Heritability of Nestling Growth in Cross-Fostered European Starlings *Sturnus vulgaris*

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ABSTRACT

In altricial birds, growth rates and nestling morphology vary between broods. For natural selection to produce evolutionary change in these variables, there must exist heritable variation. Since nestling traits are not any longer present in parents, traditional offspring-parent regressions cannot estimate heritabilities of these. In this study, a partial cross-fostering experiment was performed, where nestlings of the European Starling (*Sturnus vulgaris*) were reciprocally exchanged between nests. The experiment demonstrated a significant heritability of nestling tarsus length and body mass, but not of the growth trajectories followed by individual nestlings. The heritability estimate for tarsus length obtained in the cross-fostering experiment using full-sib analysis was lower than those obtained by offspring-parent regressions. This is likely due to a genotype-by-environment effect on tarsus length, with nestlings destined to become large but in poor condition having a low probability of appearing as parents. The main reason for the low heritability of growth was probably the large within-brood variation in growth pattern due to the initial size hierarchy of nestlings. Nestlings demonstrated targeted growth, where small-sized nestlings that initially grew slower than their siblings, managed to catch up.

I N altricial birds, there is often a considerable variation in nestling growth rates among broods (RICKLEFS 1984). Large differences in growth rates have been found within the same habitat (*e.g.*, ALATALO and LUNDBERG 1986), between different habitats (*e.g.*, QUINNEY *et al.* 1986), between geographical regions (*e.g.*, RHYMER 1992) and between years (*e.g.*, PRICE 1985). This variation can be of both genetic and environmental origin. For example, the fact that growth rate is heritable has been used to select for fast-growing poultry (KINNEY 1969) while supplemental feeding experiments have shown growth to be susceptible to prevailing food conditions (*e.g.*, CROSSNER 1977).

To estimate the degree of genotypic and environmental contribution to variation in growth is important for several reasons. First, if there exists additive genetic variation, selection may shape optimal growth rates that differ between populations (JAMES 1983). Hence, observed differences in growth rates between populations may not only be a proximate consequence of varying food supplies, but may actually be selected strategies. Growth rates may be adaptive compromises between selection for rapid growth conflicting with food availability (LACK 1968) or maturation and function (RICKLEFS 1979). Since adult morphology largely is determined during early ontogenetic processes, growth rates may also be correlated responses to selection on adult morphology (PRICE and GRANT 1985). Second, if

growth rates are variable and mainly determined by environmental factors, this might be because selection has favored reaction norms allowing nestlings to be raised in a variety of environments (*e.g.*, VAN NOORDWIJK 1989), or a nonadaptive response to varying conditions (PRICE 1985). Third, whether growth rate is mainly genotypically or environmentally determined, its variation may be a reason for female mate choice. For example, if there exist a genetically transmitted resistance to disease or ectoparasites, it may pay females to choose resistant males (HAMILTON and ZUK 1982; MØLLER 1990) and if there exists predictable differences in the quality of paternal care affecting growth rate, it may pay females to choose good parents (HOELZER 1989).

In poultry, several growth and morphological characters have proved to be highly heritable (KINNEY 1969). However, the degree of heritability will be affected by the extent of environmental variation (FALCONER 1981), which was clearly reduced in these studies. It is therefore essential to study heritability of growth and morphological characters in the wild. Since heritabilities are estimated by comparing relatives, a main problem in field studies is that similarities between relatives might arise rather because they share a common environment than because of genetic resemblance. For example, parents with long tarsi might be able to occupy better territories and therefore grow larger young. The problem is even more accentuated when studying traits like growth parameters and nestling masses that occur only in offspring, since siblings clearly share a common environment. A way to circumvent this is to cross-foster nestlings. By such studies the environmental covariation between

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parents and offspring can be broken. Such studies have demonstrated heritable variation in morphological characters for a number of birds species (BOAG and VAN NOORDWIJK 1987). To estimate heritability of offspring traits, a design where only parts of broods are reciprocally exchanged between nests may be used (RUTLEDGE *et al.* 1972). With this design, traits can be compared between siblings in different nests and nonsiblings in the same nest. In this way environmental and genotypic influences on traits can be distinguished (RUTLEDGE *et al.* 1972; ATCHLEY and RUTLEDGE 1980). This design has been successfully applied to mice in the laboratory (RUTLEDGE *et al.* 1972; ATCHLEY and RUTLEDGE 1980; RISKA *et al.* 1984) and in a few studies on wild-living birds (MØLLER 1990; GEBHARDT-HENRICH and VAN NOORDWIJK 1991; PRICE 1991; see also RICKLEFS and PETERS 1981 and RICKLEFS 1984 for a related design).

The relative contribution of genotypic and environmental factors to nestling size might change during the ontogeny of the birds (ATCHLEY 1984). When nestlings hatch, there often exists a difference in hatching time that gives rise to an initial size hierarchy. If growth is not targeted (*sensu* TANNER 1963), this initial growth hierarchy will remain or be multiplied (RISKA *et al.* 1984). However, if growth is targeted, because of canalized growth or because of selective feeding behavior of parents, chicks with an initial size disadvantage may grow to the same size as its siblings. Because of processes like targeted growth, the heritability of a trait may change during ontogeny (ATCHLEY 1984; RISKA *et al.* 1984).

In this study we investigate the heritability of growth, nestling mass and tarsus length in the European Starling (*Sturnus vulgaris*) by means of a partial cross-fostering experiment.

MATERIALS AND METHODS

Study population: The study was performed in 1993 in the Revinge area 20 km east of Lund in southern Sweden. The area is dominated by permanent pastures grazed by cattle. Starlings bred in colonies of 15–30 equally sized nestboxes. The European Starling is a facultatively polygynous, nonterritorial species (PINXTEN and EENS 1990; SMITH *et al.* 1994). In southern Sweden it is migratory. Starlings arrive at the breeding colonies in early spring (mid-March), but do not lay their eggs until late April or early May. Breeding is highly synchronous, with most females laying within a week of each other (KARLSSON 1983). Males occupy one to several nestboxes, and attract one to three females (SMITH *et al.* 1994). Monogamous males assist their females with incubation and nestling feeding and polygynous males regularly assist their primary female (MERKEL 1980; PINXTEN *et al.* 1993a; PINXTEN and EENS 1994; SMITH *et al.* 1995b).

Field methods: Adult Starlings were captured both before breeding and during the incubation and nestling feeding periods. Each bird captured was sexed (SVENSSON 1984) and its tarsus length (method of ALATALO and LUNDBERG 1986) was determined to the nearest 0.05 mm using Vernier calipers. Each bird was equipped with an aluminum ring and a unique combination of three color rings. Repeatability for tarsus length has earlier been estimated to be 0.82 (SMITH 1993).

To reduce between-observer differences in measurements of tarsus length, all measurements were scaled to the measure obtained by the senior author using linear regressions. These analyses were based on at least 12 birds measured by both the senior author and the other observer, and correlations ranged from 0.92 to 0.99.

During the egg-laying period, nestboxes were visited daily to determine laying dates and clutch sizes. Each egg was marked on the day of laying. In this population ~1.5% of nestlings originate from dumped eggs (SMITH *et al.* 1994) and two dyads (see below) were excluded from all genetical analyses since it could not be determined which nestling originated from a parasite egg. Hatching date was determined by daily nest checks around hatching. Nestlings were counted and weighed on an A&D EK120A portable electronic balance with an accuracy of 0.01 g 1, 4, 7 and 14 days after hatching of the first egg in the clutch. On the last occasion their tarsus lengths were also measured, at which time the tarsus length had reached 99.9% of adult size (SMITH 1993).

For 1- and 4-day-old nestlings, there existed a relationship between mass and time of day that they were weighed (linear regression, $\alpha = 6.55$, $\beta = 0.25$, $t = 2.71$, $n = 46$, $P = 0.010$ and $\alpha = 23.93$, $\beta = 0.40$, $t = 3.14$, $n = 46$, $P = 0.003$, respectively), but not for 7- and 14-day-old nestlings ($P > 0.15$ in both cases). For 1- and 4-day-old nestlings, mass was adjusted to noon mass using the linear regression equations.

Parents were assigned to nests by observing them incubating or feeding nestlings. Male Starlings attract 1–3 females (SMITH *et al.* 1994). For colonies in which most breeding males were known, we assigned a mating status to females. This was done by assuming that laying date reflects mating date, which seems to be true for this population (SMITH *et al.* 1994). Females were classified as monogamous, primary, secondary or tertiary. Only monogamous and primary nests were included in this study, since polygynous males allocate nearly all of their feeding effort to the primary female's brood (SMITH *et al.* 1994). One replicate (see below), where the same male fathered both broods, was excluded from all analyses.

Experimental design: We performed a partial cross-fostering experiment. Broods hatched on the same day and having the same size were matched and constituted a dyad. When perfect matching was not possible, we allowed for a brood size difference of one (nine cases) or two (two cases) nestlings. Half (or if the number of nestlings was odd, one less than half) of the nestlings of the smaller brood were randomly chosen and reciprocally exchanged between the nests. Nestlings were exchanged in the afternoon the day after hatching of the first egg in the clutch. At the same time all nestlings were individually marked with a piece of drinking straw around the tarsus (HARPER and NEILL 1990) and weighed. The piece of drinking straw was replaced by a numbered aluminum ring 7 days after hatching. In the afternoon nestlings were moved, only one nest had a single egg that had not hatched. It was left in the original nest, but the resulting nestling died soon after hatching.

Every other dyad was treated against ectoparasites by replacing the nest material and cleaning the nestbox when nestlings were swapped and all other dyads were sham-manipulated. Since this experiment had no effect on nestling growth or morphology (K.-J. WETTERMARK and H. G. SMITH, unpublished results), it is not further considered here.

Statistical methods: Variance in nestling characters among and within nonexperimental broods in 1991–1993 was estimated using the SAS VARCOMP procedure with the MIVQUE0 method (SAS INSTITUTE INC. 1988).

Growth was estimated in two ways. First, during days 1 to 7 the growth of nestlings is approximately linear (SMITH *et al.* 1995a). We therefore calculated a linear growth coefficient

for each nestling during this period using linear regression. Second, we fitted a logistic growth curve (RICKLEFS 1967) to data for each nestling using a least-squares nonlinear estimation method with the Marquardt algorithm (SAS NLIN procedure, SAS INSTITUTE INC. 1988) and obtained a growth constant (K, day^{-1}), inflection-point (I, days) and asymptotic mass (A, g). The linear growth constant and the constant obtained by assuming logistic growth were clearly related $(r = 0.63, n = 226, P < 0.001)$. The growth parameters obtained by the logistic growth curve were not independent since the growth constant was negatively related to the inflection-point $(r = -0.54, P < 0.001)$ and the asymptotic mass $(r = -0.22, P = 0.001)$ whereas the inflection point was unrelated to the asymptote $(r = 0.10, P = 0.14)$.

Two different methods were used to estimate heritabilities: offspring-parent regressions and full-sib analyses.

Offspring-parent regressions: For tarsus-length, a trait present in both parent and offspring, regression of offspring on the average value of parents was used to estimate heritability (FALCONER 1981). In the absence of assortative mating, the slope of this regression estimates heritability (FALCONER 1981; BECKER 1984). We also estimated heritability from regressions of offspring on single-parents as twice the regression coefficient.

Full-sib analyses: Sib resemblance was analyzed by means of a two-way nested analysis of variance (ANOVA) with the factors original nest, foster nest and the interaction between original and foster-nest nested within dyads (RUTLEDGE et al. 1972; ATCHLEY and RUTLEDGE 1980; RISKA et al. 1984). Following RUTLEDGE et al. (1972), resulting variance components were equated with genetic expectations. Variance components were estimated using the maximum-likelihood method of the SAS VARCOMP procedure and their significance by performing a random-factor nested ANOVA using SAS GLM (SAS INSTITUTE INC. 1988). Heritability was estimated as twice the variance component due to biological parents divided by the sum of the variance due to biological parents, guardians, the interaction between guardians and biological parents and the residual error. Since variance among dyads incorporates both environmental and genotypic differences and since the additive genetic variance was measured within dyads, variance among dyads was not included in the phenotypic variance (RUTLEDGE et al. 1972; ATCHLEY and RUTLEDGE 1980). This variance component was, however, consistently low (0–3.5%) for all morphological measurements, but somewhat higher for measurements of growth rate (10–14%). It should also be noted that estimates of additive genetic and residual environmental variance each will include half of any dominance variance and that prenatal maternal effects will be confounded with the additive genetic variance (FALCONER 1981; RISKA et al. 1984). Standard errors of the heritability estimates were calculated from the variances and covariances obtained

TABLE 1

Percent among-brood variance in tarsus length and mass for 13–15-day-old Starling nestlings in monogamous and primary nonexperimental nests in 1991–1993

Year	Tarsus length	Mass	Clutches/nestlings
1991	30.1	32.7	53/248
1992	33.4	40.0	58/281
1993	37.4	53.5	55/238

by the maximum-likelihood method (BECKER 1984). It should, however, be noted that the distribution of variance components is not normal and that standard errors therefore only give a rough description of the precision of the estimate of heritability (WRICKE and WEBER 1986). Two dyads were excluded from analyses since, due to nestling mortality, the 2×2 factorial had missing values for some cells. To keep sample sizes constant across nestling ages, only nestlings that survived until the final measurements (day 14) were included in the analyses.

Except where otherwise noted, statistical analyses were performed using SYSTAT (WILKINSON 1990).

RESULTS

Variance in natural broods: The proportion of variance in tarsus length among nests for 13–15-day-old nestlings in monogamous and primary broods was on average 33.6% (Table 1). The proportion of variance in mass among nests was somewhat higher (42.1%) and more variable between years (Table 1).

Effects of cross-fostering: Cross-fostering had no traceable effect on nestling morphology. Cross-fostered and remaining nestlings had the same mass day 1 (using mean values for cross-fostered and remaining young in each nest, paired-$t = 0.54$, $n = 46$, $P = 0.60$), day 4 ($t = 0.96$, $n = 45$, $P = 0.34$), day 7 ($t = 0.99$, $n = 45$, $P = 0.33$) and day 14 ($t = 0.86$, $n = 44$, $P = 0.40$). In addition both groups had the similar tarsus length ($t = 0.98$, $n = 44$, $P = 0.33$) and wing length ($t = 1.39$, $n = 44$, $P = 0.17$).

Heritability of tarsus length: The estimates of heritability for a given trait might be affected if variance in that trait differs between the sexes and if parents mate

TABLE 2

Estimates of heritability of tarsus-length in cross-fostered broods of Starlings

	Reared home				Cross-fostered			
	h2	r	n	P	h2	r	n	P
Midparent	0.49 ± 0.12	0.55	40	0.001	0.43 ± 0.17	0.40	39	0.01
Father	0.64 ± 0.17	0.52	41	0.001	0.40 ± 0.22	0.28	40	0.08
Mother	0.33 ± 0.20	0.26	40	0.11	0.43 ± 0.25	0.27	39	0.09
Mid-fosterparent					0.14 ± 0.18	0.13	39	0.42
Foster-father					0.23 ± 0.24	0.16	40	0.34
Foster-mother					0.02 ± 0.25	0.01	39	0.95

Values are means ± SE, estimated from mid-offspring regressed on mid-parent, father and mother, respectively.
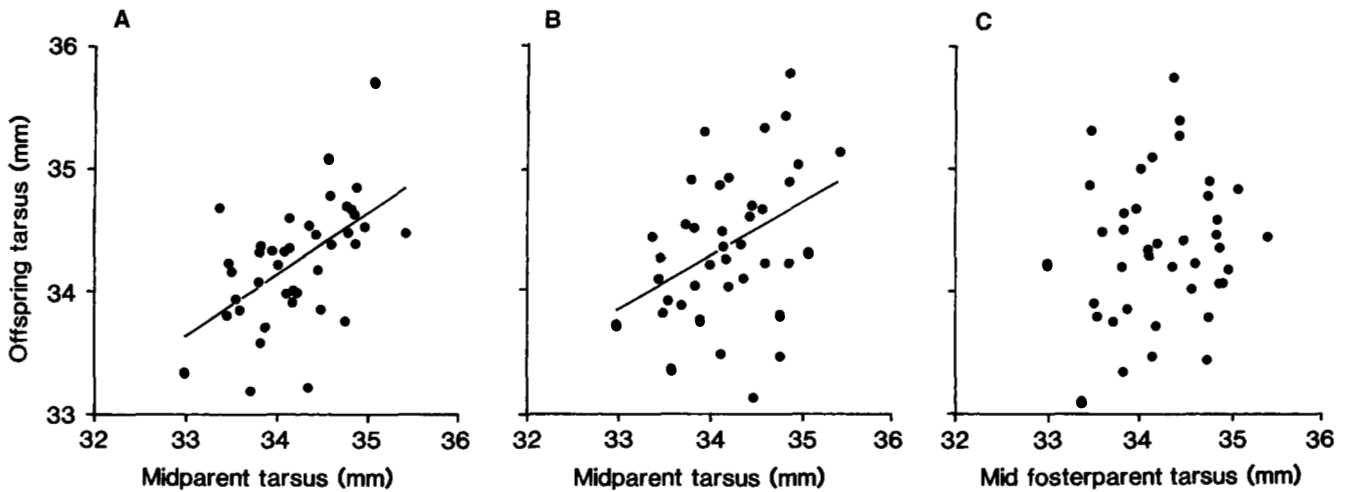
FIGURE 1.—Regression of mid-offspring tarsus on the mid-parent tarsus for nestlings reared home (A), in a foster-nest (B) and of mid-offspring on mid-foster-parent tarsus length (C).

assortatively (FALCONER 1981). Although tarsus length in the starling is sexually dimorphic, the variance is the same for both males and females (SMITH 1993). Assortative mating did not affect the cross-fostering experiment ($r = 0.06$, $n = 41$, $P = 0.70$).

In natural broods of monogamous and primary females of the starling, offspring resemble their parents (SMITH 1993). This cross-fostering experiment could be used to evaluate the degree to which this depend on genetic effects. Offspring resembled their parents both when in the same nest and when grown up in another nest but cross-fostered nestlings did not resemble their foster-parents (Table 2, Figure 1). The estimate of heritability obtained from the partial cross-fostering experiment (0.43) is similar to one previously obtained in a full cross-fostering experiment (0.49; SMITH 1993).

Heritability estimates were somewhat higher when estimated from the resemblance between offspring and father than between offspring and mother (Table 2), but none of these differences was significant ($P > 0.1$). For cross-fostered nestlings, there was no similarity between offspring and any of their foster-parents (Table 2).

A full-sib resemblance analysis demonstrated a significant effect of original nest on tarsus length (Table 3). None of the other effects were significant. Using the maximum-likelihood method, neither nest of rearing nor the interaction contributed anything to the variance in tarsus length. Heritability, as estimated by the maximum-likelihood method was 0.30 ± 0.22 (SE).

Heritability of growth: We found no additive genetic variance for linear growth or for the growth constant and inflection point obtained from the logistic growth curve (Table 4). However, asymptotic mass was affected both by the nest of origin and the nest of rearing, suggesting a heritability of 0.25 ± 0.21 (SE). For mass, there was a significant effect of nest of origin on the day nestlings were moved (Table 5). This effect then disappeared during days 4 and 7, but an effect of nest

of origin was again apparent 14 days after hatching (Table 5). This produced a pattern of apparent heritability that was highest at the beginning and end of the nestling period (Figure 2).

Targeted growth: The phenotypic variance increased from day 1 to day 7, but then decreased (Figure 3). Hence, phenotypic variance reached its maximum around the inflection point. A reduction of phenotypic variance can be explained by targeted growth (TANNER 1963; MONTEIRO and FALCONER 1966). However, changes in variance components across nestling ages could be due to scale effects (ATCHLEY 1984). Since growth is a multiplicative process, log-transforming data has been suggested to be appropriate (RISKA et al. 1984). Therefore, to investigate whether the observed

TABLE 3

Analysis of variance of tarsus length in cross-fostered starling broods

	MS	F	d.f.	P
Among dyads of nests	1.130	1.32	18	0.30
Among nest mates from different families	0.829	2.20	19	0.047
Among siblings in different nests	0.408	1.08	19	0.43
Foster × parent interaction	0.377	0.91	19	0.57
Error	0.414		114	

The analysis is based on 19 experimental dyads where at least one offspring from each treatment (nest of origin × nest of rearing) survived until the day tarsus length was measured. Data are analysed as a two-way nested ANOVA with nest of origin, nest of rearing and the interaction all nested within dyads using type III sums-of-squares. Since it is a random-factor model, the effect of nest of origin and rearing is tested against the interaction and the interaction against the error. The effect of dyad is tested against a complex error term involving the effect of nest of origin, rearing, the interaction and the error term (SAS INSTITUTE INC. 1988). $n = 190$ nestlings.

TABLE 4

Analysis of variance of growth in cross-fostered Starling broods

	d.f.	Linear growth			K			I			A		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
Among dyads of nests	18	1.68	3.04	0.15	0.0064	2.10	0.07	0.78	1.70	0.42	25.43	0.42	0.97
Among nest mates from different families	19	0.77	1.10	0.49	0.0022	1.81	0.10	0.95	1.07	0.44	41.12	2.83	0.01
Among siblings in different nests	19	0.55	0.71	0.77	0.0021	1.72	0.12	0.40	0.45	0.95	34.31	2.36	0.03
Foster × parent interaction	19	0.77	1.02	0.44	0.0012	0.75	0.76	0.89	0.97	0.51	14.53	0.78	0.72
Error	114	0.75			0.0016			0.92			18.60		

Linear growth is the mass increase per day during the linear phase of growth (days 1–7), K, I and A are the growth coefficient, inflection-point and asymptotic mass of the logistic growth curve fitted for each nestling, respectively. For computational details see Table 3. $n = 19$ dyads with 190 nestlings.

pattern was due to the particular data transformation used (none), we investigated the relationship between means and variances of mass. However, examining their correlation across ages can confound the investigation of changes in variance during growth with scale effects (RISKA et al. 1984). We therefore looked for correlations between means and variances of broods within age groups. For untransformed variables, no such correlations existed ($P > 0.15$ in all cases), whereas for logarithmically transformed data most correlations were significantly or nearly significantly negative. Furthermore, an analysis of logarithmically transformed data demonstrated a strictly decreasing phenotypic variance component with age of nestlings (data not shown).

The targeted growth was to a large extent due to small nestlings growing to similar size as other nestlings. Since nestlings were transferred between nests, we did not use hatching order to distinguish junior chicks, but instead analyzed separately the growth of the smallest nestling in each cross-fostered nest at the day of transfer, after manipulation. The smallest nestling had a lower growth rate during the first week (pairwise comparison between smallest nestling and the mean of its siblings: $d = -1.21$, $t = 6.12$, $n = 37$, $P < 0.001$; Figure 4) and a later inflection point ($d = 1.53$, $t = 6.96$, $P < 0.001$) whereas the logistic growth constant did not dif-

fer ($t = 1.32$, $P = 0.20$). The mass of the smallest nestling was 59% of the mean for its sibs during day 1, increasing to 66% on day 4 ($t = 12.10$, $P < 0.001$), 79% day 7 ($t = 9.05$, $P < 0.001$) and 95% day 14 ($t = 3.98$, $P < 0.001$; Figure 4). Its tarsus length on day 14 was 99% of that of its siblings ($t = 3.66$, $P = 0.001$) but asymptotic mass did not differ (99% of that of its siblings, $t = 0.81$, $P = 0.42$). The length of the wing, which is still growing rapidly at 14 days of age (FEARE 1984), of the initially smallest chick was 90.4% of the mean for its siblings ($t = 5.26$, $P < 0.001$).

The variance in mass due to a common nest environment was low and only at 14 days of age was a tendency, albeit not significant, for similarity between nestmates due to the common nest environment apparent (Table 5). However, by random chance, the cross-fostering experiment introduced a negative relationship between the mass of original and cross-fostered chicks within nests ($r = -0.51$, $n = 38$, $P = 0.001$) that remained until day 4 ($r = -0.38$, $P = 0.02$), but then disappeared ($r = -0.07$, $P = 0.68$ and $r = -0.06$, $P = 0.71$ 7 and 14 days after hatching, respectively). Hence, this effect may have masked effects due to common nest environment.

DISCUSSION

Heritability of tarsus length: In this study we demonstrate a heritable variation in tarsus length both by

TABLE 5

Analysis of variance of mass in cross-fostered Starling broods of different ages

|	d.f.	Day 1			Day 4			Day 7			Day 14		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
Among dyads of nests	18	6.63	0.51	0.90	35.52	0.83	0.65	74.74	2.22	0.25	30.33	0.47	0.95
Among nest mates from different families	19	16.05	4.06	0.002	58.10	1.70	0.13	58.01	1.24	0.32	49.07	2.52	0.02
Among siblings in different nests	19	0.89	0.23	0.99	15.02	0.44	0.96	22.34	0.48	0.94	35.73	1.84	0.10
Foster × parent interaction	19	3.69	0.81	0.69	34.11	1.08	0.38	46.73	1.03	0.43	19.45	1.10	0.36
Error	114	4.88			31.65			45.32			17.67		

For computational details see Table 3. $n = 19$ dyads with 190 nestlings.
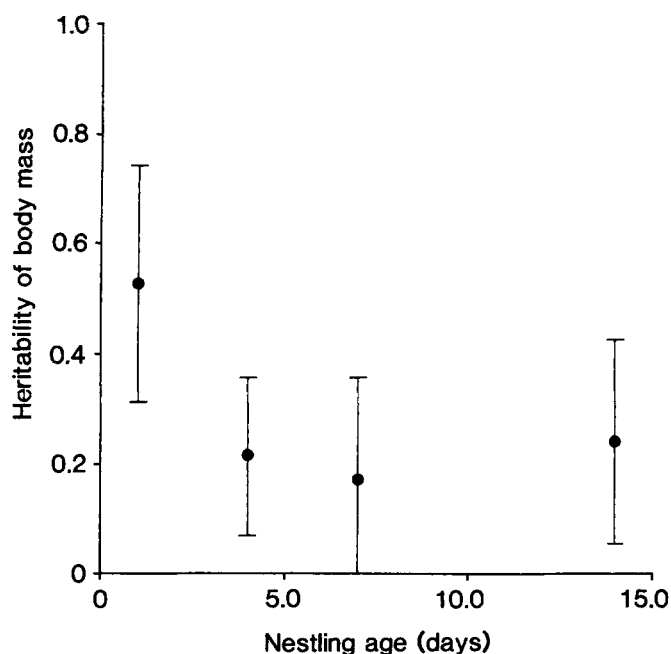
FIGURE 2.—Heritability of nestling body-mass calculated from full-sib analyses in relation to nestling age.

FIGURE 3.—Phenotypic variance (V_p; $\bigcirc$) and additive genetic variance (V_a; $\bullet$) in nestling mass in relation to nestling age.

means of offspring-parent regressions and a full-sib analysis. Several other cross-fostering experiments have demonstrated heritable variation in tarsus length in altricial birds in the wild (e.g., SMITH and DHONDT 1980; DHONDT 1982; ALATALO and GUSTAFSSON 1988; WIGGINS 1989), including the Starling (SMITH 1993).

Interestingly, the estimate obtained by the full-sib analysis tended to be lower than the one obtained by offspring-midparent regression. Furthermore, RICKLEFS (1984), using a related design, failed to show a heritable variation in tarsus length. This is unexpected since in full-sib analyses the estimate of additive genetic variance and the residual environmental variance each will include half of any dominance variance. There might be several explanations for the lower estimates obtained by the full-sib analyses. First, tarsus length is sexually dimorphic in the Starling, with the difference between the sexes being approximately equal to the variance within sexes (SMITH 1993). The offspring-midparent regression compensates for this variation by using the average of the two parents. Secondly, heritability might be higher after selection than before (VAN NOORDWIJK 1988; VAN NOORDWIJK et al. 1988). This could be the case if some chicks are more susceptible to environmental deterioration than others and those chicks that are more susceptible are the ones that would be large under good conditions (PRICE 1991). Also in agreement with this is the fact that heritability of tarsus length in the Starling estimated with offspring-parent regression is lower when conditions for nestlings are poor (SMITH 1993). If growth conditions vary mainly within nests, this genotype-by-environment interaction will not show up as a parental vs. foster-nest interaction. Also using
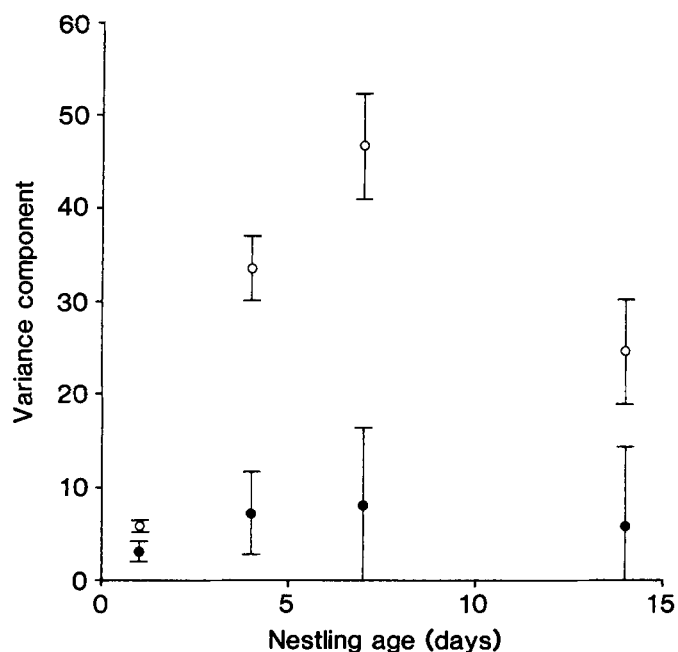
a partial cross-fostering design, PRICE (1991) found no heritability for tarsus length in the Yellow-browed Leaf Warbler (Phylloscopus inornatus), but a significant genotype-by-environment interaction that he attributed to varying growth conditions among nests. In a partial cross-fostering experiment using Great Tits (Parus major), however, GEBHARDT-HENRICH and VAN NOORDWIJK (1991), found higher heritability estimates for tarsus length during bad conditions.

It has been argued that extra-pair copulations might deflate heritability estimates obtained in the wild (ALATALO et al. 1984, 1989). However, in this study heritability estimates from offspring-father regressions were not lower than those obtained by offspring-mother regressions and the same was true for an earlier cross-fostering experiment (SMITH 1993). This is most likely due to the rather low degree of extra-pair paternity among monogamous and primary females' broods in the Starling (PINXTEN et al. 1993b; SMITH and VON SCHANTZ 1993).

Heritability of growth: The experimental design of the partial cross-fostering experiment allowed us to compare siblings in the same and different nests and thereby estimate the additive genetic variance in mass and growth (RUTLEDGE et al. 1972). However, there are several problems with the interpretation of the heritability of growth. First, by exchanging nestlings between broods, we might affect the variation in size and therefore the competitive relationships between the nestmates (SCHIFFERLI 1973; O'CONNOR 1975). Since in practice it is only possible to match broods so that they hatch on the same day, we will likely increase the environmental variance within nests. Second, the design
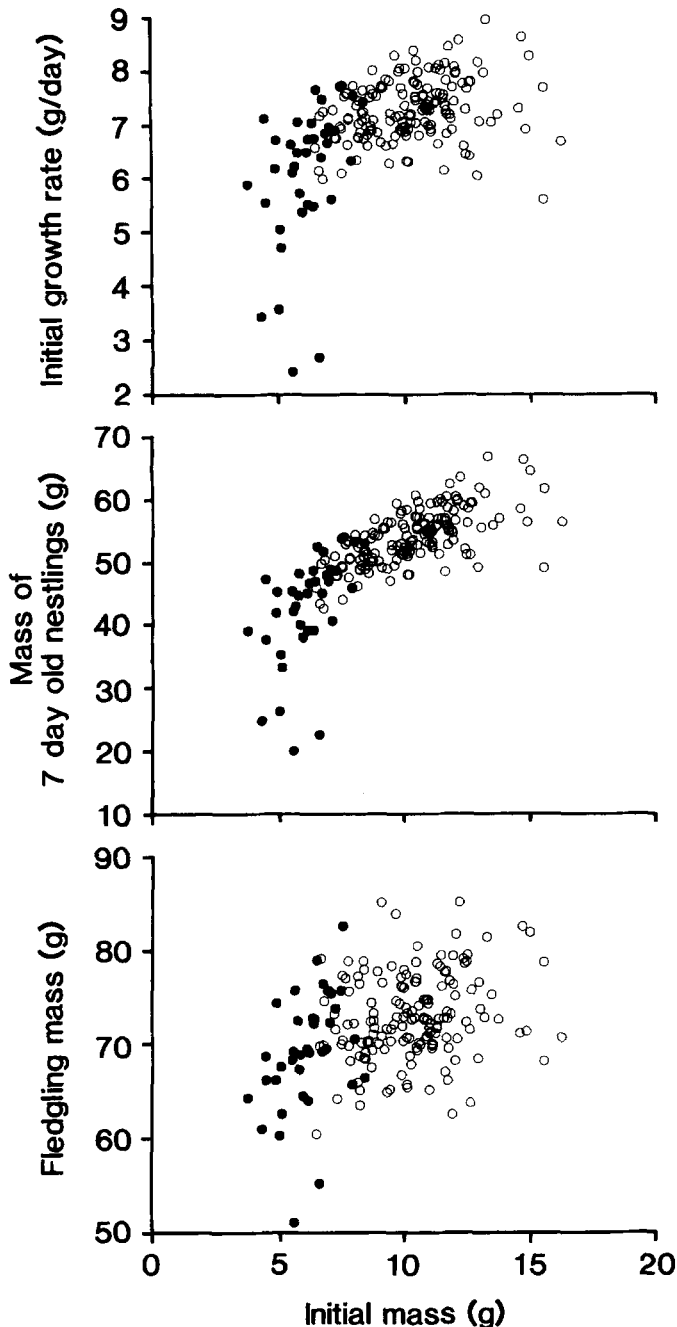
FIGURE 4.—Initial growth rate (during the first week), mass of 7-day-old nestlings and mass of 14-day-old nestlings in relation to initial mass of nestlings. The initially smallest nestling in each nest designated by a filled symbol.

confounds prenatal maternal effects, such as effects of egg size on hatchling size (SMITH et al. 1993, 1995a) with additive genetic variance. The effect of egg-size may explain the high apparent heritability on the day of experimentation, but the effect of egg-size is not traceable beyond 4 days of age and thus, cannot explain apparent heritability at the end of the nestling period (SMITH et al. 1993, 1995a; see also PRICE and GRANT 1985). Third, given the low number of times nestlings were weighed, it is only possible to fit data to a simple

growth equation even if a more complex function, like Richards' growth equation (RICHARDS 1959; BRISBIN et al. 1986) would have been preferable.

None of the growth parameters estimated, except the asymptotic mass, could be demonstrated to have any heritable component. Similarly RICKLEFS and PETERS (1981) and RICKLEFS (1984) found no heritability for growth in the starling. The heritability of asymptotic mass was corroborated by the heritable mass 14 days after hatching. Using full-sib analyses on Great Tits, GEBHARDT-HENRICH and VAN NOORDWIJK (1991) also demonstrated heritability for nestling mass, but estimates were lower than those obtained by offspring-parent regressions whereas PRICE (1991) failed to demonstrate heritability for nestling mass in the Yellow-browed Leaf Warbler. The fact that growth parameters showed no heritability, despite the large heritable variation found in domestic fowl, is probably due to the large variance within broods. This variance was partly due to the deviant growth pattern exhibited by junior chicks, which initially grew at a lower rate than siblings. Similar effects of initial size have also been demonstrated for other altricial birds (SHIFFERLI 1973; O'CONNOR 1975).

The change of the size of variance components with the age of nestlings demonstrated a targeted growth pattern for mass (ATCHLEY 1984; RISKA et al. 1984). This was largely due to the initially smallest chicks catching up with the others. The simplest explanation for this is that the increase of the tarsus and mass of siblings had reached a plateau by 14 days of age, allowing the smallest chick to catch up. Interestingly, although the wing length of 14-day-old starlings is only 62% of that of adults, the junior siblings at 14 days of age had reached a wing length that was 90% of that of its siblings. This suggests that slowly growing chicks give a priority to the growth of the wing, presumably to allow nest-leaving simultaneously with the siblings (NILSSON 1990).

The effects on growth and mass of a common nest environment were small. However, since the among-brood variance in mass theoretically measure half of the additive genetic variance, the high estimates of among-brood variance in nestling mass indicate the existence of an effect of a common nest environment. In this study, the effect of a common nest environment may partly have been masked by the negative correlation between the masses of remaining and cross-fostered chicks in a nest. RICKLEFS and PETERS (1981) and RICKLEFS (1984) demonstrated an effect of foster-parents on the growth of nestling Starlings. In their study, the variation in the quality of caretakers may have varied more than in this study, since they did not control for the fact that some nests do not receive any male help. Another reason for the small effect of caretakers on the growth and mass is that impoverished growth conditions will not only affect the among-, but also the within-brood variation. For example, for the Great Tit, SMITH

et al. (1989) found higher variance in nestling mass within broods during poor growth conditions.

Growth and mating system: One of the aims of this study was to investigate if there were genotypic or phenotypic differences between males affecting nestling growth that might select for females to be choosy (HAMILTON and ZUK 1982; HOEZLER 1989). For example, MOLLER (1990) demonstrated that female Barn Swallows (*Hirundo rustica*) increase their fitness by choosing males with a heritable resistance against ectoparasites and HILL (1991) demonstrated that female House Finches (*Carpodacus mexicanus*) might gain by selecting males providing good parental care.

In this study we found no heritable effect on growth or nestling mass. Furthermore, ectoparasites had no traceable effect on the growth and morphology of nestlings (H. G. SMITH and K.-J. WETTERMARK, unpublished results). However, even if superior male genetic quality is not demonstrable during the nestling period, it might well affect the viability of fledged young (NORRIS 1993).

We found little effect of the common nest environment on the growth of nestlings. The Starling is a colonial bird that does not defend a territory. Hence, the most likely reasons for environmental among-brood variation in growth is variation in nest-quality and in the quality of parental care. Since birds bred in nest-boxes and only monogamous and primary broods were included in the study, both these factors were minimized. Furthermore, even if there existed a difference between parents in the quality of parental care, birds compensate for deficiencies in the care given by mates (WRIGHT and CUTHILL 1989). Hence, even if males do differ in the quality of parental care they provide, this should be hard to demonstrate without actually measuring the contribution by both sexes to parental care.

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