HERITABILITY OF PARENTAL EFFORT IN A PASSERINE BIRD

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Abstract.—The study of the evolution of parental care is central to our understanding of social systems, sexual selection, and interindividual conflict, yet we know virtually nothing about the genetic architecture of parental care traits in natural populations. In this paper, we use data from a long term field study of a passerine bird, the long-tailed tit (*Aegithalos caudatus*), to examine the heritability of the rate at which parents feed offspring. This measure of effort is positively related to offspring survival, is repeatable within individuals, and does not appear to be confounded by environmental effects. Using both parent-offspring regression, and an animal model approach, with a pedigree derived from ringing data, we show that our measure of effort has a significant heritable component.

Key words.—Additive genetic variance, *Aegithalos caudatus*, animal model, cooperative breeding, long-tailed tit, nestling provisioning, parental investment.

The study of the evolution of parental care is central to our understanding of social systems, sexual selection, and interindividual conflict (Trivers 1972; Mock and Parker 1997). Additive genetic variance in parental investment must exist for parental care to evolve (Parker 1985; Winkler 1987), but has seldom been looked for in natural populations (Freeman-Gallant and Rothstein 1999; Kolliker et al. 2000). Instead, empirical work on parental care has concentrated on the short-term optimization of effort in relation to social and environmental factors, for example, offspring demand (Bengtsson and Ryden 1983), brood size (Nur 1984), and extra-pair paternity (Sheldon and Ellegren 1998). However, it is well known that substantial genetic variance exists for measures of effort in domestic mammals (e.g. milk yield, Van Tassell et al. 1999), and recently the genetics of parental care has begun to receive attention from an evolutionary perspective (Agrawal et al. 2001; Hunt and Simmons 2002; Rauter and Moore 2002).

A major reason for this recent attention has been a growth of interest in the importance of maternal and other indirect genetic effects in evolution (Cheverud and Moore 1994). Parental care has traditionally been considered to form part of the environmental effects on the phenotypes of offspring in the quantitative genetic analysis of trait evolution, but if these ''environmental effects'' are under partial genetic control, they may themselves evolve, and are called indirect genetic effects (Wolf et al. 1998). In certain circumstances genetic correlations may arise between care traits and solicitation or other traits in offspring (Agrawal et al. 2001). In species with complex social systems, such as cooperative breeders, in which the quality of the offspring environment may depend largely on the care of related individuals, indirect genetic effects may be of special importance.

The provisioning of nestling birds by their parents is a favorite exemplar among theoretical and empirical examinations of parental effort (Trivers 1972; Houston and Davies 1985; Winkler 1987), and in this paper we use data on nestling feeding rate from an eight-year field study of long-tailed tits (*Aegithalos caudatus*) to quantify the parental effort of individual birds. We examine the relationship between parental effort and offspring survival, and we estimate the heritability of effort both by parent-son regression, and an animal model using a pedigree established from ringing data. We demonstrate, for the first time in a wild population, additive genetic variance in a measure of parental care that increases offspring survival.

Methods

We studied a population of 18–53 pairs of long-tailed tits between 1994 and 2001 in the Rivelin Valley, Sheffield, U.K. (53°23′N 1°34′W). All long-tailed tits initially attempt to breed in pairs, but the rate of nest failure is high. As a result, some individuals abandon independent breeding, and help a close relative in the raising of their brood. For further details of the study area, species, and social system see Hatchwell and Russell (1996) and MacColl and Hatchwell (2002). Adults were color-ringed and weighed before breeding started, or in some cases, during the nestling period. Helpers from outside the study area were color-ringed on arrival at a nest. The disturbance caused by ringing did not affect their rate of food delivery when compared to helpers that had been ringed before they began helping ($F_{1,46} = 0.11$, NS). 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. In this way, date of first egg was recorded, and clutch size recorded after the onset of incubation. Chicks were counted (brood size), weighed (fledging weight), and ringed when 11 days old. If a pair failed in a breeding attempt, we located any subsequent nest by extensive searching of the study area. The occurrence of helping behavior in this species means that up to six adults (parents + helpers) may invest care in a single brood in our study population (Hatchwell et al. 2003). Any adult seen feeding at a nest is referred to as a ''carer'', but only the parents are referred to as ''parents''. We include only measures of effort by parents

in our analysis of heritability. Extra-pair paternity and intraspecific brood parasitism are rare in long-tailed tits ($< 5\%$ of offspring, Hatchwell et al. 2002) and unlikely to substantially bias estimates of heritability.

Nests containing nestlings were watched every other day from hatching (day 0) to fledging (day 16 or 17), usually for a period of one hour (mean total observation time per nest $\pm$ SE $= 523 \pm 30$ min). In this way we recorded the rates at which individual carers brought food to nestlings. For each individual parent we then fitted a simple linear regression line to the relationship between hourly feeding rate and age of nestlings, and individual effort was estimated as the area under the regression line between 0 and 16 days. In total, we measured the effort of 172 parents at 91 nests. Ten parents were missing because three were unringed, and seven died or disappeared late in the nestling period. The total effort invested in a brood was estimated in a similar way by calculating the area under the regression of total provisioning rate (by all carers) against nestling age over the whole nestling period. We have used ''feed units'' as the unit of effort and this is directly proportional to the total number of feeds made by an individual (or by all carers) during the nestling period. Under the assumption of constant feeding rates during daylight hours, the constant of proportionality is equal to the number of daylight hours, which is about 16 hours in the middle of the breeding season.

We calculated the repeatability of individual effort across breeding seasons for a sample of parents for which we had data from more than one season. Although long-tailed tits are not territorial, and often use widely spaced nest sites in successive years, we also examined the repeatability of individual effort attributable to location for a sample of unrelated individuals which used nest sites in the same location in different years. We used data from small blocks (< 1 ha) of homogeneous habitat for which we had at least two measures of individual effort from different nests in different years.

We used morphometric data from fathers caught during the same breeding season as their effort was measured to test for correlations between the condition of fathers and their effort. Condition of males was calculated as both weight/(tarsus)^3 and residuals from the regression of weight on tarsus. We did not estimate the condition of females in this way because they were often caught close to the egg-laying period, when their weight undergoes rapid change due to egg formation.

Interbreeding season survival of chicks that fledged successfully, and adults that survived the breeding season was assessed from resighting during intensive fieldwork at the beginning of each breeding season. Previous analyses have shown that the resighting probability of survivors is close to one (McGowan et al. 2003). We analyzed the relationships between interbreeding season survival and individual effort using generalized linear mixed models (GLMM), with a binomial error structure (SAS Institute 1999). Nest was included in these analyses as a random factor to control for nonindependence of adults and fledglings from the same nest. To estimate the heritability of our measure of individual effort, we first calculated parent-offspring regressions (Lynch and Walsh 1998) using data from mothers, fathers, and sons.

We were unable to do this for daughters because the natal dispersal of females resulted in an insufficient sample size.

The simple parent-offspring regressions take no account of fixed effects, such as brood size, which make a substantial contribution to variation in feeding rates, and nor do they make use of information from other levels of familial relationship within the pedigree. We therefore recalculated heritability using an animal model (Lynch and Walsh 1998) such that the phenotype of an individual is modeled as the sum of its additive genetic value, and other fixed and random effects. The animal model does not involve many of the restrictive assumptions about the form and structure of data required by traditional regression techniques (Lynch and Walsh 1998). It is also able to use data from all kinds of genetic relationships from across natural pedigrees. This makes more efficient use of information, and should reduce upward bias on estimates of heritability due to maternal effects. We used an animal model of the form:

$$y = Xb + Z_1a + Z_2n + e \qquad (1)$$

in which y was a vector of phenotypic values, b was a vector of fixed effects, a was a vector of the additive genetic component, n was a vector of the random effect due to the nest at which the individual worked, e was a vector of residual values and X, Z_1 and Z_2 were corresponding design matrices. The best fitting fixed effects model from a set of covariates known to affect hourly feeding rate was determined using restricted maximum likelihood (REML) in SAS (SAS Institute 1999). Year was the year of study (1994–2001). Sex was the sex of the parent. Helped was a factor taking a value of 0 or 1 depending on whether adult carers other than the parents provisioned nestlings. We used Helped rather than number of helpers, because the latter may vary during the nestling period, and previous analyses have shown that parents only make significant reductions in provisioning rates in response to the arrival of the first helper (Hatchwell 1999; MacColl and Hatchwell 2003). Hatch date was the date of hatching of the clutch as number of days after 31 March in each year. Area was a factor which coded for blocks of similar habitat (< 2.5 ha) within the study area in which a nest was situated. Attempt was the number of times that the mother of a brood had built a nest in that season.

Estimates of best linear unbiased predictors of breeding values were obtained using the software package PEST (Groeneveld and Kovac 1990; Groeneveld et al. 1992), incorporating the best fitting fixed effects model estimated in SAS. Components of variance were estimated using REML VCE (ver. 4.2; Groeneveld 1995). The additive genetic relationship matrix was created from a file of the pedigree relationships of the whole population, established from ringing of nestlings a few days before fledging. The pedigree contained 951 animals of which 122 were base animals of unknown parentage.

Total phenotypic variance (V_P) in effort was partitioned into additive genetic variance (V_A), nest variance (V_N) and the residual variance (V_R) which includes measurement error and nonadditive genetic effects: $V_P = V_A + V_N + V_R$. Narrow sense heritability (h^2) was calculated as the ratio of additive genetic to total phenotypic variance: $h^2 = V_A/V_P$. We also calculated coefficients of additive genetic variation $CV_A =$

TABLE 1. A generalized linear mixed model of fledgling survival with binomial error structure, logit link function, and nest of investment as a random effect. The analysis included data on 652 chicks from 84 nests. The variance ($\pm$ SE) due to nest = 1.42 $\pm$ 0.46, residual variance = 0.72 $\pm$ 0.04.

Effect	df	F	P
Effort	1, 74	4.48	0.034
Sex	1, 74	21.67	<0.0001
Year	7, 74	4.90	<0.0001
Nestling weight	1, 73	3.74	0.053
Helped	1, 73	3.55	0.059
Brood size	1, 73	0.04	0.84
Fledging date	1, 73	1.20	0.27

TABLE 2. Fixed effects model (REML) of effort by parents. The model had a normal error structure, identity link function, and nest of investment as a random effect. The analysis used data from 91 nests. The variance ($\pm$ SE) due to nest = 116.8 $\pm$ 113.2, residual variance = 1290 $\pm$ 170.

Effect	df	F	P
Year	7, 78	2.62	0.019
Sex	1, 78	48.2	<0.0001
Brood size	1, 78	18.4	<0.0001
Helped	1, 78	2.20	0.14
Hatch date	1, 78	5.92	0.018
Brood size $\times$ helped	1, 78	6.63	0.012
Area	28, 39	1.61	>0.08
Attempt	2, 76	0.33	0.72

$100\sqrt{V_A}/\bar{X}$ and residual variation $CV_R = 100\sqrt{V_P - V_A}/\bar{X}$ (in which $\bar{X}$ is the trait mean; Houle 1992).

RESULTS

The mean value of individual effort ($\pm$ SD) was 136.9 ($\pm$ 49.0) feed units (see Methods). For 16 fathers for which individual effort was measured in at least two years (12 of the males bred with different females), the repeatability of effort was 0.70. For 10 mothers, the repeatability of effort was 0.37 (Lessells and Boag 1987). For 56 males from 17 locations, the repeatability of individual effort attributable to location was 0.03. There was also no evidence that habitat affected effort in a model of the fixed effects affecting effort for all measured individuals (see below).

For a sample of 34 males caught in the same season as their individual effort was measured, there was no relationship between effort and condition when measured either as weight/tarsus[3] (r = 0.18, 32 df, NS) or residuals from the relationship between weight and tarsus (r = 0.005, 32 df, NS).

The survival of offspring to the following spring was positively related to the total effort invested in the brood by all individual carers, in a model which also controled for year effects (Table 1, Fig. 1). The apparent survival of male fledglings was higher than that of females for a given level of effort. This result is simply a consequence of male philopatry in this species. We could find no evidence that the individual effort of parents affected their own survival over the following winter (in a generalized linear mixed model of adult survival with binomial error structure, logit link function, and nest of investment as a random effect: sex $F_{1,82}$ = 2.17, NS; year $F_{7,76}$ = 1.7, NS; helped? $F_{1,82}$ = 0.02, NS; effort $F_{1,153}$ = 1.00, NS).

Individual effort varied between years, was higher for males than females, and was greater for larger broods (Table 2). Individual effort was also lower at nests at which helpers were present, and declined as the season progressed.

The effort of sons when they fed their own brood was significantly related to the effort of both their mothers and their fathers (for 30 sons of 19 mothers: mid-son effort = 0.34 $\times$ mother's effort + 99; $F_{1,17}$ = 7.09, P < 0.025; 95% confidence intervals for slope = 0.07, 0.60. For 33 sons of 21 fathers: mid-son effort = 0.37 $\times$ father's effort + 86; $F_{1,19}$ = 5.81, P < 0.05; 95% CI for slope = 0.05, 0.69). As there was no evidence for difference in slopes of the son-mother and son-father regressions, we calculated an overall heritability of effort from the mid-son–mid-parent regression, h^2 = 0.59 (Fig. 2, for 31 sons from 20 pairs: $F_{1,18}$ = 12.52, P < 0.005; 95% CI for slope = 0.24, 0.94). The simple relationships between sons and parents does not take account of variability in effort due to fixed effects, nor does it use the depth of information available from across the pedigree.
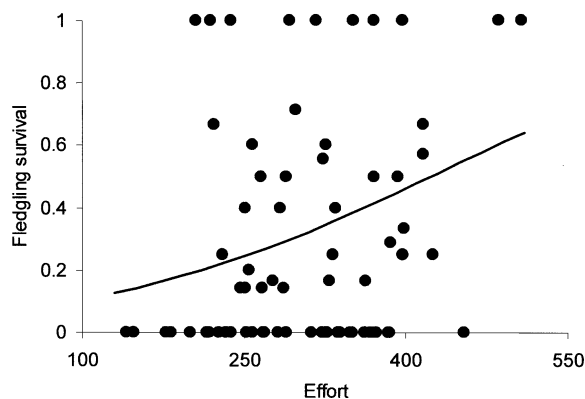

FIG. 1. The relationship between interbreeding season survival of male fledglings and the total invested in them by adult carers. Data points are within brood average survival. The fitted line is from a generalized linear mixed model of fledgling survival.
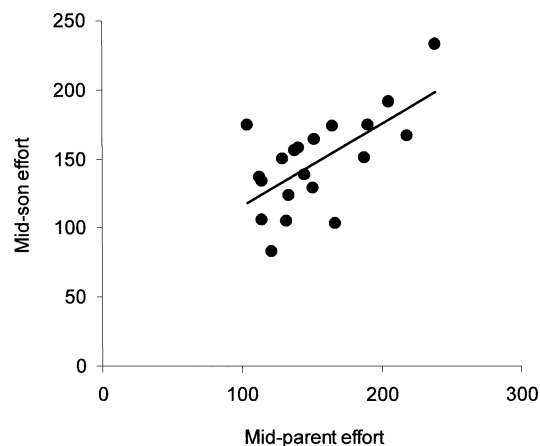

FIG. 2. Regression of mid-son on mid-parent for feeding effort in long-tailed tits. Data are for 31 sons from 20 broods. The equation of the line is $y = 0.59x + 56.7$.

When this information was used in an animal model that incorporated the fixed effects, and included birds of both sexes working as parents, estimates of the variance components were: $V_A = 697.9$, $V_N = 707.2$, and $V_R = 228.6$. This allowed us to estimate the heritability of effort $h^2 = 0.43$ ($\pm$ 0.07 SE) which is significantly different from zero ($z = 6.14$, $P < 0.001$). The coefficients of variation were $CV_A = 19.3$, and $CV_R = 22.3$.

DISCUSSION

Our results are the first to demonstrate, in a natural population, heritability of parental effort which is related to offspring survival, and which is not simply a consequence of environmental effects. Our estimate of h^2 is in the middle of the upper half of the range reported in a recent review of behavioral traits, whereas the value of CV_A for effort is close to the mean for foraging related traits, and the value for CV_R is low (Stirling et al. 2002). It is apparent from these estimates that effort should be quite free to respond to the selection that it appears to be under. It is therefore difficult to explain why substantial variation in effort should remain, especially because effort was not related to the most obvious indices of condition. This is an issue that has been much discussed (Houle 1992), and there are numerous possibilities (Kruuk et al. 2001) which include undetected costs and trade-offs among fitness components. At present we are unable to assess the applicability of these explanations to the maintenance of variation in effort in long-tailed tits.

It is possible that our estimate of heritability may be partly accounted for by nongenetic modes of inheritance. The most obvious of these is social learning, but other neurobiological mechanisms are possible, and these have been shown to be important in mammals (Fleming et al. 2002). In birds, maternal hormones in eggs are already known to exert strong effects on the development of chicks (Schwabl 1996), and it is possible that these continue into adulthood and affect parental care patterns. As the animal model uses information from across the pedigree, the magnitude of any nongenetic effects should be reduced compared with traditional regression methods for estimating heritability, but they cannot be completely eliminated without experimentation.

In any case, it is clear from our analysis that effort is partially controlled by trans-generational effects, and is not completely free to vary in response to environmental and social conditions as has often been implicitly assumed (Nur 1984). In this respect, our results are consistent with those on the repeatability and heritability of parental effort beginning to emerge from other studies of passerines (Freeman-Gallant and Rothstein 1999; Potti et al. 1999; Kolliker et al. 2000). In these studies, there were differences between the sexes in the heritability or repeatability of effort, or in the response to begging. In our study, the repeatability of effort was lower for females, similar to savannah sparrows (*Passerculus sandwichensis*) (Freeman-Gallant and Rothstein 1999), but in contrast to pied flycatchers (*Ficedula hypoleuca*) (Potti et al. 1999). Unlike Freeman-Gallant and Rothstein (1999), we found no evidence that the son-parent regression depended on the sex of the parent, but because we have few

data for daughters, we are unable to be certain that the heritability of effort does not differ between the sexes.

In quantitative genetic analyses, maternal effects in the broad sense (Cheverud and Moore 1994; Wolf et al. 1998), such as our measure of parental effort, have traditionally been considered to form part of the environmental variation in offspring traits. Where there is genetic variation in maternal effects, they are termed indirect genetic effects and may themselves evolve under selection (Cheverud and Moore 1994). The presence of indirect genetic influences on a trait can substantially alter the response of that trait to selection. For example, if parental effort increases body size, and independently has an effect on survival of offspring, then there may be evolution of larger body size, even in the absence of additive genetic variation for body size. In future analyses we intend to explore the covariance between parental effort and fledgling size in long-tailed tits. In some circumstances an indirect genetic effect may become correlated with a direct genetic effect on a parental performance trait. For example, offspring that receive good care may not only tend to be in better condition, and so give good care, but will also receive genes for giving good care. In such circumstances the evolution of a social (parental performance) trait may become very rapid (Wolf et al. 1998).

Genetic variation in measures of parental quality has consequences for our understanding of sexual selection. Certain models of mate choice have assumed that variation in parental quality is not heritable (Hoelzer 1989; Price et al. 1993). The result of this and other studies do not support this assumption, but suggest that models incorporating heritable variation in quality may be more appropriate (Iwasa and Pomiankowski 1999). In such circumstances the outcome may still depend critically on assumptions about the magnitude and direction of genetic correlations between traits (Cheverud and Moore 1994). The genetic architecture of parental effort is likely to be complex, in part because of the potential for indirect genetic effects (Wolf et al. 1998), but knowledge of it will be essential for a complete understanding of one of the most important life-history traits.

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