

Carer provisioning rules in an obligate cooperative breeder: prey type, size and delivery rate

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Abstract Providing food to developing offspring is beneficial for offspring but costly for carers. Understanding patterns of provisioning thus yields important insights into how selection shapes (allo-) parental care strategies. Broadly, offspring development will be influenced by three components of provisioning (prey type, size and delivery rate). However, all three variables are rarely considered simultaneously, leading to suggestions that the results of many studies are misleading. Additionally, few studies have

examined the provisioning strategies of breeders and non-breeding helpers in obligate cooperative breeders, wherein reproduction without help is typically unsuccessful. We investigated these components of provisioning in obligately cooperative chestnut-crowned babbler (*Pomatostomus ruficeps*). Prey type was associated with size, and delivery rate was the best predictor of the overall amount of food provided by carers. As broods aged, breeders and helpers similarly modified the relative proportion of different prey provided and increased both prey size and delivery rate. Breeding females contributed less prey than male breeders and adult helpers, and were the only carers to load-lighten by reducing their provisioning rates in the presence of additional carers. While our results suggest that breeders and helpers follow broadly comparable provisioning rules, they are also consistent with the idea that, in obligately cooperative species, breeding females benefit more from conserving resources for future reproduction than do helpers which have a low probability of breeding independently.

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Introduction

In iteroparous organisms, fitness is maximised in large part by optimising the trade-off between investment in current and future reproductive attempts (Williams 1966; Stearns 1992). One way in which reproductive investment can be quantified is through measures of offspring provisioning because provisioning is expected to be costly to carers (Clutton-Brock 1991), and the level of nutrition received by offspring is known to have pronounced fitness consequences (Lindström 1999; Metcalfe and Monaghan 2001). It is commonly assumed that those individuals reaping greater

benefits, for example, because they are more related to young, should contribute more to provisioning young than those that benefit less, and that those suffering relatively high costs of provisioning should contribute less than those suffering lower costs (Clutton-Brock 1991). However, both predictions may depend on the expected value of future reproductive attempts (e.g. Sheldon 2000). For example, where the value of current attempts exceeds that expected of future ones, selection should favour increased allocation to provisioning current young, irrespective of individual variation in the current costs and benefits involved. Quantification of provisioning behaviour thus offers significant insights into the selection pressures acting on life-history evolution, and in particular, how different classes of individual value current versus future reproduction (Clutton-Brock 1991; Hatchwell 1999).

Cooperatively breeding species provide a particularly useful system for investigating provisioning rules because carers of differing reproductive status and age contribute to rearing the same young (Brown 1987; Stacey and Koenig 1990; Solomon and French 1997). The rate at which carers of differing status provide food to developing offspring varies considerably among species, as does their response to variation in offspring age and current workforce. For example, in long-tailed tits (*Aegithalos caudatus*), breeders feed offspring more often than do helpers, but both increase feeding rates as broods age (MacColl and Hatchwell 2003) and reduce them with additional helpers (Nam et al. 2011). In white-fronted bee-eaters (*Merops bullockoides*), breeders contribute more than helpers to provisioning but maintain their work rate with increasing workforce (Emlen and Wrege 1991). Finally, in meerkats (*Suricata suricatta*), breeders feed offspring at a lower rate than do helpers and reduce their investment to a greater extent as helper number increases (Clutton-Brock et al. 2004).

Such variation can be partly explained by the likelihood of offspring starvation—where the probability of starvation is high, carers should be selected to maintain their provisioning rates with increasing workforce (Hatchwell 1999). However, this model did not consider why carers of differing breeding status should vary in their overall contributions to offspring provisioning nor why they should vary in response to changes in brood demand or workforce. While such variation might be expected to revolve around relatedness to the brood, there is little evidence that kinship contributes significantly to quantitative variation in carer provisioning rates (Cornwallis et al. 2009). Another explanation lies in the relative probability of future reproduction by helpers compared to that of current breeders and the effects of current work rates on this future probability (Clutton-Brock et al. 2004; Canestrari et al. 2008). Broadly speaking, in facultatively cooperative species, where the majority of helpers go on to secure an independent breeding position in the future, helpers will benefit significantly by

saving resources; hence, they might be expected to invest less than breeders in provisioning current young. By contrast, in obligate cooperative breeders, where most helpers never gain reproductive status and the benefits of being a breeder are substantial (Clutton-Brock et al. 2006), breeders should be under stronger selection than helpers to safeguard resources for subsequent attempts; hence, they should contribute less to caring for current offspring.

While current evidence largely supports the above predictions, two problems have been highlighted (Dickinson and Hatchwell 2004; Clutton-Brock et al. 2004). First, there are currently few data on obligate cooperatively breeding vertebrates, as they are relatively rare (Hatchwell 2009). Second, the vast majority of studies have used feeding rate as a surrogate for carer contributions to provisioning young (Hatchwell 1999). While this is likely to be satisfactory in some species, for which prey are relatively invariant (e.g. Hatchwell et al. 2004; Russell et al. 2008), this is not always the case. For example, in Arabian babblers (*Turdoides squamiceps*), breeders and helpers increase both provisioning rate and prey size in response to elevated brood demand (Wright 1998). In green woodhoopoes (*Phoeniculus purpureus*), breeders and helpers vary prey type as chicks age (Radford 2008), while in laughing kookaburras (*Dacelo novaeguineae*), both breeders and helpers reduce the size of prey fed to chicks with increasing helper number, but only helpers reduce their feeding rate (Legge 2000). Therefore, in addition to provisioning rate, prey size and type appear to represent salient elements of individual contributions.

Here, we investigate provisioning rules in an obligate cooperatively breeding bird, the chestnut-crowned babbler (*Pomatostomus ruficeps*). First, we assess the relative abundance and size of different prey types in the environment. Second, we investigate the effects of carer status, brood age and workforce, as well as their interactions, on the type and size of prey fed to nestlings; the rate at which prey is delivered; and the total amount of food fed to young by individual carers. Finally, we test the relative importance of prey size versus provisioning rate in determining variation in the overall amount of food delivered to nestlings. Chestnut-crowned babblers are medium-sized (~50 g), sexually monomorphic, obligate cooperatively breeding passerines endemic to the arid and semi-arid regions of south-eastern Australia (Higgins and Peter 2002). They are also plural breeders, with 70 % of social groups disbanding into multiple breeding units (mode=2, range 2–4) whose members associate with a single nest and with unit membership being repeatable between years (Browning et al. 2012). Breeding units comprise 2–15 independent group members (mean=6), but breeding in the absence of helpers is rare (6 % of attempts), seldom successful and never attempted unless the pair is part of a larger social group (Browning et al. 2012). Clutch size ranges from two to six eggs; brood

size varies from one to six nestlings, and fledging occurs after 21 to 25 days in the nest (Russell et al. 2010; Browning et al. 2012). Finally, babblers forage primarily on the ground (~65 % of the time), principally by digging or turning over the substrate with their bills, and have never been observed to 'hawk' flying prey (Portelli et al. 2009).

Methods

Fieldwork was conducted at the University of New South Wales Arid Zone Research Station in western New South Wales, Australia (31°05' S, 141°43' E). A colour-ringed population of chestnut-crowned babblers has been studied here since 2004 (Russell et al. 2010; Browning et al. 2012) which consists of ~80 breeding units in 56 km². The climate is arid with low, unpredictable annual rainfall. Vegetation is sparse, covering only ~30 % of the ground, and is characterised by chenopod shrubland, with trees and tall shrubs being largely confined to the ephemeral drainage channels and creek beds (Portelli et al. 2009).

Birds were captured using mist nets placed around active nests or across the drainage lines where babblers spend the majority of their time (Portelli et al. 2009). The mean size of breeding units in the study was six birds (range=2–13), and we captured an average of 98 % of all birds in the groups used in this study (range=75–100 %, $n=21$, excluding one pair where only the breeding female was caught). Excluding breeders, groups comprised on average 44 % adult (>1 year old) males (range=0–100 %) and 26 % adult females (range=0–50 %) and 20 % yearling (1 year old) males (range=0–100 %) and 10 % yearling females (range=0–33 %). Birds were banded with a uniquely numbered metal band (Australian Bird and Bat Banding Scheme issue) and three colour bands to facilitate identification in the field. All birds were injected subcutaneously along the flank with a passive integrated transponder (PIT) tag (see below). A blood sample (~100 μ l) was taken from each adult for subsequent molecular sexing, following standard P2/P8 sexing techniques (Griffiths et al. 1998). The breeding female in each group was easily identified as the sole member with a brood patch, and maternity and paternity were confirmed molecularly using 15 polymorphic microsatellite loci (Holleley et al. 2009; Rollins et al. 2012).

Breeding units were visited at least weekly to check for breeding activity (Russell et al. 2010). The hatching date of 19 of the 26 broods used in this study was known precisely. The chick ages of the seven broods found post-hatching were estimated using tarsus length, as chick tarsus and age show a strong linear relationship at least up to an age of 10 days (chick age=9.37+1.22×tarsus; $r^2=0.71$, $F_{1,74}=177.2$, $p<0.001$; determined from broods where exact hatch date was known).

Prey abundance in the environment

We examined prey abundance systematically during the 2004 breeding season and opportunistically during the 2006 season (August–September). We present the results of the former only because the results were qualitatively similar between the two seasons, presumably because rainfall during these years differed by only 14 mm. Prey abundance was measured using pitfall traps and transect lines throughout a representative part of the field site. We used these two different approaches in order to gain a more comprehensive measure of prey abundance in the babbler habitat. In particular, pitfall traps enabled us to record the frequency of nocturnal species, such as spiders and geckos, which babblers are able to catch during the day by digging in the substrate. Pitfall traps were constructed from PVC piping, 12 cm in diameter and 20 cm in depth, with a cardboard bottom wrapped in aluminium foil. Traps were organised in sets of eight in a cross formation, four at 50 m intervals from a central point along a drainage line and four at 50 m intervals running perpendicular from this central point ($n=168$ traps). Pitfall traps were checked every second day in August and September, the peak nestling period. We excluded all ant species (principally *Rhytidoponera* and *Ponerinae* spp.) and reptiles over 7 cm in length, since babblers have never been observed to prey on them. All prey items were identified at least to taxonomic order and taken back to the lab to be weighed on a top-pan balance (± 0.001 g). Transect counts of potential prey items were conducted while walking the 200 m length of each set of the four pitfall traps ($n=42$ lines). All species observed (both terrestrial and volant) within ~2 m either side of the transect line were recorded, excluding butterflies which babblers have never been observed to catch or feed to young.

Measures of provisioning behaviour: prey type, size and delivery rate

Nest observations were conducted between August and November (inclusive) during the breeding seasons of 2007 ($n=19$ breeding units) and 2008 ($n=7$ breeding units). While we acknowledge the temporal discrepancy between prey sampling (2004) and provisioning observations (2007, 2008), we have no reason to believe that the size or type of prey differed substantially between the time points. Importantly, rainfall during the 3 months before the onset of breeding (April, May, June) and the first 3 months of breeding (July, August, September) varied by just 3 mm between 2004 (prey sampling) and 2007 and 2008 (provisioning observations). In addition, the type, size and delivery rate of prey brought to the nest did not differ significantly between 2007 and 2008 ($p>0.16$ in all cases), suggesting that the similar rainfall patterns during these critical periods

resulted in prey of similar type, size and number being fed to the nestlings.

Provisioning behaviour at the nest was recorded using a remote PIT tag-reading system connected to a pen camera, fitted to the back of the nest (described in Young et al. 2012). The identity of all PIT-tagged birds that visited the nest was recorded electronically, along with the date and time. In addition, the type and size of prey items fed to young inside the nest was recorded simultaneously using the nest cameras. Observation sessions commenced at 0500–1600 hours and had a mean duration of 4 h (range=1–13 h, $n=57$ nest observations). Individuals visiting the nest with food deliver their prey item in 98 % of visits (Young et al. 2012), so all nest visits that involved an individual bringing food to the nest were classed as feeds. Overall, data were collected from 2,192 feeds by 85 individuals [22 female breeders, 21 male breeders, 28 old male helpers (>1 year), 15 yearling male helpers (see below)] during 26 breeding attempts from 22 breeding units (four units were observed in both 2007 and 2008). The mean number of observation periods per individual and per nest was two (range individuals=1–7, nests=1–5). Too few (four) female helpers were observed visiting the nest to be analysed in this study. Prey type was identified in 1,619 cases, and prey size was identified in 1,890 cases.

Factors affecting the type of prey delivered, its size and rates of delivery were analysed in R v.2.14.1 (R Development Core Team 2011). In each analysis, mixed models were used to allow random intercepts to be fitted, which consider the non-independence of data across repeated measures, in this case, individual and brood identity. The primary predictors of interest in all analyses were carer status, brood age and the number of carers, as well as two-way interactions between carer status and both brood age and carer number. Carer status was categorised as breeding female, breeding male, adult male helper (>1 year old) and yearling male helper (1 year old). Carer number was the total number of individuals observed to provision the brood at least once during each observation period (mean=4, range=2–10; including the four females). Carer number is highly correlated with breeding unit size because most group members provided care to the offspring (Spearman's $r_s=0.75$), and so both terms could not be included in the same model due to collinearity. Brood age was known to within a day (see above) and defined by the age of the eldest nestling (range=1–21 days). Both linear and non-linear relationships with brood age (brood age and brood age squared) were investigated because offspring commonly receive less food just before fledging (e.g. te Marvelde et al. 2009). We fitted brood size as a covariate (mean=3 nestlings, range=1–5) and provide the results in Tables 1, 2, 3 and 4 but do not consider the effects explicitly due to the difficulty of dissociating cause from effect. For example,

larger broods might lead to increased food delivery through increased brood demand, but increased food delivery can result in larger broods through reduced mortality. In addition, we did not consider fine scale variation in brood demand by analysing brood begging behaviour, since carers of different status are unlikely to experience significantly different levels of brood demand (no difference in average time of day that carers of different status provisioned; Kruskal–Wallis test $\chi^2=0.89$, degrees of freedom (df)=3, $p=0.82$). Highly correlated predictors ($r_s \geq |0.5|$) were not included in the same model due to potential problems of collinearity (Zuur et al. 2009). Continuous predictors were centred by subtracting the mean to aid interpretation of interaction terms (Schielezeth 2010). Finally, all analyses controlled for the duration of the observation period (results not shown).

Factors affecting the type of prey delivered were analysed by fitting the proportion of spiders and of insect larvae delivered as the response terms in a mixed-effects multinomial logistic regression model. We chose to analyse variation in spiders and larvae provisioned because they made up the majority of prey items delivered (86 %; see “Results”), and the other types were too few to analyse statistically as distinct responses. A multinomial logistic approach allowed us to model the proportions of spiders and larvae, independently, by analysing the log odds ratio of the proportion of each prey type relative to the proportion of other (non-spider and non-larva) prey items. By estimating these relative proportions simultaneously, we reduced the problem of conflating variation in the proportion of spiders delivered with that of larvae. We carried out this analysis using Bayesian generalised linear mixed models (GLMM) with the R package MCMCglmm (Hadfield 2010). The following settings were implemented: 10,050,000 iterations; burn-in period of 50,000; thinning interval of 5,000. Time-series plots showed no problems of autocorrelation. The output from this model is a posterior distribution for each of the predictors. Statistical inference of predictors was based on the 95 % confidence intervals (CI) of the model parameters, which show whether the parameter estimates are likely to equal zero, generated from a model containing all predictors of interest.

Factors affecting prey size and delivery rate were investigated using linear mixed model (LMMs) with normal errors after square root transformation in the R package lme4 (Bates et al. 2011). Prey size was analysed as the mean size of prey items delivered per observation period. This was estimated using the length and breadth of prey body size relative to the babbler's bill and converted to a multiple of bill volume to the nearest 0.25 (Wright et al. 2010). In babblers, bill length is relatively invariant (mean \pm SD=18.2 \pm 0.9 mm, $n=156$ adults) compared with the level of accuracy used to estimate prey size, so we did not control for bill size statistically in the

Table 1 Factors affecting relative proportion of feeds with spiders and larvae

Predictors	Estimate	SE	95 % CI
Spiders intercept	-0.34	0.37	-1.03, 0.42
Status ^a			
Breeding male	0.47	0.43	-0.27, 1.35
Old male helper	1.10	0.43	0.18, 1.90
Yearling male helper	0.98	0.51	-0.01, 1.97
Carer number ^b	-0.39	0.17	-0.74, -0.09
Status ^a × carer number ^b			
Breeding male	0.20	0.20	-0.14, 0.64
Old male helper	0.46	0.21	0.09, 0.90
Yearling male helper	0.46	0.23	0.04, 0.92
Brood size ^b	-0.03	0.13	-0.29, 0.20
Brood age ^b	-0.10	0.03	-0.16, -0.05
Brood age squared ^b	0.003	0.005	-0.008, 0.013
Status ^a × brood age ^b			All 95 % CI include zero
Larvae intercept	1.13	0.29	0.58, 1.70
Status ^a			
Breeding male	-0.04	0.33	-0.70, 0.58
Old male helper	0.25	0.35	-0.41, 0.90
Yearling male helper	0.56	0.41	-0.31, 1.32
Carer number ^b	-0.11	0.07	-0.25, 0.03
Brood size ^b	0.35	0.12	0.10, 0.55
Brood age ^b	0.08	0.02	0.02, 0.13
Brood age squared ^b	0.01	0.00	-0.01, 0.01
Status ^a × carer number ^b			All 95 % CI include zero
Status ^a × brood age ^b			All 95 % CI include zero

Estimates ± SE and 95 % CI are given as log odds of the proportion of either spiders or larvae relative to the proportion of other (non-spider and non-larva) prey items delivered. Nest [modal variance component (95 % CI)=0.002 (0.000, 0.444)] and individual [0.003 (0.000, 0.570)] identities were included as random terms in the model. Significant terms are shown in bold

^aBreeding female is the reference category

^bContinuous variables have been centred by subtracting the mean

analyses. Prey delivery rates were analysed as the rate at which individuals brought food to the nest (deliveries/hour).

Table 2 Factors affecting mean size of prey delivered to nest

Predictors	Estimate	SE	<i>L</i>	<i>df</i>	<i>p</i> value
Intercept	1.06	0.02			
Status ^a			24.00	3	<0.001
Breeding male	-0.10	0.03			
Old male helper	-0.12	0.03			
Yearling male helper	-0.12	0.03			
Carer number ^b	-0.001	0.008	0.003	1	0.956
Feeding rate ^b	0.004	0.005	0.43	1	0.512
Brood size ^b	0.03	0.01	6.63	1	0.010
Brood age ^b	0.02	0.003	36.24	1	<0.001
Brood age squared ^b	-0.002	0.000	18.37	1	<0.001
Status ^a × carer number			2.39	3	0.596
Status ^a × brood age			3.44	3	0.328

Estimates ± SE are given on the square root scale. Nest (variance component ± SE=0.002 ± 0.009) and individual (0.000 ± 0.000) identities were included as random terms in the model. Significant terms are shown in bold

^aBreeding female is the reference category

^bContinuous variables have been centred by subtracting the mean

Here, the minimal adequate model was selected from a maximal model containing random terms and all predictors and interactions of interest (see above). The decision to retain or drop terms from the model was based on likelihood ratio tests, where the fit of the model with and without the term of interest are compared (Zuur et al. 2009). Effect sizes were estimated from the minimal adequate model fitted using restricted maximum likelihood. Effect sizes and *p* values for all dropped terms were obtained by adding them, one at a time, back into the minimal model. Residuals from the minimal model were checked visually to ensure that model assumptions were met.

Estimates of the amount of prey delivered

We combined prey size and delivery rate into a composite estimate of the mean amount of prey delivered per hour by multiplying mean provisioning rate by mean prey size per individual. The amount delivered was then analysed using LMMs in the R package lme4 (Bates et al. 2011) with normal errors, following square root transformation. First, we investigated the relationship between the amount delivered and carer status, carer number and brood age, as well as their interactions, after controlling for brood size and

Table 3 Factors affecting individual mean provisioning rate per hour

Predictors	Estimate	SE	<i>L</i>	<i>df</i>	<i>p</i> value
Intercept	1.37	0.10			
Status ^a			24.75	3	<0.001
Breeding male	0.63	0.13			
Old male helper	0.37	0.12			
Yearling male helper	0.27	0.15			
Carer number ^b	-0.15	0.05	1.98	1	0.160
Status ^a ×carer number ^b			9.79	3	0.021
Breeding male	0.09	0.06			
Old male helper	0.13	0.06			
Yearling male helper	0.20	0.07			
Proportion spiders ^b	-0.10	0.15	0.58	1	0.445
Brood size ^b	0.14	0.04	10.34	1	0.001
Brood age ^b	0.02	0.01	4.43	1	0.035
Brood age squared ^b	-0.003	0.001	4.72	1	0.030
Status ^a ×brood age ^b			3.41	3	0.333

Estimates±SE are given on the square root scale. Nest (variance component±SE=0.042±0.040) and individual (0.051±0.025) identities were included as random terms in the model. Significant terms are shown in bold

^a Breeding female is the reference category

^b Continuous variables have been centred by subtracting the mean

observation duration. Second, we investigated whether variation in the amount of prey was most influenced by

Table 4 Factors affecting mean amount of food delivered (in bill volumes per hour)

Predictors	Estimate	SE	<i>L</i>	<i>df</i>	<i>p</i> value
Intercept	1.44	0.11			
Status ^a			16.46	3	<0.001
Breeding male	0.50	0.13			
Old male helper	0.23	0.12			
Yearling male helper	0.15	0.15			
Carer number ^b	-0.16	0.05	2.71	1	0.100
Status ^a ×carer number			8.31	3	0.040
Breeding male	0.12	0.06			
Old male helper	0.14	0.06			
Yearling male helper	0.17	0.07			
Brood size ^b	0.19	0.04	17.73	1	<0.001
Brood age ^b	0.05	0.01	22.88	1	<0.001
Brood age squared ^b	-0.01	0.00	15.34	1	<0.001
Status ^a ×brood age ^b			3.02	3	0.338

Estimates±SE are given on the square root scale. Nest (variance component±SE=0.048±0.043) and individual (0.046±0.023) identities were included as random terms in the model. Significant terms are shown in bold

^a Breeding female is the reference category

^b Continuous variables have been centred by subtracting the mean

provisioning rate or prey size. In this analysis, both variables were standardised by subtracting the mean and dividing by two standard deviations in order to enable direct comparison of their effect sizes (regression slopes) (Gelman 2008). The rationale for doing so was to elucidate how variation in prey size and delivery rates might translate into overall differences in total amounts of food provided, as well as to evaluate whether variation in prey load size or provisioning rate was most likely to contribute to variation in the amount of prey delivered to young.

Results

Prey abundance in the environment

A total of 313 potential prey items were captured in the pitfall traps. These included spiders (Araneae 42 %), crickets (Orthoptera 29 %), adult beetles (Coleoptera 16 %), caterpillars (Lepidoptera 11 %), lizards (Scincidae, Gekkonidae, Agamidae; <2 %) and lesser percentages (<1 % each) of centipedes (Chilopoda), silverfish (Thysanura), slaters (Isopoda) and desert cockroaches (Blattaria). In addition, 2,464 potential prey items were counted along the line transects. These included moths (54 %), caterpillars (36 %), crickets (3 %), spiders (2 %), lizards (2 %), beetles (1 %), shield bugs (Acanthosomatidae, <1 %), dragonflies (Odonata, <1 %) and antlions (Neuroptera, <1 %). Thus, combining the data from both forms of sampling method suggested that the four most common potential prey items were moths, caterpillars, spiders and crickets. The wet mass of those items captured in pitfall traps varied from 0.0005 to 2.5 g (median=0.1 g) and differed significantly among prey types [spiders<adult insects (mainly crickets and beetles)<caterpillars<lizards; Kruskal–Wallis $K=138$, $df=3$, $p<0.001$]. Of particular note, given their prevalence in the diet of nestling babblers (see below), is that spiders appeared rarer than caterpillars overall and were an order of magnitude lighter (median, interquartile range; spiders=0.008 g, 0.001–0.016; larvae=0.27 g, 0.17–0.39; Mann–Whitney $U=151$, $p<0.001$). Despite being rarer overall, the lack of overlapping quartiles shows that spiders dominated the small prey size categories.

Measures of provisioning behaviour: prey type, size and delivery rate

Carers always delivered food to broods in the form of a single prey item ($n=1,619$ feeds). The most common prey items fed to nestlings were insect larvae (Lepidoptera and Coleoptera 61 %) and spiders (25 %), with lesser numbers of crickets (7 %) and the remaining 7 % comprising adult insects (desert cockroaches, moths, dragonflies, Diptera,

Mantodea, Dermaptera, Hemiptera), slaters, centipedes, Diplopoda and squamate reptiles (principally geckos and skinks) (Fig. 1a). Thus, insect larvae and spiders comprised 86 % of all prey items delivered, with the former being more than twice as common as the latter. In addition, the spiders fed to nestlings were significantly smaller than the insect larvae, indicating an association between prey type and size in the nestling diet (mean, range; spiders=0.5 bill volumes, 0.25–2.5; larvae=1.0 bill volume, 0.25–4; Mann–Whitney $U=4,672$, $n_s=446$, $n_l=1144$, $p<0.001$; Fig. 1b).

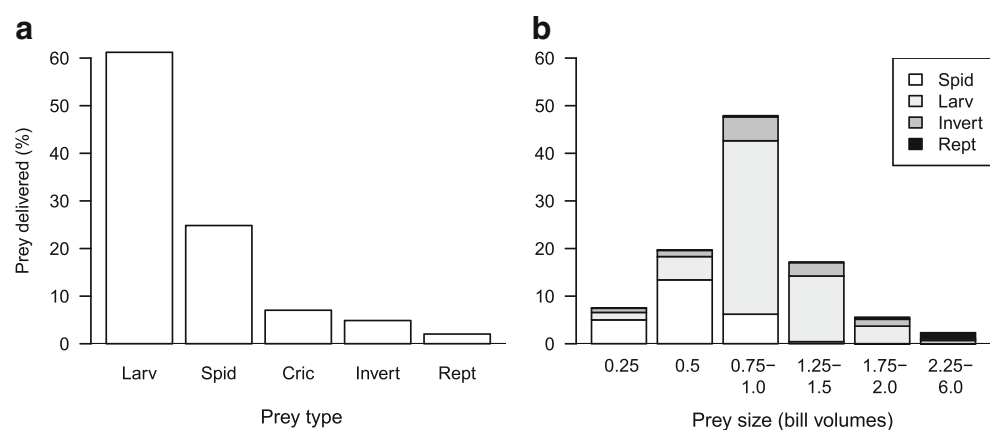
All carers provisioned progressively fewer spiders and more insect larvae relative to other prey items as broods aged (Table 1). That the relative proportions of each prey type were modified as broods aged suggests that they might be selected differentially for offspring of different ages. To verify this conclusion, we analysed the total number of each delivered by the group as a function of brood age, using a GLMM with Poisson errors and a log link function. Indeed, we found that the group delivered fewer spiders [slope (95 % CI); brood age, -0.05 (-0.09 , -0.02)] and more larvae [brood age, 0.12 (0.09 , 0.15)] as nestlings aged.

The strong association between prey type and size (above) suggests that carers might preferentially feed young chicks spiders because spiders are small, rather than because they are spiders per se. To test this possibility further, we added mean prey size as a covariate in this analysis and found that higher proportions of spiders were no longer significantly associated with young chicks [brood age estimate (95 % CI) -0.02 (-0.08 , 0.03)]. This suggests that young broods receive more spiders simply because spiders are smaller than insect larvae and so presumably are more manageable for small chicks. Breeders delivered relatively fewer spiders than helpers (Fig. 2a), but there was no effect of carer status on the relative proportion of larvae fed to young (Fig. 2b). In addition, only breeding females showed a significant decrease in the relative proportion of spiders (but not larvae) delivered with increasing carer number, while other carers maintained constant amounts (Fig. 2a).

The mean size of prey delivered to broods was equivalent to 1.0 bill volume (range=0.25–6.0). Mean prey size was influenced by brood age and carer status, but there was no effect of mean provisioning rate or carer number and no significant interactions between carer status and either brood age or carer number (Table 2). As broods aged, mean prey size increased, although it decreased again as broods approached fledging age. Breeding females delivered prey items that were 27 % larger than the other carer classes (Fig. 3a). This effect could have arisen due to the fact that only breeding females brood the chicks and, hence, feed more when the chicks no longer require brooding, namely, when they are older and can manage larger prey. However, females were still found to deliver larger prey items than other carers even when the analysis was restricted to chicks older than 10 days old ($L=8.69$, $df=3$, $p=0.034$), suggesting that breeding females might have different provisioning rules compared to other group members.

The rate at which carers visited the nest with food ranged from an average of <0.1 to 13 times/h (mean=3.0). Individual provisioning rates were associated with variation in brood age and carer status. However, there were no main effects of either prey type or the number of carers feeding at the nest (Table 3). Carers fed older broods more often, although provisioning rates began to decline as nestlings reached fledging age as indicated by the significant quadratic brood age term. On average, breeding females and yearlings delivered food at the lowest rate, and breeding males did so at the highest rate, with older helpers feeding at an intermediate rate (Fig. 3b). Again, breeding females showed reduced provisioning rates following restriction of the analysis to data collected after chicks cease to require brooding (>10 days) ($L=11.0$, $df=3$, $p=0.012$), suggesting that this result was not confounded by breeding female brooding behaviour. Although we found no evidence of a main effect of carer number on provisioning rate, there was a significant interaction with carer status—breeding females reduced their rate of provisioning with increasing carer number, while breeding and non-breeding males did not (Fig. 3b).

Fig. 1 Relative frequency (a) and size distribution (b) of prey types fed to nestlings. *Larv* insect larvae, *Spid* spiders, *Cric* crickets, *Invert* other invertebrates (see “Results” for details; **b** also includes crickets), *Rept* reptiles



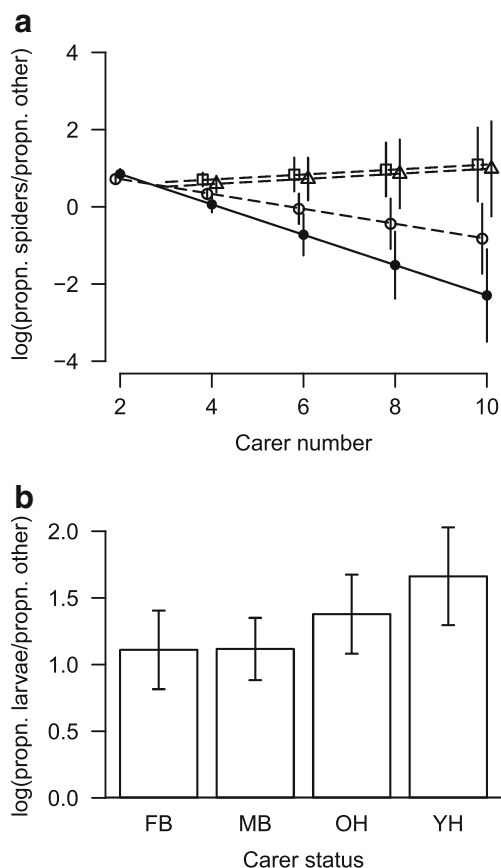


Fig. 2 Effect of carer status on prey type provisioned: **a** spiders and **b** larvae. *FB* female breeder (filled circle/solid line), *MB* male breeder (empty circle/dashed line), *OH* old male helper (>1 year old; empty square/dashed line), *YH* yearling male helper (1 year old; empty triangle/dashed line). The predicted log odds ratios of proportion of **a** spiders and **b** larvae relative to the proportion of other prey types (± 1 SE) from Table 1, are shown. The slope of dashed lines does not differ from zero

Estimate of amount of prey delivered

The amount of prey delivered per hour averaged 2.7 bill volumes/h (range= <0.1 –13.7) and varied with brood age and carer status, but there was no main effect of carer number (Table 4). Carers delivered a greater amount of prey as broods aged, although this decreased as fledging age approached. Breeding females and yearlings delivered the least amount of prey overall to nestlings compared with male breeders and adult helpers (Fig. 3c). In addition, breeding females reduced the amount of food they fed nestlings as the number of carers increased, whereas other classes of carers maintained constant amounts (Fig. 3c).

In a separate analysis, we found that amount of prey delivered increased with both provisioning rate ($L=461.89$, $df=1$, $p<0.001$) and prey size ($L=210.93$, $df=1$, $p<0.001$). However, comparison of the standardised effect sizes of provisioning rate versus prey size indicated that the effect

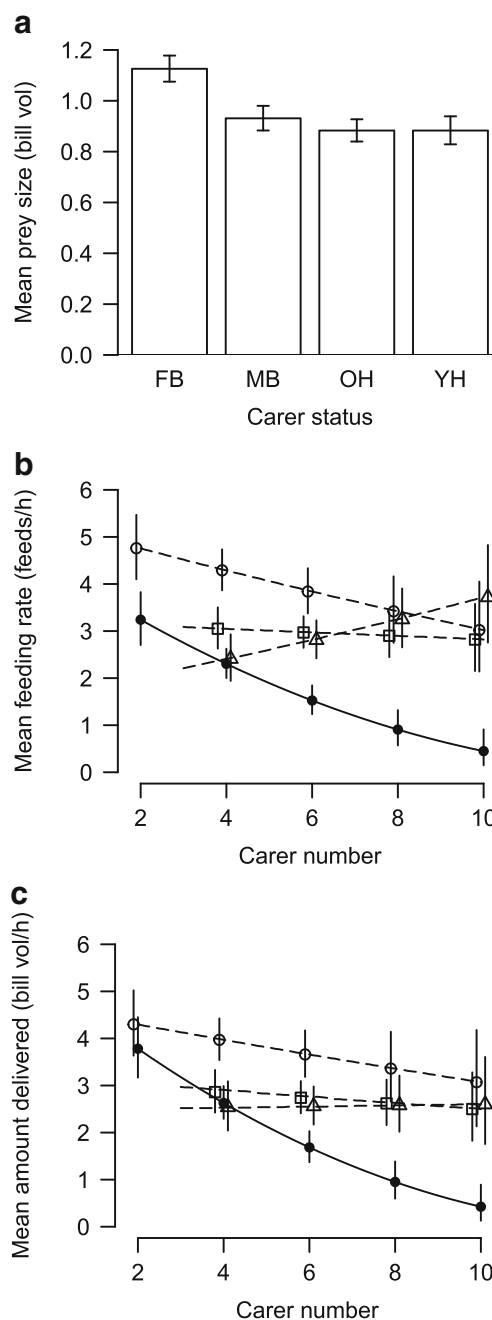


Fig. 3 Effect of carer status on mean **a** prey size delivered, **b** delivery rate and **c** amount of food delivered. *FB* female breeder (filled circle/solid line), *MB* male breeder (empty circle/dashed line), *OH* old male helper (>1 year old; empty square/dashed line), *YH* yearling male helper (1 year old; empty triangle/dashed line). The predicted values (± 1 SE) from Tables 2, 3 and 4, respectively, are shown. The slope of dashed lines does not differ from zero

of the former was over two and a half times stronger than the effect of the latter (estimate \pm standard error (SE) rate=1.20 \pm 0.03; size=0.46 \pm 0.02). This suggests that, while prey size is associated with the amount of prey delivered, it is substantially less important than the rate at which food is delivered.

Discussion

Chestnut-crowned babblers always provisioned broods with a single prey item at a time. Prey type and size were correlated, but delivery rate was not associated with either. Breeders and helpers alike adjusted all three components of provisioning in response to changes in brood age: the relative proportion of larvae, load size and delivery rate all increased as nestlings aged. However, only breeding females, which also provisioned at a lower rate than breeding males and adult helpers, reduced their provisioning rate in response to the presence of additional carers. While they also delivered larger prey items than other carer classes, this appeared insufficient to compensate for their low provisioning rate, resulting in a lesser contribution to provisioning overall compared to adult male helpers and also to male breeders which contributed most.

Models of provisioning rules in cooperative breeders have tended to emphasise the importance of the current benefits of contributing to offspring care (reviewed in Heinsohn 2004). Here, we found little evidence that variation in current benefits alone explains patterns of provisioning in chestnut-crowned babblers. In this species, all carers can increase the production of young by provisioning at the nest (Browning et al. 2012), but the current kin-selected benefits of doing so vary among classes of carer due to differences in relatedness to the current brood (Hamilton 1964; Maynard Smith 1964). A single female produces all offspring in a brood, and on average, her partner sires most of these young (Griffith and Russell unpublished results). In addition, relatedness between helpers and young will decrease over time due to breeder turnover (Rabenold 1985), meaning that yearling helpers are likely to be more related, on average, to broods than are older helpers. Therefore, according to the current kin-selected benefits alone (Hamilton 1964; Maynard Smith 1964), breeding females should contribute most to rearing offspring; breeding males and younger helpers should contribute intermediate amounts, and older helpers should contribute least. This was not the case in our study. Breeding males contributed most overall, followed by adult helpers, yearling helpers and breeding females. The fact that variation in relatedness to the brood among helpers seldom explains quantitative variation in their contributions to cooperation across species (Cornwallis et al. 2009) also provides general support for the idea that current kin-selected benefits are a poor predictor of provisioning rules in cooperative breeders.

By contrast, there is increasing evidence that the short-term costs of provisioning have greater power in explaining carer investment in offspring care. For example, the poor foraging skills typical of helpers in their first year of life (Heinsohn 1991; Langen 1996) may exaggerate the short-term costs of care and thus explain the observation that

young helpers frequently contribute less to offspring care (Boland et al. 1997; Clutton-Brock et al. 2002). In support of this, supplementary feeding can eliminate this difference, presumably by alleviating such costs (Boland et al. 1997). Additionally, the costs of offspring production (Monaghan and Nager 1997) may prohibit breeding females from investing as much as male carers in offspring provisioning. Although the costs of both offspring production and provisioning have yet to be determined in chestnut-crowned babblers, a variable short-term costs model might explain our observations that both breeding females and yearlings contributed least overall to feeding young.

Nevertheless, short-term costs in isolation are not wholly consistent with our observations. First, we would expect that both breeding females and yearling helpers attempt to mitigate such costs of provisioning by load lightening in the presence of additional carers; yet, only breeding females did so. Second, a short-term cost model would predict that both breeding females and yearling helpers should deliver a higher proportion of the most abundant, easily obtainable prey items and/or reduce their contribution of rarer, less easily obtainable prey types. Our estimates of prey abundance in the environment suggest that caterpillars are the most common prey type which are also the most easily obtainable, due to the fact that they are relatively immobile and do not need to be dug out of the substrate, unlike spiders which typically must be excavated from burrows. Contrary to prediction, carers did not vary in their propensity to deliver larvae, nor did yearlings deliver a lower proportion of spiders than other carers. By contrast, breeding females did provision the lowest proportion of spiders compared to other carers and reduced this proportion in the presence of additional carers.

Instead, the provisioning rules of cooperative breeders might be better viewed as a function of the current versus expected future fitness potential and the long-term effect of current costs on this future potential (Heinsohn 2004; Clutton-Brock et al. 2004; Canestrari et al. 2008). One feature of more obligate cooperative breeders, which is seldom incorporated into models of provisioning rules (Heinsohn 2004), is that most group members never gain reproductive status, and so the survival and breeding potential of the breeding female has a fundamental bearing on the opportunity of all group members to gain fitness through rearing her offspring (Clutton-Brock et al. 2006). Under a more comprehensive life-history model (Heinsohn 2004), we might expect the fitness of all group members to be linked to the fecundity of the breeding female through kin selection (Hamilton 1964; Maynard Smith 1964). Such a model would predict that helpers invest heavily, irrespective of their level of relatedness, because they both (1) have a low probability of gaining direct fitness in the future, and (2) their relatedness to recipients will decline over time due to

breeder turnover. This prediction cautions against using asymmetries in carer relatedness to the brood when testing kin selection theory (Hamilton 1964; Maynard Smith 1964), unless both the short- and long-term costs are also considered (Heinsohn 2004). In addition, a life-history model would also predict that female breeders invest little in offspring care generally, and that breeding males and helpers benefit from female breeders saving resources for the future where possible. While further work is required in this area, our results are fully consistent with this possibility—helpers worked similarly hard irrespective of their age, and breeding females not only invested less than breeding males and adult helpers but were also the only carer class to reduce their contribution in the presence of additional helpers.

In addition to the importance of future prospects of gaining direct and/or indirect fitness in understanding provisioning rules in cooperative breeders, our study has a number of broader implications. First, the fact that breeding females reduced their contributions using visit rate rather than prey size, and that the effect of delivery rate was more than twice the effect of prey size on overall food delivery suggests that the primary cost of provisioning in chestnut-crowned babblers involves travel costs in the form of energy and time (and possibly, predation risk to carers; Sorato et al. 2012). We hypothesise that such costs may be salient in those species, such as babblers, that must travel relatively large distances over open terrain to feed young, and for which larger food items are readily available. Second, a high proportion of spiders in the diet of young nestlings has been reported in a number of bird species (this study; Royama 1970; Cowie and Hinsley 1988; Radford 2008) and has previously been suggested to occur because spiders meet nutritional requirements that are particular to young chicks (Ramsay and Houston 2003; Arnold et al. 2007). While we cannot yet rule out this possibility, our data suggest a simpler explanation—spiders were the most common small prey items in the environment and, hence, represent the most suitable food for small nestlings (Bañbura et al. 1999). In support of this, when we controlled for variation in mean prey size in the analysis of prey type, chick age was no longer associated with higher proportions of spiders in the nestlings' diet. This suggests that carers preferentially feed spiders to young chicks because spiders are smaller, rather than because they are spiders per se.

In conclusion, this study adds to a limited number that have examined the investment strategies of breeders versus helpers in obligate cooperatively breeding vertebrates (Clutton-Brock et al. 2004; Woxvold et al. 2006; Gilchrist and Russell 2007). Despite breeding females provisioning larger prey items to young, they contributed less overall than other adults and were the only carer to load-lighten in the presence of additional helpers. This result is explained, in part, by the fact that the delivery rate is the best predictor of the amount of food fed to

young in chestnut-crowned babblers, and breeding females were found to deliver food at the lowest rate. The lack of load lightening by other carers, in conjunction with the fact that brood reduction is common in this species (Russell et al. 2010; Browning et al. 2012), is consistent with the hypothesis that higher risks of nestling starvation favour additive care (Hatchwell 1999). Nevertheless, our results extend this hypothesis by supporting the suggestion that breeding females benefit most from reducing their own investment in offspring care in obligate cooperative breeders, wherein the future prospects of reproduction differ dramatically between breeders and helpers (Clutton-Brock et al. 2004).

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Ethical standards Fieldwork was carried out under the approval of UNSW Animal Care and Ethics Committee (license no. 06/40A) and the authority of NSW National Parks and Wildlife Service and the Australian Bird and Bat Banding Scheme.

Conflict of interest None.

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