Determinants of lifetime fitness in a cooperative breeder, the long-tailed tit *Aegithalos caudatus*

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Summary

1. Long-tailed tits (*Aegithalos caudatus*) are a cooperatively breeding species in which helpers often invest effort in the provisioning of young that are not their own.

2. We quantified the lifetime reproductive success (LRS) and the individual fitness, lambda, of 228 long-tailed tits using 8 years of field data. Calculation of lambda took account of the effect of helpers on reproductive success, and thus lambda estimates the inclusive fitness of individuals. We examined the relationships between the fitness estimators and the provisioning effort, cohort, body size and dispersal status of individuals.

3. LRS of individuals which bred successfully varied between 0 and 13 local recruits (mean 0·71 ± 0·11 SE); lambda varied between 0 and 2·54 (mean 0·28 ± 0·04). The measures were highly correlated, and their distributions were strongly skewed. Helping by individuals contributed little to their fitness, but one-fifth of birds that accrued fitness did so only through helping. In general, individuals that gained fitness from helping did not gain fitness directly.

4. Both LRS and individual fitness were significant predictors of the number of grand-offspring that an individual had, but they accounted for only about one-third of the variation.

5. When variance in LRS was partitioned between length of breeding life span, average fecundity and offspring survival, the latter component was the most important in accounting for variance in LRS.

6. Offspring local survival was positively related to the provisioning effort of mothers, but was unrelated to that of fathers. As a result, the fitness of females was positively related to their provisioning effort.

7. Immigrant birds tended to be more reproductively successful than philopatric ones. Among females, only immigrant birds accrued any LRS or individual fitness.

8. The probability that an individual had at least one offspring recruit to the local breeding population varied among cohorts, probably as a result of variation among years in offspring local survival. This resulted in variation among cohorts in the individual fitness of females, but not in their LRS, nor in the LRS or individual fitness of males.

Key-words: dispersal, helpers-at-the-nest, inclusive fitness, lifetime reproductive success, parental care.

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Introduction

A defining aspect of cooperatively breeding species is that some individuals invest effort in the rearing of young that are not their own offspring. An important com-

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ponent of this effort is often the provisioning of offspring with food (Stacey & Koenig 1990; Clutton-Brock *et al.* 2001). Many studies have demonstrated that helpers can increase the production of offspring by helped pairs, and their authors have thus claimed that inclusive fitness gains play an important role in the evolution of co-operative breeding. However, few studies have been able to examine the contribution of helping to fitness over the lifetime of individuals (Fitzpatrick & Woolfenden 1988).

Measurement of fitness of individuals in natural populations is not trivial (Grafen 1988; McGraw &

Caswell 1996). The total number of offspring produced over a lifetime, 'lifetime reproductive success' (LRS) (McGregor, Krebs & Perrins 1981; Clutton-Brock 1988) has often been used as an estimate. In numerous detailed empirical studies LRS has usually been shown to have a high degree of skew among individuals and this has been used to draw conclusions about selection on life-history traits (Clutton-Brock 1988; Newton 1989). However, LRS and fitness are not the same thing (Grafen 1988). LRS has been criticized as a measure of fitness principally because it does not take account of the timing of reproductive events (McGraw & Caswell 1996). This problem can be overcome by explicit incorporation of age at reproduction in the calculation of a measure that has come to be called 'individual fitness' (McGraw & Caswell 1996; Brommer, Merila & Kokko 2002). McGraw & Caswell (1996) used empirical data to demonstrate how conclusions about selection on life-history traits could be altered substantially by considering individual fitness instead of LRS. However, individual fitness has been criticized in its turn because it, also, is not a perfect measure of fitness because for example, it is sensitive to the age at which offspring are censused, which LRS is not (Brommer *et al.* 2002).

In cooperatively breeding species the measurement of fitness is complicated further by the need to take account of the social situation of individuals. Attempting to estimate inclusive fitness is the recognized way to do this (Hamilton 1964), but this has proved to be controversial in practice (Grafen 1982; Creel 1990; Queller 1996). Oli (2003) has recently published an adaptation of McGraw & Caswell's (1996) method that allows inclusive fitness to be accounted for when calculating individual fitness. In this study of the cooperatively breeding long-tailed tit *Aegithalos caudatus* (L.) we use Oli's (2003) method to calculate individual fitness, and we also calculate the LRS of individuals. We compare the distributions of these fitness estimators, examine the relationship between them and compare their ability to predict the production of grand-offspring. We then explore how they vary among individuals. We do this in two ways. We first partition variance in LRS among component terms to assess their relative contributions to LRS, following Brown (1988). We then examine the relationship of these components, of LRS itself and of individual fitness to variables which have been found previously to be related to fitness in other species, such as body size, cohort and dispersal status. In long-tailed tits higher levels of provisioning effort by parents and helpers are associated with increased survival of fledglings, and we have found that the provisioning effort of parents is heritable (MacColl & Hatchwell 2003a). We were therefore interested in quantifying the relationship between provisioning effort and fitness.

Although there are now several studies that have evaluated LRS and/or individual fitness in natural avian populations (Clutton-Brock 1988; Newton 1989; Brommer *et al.* 2002), there are few studies of these measures of fitness for cooperative breeders, and those that do exist have been unable to control for the complication of extra-pair parentage. This analysis enables us to assess the main determinants of variation in fitness in long-tailed tits and to compare the relative importance of direct and indirect components of inclusive fitness. We are also able to make the first test of the hypothesis that in cooperative breeders the sex with the greater variance in reproductive success should be more likely to help, because individuals are more likely to die without breeding, and thus helping may be their only route to gaining inclusive fitness (Koenig, Mumme & Pitelka 1983).

Methods

STUDY SITE AND POPULATION

A population of 18–53 pairs of long-tailed tits was studied between 1994 and 2002 in the Rivelin Valley, Sheffield, UK. (53°23′N 1°34′W). The study area occupies a 3-km long section of the valley which is approximately 1 km wide and runs West to East. Suitable habitat for long-tailed tits within this part of the valley consists of about 160 ha of interconnected patches of woodland and scrub. The part which is not woodland is almost entirely grassland (agricultural pasture and golf course) that is unsuitable habitat for long-tailed tits. Woodland in the study area is connected at both ends by narrow corridors to poorer-quality habitat.

Long-tailed tits spend most of the year, from June to January, in flocks of 10–30 individuals. These flocks break up when pairs form in late winter. All long-tailed tits attempt initially to breed in pairs, but the rate of nest failure is high because of predation by corvids. As a result some individuals abandon independent breeding, and help a close relative to raise their brood. The major contribution of helpers to nestlings is in the provisioning of food. For further details of the study area, species and social system see Hatchwell *et al.* (2001, 2004) and MacColl & Hatchwell (2002).

Unringed adults were colour-ringed and weighed before breeding started, or in some cases during the nestling period. Birds ringed as adults in the first year of the study (1994) were not included in our calculations of fitness. Birds ringed as adults in all subsequent years were classed as immigrants, and were assumed to be 1 year of age when first recorded breeding. Helpers from outside the study area were colour-ringed soon after first appearance at a nest. Birds that were caught were weighed (to 0·1 g) and had their right tarsus measured (to 0·1 mm). Nests were located by observation of pairs and checked at least every other day. If a pair failed in a breeding attempt we relocated the birds and any subsequent nest by extensive searching of the study area. Chicks were counted ('number of fledglings'), weighed to 0·1 g ('nestling weight') and ringed with unique colour combinations when 10–13 days old. Ninety per cent (*n* = 104 broods) were weighed at

11 days. The survival of chicks in nests which were not depredated was very high (97·7% from hatching to day 11; Hatchwell *et al*. 2004). Chicks were sexed using a molecular technique (Griffiths *et al*. 1998), using blood taken by brachial venipuncture at the time of ringing.

Chicks that were known to have fledged were counted as recruits to the local breeding population if they were resighted during intensive fieldwork at the beginning of each breeding season. As well as the study area itself we searched the first few hundred metres of the woodland areas adjacent to the study area at its East and West ends in several years of the study as time allowed. Very few marked birds were ever found. To the North the study area is bounded almost entirely by pasture, and we believe that there is little dispersal in that direction. To the South the study area is bounded by residential housing, and most short-distance dispersal out of the study area probably takes place into the gardens of these houses. It is difficult to quantify this dispersal because this land is privately owned. However, neither public appeals for sightings nor the personal observations of the second author (B. J. H.) on adjacent public land have ever provided any records of colour-ringed birds. These facts, coupled with a previous formal survival analysis on this population that indicated a between-year resighting probability of close to one for living adults (McGowan, Hatchwell & Woodburn 2003), suggests that few birds disperse just past the margins of the study area. We were unable to control for longer distance dispersal in our calculations, although we have no reason to believe that this should effect our conclusions.

The complete reproductive histories of birds which hatched between 1994 and 2000 and had died by 2002 were recorded. Long-tailed tits raise a maximum of one brood per year, and always attempt to breed in every year from the age of 1 year. Lifetime reproductive success and individual fitness of birds were estimated from the number of their offspring that recruited to the local breeding population. We believe that recruits are the correct unit of reproductive success in this species because of the extended period of parental care (Brommer *et al*. 2002). Previous work has shown that helpers do not affect the number of chicks that fledge from the nest where they help because they arrive too late to affect clutch size, while nestling mortality due to causes other than catastrophic predation is generally very low. However, helpers do increase the number of fledglings that recruit locally (Hatchwell *et al*. 2004).

Extra-pair paternity and intraspecific brood parasitism are rare in long-tailed tits (< 5% of offspring), and unlikely to affect estimates of fitness. However, in calculations all known extra-pair young were assigned to their most likely true parents (Hatchwell *et al*. 2002).

Nests containing nestlings were watched every other day from hatching (day 0) to fledging (day 16 or 17), usually for a period of 1 h (mean total observation time per nest ± SE = 523 ± 30 min). In this way the rates at which individual carers brought food to nestlings were recorded. For each individual parent a simple linear regression line was then fitted to the relationship between hourly feeding rate and age of nestlings, and 'provisioning effort' was estimated as the area under the regression line between 0 and 16 days (MacColl & Hatchwell 2003a). The effort of individuals is repeatable across years (MacColl & Hatchwell 2003a), so the mean of all estimates of provisioning effort over an individual's lifetime was used to calculate 'mean provisioning effort'. Provisioning effort is related only weakly to the size of the brood that was provisioned ($R^2 = 0·05$) (MacColl & Hatchwell 2003b). However, in analyses where mean provisioning effort was used as a predictor variable, the analyses were repeated using the residuals of provisoning effort from brood size instead. This did not alter the conclusions. Only the results from analyses using mean provisioning effort itself are presented, as these are more easily understandable.

MEASUREMENT OF FITNESS

Lifetime reproductive success

Lifetime reproductive success is the sum of all local recruits produced by an individual in its lifetime. Following Brown (1988), in the partition of variance in LRS among components (see below) only those birds that succeeded in fledging at least one offspring were considered. It was then necessary to calculate the contribution of these individuals to overall variance in LRS, compared with that of the 'invisible fraction' that fledge no young (Grafen 1988). For n_t total birds, of which n_b succeeded in fledging at least one offspring, the overall variance in LRS for all birds is given by: $p \cdot V(LRS) + p \cdot (1 - p) \cdot LRS^2$, where $p = n_b/n_t$, and V(LRS) is the variance in LRS of birds that fledged at least one offspring (Brown 1988). The first term in this equation gives the proportion of the variance accounted for by those that fledged young, the second term gives the proportion accounted for by all other birds that attempted to breed.

Individual fitness

Data on the annual reproductive success and survival of each bird were used to construct individual projection matrices according to the method of McGraw & Caswell (1996). The individual fitness of each bird was then calculated as the dominant eigenvalue of its matrix (using MATHCAD 5·0 (Fausett 2002)). In this way the fitness of each bird was calculated using three different methods to estimate their annual reproductive success. First, half the number of local recruits from each year was used to calculate 'recruit fitness' λ_r, under the assumption that the relatedness of parents and offspring was 0·5. The direct fitness (λ_d) of individuals was then calculated by stripping from each the component of its annual reproductive success that was due to having been helped (see below). This indirect fitness component was divided among the helpers at each nest

in accordance with their relatedness, and these fractions were added to their annual reproductive success values (λ_d) to calculate inclusive, or individual fitness (λ_i) for all birds (Hamilton 1964; Oli 2003).

To calculate the component of an individual's annual reproductive success that was attributable to having been helped a logistic regression model was constructed of the relationship between the proportion of fledglings that recruited locally and the number of helpers at a nest (Hatchwell *et al.* 2004). The model controlled for year effects, lay date and the sex ratio of the brood at fledging. This model was used to find the predicted proportion of fledglings that would have recruited locally from nests with helpers if they had had either no helpers or their observed number of helpers. Following Fitzpatrick & Woolfenden (1989), these two quantities were used to calculate the proportion of observed local recruitment from these nests that was due to the effect of helping.

To understand better the usefulness of LRS and individual fitness as measures of fitness, their ability to predict the number of grand-offspring (fledglings) produced by individuals was examined. The number of grand-offspring produced by a sample of individuals whose offspring had all completed their reproductive life spans were counted.

Partition of variance in LRS

A 'Brownian' partition of variance (Brown 1988) was used to assess the relative importance of three component terms: breeding life span (L), fecundity (F) and offspring local survival (S) and their products to overall variation in LRS. Breeding life span was the number of breeding seasons in which an individual attempted to breed. Fecundity was the average number of fledglings produced by an individual per season over its breeding life span, and offspring local survival was the total number of local recruits produced by an individual divided by the total number of fledglings. The product of L, F and S was therefore lifetime reproductive success.

Correlates of variation in components of fitness

A series of statistical models was used to examine how individual fitness and LRS and its components were related to cohort effects and to the provisioning effort of parents, their sex, body size and their 'dispersal status' (philopatric or immigrant). There were many pairs of males and females in the data set which had the same LRS and/or individual fitness because all their successful nesting attempts (in most cases only a single attempt) were with each other. In analyses where we judged that there was a problem of pseudoreplication the data for males and females were split and analysed separately. Generalized linear models (GLMs) were used to examine relationships. These were performed using PROC GENMOD in SAS (SAS Institute 1999; Der &

Everitt 2002). The significance of terms and relevant two-way interactions was assessed from analysis of deviance when terms were fitted last in models. Error distributions and link functions were chosen to be appropriate for each dependent variable, and residuals were checked for normality by visual inspection of residual and normal probability plots (Der & Everitt 2002).

Results

LIFETIME REPRODUCTIVE SUCCESS

The complete reproductive histories of 228 birds (n_t) were recorded: 119 females and 109 males from seven cohorts. The sample comprised at least 90% of the individuals from each cohort except 2000 (1994, 100%; 1995, 100%; 1996, 97%; 1997, 97%; 1998, 94%; 1999, 91%; 2000, 55%). Ninety-eight birds (n_b) (54 females and 44 males) fledged at least one offspring. Fifty-five birds had at least one offspring recruit to the study population. The mean (variance) LRS of birds that fledged at least one offspring was 1·70 (6·14) for females and 1·61 (3·68) for males (Wilcoxon's two-sample test $t = 0·17$, $P = 0·87$). According to Brown's (1988) equation 76% of the variance in overall breeding success can then be attributed to breeders.

INDIVIDUAL FITNESS

In the model that was used to estimate the effect of helping on annual reproductive success, the proportion of fledglings from a brood that recruited in the study area was positively related to the number of helpers that worked at the nest, the lay date and the brood sex ratio (Table 1). It varied between years and there was a significant interaction between year and lay date.

Seventy birds had non-zero individual fitness. Fifteen individuals (13 males) that had zero LRS accrued non-zero inclusive fitness by helping at the nests of others (mean $\lambda_i = 0·18 \pm 0·04$). This compared with a mean λ_i of 1·10 ± 0·08 for 55 individuals with non-zero LRS. The average contribution of indirect fitness to individual fitness was 22 ± 5%; however, this was distributed unevenly among individuals. Only two individuals (one bird of each sex) that gained fitness directly also gained fitness by helping. Mean λ_r for 98

Table 1. Estimate of the effect of helping on annual reproductive success. The proportion of fledglings from a brood that recruited in the study area was modelled as binomial in a GLM with a logit link function, for $N = 88$ nests

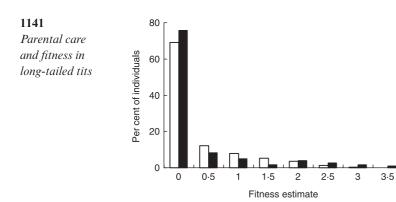| Effect	d.f.	χ^2	P
No. of helpers	1	6·81	0·009
Year of fledging	7	35·59	< 0·0001
Lay date	1	16·07	< 0·0001
Brood sex ratio	1	22·89	< 0·0001
Year × lay date	7	32·46	< 0·0001

Fig. 1. The distribution of estimates of LRS ($\times 0.5$, filled bars) and individual fitness (λ_i, open bars) for 228 long-tailed tits hatched between 1994 and 2000 which attempted to breed in our study area.

Table 2. Means and variances of individual components of lifetime reproductive success and their products for long-tailed tits. L = beeding life span (seasons), F = fecundity (fledglings per season), S = offspring survival to local recruitment. G gives the variances of individual variables and their products after the individual variables have been divided by their means. G′ gives the G-values as a percentage of the G-value for LRS

Component	Mean	Variance	G	G′
L	1·89	1·28	0·358	23·6
F	6·52	8·22	0·194	12·8
S	0·15	0·03	1·529	101·0
LF	10·45	24·52	0·162	10·7
LS	0·29	0·16	2·083	137·6
FS	1·02	2·09	2·262	149·4
LFS	1·66	4·99	1·514	100·0

Table 3. Percentage contribution of the components of lifetime reproductive success to variation in LRS. This gives a breakdown of the variances of the original components after scaling by their means, expressed as a percentage of V(LRS). The two component contributions are shown as the below-diagonal entries. They give the extra variance induced in the product by joint variation, in excess of the sum of the single-component contributions

Component	L	F	S
L	23·6		
F	−25·7	12·8	
S	13·0	35·7	101·0
LFS	−60·3		

birds that fledged at least one offspring was 0.70 ± 0.08 (SE). There was no difference between males (0.73 ± 0.13, $N = 44$) and females (0.68 ± 0.11, $N = 54$) (Wilcoxon's two-sample test $t = 0.27$, $P = 0.78$). The two other measures of individual fitness, λ_f and λ_I, were highly correlated with λ_r (0.98 and 0.97, respectively, both $P < 0.0001$, $N = 228$). The correlation between λ_i and LRS was also high (0.90, $P < 0.0001$, $N = 228$), and this fell only slightly when individuals which neither fledged young nor accrued fitness by helping were excluded (0.88, $P < 0.0001$, $N = 112$). The distribution of LRS and individual fitness did not differ significantly (Fig. 1, Kolmogorov–Smirnov $D = 0.066$, $P = 0.71$).

Both LRS and λ_i significantly predicted the number of grand-offspring that a bird produced (for males $F_{1,12} = 5.64$, $P = 0.035$ and $F_{1,12} = 7.24$, $P = 0.02$, respectively; for females $F_{1,14} = 21.18$, $P = 0.0004$ and $F_{1,14} = 5.39$, $P = 0.036$), but they accounted for only about a third of the variation ($R^2 = 0.32$, 0.38, 0.60, 0.28, respectively). The stronger relationship between grand-offspring produced by females and their LRS was the result of a single outlying point, without which $R^2 = 0.15$.

PARTITION OF VARIANCE IN LRS

The data on the components of LRS are summarized in Table 2. The average breeding life span of these individuals was about 2 years, during which long-tailed tits produced on average about six-and-a-half fledglings per year. About one in seven of these survived to recruit in the study area. The average LRS was 1·66 offspring recruited. The most important single component of variance in LRS [V(LRS), see G′ in Table 2] was offspring local survival (S), because if breeding life span (L) and average fecundity (F) were set equal to their means, LRS would have had variance almost exactly the same as that (101%) when variation in all three components was allowed (Brown 1988). In the same way, only 13% of V(LRS) was accounted for by variation in F only, and variation in life span also contributed little (24%). Both products involving S (LS and

FS) also demonstrate the importance of S in determining V(LRS), and the contribution of the product LF was very small.

Table 3 gives a breakdown of the variances of the original components after scaling by their means, expressed as a percentage of V(LRS). The diagonal in this table thus represents the same information about the single components of LRS, as shown in the last column of Table 2. The two component contributions are shown as the below-diagonal entries, and accounted for a moderate amount of the overall variation, although some of the contributions were negative. Thus, for example, the extra variance induced in the product by joint variation in L and S, in excess of the sum of their single-component contributions (24% + 101% = 125%), is 13%, giving a total for these two components of 138% (Table 2). This means that if the average fecundity of each long-tailed tit were set to 6·5, the LRS would have had a variance of 138% of its value when all three components took their real values. The 13% by which this is greater than the sum of the individual component contributions can be broken down further into more meaningful terms, depending on the degree of correlation between L and S.

Table 4 shows the partition of two component contributions into simultaneous independent terms and

Table 4. The partition of two component contributions into independent variation and covariation in components of lifetime reproductive success. Simultaneous independent terms are shown below the diagonal (bold), and covariation terms above the diagonal (italic). The three variable term is partitioned at the bottom of the table

Component	L	F	S
L	23·6	*–30·3*	*–23·2*
F	**4·6**	12·8	*16·1*
S	**36·2**	**19·6**	101·0
LFS	ind **7·0**	covar	–67·3

covariation terms. The simultaneous independent contribution of L and F was small, other terms were of moderate size. The breeding life span and fecundity of long-tailed tits were negatively correlated such that the variance of their product LF was less, by 30% of V(LFS) than it would have been if they were independent. The variance of the three-way product was also much less than it would have been if the components were independent. Variations in fecundity and offspring local survival were slightly (16%) synergistic, suggesting that fledglings from larger broods survive better.

CORRELATES OF VARIATION IN COMPONENTS OF FITNESS

Life span

There was significant variation among cohorts in the length of the reproductive life span (L), although this was mainly because of short apparent life spans of birds from the last two cohorts (1999 and 2000) for which data were censored (Table 5a). There was no difference between the sexes in the length of the reproductive life span (Fig. 2), nor was there a difference between philopatric and immigrant birds. The length of the breeding life span was unrelated to mean provisioning effort or the interaction between sex and effort (Table 5a). However, parameter estimates suggested a negative relationship between length of the breeding life span and effort for females ($\beta = -0.004 \pm 0.0024$ seasons per provisioning unit). In a subset of 90 philopatric birds, breeding life span was unrelated to the weight or tarsus length of an individual at fledging ($\chi_1^2 = 0.18$, $P = 0.67$; $\chi_1^2 = 0.33$, $P = 0.57$) and was unrelated to whether it had been raised in a nest with helpers ($\chi_1^2 = 0.15$, $P = 0.70$).

Fecundity

The probability that an individual which attempted to breed would successfully fledge offspring of its own at some time during its reproductive life was positively related to the number of seasons during which it attempted to breed (Fig. 3; Table 5b) and was higher for immigrant than philopatric birds. The probability of fledging at least one offspring did not differ between

Table 5. Correlates of variation in components of fitness for individual long-tailed tits that attempted to breed at least once. (a) Results of a GLM (Poisson errors, logarithm link) for life span (L) defined as the number of seasons in which an individual attempted to breed; (b) results of a GLM (binomial errors, logit link) for the binary probability of producing at least one fledgling; (c) results of a GLM (normal errors, identity link) for average fecundity (F) of females, defined as the total number of fledglings produced divided by L; (d) results of a GLM (binomial errors, logit link) for offspring survival (S) defined as the offspring that recruited locally as a proportion of those that fledged

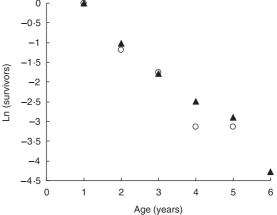| Effect	d.f.	N	χ^2	P
(a) Life span (number of breeding seasons)				
Cohort	6	228	15·89	0·014
Sex	1	228	0·0	0·99
Dispersal	1	228	0·06	0·81
Provisioning effort	1	228	0·93	0·34
Sex × effort	1	228	2·24	0·13
(b) Probability that a bird fledged at least one offspring				
Life span	1	228	28·5	< 0·0001
Cohort	6	228	3·96	0·68
Sex	1	228	0·01	0·93
Dispersal	1	228	4·05	0·044
(c) Average fecundity of females				
Life span	1	54	15·1	< 0·0001
Cohort	6	54	3·04	0·80
Dispersal	1	54	2·22	0·14
Provisioning effort	1	54	2·86	< 0·09
Tarsus length	1	54	1·09	0·30
(d) Survival of the offspring of females to local recruitment				
No. fledged	1	54	6·12	0·013
Cohort	6	54	19·01	0·0042
Dispersal	1	54	7·16	0·0074
Provisioning effort	1	44	7·64	0·0057
Tarsus length	1	44	1·95	0·16

Fig. 2. Log-linear survivorship curves for philopatric male ($N = 72$, triangles) and female ($N = 23$, circles) long-tailed tits that were known to have attempted to breed at least once. Birds seen breeding in 1994, and those of unknown provenance ('immigrants') are omitted.

the sexes or between cohorts (Table 5b). In a subset of 87 philopatric birds the probability of fledging at least one offspring was related to number of breeding seasons ($\chi_1^2 = 5.54$, $P = 0.019$) and to the bird's own tarsus length
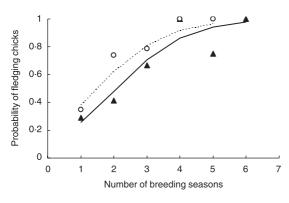
Fig. 3. Probability of fledging at least one chick as a function of number of breeding seasons. Filled triangles (solid line) show the data (fit) for philopatric birds ($N = 62, 17, 9, 2, 4, 1$, respectively), open circles (dashed line) show the data (fit) for immigrants ($N = 95, 27, 14, 5, 2$, respectively).
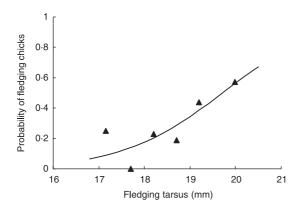

Fig. 4. The relationship between probability of fledging young as an adult, and length of tarsus at fledging, for individuals which bred in a single season. The model was fitted to the binary data for individuals, but for clarity, mean probabilities for binned data are shown, with $N = 4, 6, 13, 16, 16, 7$ for points from left to right, respectively. The fitted line covers the full range of the data.

at fledging (Fig. 4; $\chi_1^2 = 5{\cdot}96$, $P = 0{\cdot}015$), but unrelated to its own fledging weight ($\chi_1^2 = 0{\cdot}67$, $P = 0{\cdot}41$). There was a weak tendency for birds which were reared in nests at which helpers were present to be less likely to fledge offspring of their own ($\chi_1^2 = 2{\cdot}89$, $P = 0{\cdot}09$).

For females that fledged at least one offspring, the total number of offspring fledged was positively related to the length of the breeding life span (Table 5c). There was a non-significant positive relationship between total offspring fledged and mean provisioning effort. Total offspring fledged did not vary between cohorts or between philopatric and immigrant birds. There was no relationship between total offspring fledged and adult tarsus length (Table 5c). The patterns for 44 males were almost identical.

Offspring local survival

For females that fledged at least one offspring, the probability that at least one offspring recruited to the breeding population in the study area was positively related to the number of offspring fledged (Table 5d),
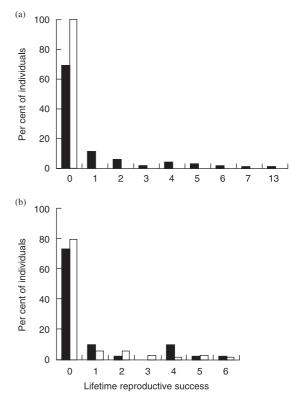

Fig. 5. Distribution of lifetime reproductive success, measured as number of recruits to the local breeding population, for (a) female and (b) male philopatric (open bars) and immigrant (filled bars) long-tailed tits that attempted to breed.
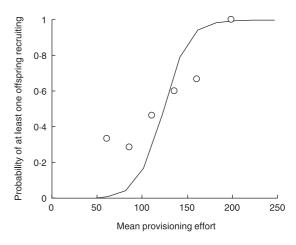

Fig. 6. The relationship between the probability of at least one fledgling recruiting in the local breeding population and the mother's feeding effort. The model was fitted to the binary data for individuals, but for clarity, mean probabilities for binned data are shown, with $N = 6, 7, 13, 10, 9, 5$ for points from left to right, respectively. The fitted line covers the full range of the data.

and varied among cohorts. The chance of at least one offspring recruiting locally was lower for philopatric than for immigrant birds. Figure 5 shows that this was because only immigrant females mothered local recruits. Females with higher mean provisioning effort had a greater chance of at least one offspring recruiting locally (Fig. 6), and there was no relationship between local recruitment and adult tarsus length (Table 5d).

Table 6. Results of GLMs of measures of fitness for females and males. LRS was modelled with Poisson errors and logarithm link. Individual fitness was square root-transformed and modelled with normal errors and identity link

Effect	LRS				Individual fitness (λ_i)			
	d.f.	N	χ^2	P	d.f.	N	χ^2	P
(a) Females								
Life span	1	30	27·28	< 0·0001	1	27	30·52	< 0·0001
Fecundity	1	30	13·19	0·0003	1	27	16·35	< 0·0001
Offspring survival	1	30	22·64	< 0·0001	1	27	26·87	< 0·0001
Cohort	5	30	0·76	0·98	5	27	19·49	0·0016
Provisioning effort	1	30	0·06	0·80	1	27	19·38	< 0·0001
Tarsus length	1	30	0·35	0·55	1	26	0·99	0·32
(b) Males								
Life span	1	25	0·01	0·93	1	38	24·28	< 0·0001
Fecundity	1	25	0·03	0·86	1	38	12·21	0·0005
Offspring survival	1	25	16·95	< 0·0001	1	38	49·36	< 0·0001
Cohort	5	25	5·55	0·48	6	38	3·13	0·79
Dispersal	1	24	0·18	0·67	1	38	0·46	0·50
Provisioning effort	1	24	1·14	0·29	1	26	0·01	0·91
Tarsus length	1	24	0·14	0·71	1	18	0·60	0·44

For males that fledged at least one offspring, the probability that at least one offspring recruited to the breeding population in the study area was positively related to the number of offspring fledged ($\chi^2_1 = 5·52$, $N = 44$, $P = 0·019$ in a GLM with binomial errors and logit link function), but did not vary among cohorts, between philopatric and immigrant birds, with mean provisioning effort, or with adult tarsus length (all $P > 0·30$).

Lifetime reproductive success

For females that had at least one offspring recruit locally, the number of offspring recruited locally (LRS) was positively related to the length of the breeding life span (L) (Table 6a), was higher for females with higher average fecundity (F) and increased as average offspring survival increased. LRS was not related to the female's mean provisioning effort or to adult tarsus and did not vary among cohorts (Table 6a). Only immigrant females gained any LRS. For males that had at least one offspring recruit locally, LRS was positively related to offspring local survival (S) (Table 6b), but was not related to any of the other explanatory variables.

Individual fitness

Non-zero measures of individual fitness (λ_i) were square root-transformed for analysis. For females λ_i was positively related to the length of the breeding life span, average fecundity and offspring local survival (Table 6a). Individual fitness was higher for females with higher mean provisioning effort (Fig. 7), and varied significantly among cohorts (Fig. 8, Table 6a).

For males with non-zero individual fitness (λ_i), fitness was positively related to the length of the breeding life span, average fecundity and offspring local survival (Table 6b). Individual fitness of males was not related to their mean provisioning effort (Fig. 7) or their adult
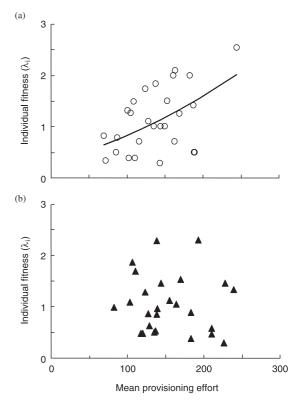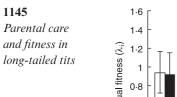

Fig. 7. The relationship between individual fitness and mean provisioning effort for female (a) and male (b) long-tailed tits. The line is the fitted estimate for females. There was no relationship for males.

tarsus length, and did not vary significantly among cohorts (Fig. 8, Table 6b).

Discussion

MEASUREMENT OF FITNESS

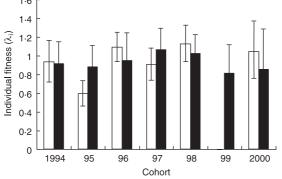As in most previous studies of bird species (Newton 1989; McGraw & Caswell 1996; Brommer, Pietiainen &

Fig. 8. Variation in mean ($\pm$ 95% CI) individual fitness among cohorts for female (open bars, N = 4, 6, 6, 5, 4, 0, 2) and male (filled bars, N = 6, 7, 4, 7, 8, 4, 2) long-tailed tits. Values are estimates from a GLM with other covariates set to their mean values. Estimates for males are from a model containing cohort as a factor, for comparison with females, although there was no significant variation between cohorts for males. No females from 1999 bred in the study area.

Kolunen 1998), lifetime reproductive success and individual fitness were strongly skewed in long-tailed tits. Most individuals that attempted to breed were unsuccessful in producing local recruits, or even fledglings, during their lifetimes. Means were similar for males and females, as expected in a short-lived monogamous animal. The variance in LRS was slightly higher for females, and there was no evidence of a difference in variance in individual fitness. This contradicts directly the hypothesis that sex ratio bias among helpers results from individuals of the sex with higher variance in success helping in order to attain inclusive fitness (Koenig *et al.* 1983), as in long-tailed tits most helpers are male (Hatchwell *et al.* 2004).

Individual fitness and LRS were highly correlated in this species, probably because the majority of birds have only a single breeding season. As a result inferences about patterns of selection on life history traits are broadly similar, irrespective of whether LRS or individual fitness are considered, although there are important exceptions to this, notably with respect to provisioning effort. This underscores the point made by McGraw & Caswell (1996) that the interpretation of analyses of selection can change when individual fitness is considered instead of LRS. The differences that McGraw & Caswell (1996) found between individual fitness and LRS were greater for both sparrowhawks (*Accipiter nisus*) and blue tits (*Parus caeruleus*) than we have found for long-tailed tits. Both those species often have several successful breeding attempts, and this makes consideration of the timing of reproduction more important.

It is not clear from our results whether either LRS or individual fitness is useful as a predictor of subsequent spread of an individual's genes through a population (Brommer *et al.* 2002). Neither accounted for very much of the variation in the number of grand-offspring produced. This may be partly a problem of using data from a finite study area to estimate fitness. The errors that inevitably occur are bound to amplify with each passing generation. Such random error could disguise any relationship between predictors of fitness and true fitness. Studies of island populations, from which there is less dispersal, may give more reliable estimates of this relationship.

About one-fifth of birds with non-zero individual fitness accrued their only fitness by helping, and the magnitude of the fitness they gained was less than a fifth of that accrued by birds which gained fitness through direct reproduction. This confirms our previous assessment that helping in this species is a best-of-a-bad-job tactic (MacColl & Hatchwell 2002; Hatchwell *et al.* 2004). The distribution of fitness in long-tailed tits may therefore resemble that in other species with 'redirected helping', in which birds become helpers after failing to breed independently (e.g. Lessells 1990; Dickinson, Koenig & Pitelka 1996; Sloane 1996). However, there are no complete descriptions of lifetime fitness in any of these species.

PARTITION OF VARIANCE IN LRS

Variation in the survival of fledglings to local recruitment is clearly the single most important source of variation in LRS for long-tailed tits. This is similar to results for other short-lived passerines [e.g. great tits *Parus major* (van Noordwijk & van Balen 1988); song sparrows *Melospiza melodia* (Smith 1988)]. For a non-migratory, insectivorous passerine the size of a long-tailed tit the many uncertainties of weather, food supply and predation make the first winter a hazardous time (McGowan *et al.* 2003), and chance must be important in determining whether individuals survive. However, we have consistently found evidence which suggests that the social circumstances of fledglings affects their probability of survival. The positive synergism between fecundity and survival in this study suggests that fledglings from larger broods survive better. Although we have not found this in previous analyses (e.g. MacColl & Hatchwell 2002), such a pattern could easily come about because of the benefits that long-tailed tits obtain from foraging and roosting together (McGowan 2002). We intend to explore this possibility in a future analysis of long-tailed tit demography and population dynamics.

The small contribution of average fecundity and breeding life span to determining LRS is unsurprising. Clutch size in long-tailed tits is comparatively invariant and nestling mortality (excluding predation) is low (Hatchwell *et al.* 2004), while the high rate of predation on long-tailed tit nests devalues the contribution of additional years of breeding. However, as in any lottery you have to buy a ticket to win, and longer-lived birds reaped the benefit by increasing their probability of having at least one year in which they fledged offspring. The negative correlation between breeding life span and fecundity suggests that individuals with lower average fecundity may have longer breeding life spans.

However, this probably arises from a sampling bias, because the analysis uses only those individuals that successfully produced at least some offspring, and thus the average fecundity of birds which produced offspring in only a single year is almost certain to be higher than that of birds which produced over more seasons, but were likely to have failed in at least one of these.

We also found evidence of negative covariance between life span and offspring local survival among long-tailed tits, and we cannot think of a sampling explanation for this. This suggests that birds that live longer have offspring that survive less well. It is consistent with the suggestion in our data that females with higher provisioning effort have shorter breeding life spans, and may throw light on the mechanism that maintains heritable variation in effort (MacColl & Hatchwell 2003a). We consider this in more detail below.

CORRELATES OF VARIATION IN COMPONENTS OF FITNESS

The large contribution of offspring local survival to LRS gives rise to the potential for anything that improves survival of fledglings to be strongly selected. This is of particular interest in a cooperatively breeding species in which the social system is based around the care of young, and it is tempting to infer that helping has arisen as an evolutionary mechanism to reduce variance in fledgling survival. Variation in offspring survival is also a major contributor to variation in LRS in some non-cooperatively breeding passerine species (e.g. great tits, van Noordwijk & van Balen 1988; and song sparrows, Smith 1988) which makes it unlikely that high variability in offspring survival is a general explanation for helping behaviour. It is still possible that behaviours that increased offspring survival in long-tailed tits have arisen as evolutionary solutions to the 'problem' of high variance in offspring survival.

We have found previously a relationship between the total care invested in a brood by parents and helpers and offspring local survival (MacColl & Hatchwell 2003a). The present analysis suggests that this effect was due mainly to the efforts of the mother, and that these efforts increase females' fitness. This makes our previous observation of heritable variation in effort all the more surprising (MacColl & Hatchwell 2003a). Such variation in effort could be maintained by trade-offs between different components of reproductive investment by females. Trade-offs among components of investment should not lead to a relationship between overall fitness and any single component such as effort across individuals, although such correlations might be apparent in a finite sample. In the present analysis there was some suggestion of a trade-off between mean provisioning effort and the length of the breeding life span for females, although this was not significant. This pattern would be most likely to result directly from the effort involved in parental care, as there does not appear to be any cost to retaining philopatric offspring

over winter (McGowan 2002; McGowan *et al.* 2003). Another possibility is that effort and fitness are associated because both are linked to condition. Unfortunately condition is hard to define or quantify, but we were unable to find any relationship between effort and simple biometric measures of the condition of males (e.g. weight/tarsus^3) in our previous analysis (MacColl & Hatchwell 2003a). We were unable to calculate even these simple measures of condition for females because they were usually weighed close to laying when weight fluctuates substantially.

Differences in fitness or quality between philopatric and dispersing individuals have been found often in studies which have looked for them. In some species philopatric individuals are of higher quality (Brown & Brown 1992; Wauters, Bijnens & Dhondt 1993; Wheelwright & Mauck 1998; Hansson *et al.* 2001), while in others they are of lower quality than immigrant or dispersing individuals (Lena *et al.* 1998; Heeb *et al.* 1999; Altwegg, Ringsby & Saether 2000), and at least one study has found an interaction between dispersal status and habitat quality (Verhulst, Perrins & Riddington 1997). This latter study is of particular interest in the present context, because in a previous analysis of a different subset of years (MacColl & Hatchwell 2002) we found that philopatric recruitment in our population was greater for heavier and earlier-fledged birds, suggesting that better-quality long-tailed tits are more likely to be philopatric. This is apparently at odds with the finding in the present study, that immigrant females have higher fitness than philopatric ones. At least three possible explanations might account for this discrepancy. (1) A habitat by dispersal interaction of the kind found by Verhulst *et al.* (1997): because our study area is relatively high-quality long-tailed tit habitat (the reason it was chosen as a study area), on the basis of the pattern observed by Verhulst *et al.* (1997) we would expect immigrants to be high-quality birds, but philopatric birds to be a mix of low and high quality, and this could contribute to a difference in fitness between the two groups. (2) An interaction between sex and quality in determining dispersal: it may be that high-quality males are philopatric while low-quality ones disperse, but that the opposite is true for females. In our previous analysis, the relationship between measures of quality and recruitment was driven mainly by males, as a higher proportion of them are philopatric (MacColl & Hatchwell 2002). (3) In our analyses survival and dispersal are partially confounded, because the probability of local recruitment that we call local survival is actually a combination of survival and philopatry. This means that quality could appear to be positively related to dispersal when in reality it is only associated with survival, or vice versa. In this respect, the measure of dispersal status used in this paper is a better estimate of true dispersal status than is our measure of local recruitment.

Variation in fitness among cohorts has also been found commonly in empirical studies (Clutton-Brock,

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Albon & Guiness 1988; Smith 1988), where it has been related to variations in food supply (van Noordwijk & van Balen 1988; Korpimaki 1992; Brommer *et al.* 1998) or density (Coltman *et al.* 1999). For long-tailed tits there was little variation among cohorts in the fledging of offspring, but significant variation among cohorts for females in the probability of offspring recruiting locally. This again reflects the relatively invariant nature of fecundity in long-tailed tits and the large variation among years in offspring survival, which is affected strongly by weather (McGowan *et al.* 2003).

Our results show that there is a large amount of variance in fitness among long-tailed tits. This is partly because many individuals do not manage to fledge young, which is mainly the result of random predation events. Variance is still large even among those tits that succeed in fledging young, and most of this variance is due to the variability in offspring local survival. Much variation in offspring local survival is undoubtedly the result of environmental conditions, in particular the weather between fledging and recruitment (McGowan 2002). However, the local survival of offspring is also related to the amount of effort invested in feeding them, at least by their mothers. This results in females which put more effort into feeding their offspring having higher fitness. The opportunity for selection that is created by large variation in offspring local survival and its effect on fitness also means that individuals which fail in independent reproduction can accrue indirect fitness by provisioning offspring in the nests of relatives.

Acknowledgements

References

Altwegg, R., Ringsby, T.H. & Saether, B.E. (2000) Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows *Passer domesticus*. *Journal of Animal Ecology*, **69**, 762–770.

Brommer, J.E., Merila, J. & Kokko, H. (2002) Reproductive timing and individual fitness. *Ecology Letters*, **5**, 802–810.

Brommer, J.E., Pietiainen, H. & Kolunen, H. (1998) The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. *Journal of Animal Ecology*, **67**, 359–369.

Brown, D. (1988) Components of lifetime reproductive success. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 439–453. University of Chicago Press, Chicago.

Brown, C.R. & Brown, M.B. (1992) Ectoparasitism as a cause of natal dispersal in cliff swallows. *Ecology*, **73**, 1718–1723.

Clutton-Brock, T.H., ed. (1988) *Reproductive Success*. University of Chicago Press, Chicago.

Clutton-Brock, T.H., Albon, S.D. & Guiness, F.E. (1988) Reproductive success in male and female red deer. *Reproductive Success* (ed. T.H. Clutton-Brock), p. 538. University of Chicago Press, Chicago.

Clutton-Brock, T.H., Brotherton, P.N.M., O'Riain, M.J., Griffin, A.S., Gaynor, D., Kansky, R., Sharpe, L. & McIlrath, G.M. (2001) Contributions to cooperative rearing in meerkats. *Animal Behaviour*, **61**, 705–710.

Coltman, D.W., Smith, J.A., Bancroft, D.R., Pilkington, J., MacColl, A.D.C., Clutton-Brock, T.H. & Pemberton, J.M. (1999) Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. *American Naturalist*, **154**, 730–746.

Creel, S. (1990) How to measure inclusive fitness. *Proceedings of the Royal Society of London Series B*, **241**, 229–231.

Der, G. & Everitt, B.S. (2002) *A Handbook of Statistical Analyses Using SAS*. Chapman & Hall, Boca Raton.

Dickinson, J.L., Koenig, W.D. & Pitelka, F.A. (1996) Fitness consequences of helping behavior in the western bluebird. *Behavioral Ecology*, **7**, 168–177.

Fausett, L. (2002) *Numerical Methods Using Mathcad*. Prentice Hall, Upper Saddle River, NJ.

Fitzpatrick, J.W. & Woolfenden, G.E. (1988) Components of lifetime reproductive success in the Florida scrub jay. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 305–320. University of Chicago Press, Chicago.

Fitzpatrick, J.W. & Woolfenden, G.E. (1989) Florida scrub jay. *Lifetime Reproduction in Birds* (ed. I. Newton), pp. 201–218. Academic Press, London.

Grafen, A. (1982) How not to measure inclusive fitness. *Nature*, **298**, 425–426.

Grafen, A. (1988) On the uses of data on lifetime reproductive success. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 454–471. University of Chicago Press, Chicago.

Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998) A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.

Hamilton, W.D. (1964) The genetical evolution of social behaviour. *Journal of Theoretical Biology*, **7**, 1–52.

Hansson, B. Bensch, S. Hasselquist, D. & Akesson, M. (2001) Microsatellite diversity predicts recruitment of sibling great reed warblers. *Proceedings of the Royal Society of London Series B*, **268**, 1287–1291.

Hatchwell, B.J., Anderson, C., Ross, D.J., Fowlie, M.K. & Blackwell, P.G. (2001) Social organisation of cooperatively breeding long-tailed tits: kinship and spatial dynamics. *Journal of Animal Ecology*, **70**, 820–830.

Hatchwell, B.J., Ross, D.J., Chaline, N., Fowlie, M.K. & Burke, T. (2002) Parentage in the cooperative breeding system of long-tailed tits *Aegithalos caudatus*. *Animal Behaviour*, **64**, 55–63.

Hatchwell, B.J., Russell, A.F., MacColl, A.D.C., Ross, D.J., Fowlie, M.K. & McGowan, A. (2004) Helpers increase long-term but not short-term productivity in cooperatively breeding long-tailed tits. *Behavioral Ecology*, **15**, 1–10.

Heeb, P., Werner, I., Mateman, A.C., Kolliker, M., Brinkhof, M.W.G., Lessells, C.M. & Richner, H. (1999) Ectoparasite infestation and sex-biased local recruitment of hosts. *Nature*, **400**, 63–65.

Koenig, W.D., Mumme, R.L. & Pitelka, F.A. (1983) Female roles in cooperative breeding acorn woodpeckers. *Social Behaviour of Female Vertebrates* (ed. S.K. Wasser), pp. 235–261. Academic Press, New York.

Korpimaki, E. (1992) Fluctuating food abundance determines the lifetime reproductive success of male Tengmalms owls. *Journal of Animal Ecology*, **61**, 103–111.

Lena, J.P., Clobert, J., de Fraipont, M., Lecomte, J. & Guyot, G. (1998) The relative influence of density and kinship on dispersal in the common lizard. *Behavioral Ecology*, **9**, 500–507.

Lessells, C.M. (1990) Helping at the nest in European bee-eaters: who helps and why? *Population Biology of Passerine Birds* (ed. J. Blondel), pp. 357–368. Springer-Verlag, Berlin.

MacColl, A.D.C. & Hatchwell, B.J. (2002) Temporal variation in fitness pay-offs promotes cooperative breeding in long-tailed tits *Aegithalos caudatus*. *American Naturalist*, **160**, 186–194.

MacColl, A.D.C. & Hatchwell, B.J. (2003a) Heritability of parental effort in a passerine bird. *Evolution*, **57**, 2191–2195.

MacColl, A.D.C. & Hatchwell, B.J. (2003b) Sharing of caring: nestling provisioning behaviour of long-tailed tit (*Aegithalos caudatus*) parents and helpers. *Animal Behaviour*, **65**, 965–964.

McGowan, A. (2002) *Fitness benefits of cooperative breeding in long-tailed tits (*Aegithalos caudatus*)*. PhD thesis, University of Sheffield.

McGowan, A., Hatchwell, B.J. & Woodburn, R.J.W. (2003) The effect of helping behaviour on the survival of juvenile and adult long-tailed tits *Aegithalos caudatus*. *Journal of Animal Ecology*, **72**, 491–499.

McGraw, J.B. & Caswell, H. (1996) Estimation of individual fitness from life-history data. *American Naturalist*, **147**, 47–64.

McGregor, P.K., Krebs, J.R. & Perrins, C.M. (1981) Song repertoires and lifetime reproductive success in the great tit (*Parus major*). *American Naturalist*, **118**, 149–159.

Newton, I., ed. (1989) *Lifetime Reproduction in Birds*. Academic Press, London.

van Noordwijk, A.J. & van Balen, J.H. (1988) The great tit, *Parus major*. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 119–135. University of Chicago Press, Chicago.

Oli, M.K. (2003) Hamilton goes empirical: estimation of inclusive fitness from life-history data. *Proceedings of the Royal Society of London Series B*, **270**, 307–311.

Queller, D.C. (1996) The measurement and meaning of inclusive fitness. *Animal Behaviour*, **51**, 229–232.

SAS Institute, Inc. (1999) *Onlinedoc*, Version 8·0. SAS Institute, Inc., Cary, NC.

Sloane, S.A. (1996) Incidence and origins of supernumeraries at bushtit (*Psaltriparus minimus*) nests. *Auk*, **113**, 757–770.

Smith, J.N.M. (1988) Determinants of lifetime reproductive success in the song sparrow. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 154–172. University of Chicago Press, Chicago.

Stacey, P.B. & Koenig, W.D., eds (1990) *Cooperative Breeding in Birds*. Cambridge University Press, Cambridge.

Verhulst, S., Perrins, C.M. & Riddington, R. (1997) Natal dispersal of great tits in a patchy environment. *Ecology*, **78**, 864–872.

Wauters, L., Bijnens, L. & Dhondt, A.A. (1993) Body mass at weaning and juvenile recruitment in the red squirrel. *Journal of Animal Ecology*, **62**, 280–286.

Wheelwright, N.T. & Mauck, R.A. (1998) Philopatry, natal dispersal, and inbreeding avoidance in an island population of savannah sparrows. *Ecology*, **79**, 755–767.