



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 babbler, *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.

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