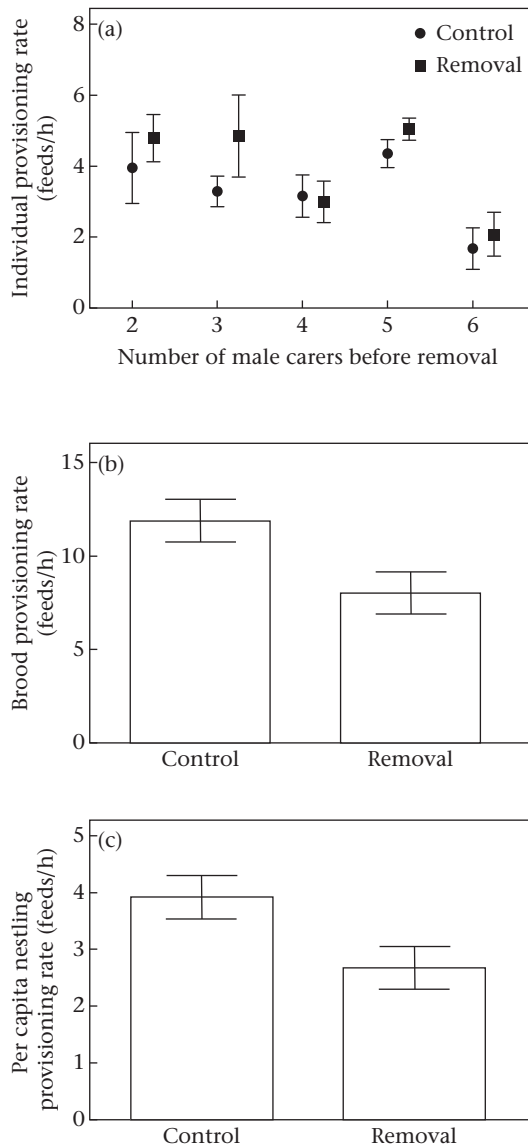
Responses to Male Carer Removal

Temporary removal of one to three male carers did not significantly influence the provisioning rate of those male carers remaining (LMM: main effect $F_{1,26} = 1.04$, $P = 0.31$, N = 36), and we found no evidence of an interaction between treatment and carer number on provisioning rates (LMM: $F_{1,26} = 0.26$, $P = 0.61$; Fig. 2a). Although using nonsignificant results to support evidence for a hypothesis can be susceptible to type II errors, our result that male carers were unresponsive to the loss of contributions by removed group members is further supported by the following four points. First, on control days, the median combined provisioning rate of those males that were eventually removed was 4.7 items/h (interquartile range 3.7—6.0). On experimental days, broods were provisioned in total at a median rate of 3.9 items/h less than on control
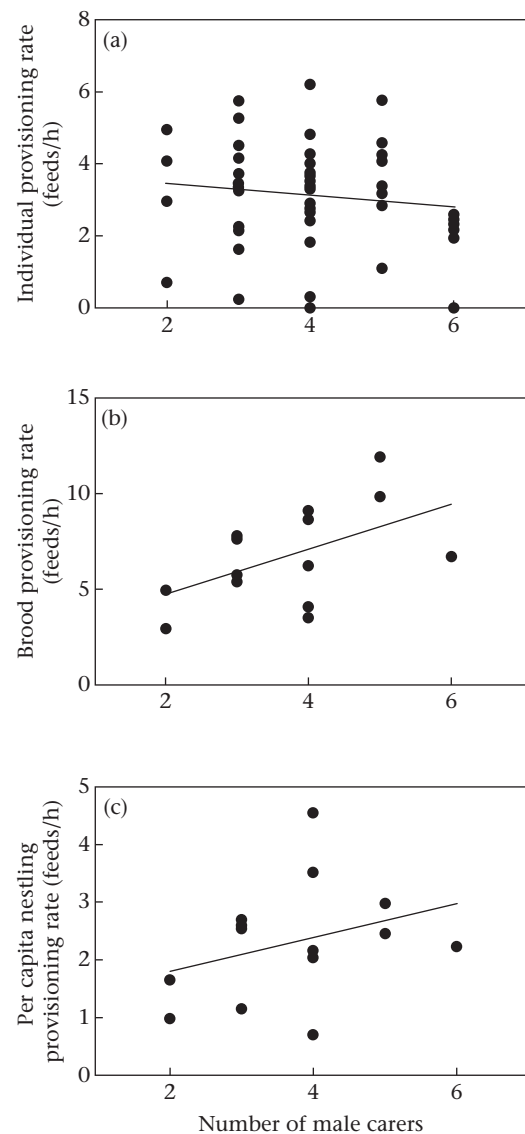
Figure 1. Provisioning rates in relation to number of male carers in premanipulated units. (a) Individual male carer provisioning rate. (b) Brood provisioning rate. (c) Provisioning rate per nestling. Raw values are shown with best fit lines.

days, suggesting that the remaining male carers only made up for 17% of the rate lost by the removal experiment. Second, we found no evidence to suggest that remaining male carers individually increased their provisioning rate as a function of the number of male carers remaining (LMM: $F_{1,9} = 0.40$, $P = 0.54$, estimate $= 0.33$, ± 0.52 SE) or the amount of provisioning lost (i.e. the total provisioning rate on control days of all individuals removed: $F_{1,12} = 0.61$, $P = 0.45$, estimate $= -0.14$, ± 0.18 SE). Third, the total reduction in provisioning rate to the brood (i.e. the brood level difference between the control and removal day) was not significantly different from the total provisioning rate of those removed on the control day (Student's t test: $t_{28} = -1.22$, $P = 0.23$). This again suggests remaining individuals did not compensate significantly for any of the reduction in brood provisioning caused by the removal of other carers. Finally, broods were provisioned significantly less often on experimental days than on control days (i.e. 3.5 fewer feeds/h; GLM: $F_{1,13} = 12.02$, $P = 0.004$; Fig. 2b), which led to a significant reduction in food delivered per nestling (i.e. 1.3 fewer feeds/h;

GLM: $F_{1,13} = 13.33$, $P = 0.003$; Fig. 2c). Taken together, these results corroborate the correlational findings above, that male carers show, at best, very weak responses to changes in the investment of cocarers, at least as determined through removal experiments and at least over the range considered.
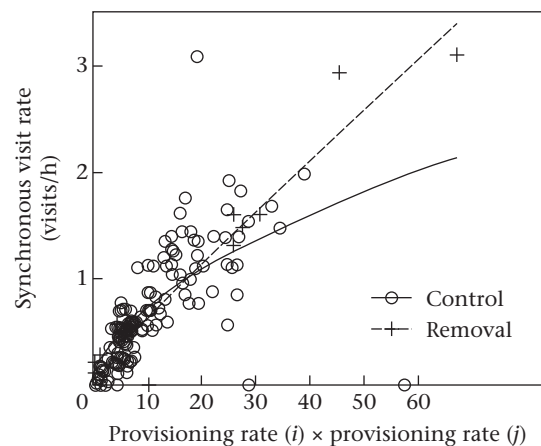
Testing the Disruption Hypothesis

On average, 43% (range 0–79%, SD = 18) of nest visits were synchronous, and the number of such visits/h varied within and among nests (coefficient of variation = 0.88). This variation was largely explained positively by individual provisioning rate (GLMM: $Z = 14.20$, $P < 0.0001$; estimate $= 0.79 \pm 0.06$ SE) and, to a lesser extent, negatively by the degree of asymmetry in provisioning rates within dyads ($Z = -1.79$, $P = 0.07$; estimate $= -0.06 \pm 0.034$ SE). By contrast, we found no evidence to suggest that the number of male carers ($Z = -1.0$, $P = 0.32$; estimate $= -0.25 \pm 0.25$ SE), treatment ($Z = 0.50$, $P = 0.62$; estimate $= 0.28 \pm 0.56$ SE; Fig. 3) or the interaction between the two ($Z = 0.70$, $P = 0.49$; estimate $= 0.17 \pm 0.24$ SE) influenced visit synchrony. These results suggest helper removals had little impact on the way in which individuals visit the nest, and thus the lack of response to removal by male carers was not generated by disruptive effects of carer removal on group dynamics or foraging ability.

DISCUSSION

We provide evidence that chestnut-crowned babbler male carers follow a no compensation rule in response to changes in provisioning by others; this leads to their contributions being fully additive to one another. First, under control conditions, the provisioning rates of male carers were independent of the number of carers (up to seven). Further, male carer provisioning rates were unresponsive to the removal of one to three carers (i.e. mean reductions in brood provisioning rates of 25%). Second, as a consequence, the rates at which both broods and nestlings received food were positively, and linearly, associated with the number of male carers, with each declining significantly following carer removal. Finally, we found no evidence to suggest that helper removals disrupted group provisioning ability, at least as measured through nest visit synchrony.

Although the use of our PIT-tag system allows provisioning data to be collected over protracted timescales, one drawback is our inability to monitor the provisioning behaviour of breeding females. Inclusion of the breeding female's contribution should not

Figure 2. Provisioning rates in response to removals. (a) Individual male carer provisioning rate. (b) Brood provisioning rate. (c) Provisioning rate per nestling. Figures show raw data ± SEM.

Figure 3. Frequency of synchronous visits for dyad composed of individuals i and j ($i \neq j$). Raw values are shown with best fit lines.

change the basic result that male carers are unresponsive to each other's contributions, so we can conclude their contributions are fully additive, at least over the range considered. Nevertheless, it is conceivable that the breeding female's provisioning contribution might confound the interpretation that the contribution of male carers is additive overall. To be fully confounding, however, breeding females would have to provision between 13 times/h in units of three and zero in units of seven. Observations using nest cameras suggest this is far from the case: females contribute only 2.7 prey items/h in units of three and reduce this rate by ca. 15% per additional carer (i.e. contributing 1.3 items/h in units of seven; Browning, Young, et al., 2012). Thus, the breeding female contributes insufficiently overall and shows insufficient reductions relative to that provided by each additional male carer (i.e. just 11%) to confound the additive contribution of male carers.

Another potential confound stems from the experimental method used, as any experimental manipulation can generate undesired consequences (Harrison et al., 2009). In the case of carer removals, many of the potential consequences are intuitive (Cockburn, 1998). Much theory on the evolution of cooperative breeding proposes that nonbreeding carers gain group-living benefits while competing for an opportunity to breed (e.g. Koenig, Pitelka, Carmen, Mumme, & Staback, 1992). By extension, remove group members and you run the risk of changing a group's foraging efficiency, or influencing predation risk and conflict over dominance within the group; in each case, a spurious response to carer removal could be generated. However, whether or not any such effects occur, let alone confound carer responses to removals, remains untested. We hypothesized that many such consequences would manifest in the synchrony of provisioning visits by individuals in the group. Specifically, if carer removal reduced foraging efficiency and increased dominance interactions, visit synchrony should decline following manipulation. We found no evidence to suggest that this was the case, lending support to the hypothesis that helper removals in chestnut-crowned babblers are unlikely to confound carer responses.

As our findings are unlikely to be confounded, the obvious question is: why do we find evidence for fully additive care among male carers? One possibility is that evolutionarily, each carer has a fixed provisioning rule and is therefore insensitive to the contribution of co-carers (sensu Houston & Davies, 1985). We find this explanation unlikely as breeding females appear to be responsive to carer numbers and male carers are responsive to brood age and demand (Browning, Young, et al., 2012; Liebl, Browning, & Russell, 2016). Hatchwell (1999) found that nonbreeding carers' contributions were more additive in species of cooperative birds in which nestling starvation was prevalent. He hypothesized that this would arise when marginal benefits of care exceed marginal costs (Russell et al., 2008). Johnstone (2011), using game-theoretic modelling, showed that this can occur when the costs of increasing care are particularly steep, and individuals provide relatively low levels of care overall. Both are true of chestnut-crowned babblers: nestling starvation is the primary moderator of fledging success (Russell et al., 2010) and an average of one prey item per nestling per h is relatively low. Alternatively, additive care can also be stable if mothers increase productivity as a function of carer numbers (Savage et al., 2013a,b), a common observation in cooperative breeders (Russell & Lummaa, 2009), including chestnut-crowned babblers (Liebl et al., n.d.). This is because increased productivity allows additional carers the potential to accrue equivalent fitness to existing carers. Thus, fully additive care is likely to have evolved in chestnut-crowned babblers due to high nestling starvation mediated through a combination of prohibitive costs of increasing investment and increased productivity by the breeding female with increasing carer numbers.

Although these hypotheses help explain our experimental findings, they also illuminate another question: why should the offspring of some species be prone to nestling starvation? Given the costs of only partially rearing offspring, one might expect strong selection on mothers to produce the number of offspring that minimizes offspring starvation. On the contrary, despite having both the highest level of nestling starvation and additive care of any Australian babbler, chestnut-crowned babblers also modally lay twice as many eggs (four or five eggs per clutch, as opposed to two or three in other Australian babbler species; Blackmore & Heinsohn, 2007; Brown, Brown, & Brown, 1982; Higgins, Peter, & Cowling, 2006; Russell et al., 2010). We hypothesize that one potential answer, and the reason why both additive care and relatively steep cost functions appear generally associated with high offspring starvation, lies effectively in a 'cooperation trap'. In biparental care species, all female offspring derive from similarly sized groups carrying the genes for the fecundity that produced them. In increasingly obligate cooperative breeders, female recruits will derive disproportionately from large groups and carry the genes for the fecundity that such groups are able to rear. However, because of inevitable variance in ecological conditions, many groups will be suboptimally composed to rear the number of progeny that the females have been selected to produce, leading to high offspring starvation. Further, steep individual cost functions combined with large numbers of progeny might be expected to select for carers to invest 'maximally' and so be relatively insensitive to the contributions of co-carers (Johnstone, 2011). As a consequence, and contrary to the assumption of most existing formal care models, we propose that carers in many groups of cooperative breeders will be operating on the linearly increasing zone of the benefit function (McAuliffe, Wrangham, Glowacki, & Russell, 2015). Here, additive care will be under selection because reducing investment in this area (e.g. partial compensation for additional contributions from other carers) leads to proportional reductions in fitness, and increasing investment is prohibitively costly (Johnstone, 2011).

Our hypothesis generates three testable predictions, at least for cooperative breeders. First, additive care will be more prevalent in species in which a strong relationship exists between carer numbers and offspring recruitment, leading offspring to derive disproportionately from large groups which are capable of rearing large numbers of offspring successfully. Second, as a consequence, we predict species showing additive care will be more fecund than congeners for which carer effects are less additive. As indicated above, chestnut-crowned babblers show at least some supporting evidence for these predictions relative to other Australian Pomatostomidae. Finally, partial compensation is predicted among carers in group sizes that maximize offspring production. We do not have the power to test this here because enough groups of the required size were lacking. Testing response rules in the largest groups either will require an overrepresentation of large group sizes in the data set or might dictate helper additions (rather than removals); however, these are seldom feasible. Either way, further studies are required to clarify why nestling starvation is prevalent in some cooperative breeders, particularly those in which fecundity is high, and whether carer response rules are nonlinear across the full range of possible group sizes.

We have three key take-home messages. First, we suggest measuring responses to qualitative changes in group contributions, induced through temporary removal experiments, is an appropriate means of investigating carer response rules, although confounding disruptive effects need to be considered. Second, although we concur with Hatchwell (1999) that additive care will be selected in systems wherein nestling starvation is prevalent, we hypothesize this to be potentially symptomatic, rather than specifically

deterministic, of additive care. This might be because many groups are caught in a 'cooperation trap', suboptimally composed to rear the numbers of offspring produced. As such, we predict the greatest levels of additive care in those cooperative breeders showing a mismatch between average and optimal carer numbers in the population, where the latter produces the majority of recruits. Finally, this hypothesis might be generalized to some biparental care systems wherein individual or territory quality varies significantly, such that the majority of recruits derive predictably from a subset of individuals or locales. In short, we predict fully additive care to be more common than is generally assumed, and to be stable when carers are operating much lower on the investment—benefit curve than is usually assumed by formal parental care models (McAuliffe et al., 2015).

Acknowledgments

References

Blackmore, C. J., & Heinsohn, R. G. (2007). Reproductive success and helper effects in the cooperatively breeding grey-crowned babbler. *Journal of Zoology, 273*(3), 326—332.

Brown, J. L., Brown, E. R., & Brown, S. D. (1982). Morphological variation in a population of grey-crowned babblers: correlations with variables affecting social behavior. *Behavioral Ecology and Sociobiology, 10*(4), 281—287. http://dx.doi.org/10.1007/BF00302818.

Browning, L. E., Patrick, S. C., Rollins, L. A., Griffith, S. C., & Russell, A. F. (2012). Kin selection, not group augmentation, predicts helping in an obligate cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences, 283*(1823). http://dx.doi.org/10.1098/rspb.2012.1080.

Browning, L. E., Young, C. M., Savage, J. L., Russell, D. J. F., Barclay, H., Griffith, S. C., et al. (2012). Carer provisioning rules in an obilgate cooperative breeder: prey type, size and delivery rate. *Behavioral Ecology and Sociobiology, 66*(12), 1639—1649.

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

Dickinson, J. L., & Hatchwell, B. J. (2004). Fitness consequences of helping. In W. D. Koenig, & J. L. Dickinson (Eds.), *Ecology and evolution of cooperative breeding in birds* (pp. 48—66). Cambridge, U.K.: Cambridge Books.

Engesser, S., Crane, J. M. S., Savage, J. L., Russell, A. F., & Townsend, S. W. (2015). Experimental evidence for phonemic contrasts in a nonhuman vocal system. *PLoS Biology, 13*(6), e1002171. http://dx.doi.org/10.1371/journal.pbio.1002171.

Harrison, F., Barta, Z., Cuthill, I., & Szekely, T. (2009). How is sexual conflict over parental care resolved? A meta-analysis. *Journal of Evolutionary Biology, 22*(9), 1800—1812.

Hatchwell, B. J. (1999). Investment strategies of breeders in avian cooperative breeding systems. *American Naturalist, 154*(2), 205—219.

Hatchwell, B. J., & Russell, A. F. (1996). Provisioning rules in cooperatively breeding long-tailed tits *Aegithalos caudatus*: an experimental study. *Proceedings of the Royal Society B: Biological Sciences, 263*(1366), 83—88.

Higgins, P. J., Peter, J. M., & Cowling, S. J. (2006). *Handbook of Australian, New Zealand and Antarctic birds: Volume 7 Boatbill to Starlings*. Melbourne, Australia: Oxford University Press.

Houston, A. I., & Davies, N. B. (1985). The evolution of cooperation and life history in the Dunnock, *Prunella modularis*. In R. Sibley, & R. Smith (Eds.), *Behavioral ecology: Ethologcal consequences of adaptive behaviour* (pp. 471—487). Oxford, U.K.: Blackwell Scientific Publications.

Johnstone, R. A. (2011). Load lightening and negotiation over offspring care in cooperative breeders. *Behavioral Ecology, 22*(2), 436—444. http://dx.doi.org/10.1093/beheco/arq190.

Johnstone, R. A., & Hinde, C. A. (2006). Negotiation over offspring care—how should parents respond to each other's efforts? *Behavioral Ecology, 17*(5), 818—827. http://dx.doi.org/10.1093/beheco/arl009.

Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L., & Staback, M. T. (1992). The evolution of delayed dispersal in cooperative breeders. *The Quarterly Review of Biology, 67*(2), 111—150.

Lessells, C. M., & McNamara, J. M. (2012). Sexual conflict over parental investment in repeated bouts: negotiation reduces overall care. *Proceedings of the Royal Society B: Biological Sciences, 279*(1733), 1506—1514.

Liebl, A. L., Russell, D., Nomano, F., Browning, L., & Russell, A. (n.d.). *Maternal effects of chestnut crowned babblers*. Manuscript in preperation.

Liebl, A. L., Browning, L. E., & Russell, A. F. (2016). Carer removal and brood size manipulation: not equivalent to quantify carer impacts on provisioning. *Behavioral Ecology*. http://dx.doi.org/10.1093/beheco/arw038 (in press).

MacGregor, N. A., & Cockburn, A. (2002). Sex differences in parental response to begging nestlings in superb fairy-wrens. *Animal Behaviour, 63*(5), 923—932.

McAuliffe, K., Wrangham, R., Glowacki, L., & Russell, A. F. (2015). When cooperation begets cooperation: the role of key individuals in galvanizing support. *Philosophical Transactions of the Royal Society B: Biological Sciences, 370*, 20150012. http://dx.doi.org/10.1098/rstb.2015.0012.

McDonald, P. G., Kazem, A. J. N., & Wright, J. (2009). Cooperative provisioning dynamics: fathers and unrelated helpers show similar responses to manipulations of begging. *Animal Behaviour, 77*(2), 369—376. http://dx.doi.org/10.1016/j.anbehav.2008.10.009.

McNamara, J. M., Gasson, C. E., & Houston, A. I. (1999). Incorporating rules for responding into evolutionary games. *Nature, 401*(6751), 368—371.

Nomano, F. Y., Browning, L. E., Nakagawa, S., Griffith, S. C., & Russell, A. F. (2014). Validation of an automated data collection method for quantifying social networks in collective behaviours. *Behavioral Ecology and Sociobiology, 68*(8), 1379—1391.

Nomano, F. Y., Browning, L. E., Rollins, L. A., Nakagawa, S., Griffith, S. C., & Russell, A. F. (2013). Feeding nestlings does not function as a signal of social prestige in cooperatively breeding chestnut-crowned babblers. *Animal Behaviour, 86*, 277—289.

Nomano, F. Y., Browning, L. E., Savage, J. L., Rollins, L. A., Griffith, S. C., & Russell, A. F. (2015). Unrelated helpers neither signal contributions nor suffer retribution in chestnut-crowed babblers. *Behavioral Ecology, 26*(4), 986—995. http://dx.doi.org/10.1093/beheco/arv023.

Peters, A., Cockburn, A., & Cunningham, R. (2002). Testosterone treatment suppresses paternal care in superb fairy-wrens, *Malurus cyaneus*, despite their concurrent investment in courtship. *Behavioral Ecology and Sociobiology, 51*(6), 538—547. http://dx.doi.org/10.1007/s00265-002-0472-4.

Portelli, D. J., Barclay, H., Russell, D. J. F., Griffith, S. C., & Russell, A. F. (2009). Social organisation and foraging ecology of the cooperatively breeding Chestnut-crowned Babbler (*Pomatostomus ruficeps*). *Emu, 109*, 153—162.

R Core Development Team. (2013). *R: A language and environment for statistical computing*.

Rollins, L. A., Browning, L. E., Holleley, C. E., Savage, J. L., Russell, A. F., & Griffith, S. C. (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. http://dx.doi.org/10.1111/j.1365-294X.2012.05492.x.

Russell, A. F. (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, MA: Cambridge University Press.

Russell, A. F., Langmore, N. E., Gardner, J. L., & Kilner, R. M. (2008). Maternal investment tactics in superb fairy-wrens. *Proceedings of the Royal Society B: Biological Sciences, 275*(1630), 29—36. http://dx.doi.org/10.1098/rspb.2007.0821.

Russell, A. F., & Lummaa, V. (2009). Maternal effects in cooperative breeders: from hymenopterans to humans. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1520), 1143—1167.

Russell, A. F., Portelli, D. J., Russell, D. J. F., & Barclay, H. (2010). Breeding ecology of the chestnut-crowned babbler: a cooperative breeder in the desert. *Emu, 110*, 324—331.

Savage, J. L., Russell, A. F., & Johnstone, R. A. (2013a). Intra-group relatedness affects parental and helper investment rules in offspring care. *Behavioral Ecology and Sociobiology, 67*(11), 1855—1865. http://dx.doi.org/10.1007/s00265-013-1595-5.

Savage, J. L., Russell, A. F., & Johnstone, R. A. (2013b). Maternal costs in offspring production affect investment rules in joint rearing. *Behavioral Ecology, 24*(3), 750—758.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution, 1*(2), 103—113.

Sorato, E., Gullett, P. R., Griffith, S. C., & Russell, A. F. (2012). Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. *Animal Behaviour, 84*, 823—834.

Whitehead, H., & Dufault, S. (1999). Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behavior, 28*, 33—74.

Wright, J., & Dingemanse, N. J. (1999). Parents and helpers compensate for experimental changes in the provisioning effort of others in the Arabian babbler. *Animal Behaviour, 58*(2), 345—350. http://dx.doi.org/10.1006/anbe.1999.1152.

Young, C. M., Browning, L. E., Savage, J. L., Griffith, S. C., & Russell, A. F. (2013). No evidence for deception over allocation to brood care in a cooperative bird. *Behavioral Ecology, 24*(1), 70—81.