Sharing of caring: nestling provisioning behaviour of long-tailed tit, *Aegithalos caudatus*, parents and helpers

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The optimal investment strategies of parents in biparental systems are well studied. This contrasts with a poor theoretical and empirical understanding of variation in individual investment in breeding systems with multiple carers. We used the cooperative breeding system of long-tailed tits, to investigate how parents and helpers adjust their rate of nestling provisioning in relation to measures of nestling demand and the number of helpers. Our aim was to examine whether parents and helpers follow the same provisioning rules. Overall provisioning rates were higher for parents than for helpers. However, both parents and helpers increased their provisioning rates as nestlings aged and provisioned at higher rates early in the day. Parents brought more food to larger broods when not helped, but at nests with helpers, neither parents nor helpers had significantly higher provisioning rates at larger broods. However the total provisioning rate was higher at larger broods at both nests with and without helpers. Parents reduced their work rate in response to the arrival of a helper, but neither parents nor first helpers reduced their work rates further with arrival of additional helpers. Variation in provisioning rates between parents and helpers may be the result of different cost–benefit relations, and a theoretical framework is needed within which to explore the consequences of such differences.

Variation in systems of parental care results in different solutions to the problem of optimal investment in offspring. Carers in uniparental systems should invest according to the optimal trade-off between the benefits of current investment and the costs of that investment for future survival and reproduction (Williams 1966; Stearns 1992). In biparental systems, an individual's optimal investment depends not only on that trade-off, but also on the care invested by the cooperating partner. Theory predicts that stable biparental care can evolve when each parent compensates incompletely for a reduction in care by its partner (Chase 1980; Houston & Davies 1985; Winkler 1987). There is considerable empirical support for this prediction (Wright & Cuthill 1989; Hatchwell & Davies 1990; Sanz et al. 2000).

Optimal investment strategies are more complex, and the potential outcomes more variable when there are multiple carers, as in cooperatively breeding animals (Houston & Davies 1985). The optimal investment of carers has been modelled and tested in polyandrous and polygynandrous dunnocks, *Prunella modularis* (Houston & Davies 1985; Davies & Hatchwell 1992; Sozou & Houston 1994). In this species, individual carers

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share parentage of the brood, but are unrelated to one another. Males adjust their provisioning effort according to their probability of paternity (Burke et al. 1989; Davies et al. 1992), and the most stable division of care between three parents is a simple extension of the division of care between two parents, in which the optimum effort of each individual depends on the total work done by others (Houston & Davies 1985; Davies & Hatchwell 1992; Sozou & Houston 1994).

In contrast, in systems where cooperation by more than two carers is based on kinship rather than shared parentage, there has been little theoretical or empirical study of the factors determining the optimal effort of individual carers (Heinsohn & Legge 1999). We still expect effort to depend on the value of the current brood (size and probability of survival) and the amount invested by other carers (i.e. the work force).

In Arabian babblers, *Turdoides squamiceps*, the provisioning behaviour of helpers, which are commonly full siblings of the chicks they help, is indistinguishable from that of parents (Wright 1998; Wright & Dingemanse 1999). However, individuals in multiple-carer systems may not always behave as predicted from a simple extension of biparental situations. Hatchwell (1999) argued that parents should not necessarily respond to the presence of helpers by reducing their own effort. Instead,

the expected reduction in breeder effort when helped should be sensitive to the cost–benefit functions for parental care. In particular, the prediction that parents should reduce their effort less in the presence of helpers when the risk of nestling starvation is high was supported by a comparative analysis. Helpers in cooperative breeding systems may also have very different costs and benefits from parents (Heinsohn & Legge 1999), which may affect their optimal investment. For example, the value of the current brood's fitness may be very different for parents and helpers. For helpers, the fitness benefit that they gain may depend on their relatedness to the brood or the magnitude of direct fitness benefits that they gain through cooperation.

In long-tailed tits, helpers may gain both direct and indirect fitness benefits from caring for young that are not their own. First, helpers usually help at the nests of close relatives; their average coefficient of relatedness to the nestlings that they help is 0.22 (Russell & Hatchwell 2001), and they increase the fledging weight and recruitment rate of helped nestlings (Russell 1999; MacColl & Hatchwell 2002), thereby gaining indirect fitness. If this represents the major benefit of helping, helpers would be expected to respond to the needs of nestlings in a similar way to parents, although the amount of care provided may be less if their relatedness to nestlings is more distant than that of parents. Second, helpers may gain direct benefits associated with living in a group. In long-tailed tits, helpers have a higher survival rate than nonhelpers (McGowan et al. 2003) and if this is an important benefit of helping, then helpers may not respond to the needs of nestlings as parents do. In such situations, helpers may simply provision nestlings to be allowed to remain in the group, a behaviour that has been called 'payment of rent' (Gaston 1978) and 'pay to stay' (Mulder & Langmore 1993; Kokko et al. 2002).

In this study, we examined the patterns of provisioning of parents and helpers in the long-tailed tit, using observational data from an 8-year field study, to investigate whether parents and helpers followed the same provisioning rules in the cooperative system of this species. We examined how the provisioning rates of carers varied in relation to sex, role (parent or helper), number of carers, value of the brood and likely correlates of offspring need. We found differences in the amount of care provided by carers of different role, and we discuss these differences in terms of the fitness benefits of cooperation in this species.

The analysis builds on that presented by Hatchwell & Russell (1996), but is an improvement in several ways. As recommended by Cockburn (1998), we used mixed models fitted by restricted maximum likelihood (REML) techniques to analyse our data (Dunn & Cockburn 1996). This allowed us to control for systematic differences between nests and individual carers in rates of food delivery, while simultaneously controlling for several fixed effects likely to be important in determining provisioning rates. This improves the estimation of parameters, and enables us to present all results as true provisioning rates, rather than as residual rates as Hatchwell & Russell (1996) did. Furthermore, the primary focus of Hatchwell & Russell (1996) was an experimental manipulation of the number of helpers, and in their analysis of observational data they did not consider the effects of year, time and temperature, and nor were the effects of date, nestling age, brood size or number of helpers fully controlled or explored, which could have resulted in misleading conclusions.

METHODS

Study Population

The data were collected between 1994 and 2001 in the Rivelin Valley, Sheffield, U.K. (130–280 m above sea level, 53°23′N 1°34′W). The study site comprises approximately 3 km² of mature oak, *Quercus robur*, and beech *Fagus sylvatica*, woodland, birch, *Betula* spp., and hawthorn, *Crataegus* spp., scrub, farmland and gardens. The study population varied between 18 and 53 breeding pairs of long-tailed tits. Birds were captured in mist nets and colour ringed (under British Trust for Ornithology licence) before breeding started, or in some cases during the nestling period. Helpers from outside the study area were colour ringed on arrival at a nest. This did not affect their provisioning rate compared with helpers that had been ringed before they began helping (means: previously ringed: 5.34 feeds/h; previously unringed: 5.69 feeds/h; SE of difference=1.08; $F_{1,46}=0.11$, NS). Rates of extrapair fertilizations and intraspecific brood parasitism are very low in long-tailed tits, so the average relatedness of parents to offspring is 0.48 (Hatchwell et al. 2002). For further details of the study population and methods, see Hatchwell & Russell (1996) and Hatchwell et al. (1999b).

Long-tailed tits spend the winter in flocks of about 6–30 birds (Gaston 1973; Hatchwell et al. 2001a). Flocks split up and pairs form in early spring. All pairs attempt to breed independently, but the rate of nest failure is high (Hatchwell et al. 1999b). Failed breeders may attempt to renest or, especially later in the season, they may help another pair to rear their young by provisioning nestlings (Glen & Perrins 1988; MacColl & Hatchwell 2002). The way in which cooperative groups form in long-tailed tits means that analysis of their reproductive behaviour is less affected by confounding variables than in many cooperative bird species. For example, because groups form afresh each year, there is not the same pattern of feedback between reproductive success in one year and group size in the next. Helpers are also commonly of the same age and experience as parents, because helpers are most likely to be a sibling of one of the breeding pair (Russell & Hatchwell 2001). Similarly, the absence of territoriality (Hatchwell et al. 2001a) means that reproductive success is not confounded by habitat or territory quality to the extent that it is in many other cooperative species. Consistent with this, we can find no evidence of variability in provisioning rates or reproductive success between blocks of habitat within our study area (B. J. Hatchwell, unpublished data).

Provisioning rates were recorded by observing nests either from hides 10–15 m from nests, or using a telescope at 30–50 m. We noted the identity of all birds

visiting the nest with food and recorded the length of observation periods so that we could calculate hourly visit rates by all individuals. Most observation periods lasted 1 h ($\bar{X} \pm$ SE$=66 \pm 10$ min, $N=864$; range 15–1020 min). Observations were made throughout the 16–17-day nestling period (the period from hatching to fledging), usually on alternate days (weather permitting), but the number of watches per nest varied because of predation of some broods ($\bar{X} \pm$ SE watches per nest$=6.4 \pm 3.0$, $N=135$; mean total observation time per nest$=424 \pm 26$ min, $N=135$). There were no differences in provisioning rates between nests that were predated and those that were not, either for parents (mean feeds/h: predated: 7.20; not predated: 6.93; SE of difference$=0.73$; $F_{1,134}=0.14$, NS) or helpers (predated: 4.87; not predated: 5.34; SE of difference$=0.97$; $F_{1,46}=0.25$, NS). Most observations were made between 0600 and 1600 hours, and all took place between 19 April and 17 June.

The total provisioning effort of individual birds, calculated as the area under the regression line of provisioning rate against nestling age for the whole nestling period, has high repeatability between breeding seasons. For 16 males for which we have good estimates of provisioning rates in at least two breeding seasons, repeatability$=0.70$ (A. D. C. MacColl & B. J. Hatchwell, unpublished data). We also know that the repeatability of individual effort attributable to location is low, supporting the contention that within-individual repeatability is not the result of environmental effects. For 17 homogeneous habitat blocks of less than 1 ha that were nested in by different, unrelated individuals in at least 2 years ($N=56$ nesting attempts), the repeatability that was due to 'location' was 0.03. We therefore believe that provisioning rate is a good and stable indicator of individual investment.

Analysis of Data

We examined the relation between provisioning rates and the following variables: year, date, time, temperature, nestling age, brood size, sex and size of workforce. 'Date' was the number of days after 1 March each year. 'Time' was the midpoint of each watch, as minutes after midnight. 'Temperature' was the dry bulb temperature at 0900 hours GMT at Weston Park, Sheffield, 5 km from the centre of the Rivelin study site at an altitude of 140 m. 'Nestling age' was calculated in days, taking the day of hatching of a brood as day 0. 'Brood size' was the number of nestlings in the nest when they were ringed at day 11; nestling starvation is rare in long-tailed tits (Hatchwell 1999) so this is a good measure of brood size. 'Sex' was the sex of the carer. We quantified the size of the workforce in two ways. (1) In selecting the most parsimonious model, we used a discrete variable, 'Helped?', which took a value of zero if only the parents were seen provisioning the nestlings during a provisioning watch or a value of one otherwise. In 90% of 70 instances of helpers seen to provision young for the first time, the helper was observed to continue provisioning at the nest during all subsequent watches on that nest. (2) When the most parsimonious model had been constructed, we substituted 'Number of helpers' into the model in place of

'helped?' to quantify differences in the mean work rates of birds at nests with different numbers of helpers. We had a priori reason (Hatchwell & Russell 1996; Hatchwell 1999) for believing that the change in provisioning rate might not be a linear function of size of workforce, so we fitted 'number of helpers' as a discrete variable. Number of helpers included helpers of both sexes seen to provision nestlings during a watch. Imbalances in the data set would have made it difficult to use 'Number of helpers' in the initial model-fitting process. For example, data were not available for the full range of brood sizes for nests with more than one helper.

We carried out two analyses of provisioning rates by individuals. In the first analysis, we modelled the provisioning rates of parents. In the second, we modelled the provisioning rates of all males to allow us to compare directly parents and helpers. We chose to split the analysis because of inherent imbalances in the data set. First, helpers provision only at helped nests, but parents may be either helped or not. This would have made interpretation of models containing the variable 'helped?' difficult. Second, there were few female helpers (18% of 62 helpers), so it would have been difficult to compare them directly with either female parents or male helpers. To test for differences in intercepts and slopes between helpers, helped male parents and unhelped male parents, we coded each with a unique value of an additional discrete variable 'status'. We also analysed the total rate of provisioning by all carers at a nest.

Statistical Methods

Provisioning rate data were modelled with mixed models fitted by REML (SAS version 8, Proc MIXED; Littell et al. 1996). Mixed models can be used to model data with normal errors with fixed and random effects. Random effects in mixed models allow for the analysis of stratified data with more than one error term (Brown & Prescott 1999). The incorporation of a random effect in a model, for example 'nest', controls for nonindependence between observations of the same nest. In the present data set, this was necessary to account for the repetition of observations on individual birds within a nesting attempt, as well as nonindependence of observations of the same marked individuals at different nesting attempts, and the nonindependence of different individuals working at the same nest. The interactions between 'nest' and 'individual', and between 'nest', 'individual' and nestling age were fitted as random factors in a model structure directly analogous to that being increasingly used in medical trials to analyse the response of patients to different treatments over time (Verbeke & Molenberghs 1997; Brown & Prescott 1999). The best-fitting model of fixed effects was constructed from a maximal model containing all effects and biologically meaningful two- and three-way interactions by the sequential dropping and readdition of individual terms, until all terms remaining in the model were significant (Crawley 1993). Significance of terms was assessed from type I F tests when the term was fitted last in the model.

Table 1. Results from a mixed model (REML) of provisioning rate for parents

Effect	df	F	P
Year	7,117	3.18	<0.005
Time	1,117	20.98	<0.0001
Temperature	1,117	11.16	<0.001
Sex	1,117	89.24	<0.0001
Helped	1,117	33.04	<0.0001
Brood size	1,117	26.27	<0.0001
Nestling age	1,117	119.25	<0.0001
Nestling age^2	1,117	25.40	<0.0001
Sex×nestling age	1,117	25.51	<0.0001
Sex×nestling age^2	1,117	13.67	<0.001
Helped×nestling age	1,117	13.36	<0.001
Helped×brood size	1,117	5.82	<0.025
Date	1,116	3.58	0.06

F values are those obtained from fitting a term last. Nest identity×individual identity and nest×individual×nestling age were included in the model as random factors. Estimates of their variances±SE were 3.50±1.01 and 0.128±0.012, respectively. All biologically meaningful two-way and three-way interaction terms were also tested, and those not shown were not significant (*P*>0.05). Total degrees of freedom is based on number of nests.

Denominator degrees of freedom were calculated from the number of nests used in each analysis.

Parameter values of the best-fitting models were examined to see if models could be further simplified, for example by the amalgamation of categories of class variables, or by constraining slopes for certain categories to be zero by fitting dummy variables (Crawley 1993; Verbeke & Molenberghs 1997). The significance of parameter estimates was assessed with *t* tests, with degrees of freedom calculated from the number of individual birds.

RESULTS

Parents

Males brought food more frequently than females did, and both sexes worked harder when not helped than when helped (Table 1, Fig. 1). Parents increased their provisioning rates as nestlings aged, but females increased their provisioning rates more rapidly than males when the nestlings were young (Fig. 1). Provisioning rates were related to nestling age^2, suggesting that rates increased to an asymptote. However, the estimate of the nestling age^2 term was significant only for females (females: $\bar{X} \pm$ SE$= -3.3 \times 10^{-2} \pm 0.63 \times 10^{-2}$; $t_{116} = -5.23$, $P<0.0001$; males: $-1.7 \times 10^{-3} \pm 6.4 \times 10^{-3}$; $t_{116} = -0.26$, NS), showing that the provisioning rates of males did not asymptote, but increased throughout the nestling period. The fit of the model (Fig. 1) suggests that the provisioning rates of male and female parents became similar as nestlings got older, probably because females brood young nestlings. However, the difference in provisioning rates between the sexes was still significant ($F_{1,85}=5.85$, $P<0.025$) when observations up to day 6 were excluded; females did virtually no brooding from this age onwards (Hatchwell et al. 1999a).
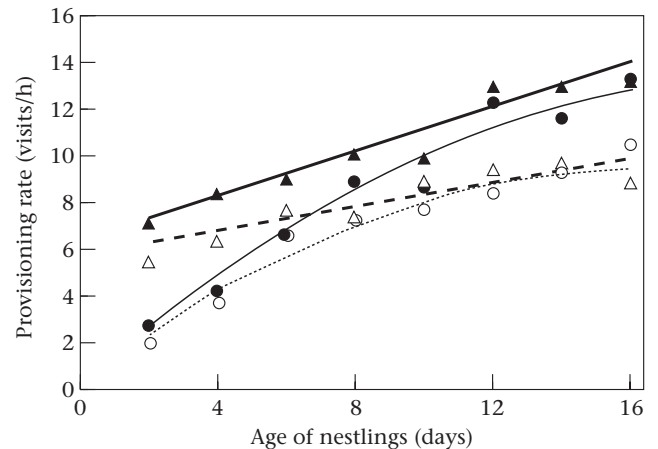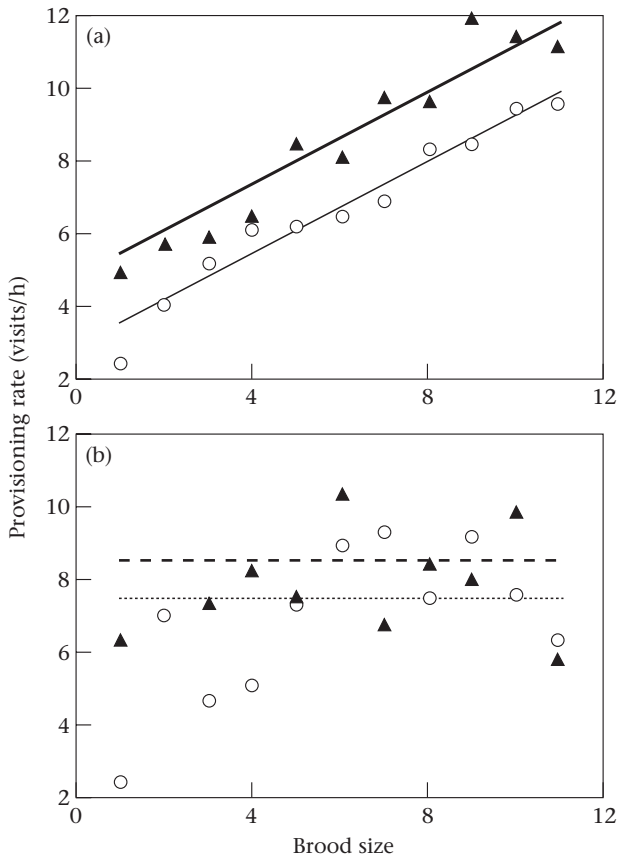

Figure 1. Relation between provisioning rate/h and nestling age for male (——, – – –, ▲, △) and female (——, ..., ●, ○) parents of each sex at helped (– – –, ..., △, ○) and unhelped (——, ——, ▲, ●) nests. The lines show predicted values from the model (Table 1) with other parameters set to their mean values. Symbols show means from data.
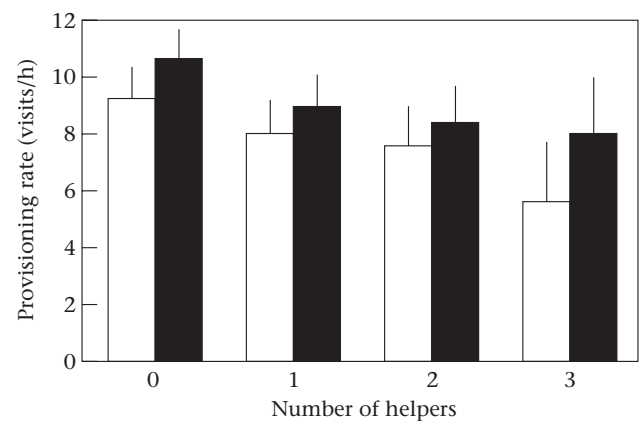
Figure 2. Variation in provisioning rate +95% confidence interval of female (□) and male (■) parents with size of the workforce, measured as number of helpers additional to the parents of the brood. The figure shows predicted values from the model (Table 1) with other parameters set to their mean values. *N*=122, 46, 21 and 8 nests for nests with 0, 1, 2 and 3 helpers, respectively.

To look in more detail at the effect of changes in the size of the workforce on provisioning rates, rather than simply whether helpers were present, we substituted 'number of helpers' for 'helped?' into the model in Table 1. Provisioning rates varied significantly with the number of helpers ($F_{3,117}=39.3$, $P<0.0001$), showing a significant drop from nests with no helper to nests with one helper (females: $t_{103}=2.87$, $P<0.005$; males: $t_{103}=4.01$, $P=0.0001$; Fig. 2). There were no further significant reductions in provisioning rates with the arrival of additional helpers.

Parents provisioned larger broods more than smaller ones (Table 1, Fig. 3), although parameter estimates show that this response was significant only for unhelped parents ($\bar{X} \pm$ SE slope: unhelped: 0.43 ± 0.07 feeds/h per nestling; $t_{117}=5.72$, $P<0.0001$; helped: 0.15 ± 0.11 feeds/h per nestling; $t_{117}=1.27$, NS). Even at unhelped nests, the

Figure 3. Relation between provisioning rate/h and brood size for male (——, – – –, ▲) and female (——, . . ., ○) parents at (a) unhelped and (b) helped nests. The lines show predicted values from the model (Table 1) with other parameters set to their mean values. Symbols show means from data. N (number of nests) for brood sizes 1 to 11, 1, 2, 3, 3, 4, 6, 8, 16, 15, 25, 6 and 1, 1, 2, 1, 2, 3, 4, 8, 11, 12, 2 for unhelped and helped nests, respectively.

Table 2. Results from a mixed model (REML) of provisioning rate for males

Effect	df	F	P
Year	7	2.01	0.06
Time	1	12.55	<0.001
Temperature	1	5.01	<0.05
Status	2	10.40	<0.0001
Nestling age	1	34.24	<0.0001
Brood size	1	10.95	0.001
Nestling age×status	2	7.73	<0.001
Date	1	1.55	NS
Nestling age^2	1	0.69	NS

Estimates of the variances±SE for nest identity×individual identity and nest×individual×nestling age, which were included in the model as random factors, were 6.51±1.53 and 0.087±0.018, respectively. See footnote to Table 1 for other details.

Figure 4. Relation between provisioning rate/h and nestling age for male parents at unhelped (——, ▲) and helped (– – –, △) nests, and male helpers (. . ., □). The lines show predicted values from the model (Table 2) with other parameters set to their mean values. Symbols show means from data.

magnitude of the increase meant that provisioning rates per nestling were lower in larger broods.

Parents also altered their provisioning rates in response to temperature and time of day (Table 1), but there were no significant differences in response to either of these variables between sexes or between helped and unhelped nests. Parents provisioned significantly less later in the day, although the rate of change in provisioning rate was small $(\bar{X} \pm SE = -2.7 \times 10^{-3} \pm 0.6 \times 10^{-3}$ feeds/h per min). Parents also provisioned significantly less on warmer days $(-8.9 \times 10^{-2} \pm 2.7 \times 10^{-2}$ feeds/h per °C) so that, on average, provisioning rates would have been about 1.6 feeds/h lower on the warmest than on the coolest days. The responses to time of day and temperature, although significant, are of small magnitude and may be of limited biological significance. Parents did not alter their provisioning rates significantly during the course of the season (Table 1).
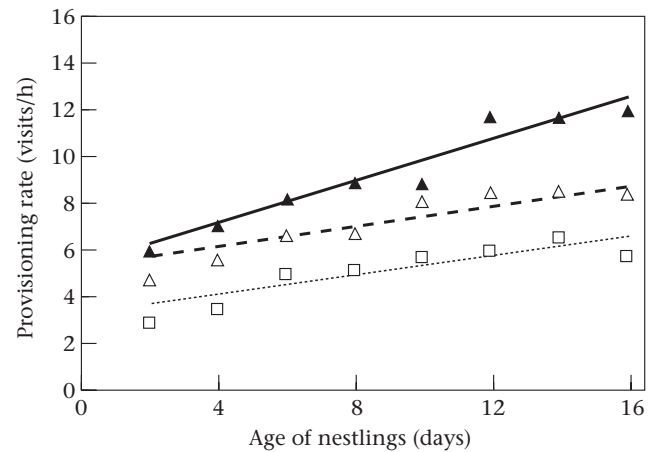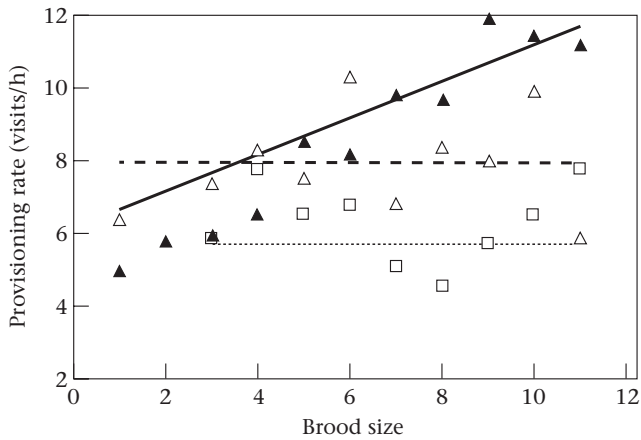
Male Parents and Helpers

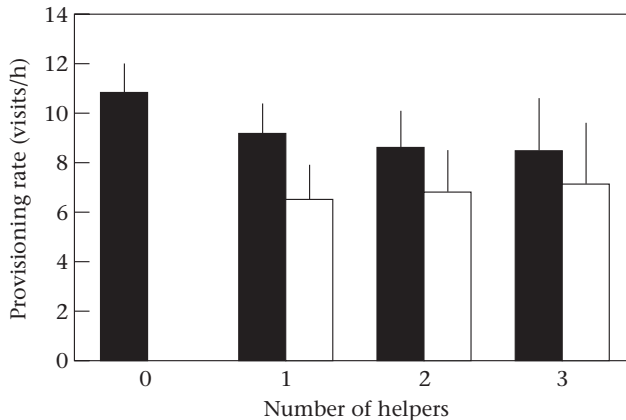Overall, male parents provisioned at a higher rate than male helpers did (Table 2, Fig. 4). Parameter estimates suggested that the response of males to changes in nestling age and brood size were determined primarily by whether they were working at a helped or an unhelped nest, rather than whether they were a parent or a helper. A better fit was obtained when the interaction between nestling age and 'helped?' was substituted in the model for that between nestling age and status $(F_{1,117}=18.17, P<0.0001)$. Thus, unhelped male parents increased their provisioning rates more rapidly as nestlings got older than either helped parents or helpers did, which did not differ from each other (Fig. 4).

The response of males to differences in brood size depended more on whether they were working at a helped or an unhelped nest than on whether they were a parent or a helper $(F_{1,117}=5.87, P<0.02,$ for the interaction between brood size and 'helped?'). In fact, males at helped nests showed a weak response to changes in brood size $(\bar{X} \pm SE$ slope=0.20 ± 0.16 feeds/h per nestling; $t_{121}=1.49$, NS; Fig. 5).

Figure 6 shows the change in provisioning rate of males with increases in the size of the workforce, when number

Figure 5. Relation between provisioning rate/h and brood size for male parents at helped and unhelped nests, and male helpers (see Fig. 4 for key). The lines show predicted values from the model (Table 2) with other parameters set to their mean values. Symbols show means from data. See the legend of Fig. 3 for sample sizes.

Table 3. Results from a mixed model (REML) of total provisioning rate

Effect	df	F	P
Year	7,120	3.72	0.001
Time	1,120	12.73	0.0005
Temperature	1,120	5.46	<0.025
Helped	1,120	22.28	<0.001
Nestling age	1,120	12.49	<0.001
Nestling age^2	1,120	21.70	<0.0001
Brood size	1,120	39.04	<0.0001
Nestling age×brood size	1,120	11.92	<0.001
Date	1,119	0.14	NS
Date^2	1,118	0.03	NS

Estimates of the variances±SE for nest identity and nest×nestling age, which were included in the model as random factors were 3.31±3.53 and 0.30±0.08, respectively. See footnote to Table 1 for other details.

Figure 6. Variation in provisioning rate +95% confidence interval of male parents (■) and helpers (□) with size of the workforce, measured as number of helpers additional to the parents of the brood. The figure shows predicted values from the model (Table 3) with other parameters set to their mean values. N=122, 46, 21 and 8 nests for nests with 0, 1, 2 and 3 helpers, respectively.

Figure 7. Relation between total provisioning rate/h and nestling age for broods of seven (——, ■) and 10 (– – –, □). The lines show predicted values from the model (Table 3) with other parameters set to their mean values. Symbols show means from data.

Total Provisioning Rates

Total provisioning rates were greater to older nestlings, but approached an asymptote as the nestlings neared fledging (Table 3, Fig. 7). Larger broods were provisioned more (Fig. 8), and this disparity increased as nestlings aged (Table 3, Fig. 7), but provisioning rates per nestling were always lower in larger broods. The total number of visits was higher at nests with helpers than at unhelped nests (Fig. 8). To look in more detail at the effect of changes in the workforce on provisioning rates, we substituted 'number of helpers' for 'helped?' into the model in Table 3. Provisioning rates varied significantly with the number of helpers ($F_{3,120}$=13.39, P<0.0001; Fig. 9), showing a significant increase from nests with no helper to nests with one helper (t_{119}= −2.58, P=0.01), and a larger increase to nests with two helpers (t_{119}= −3.53, P<0.001). However, total provisioning rates at nests with three helpers were not significantly higher than at nests with two helpers (t_{119}= −0.68, NS), although the sample of nests with three helpers was small (N=8).
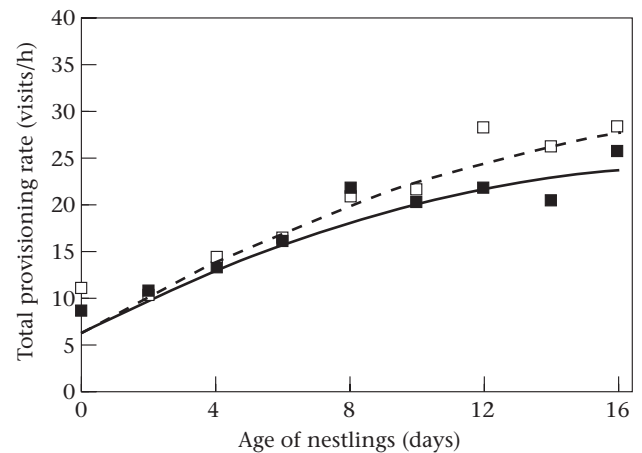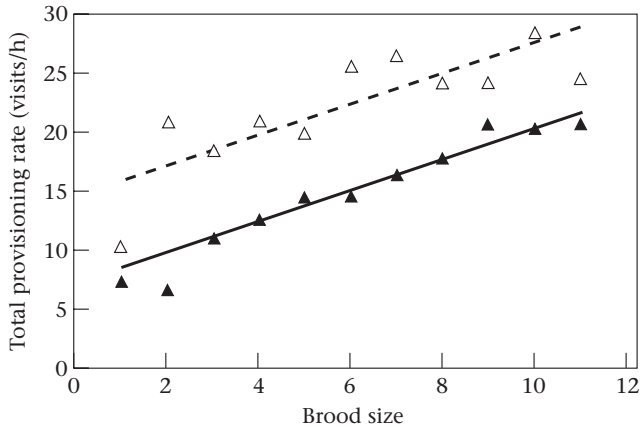
of helpers was substituted into the model for 'helped?', and birds were classified as either parents or helpers. We used only data for the father and the first helper to arrive at a nest. Male parents showed a large reduction in effort when there was a single helper at a nest (t_{103}=3.92, P=0.0002; Fig. 6). Beyond that, neither parents nor helpers showed significant changes in provisioning rate as the number of helpers increased (all P>0.25).

Males provisioned less later in the day, although the rate of change in provisioning rate through the day was small ($\bar{X} \pm SE$ = $-2.4 \times 10^{-3} \pm 0.7 \times 10^{-3}$ feeds/h per min), such that the reduction over the course of the day amounted to fewer than 2 feeds/h. Males also provisioned significantly less on warmer days ($-7.7 \times 10^{-2} \pm 3.1 \times 10^{-2}$ feeds/h per °C). Males did not alter their provisioning rates as the season progressed (Table 2).

Figure 8. Relation between total provisioning rate/h and brood size for unhelped (——, ▲) and helped (– – –, △) nests. The figure shows predicted values from the model (Table 3) with other parameters set to their mean values. Symbols show means from data.
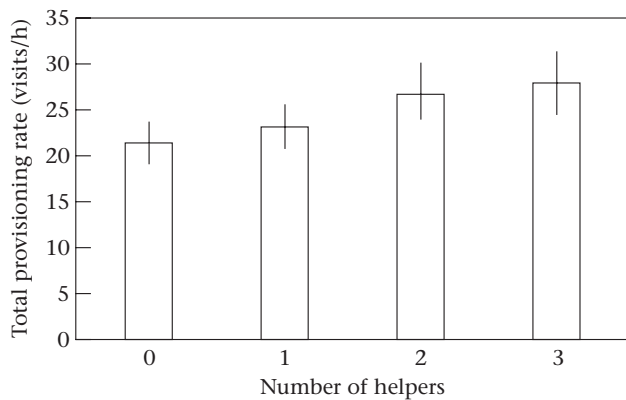
Figure 9. Variation in total provisioning rate ±95% confidence interval with size of the workforce, measured as number of helpers additional to the parents of the brood. $N=122$, 46, 21 and 8 nests for nests with 0, 1, 2 and 3 helpers, respectively.

In common with the results of the other analyses, total provisioning rates varied significantly between years, were lower later in the day and on warmer days, but did not vary significantly through the season (Table 3).

DISCUSSION

Differences between mothers, fathers and helpers in the amount of care invested in offspring by long-tailed tits were mainly quantitative rather than qualitative. Fathers provisioned more than mothers, who worked harder than helpers. Much of the variation in provisioning rates was related to the age of nestlings. All types of carers provisioned older nestlings more than younger ones. Mothers and fathers at unhelped nests worked harder when provisioning larger broods than smaller ones, but, at helped nests, the responses of parents and helpers to differences in brood size were not significant. Mothers and fathers reduced their work rate as the number of helpers increased, although the reduction was significant

only in response to the arrival of the first helper. Neither parents nor first helpers showed significant changes in work rates with additional increases in the number of helpers. However, the total provisioning rate increased in response to the arrival of one and two helpers. All classes of carers worked slightly, but consistently, less hard later in the day, and on warmer days. Carers did not change their provisioning rates during the course of the breeding season.

The patterns of provisioning in relation to nestling age and number of helpers that we describe in this paper are similar to those obtained in the observational and experimental study of Hatchwell & Russell (1996). However, with the increase in power afforded by increased sample size and an improved statistical method, we have been able to add considerable detail. For example, we have added comparisons of male parents and helpers in their responses to changes in covariates such as chick age, brood size and number of helpers. We have also explored in more detail the variation in total provisioning rates.

The provisioning rate of female parents may be less than that of male parents because females invest more in other ways. Females bear the full cost of laying the clutch, and, in long-tailed tits, females also do all of the incubation. However, it is not a general tendency among cooperative breeders (or birds in general) for male parents to work harder at provisioning nestlings. In several species, males do work harder (e.g. pygmy nuthatches, *Sitta pygmaea*: Sydeman 1989; rifleman, *Acanthisitta chloris*: Sherley 1990; green woodhoopoe, *Phoeniculus purpureus*: du Plessis 1991), but in others females do more provisioning (e.g. splendid fairy-wren, *Malurus splendens*: Rowley 1981; acorn woodpecker, *Melanerpes formicivorus*: Mumme et al. 1990; white-winged fairy-wren, *Malurus leucopterus*: Tidemann 1986), and in some species there is no difference (e.g. western bluebird, *Sialia mexicana*: Dickinson et al. 1996; Arabian babbler: Wright 1997). These differences between species may be linked to differences in other components of reproductive care such as incubation behaviour, or they may be the result of differences in the shape of cost–benefit functions between sexes. For example variation in extrapair paternity will tend to make the slope of the benefit function different for males and females, and differences in survival between the sexes will alter the shape of cost functions. Such differences will mean that the optimal investment by each sex differs between species.

Inclusive fitness considerations lead to the general expectation that helpers in cooperative breeding systems should work less hard than parents, because they are likely to be less related to the offspring. An obvious exception to this prediction is where helpers are the full siblings of the offspring that they provision. However, long-tailed tit helpers are usually a first-order relative of only one of the parents (Russell & Hatchwell 2001), and their relatedness to the offspring that they help is thus approximately half that of the parents. There are several other cooperative breeders in which helpers do work less hard than parents when provisioning young (e.g. acorn woodpecker: Mumme et al. 1990; common babbler,

Turdoides caudatus: Gaston 1978); however, this is again not a general rule, and in several species, helpers work as hard as one or both parents (e.g Arabian babbler: Wright 1997; Galapagos mockingbird, *Nesomimus parvulus*: Kinnaird & Grant 1982; Florida scrub jay, *Aphelocoma c. coerulescens*: Stallcup & Woolfenden 1978; Mumme 1992). There are several possible reasons for this variation, linked to the type and magnitude of benefits that helpers gain by helping. If helpers are related to the nestlings they help, then the amount of effort that they expend should be proportional to their relatedness and to the amount of difference they can make by helping. If, on the other hand, helpers are unrelated to nestlings, suggesting that they are helping only to gain the direct benefits of living in the group, then they should work only as hard as needed to be allowed to remain (Gaston 1978; Kokko et al. 2002).

The positive relation that we found between brood size and provisioning rate at unhelped nests has been observed many times in passerine birds, and it is normal for nestlings in larger broods to receive less food per individual (Klomp 1970). This decrease in investment per individual is probably partly the result of the thermal benefits enjoyed by nestlings in larger broods (Royama 1966), and partly because of parents optimizing costs and benefits of care (Nur 1984). The lack of a significant relation between work rate and brood size at helped nests in the present study may be a result of lack of statistical power, because helpers were present at only a subsample of nests. However, the data were much more variable for helped nests, and this suggests another possibility. In larger workforces, more complex patterns of compensation among carers are possible, and these may make the response of individual birds less clear. For example, at some nests with large broods, the father might work harder, but at others it might be a helper or the mother. Individuals might also behave differently from day to day, depending on short-term variation in their condition (Clutton-Brock et al. 2000).

The pattern of response of carers to changes in the number of helpers is consistent with previous observational and experimental work on this species (Hatchwell & Russell 1996; Hatchwell 1999). Parents at unhelped nests reduced their provisioning rate in response to the arrival of one helper, but carers at nests that already had a helper did not significantly alter their provisioning rates in response to the arrival of further helpers. Although it is possible that the sample size of helped nests was not large enough to detect an effect, the parameter estimates, for helpers at least, do not suggest any decrease in provisioning rates. Perhaps the first priority for unhelped parents is to reduce their costs, but carers at helped nests, which are already working less hard, prefer to increase their benefits by maintaining their work rate when further helpers arrive, and thus increase total provisioning rates (Hatchwell 1999). However, although we have been able to measure a significant effect of a single helper on the productivity of the brood that they help, helpers appear to have no effect on the survival of helped adults, despite this reduction in reproductive effort (McGowan et al. 2003).

It is likely that the response of carers to temperature and time of day are mediated through begging signals by variation in hunger state (Kilner & Johnstone 1997). Nestlings should be hungriest first thing in the morning after not being fed all night, and they are lightest at this time of the day (unpublished data). Weight increases through the day, and hunger probably declines as the nestlings receive food. On warmer days, nestlings should have a more favourable energy balance, and so might beg less. However, it is also possible that the carers are able to exploit larger prey on warmer days, and that their visit rates might go down as a result. We intend to examine this possibility in the future.

It is surprising that the work rate of carers did not change consistently through the season, because the value of nestlings that fledge later was less, because of lower overwinter survival (MacColl & Hatchwell 2002). We therefore expect carers to put less effort into later broods (Winkler 1987). The lack of such a relation in the present analysis may be caused by a lack of statistical power, because in other analyses the total effort that individuals devoted to provisioning nestlings over the whole nestling period did decline through the season (unpublished data). An alternative explanation is that the reduction in value of fledglings as the season progresses is offset by a reduction in the cost of provisioning them because food availability increases. We cannot rule out this possibility for long-tailed tits, but for ecologically similar insectivorous birds such as the parid tits, prey abundance peaks in the middle of the breeding season (Woodburn 1997; Verboven et al. 2001). We are currently investigating the seasonal change in food availability for long-tailed tits.

Although we have examined several factors that make important contributions to observed variations in provisioning rates, substantial variation still remains to be explained. Several additional factors that we did not examine in these analyses might be important in this regard. Relatedness between carers and offspring is one candidate (Emlen & Wrege 1988; Komdeur 1994). Relatedness is unlikely to affect substantially the provisioning rates of long-tailed tit parents because there is so little extrapair fertilization or brood parasitism (Hatchwell et al. 2002). It is more difficult to test this hypothesis for helpers because of imperfect data on the relatedness between helpers and the birds they help. We know many first-order relationships from ringing data, but without extensive genetic work, it is impossible to know whether helpers of unknown relatedness are less related or completely unrelated. Basic comparisons between the provisioning rates of helpers that are known first-order relatives of at least one parent and those that are not do not support the idea that closely related birds work harder (unpublished data). In any case, less related or completely unrelated helpers may provision at nests only because of limitations in their ability to recognize relatives, and hence we might not expect distant relatives to work less hard than close relatives (Hatchwell et al. 2001b).

Some of the variation in provisioning rates was the result of consistent behavioural differences between

individual carers. The provisioning effort of individual long-tailed tits is consistent between years, and an animal model analysis (Lynch & Walsh 1998) showed that some of the variation between individuals is the result of heritable differences (unpublished data). We also found that variations in provisioning rates caused by nest site or habitat type were small. Parental care may be heritable in another passerine, the Savannah sparrow, *Passerculus sandwichensis* (Freeman-Gallant & Rothstein 1999). Studies of nestling provisioning in birds have usually focused on the environmental causes of variation such as brood size, age and relatedness. Thus, the discovery of individual differences in behaviour from transgenerational causes is important for our understanding of the regulation of parental effort.

Although helpers responded similarly to parents to differences in circumstances, overall they worked less hard than parents. This contrasts with work on Arabian babblers (Wright 1998; Wright & Dingemanse 1999), in which the provisioning behaviour of parents and helpers was indistinguishable. The main difference between Arabian babbler helpers and long-tailed tit helpers may be their relatedness to the brood. Arabian babbler helpers are usually full siblings (Wright et al. 1999), and long-tailed tit helpers are often half siblings (Russell & Hatchwell 2001). This difference highlights the sensitivity of behaviour to the relative magnitude of different benefits. In cooperative systems where the fitness benefits of cooperation are primarily indirect, helpers have similar interests in the brood to parents and may show qualitatively similar responses to parents to different circumstances, with absolute effort being determined by relatedness. However, the interests of helpers and breeders in nestling provisioning are likely to diverge as the relative importance of direct fitness benefits increase. Long-tailed tit helpers have higher overwinter survival than failed breeders that do not help (McGowan et al. 2003). Therefore, multiple carer systems cannot be considered as simple extensions of biparental systems, because helpers may have fitness functions that differ from those of parents. This difference highlights a need to develop a theoretical understanding of care in multiple carer systems so that variation in provisioning behaviour may be more rigorously explored.

Acknowledgments

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