HERITABILITY OF NESTLING BEGGING INTENSITY IN THE HOUSE SPARROW (*PASSER DOMESTICUS*)

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Evolutionary theory of parent–offspring conflict assumes that offspring food solicitation behavior, known as begging, and parental response to begging are subjected to selection and coevolution. This assumption implies that begging intensity should be heritable, at least to some degree. Although some studies have suggested that begging is heritable, the evidence for this is rare and mostly indirect. To assess the heritability of begging we used artificial selection, sibling analysis, and the monitoring of begging intensity in four generations of cross-fostered captive house sparrow nestlings. We also contrasted the heritability of begging with that of morphological traits, known to be heritable in this species. Our results show that adult wing length and body mass were heritable as expected. The heritability estimates of the visual and vocal components of nestling begging (standardized for food deprivation and body mass) were low to moderate, as expected for behavioral traits in general, and lower than previously reported for passerine birds. Our sibling analysis shows that common environment had much greater effect on begging than genetic origin, suggesting that begging evolution may be strongly influenced by gene–environment interaction, probably through the mechanisms that adjust begging response to environmental and social conditions.

KEY WORDS: Parent–offspring communication, parent–offspring conflict, signaling evolution.

In sexually reproducing organisms, genetic differences between parents and offspring result in a conflict over parental investment (Trivers 1974). Evolutionary theory of this parent–offspring conflict suggests that offspring are selected to demand more resources than the parents are selected to provide (Trivers 1974; Parker and Macnair 1979; Mock and Parker 1997). Accordingly, offspring food solicitation behavior, known as begging, may evolve to become conspicuous signals of food demand, whereas parental behavior may evolve either to respond to these signals or to ignore them (Kilner and Johnstone 1997; Godfray and Johnstone 2000). Several attempts to find a theoretical resolution for such a parent–offspring conflict predicted

a range of possible evolutionary outcomes (Parker and Macnair 1979; Godfray 1991, 1995; Rodríguez-Gironés et al. 1996; Mock and Parker 1997; Godfray and Johnstone 2000). Regardless of the exact nature of each resolution, these models are based on the assumption that begging behavior and parental response to begging are genetically variable and therefore have the ability to coevolve. Against this background, it is perhaps surprising to see that only a few attempts have been made to investigate the genetic basis of offspring begging and parental response to begging, or to measure their degree of heritability.

Three cross-fostering studies that investigated the genetic basis for parent–offspring communication identified a genetic covariance between parental behavior and offspring levels of solicitation (Kölliker et al. 2000; Agrawal et al. 2001; Lock et al. 2004). This covariance was expressed by a negative correlation

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between food solicitation and parental provisioning levels in one of these studies (Agrawal et al. 2001 in burrower bugs *Sehirus cinctus*), and by a positive correlation between the two in the other two studies (Kölliker et al. 2000 in great tits *Parus major*, and Lock et al. 2004 in burying beetles *Nicrophorus vespilloides*). The existence of such correlations is consistent with an arms-race coevolutionary scenario of parent–offspring communication (Dawkins and Krebs 1979; Parker and Macnair 1979; Kölliker and Richner 2001), with coadaptation theory (Wolf and Brodie 1998; Kölliker et al. 2005), and also suggests that these traits must be heritable to some degree, as otherwise it is difficult to explain the emergence of such correlations in a cross-fostering experiment. One of these studies provided a more direct assessment of the heritability of begging by analyzing data of cross-fostered siblings of great tits (Kölliker et al. 2000). That study is particularly interesting because begging of passerine nestlings has been the main focus of studies on parent–offspring communication in the past two decades (reviewed by Kilner and Johnstone 1997, and by Wright and Leonard 2002). Kölliker and his colleagues found that a significant part of the variation in begging call intensity among nestlings can be explained by genetic origin, and estimated the heritability of begging at the range of 40–52% (Kölliker et al. 2000; Kölliker and Richner 2001).

Although only one such study on the genetic basis of nestling begging has been carried out so far, the phenotypic flexibility of nestling begging has been studied extensively. Phenotypic variation in begging behavior has been attributed to many factors, such as short-term need or "hunger" (Redondo and Castro 1992; Price and Ydenberg 1995; Leonard and Horn 1996; Kilner and Johnstone 1997; Kilner et al. 1999; Clark 2002), long-term need (Price et al. 1996), relative rank in the brood (Lotem 1998; Cotton et al. 1999), nestling's sex (Hauber and Ramsey 2003), parasite load (Christe et al. 1996), immunocompetence (Saino and Møller 2002), nest predation (Briskie et al. 1999), sibling relatedness (Briskie et al. 1994), sibling competition (Smith and Montgomerie 1991; Kacelnik et al. 1995), and past experience (Kedar et al. 2000; Rodriguez-Girones et al. 2002; Grodzinski et al. 2008). In addition to all these nongenetic factors that may contribute to the observed variation in begging intensity, it is still possible that more than 40% of this variation may be genetic. It should be noted, however, that Kölliker and his colleagues acknowledged that maternal effects could possibly have inflated their heritability estimate, and emphasized the need for further research (Kölliker et al. 2000; Kölliker and Richner 2001). Furthermore, because heritability estimates of quantitative traits may vary across species and populations (Pomiankowski and Møller 1995; Hoffmann and Merilä 1999; Merilä and Sheldon 2001; Christians 2002), more than one study is necessary to provide a reliable estimate of the heritability of nestling begging.

In this study, we attempted to measure the heritability of nestling begging in a captive population of house sparrows (*Passer domesticus*). To that aim we used a combination of artificial selection, sibling analysis, and monitoring of begging intensity in four generations of cross-fostered nestlings. We also compared the heritability of begging with that of adult wing length and body mass, which are known to be heritable in this species. We predicted that if begging is strongly heritable we should be able to generate differences between selection groups, and find positive correlations in begging intensity between parent and offspring and between siblings raised by different fostered parents. On the other hand, small differences or weak correlations in respect to begging, along with significant results with respect to the heritability of morphological traits, would suggest that the heritability of begging is relatively low.

Materials and Methods
THE HOUSE SPARROW COLONY

The study was conducted in a large captive colony of house sparrows in the I. Meier Segals Garden for Zoological Research at Tel Aviv University. This colony was initially established in 1996 from hand-raised sparrow nestlings and wild-caught individuals, all from the Tel-Aviv area. In previous years, the captive population had been rejuvenated every winter by releasing 40–60% of the birds, and introducing new wild-caught sparrows. The study reported here was conducted from 2003 to 2007, on a population of about 50 breeding pairs that were hosted in five adjacent aviaries (8–12 pairs in each aviary of 4 × 4 × 3 m, width, length and height, respectively). The sparrows nested in wooden boxes with one compartment for the nest and another, separated by a glass plate, fitted for an infrared video camera. The sparrows were fed with a combination of commercial birds' mixture, boiled eggs, Dora seeds, and fly larvae ad lib. The breeding season lasted from March to August of each year, allowing many of the same pairs to have up to three or four successive broods (average number of broods in the colony during the 4 years of the study was 3.04 ± 1.08 SD). During the nesting period, we monitored nests in the colony twice a week for egg laying and then daily from 2 days before the expected day of hatching (day 0). All nestlings were weighed at the age of 3, 6, and 9 days, and were individually marked with a metal ring at the age of 9 days (the nestlings usually fledge when they are 14–15 days old). Before each breeding season (usually during January or February) we caught all the sparrows in the colony with a mist net, weighed them (to the nearest 0.1 g using OHAUS scale), measured their wing length (to the nearest 1 mm), and took a blood sample for further analysis (not reported here). At this time, we also redistributed the individuals among the different cages as necessary: Breeders from the previous year were released (into the zoo area, where food and

shelter are abundant and formerly captive adults survived well), and yearlings were distributed according to the selection regime (see below).

CROSS-FOSTERING AND EXPERIMENTAL SETUP

All clutches in the colony were cross-fostered 2–3 days before the expected day of hatching. As a result, each brood was raised by foster parents that were assigned randomly. This cross-fostering allows controlling for parental effects (excluding those that can be passed through the eggs) and for possible dynamic interaction between offspring begging and the responsiveness to begging of their genetic parents (that may be negatively or positively correlated, see introduction, and in Kölliker et al. 2005). As a result of possible extra pair mating in house sparrows (Griffith et al. 1999; Whitekiller et al 2000; Stewart et al. 2006; Edly-Wright et al. 2007), our paternity record may include some errors that could confound our heritability measurements. As discussed below, we tested this possible error by comparing begging heritability to that of morphological traits whose heritability estimates were subject to the same error due to extra-pair paternity.

When nestlings were 3 days old, we video recorded their begging behavior in as many nests as possible (subject to time, labor, and equipment constraints). A day before the video recording, an infrared CCD camera was placed in the designated compartment in the nest box, to allow the sparrows to habituate to its presence. The camera was connected to a distant video in a surveillance room by 30-m cables. On the morning of the video recording, the 3-day-old nestlings were weighed (using OHAUS scale to the near 0.1 g), measured for wing length (with a caliper to the near 0.1 mm) and individually marked using nontoxic color paints (Tulip, Duncan Enterprises, Fresno, CA). After the nestlings' and parents' behavior appeared normal (and at least 30 min after disturbance), a continuous video recording of 2 h was taken (recording begun between 09:00 and 10:00 a.m.).

MEASURING BEGGING INTENSITY THROUGH VIDEO ANALYSIS

We analyzed the second hour of the 2 h recorded (thereby starting to measure begging only one-and-a-half hours after disturbing the nest to take measurements). We used begging posture as our primary measure of begging intensity (see also vocal measurements below). Begging posture was measured on a graphic scale from 0 (no begging) to 3 (erect position of begging) as described in detail in Kedar et al. 2000 and Grodzinski et al. 2008, and following similar methods established by others (Redondo and Castro 1992; Kilner 1995; Lotem 1998; Leonard et al. 2003; Kacelnik et al. 1995; Dor et al. 2007; Grodzinski and Lotem 2007). We scored begging posture based on a sample of one video frame per second during the first 10 sec of a parental visit (or until the first nestling was fed, whichever came first). We analyzed the 25th

frame of each second (in a PAL video system of 25 frames per second), start counting from the frame of the parental stimulus. We then calculated a mean begging posture score for a visit and an average score across all visits for each nestling ("average begging intensity"). These average begging scores were later standardized to control for variation in food deprivation and body size (see statistical methods below). To control for food intake we also scored from the video the number of feedings received by each nestling and the size of each meal (three meal sizes estimated relative to the parent's beak size, see similar method in Schwagmeyer and Mock 2008).

MEASURING THE ACOUSTIC ENERGY OF BEGGING CALLS

Previous assessment of the heritability of nestling begging was based on measuring the acoustic energy of nestling begging rather than on begging posture (Kölliker et al. 2000). To control for the possible differences between studies that are due to different methods of measuring begging, we also carried out a set of experiments in which we measured the acoustic energy of begging calls as in Kölliker et al. (2000). These experiments were carried out during the breeding seasons of 2006 and 2007, and included 82 pairs of siblings taken from the same brood. From these pairs, 36 were of siblings taken from consecutive broods of the same genetic parents (forming 18 opportunities to compare between siblings raised in different fostered nests). Some of the nestlings participating in the experiment during 2007 were offspring of individuals that had participated in the experiment in 2006, also providing a small sample for parent–offspring comparison.

Two randomly selected siblings from each brood were brought to the laboratory at the age of 3 days and were individually placed in two custom-made temperature-controlled nest boxes (Made by D.M.P. Engineering Ltd. and set to 37°C). The nestlings were kept in the box for 90 min and were stimulated to beg 30, 60, and 90 min after removal from the nest (a procedure that minimizes variation in begging due to recent satiation). We elicited begging by tapping three times on the box and closing the box's entrance hole (thereby darkening the nest). We repeated this three times, forming a begging session during which nestlings were stimulated to beg in three consecutive trials. No food was given to the nestlings during the experiment, after which they were returned to their nest. Begging calls were recorded using a condenser microphone positioned within the box above the nestlings, and connected to an analog Sony Hi-8 VCR (Sony, Tokyo, Japan). Begging calls were then digitized to a computer (16 bit and 48 kHz), calibrated (using standard sound output), and analyzed for the acoustic energy between 3 and 15 kHz during the first 3 sec of begging (using Avisoft-SASlab Pro, ver. 4.40 software, Avisoft Bioacoustics, Berlin, Germany). For each nestling, we calculated the mean acoustic energy during each begging

session and a total average of the acoustic energy across all sessions (30, 60, and 90 min away from the nest and without food). The total average acoustic energy was then standardized statistically for variation in body mass (see statistical analysis).

ARTIFICIAL SELECTION PROCEDURE

To create a bidirectional selection regime for high and low begging intensities, yearlings caught before their first breeding season (see above) were divided into two separate cages according to their standardized begging posture score (see statistical analysis section below), which had been measured while they were at the nest during the previous spring (see above). We conducted two single-generation selection experiments: before the second breeding season (the spring of 2005) we created the two selection groups by taking the upper third ("high begging") and lower third ("low begging") of the population, whereas before the third breeding season (the spring of 2006) we divided the population of young sparrows into two (upper and lower) halves (due to a lower sample size of sparrows). The selected sparrows nested during the spring, their eggs were cross-fostered, and their nestlings' begging behavior was measured at their foster parents nest, using the same procedure as in the previous year (described above). Note that because high and low beggars were in separate cages, they could only mate with their own type. Therefore, extra-pair paternity could not confound the response to selection and its resulting heritability estimates.

MEASURING THE HERITABILITY OF BEGGING

Using the research setup described above we were able to assess the heritability of nestling begging (and of some other traits) using three different methods:

(1) *Response to artificial selection*: using the formula $h^2 = R/S$ (Falconer and Mackay 1996) we estimated the heritability of begging posture as the ratio between the response to selection (the difference between the mean value of the offspring of the selected group and the mean value of the entire parents' population), and the selection differential (the differences between the mean value of the selected parents' group and the mean value of the entire parents' population).

(2) *Parent–offspring analysis*: The trait value of 1 randomly selected individual (or the mean trait value of the entire brood) was plotted against midparental value, giving the slope as the heritability estimate (Falconer and Mackay 1996). Offspring data can also be plotted separately against mother and father data, giving a slope that is equal to half of the heritability estimate (Falconer and Mackay 1996).

(3) *Sibling analysis*: The trait value of a randomly selected individual from one brood was plotted against that of a randomly selected individual from a consecutive brood of the same genetic

parents (successive broods of the same parents were always fostered by different pairs). A significant correlation would suggest a significant effect of genetic origin (although it cannot preclude a common maternal effect as an alternative explanation or as a contributing factor). This correlation between broods can then be compared with a within-brood analysis (of two randomly selected individuals from the same brood), illustrating the relative contribution of common environment. Finally, we also estimated the variance components of genetic and environmental factors in our begging data by applying a nested analysis of variance (ANOVA) model on standardized begging parameters (body posture and acoustic energy) with consecutive broods as a nested factor within parental origin. We validated the application of a nested ANOVA model by confirming that there were no significant differences in begging between first and second broods, allowing treating them as "nested" within "parental origin."

STATISTICAL ANALYSIS

Each of the three methods described above was applied to all the relevant data in our dataset that were suitable for this particular analysis. As a result, we could use part of the data for more than one analysis (e.g., begging data of a brood participating in the selection experiment could also be used in the parent–offspring and the sibling analysis). This implies that our three analyses are not statistically independent. We simply used three different methods to estimate the heritability of begging in the same population. Normally, this would require a correction for multiple testing, but given our negative results (see below) the use of such a correction was not necessary.

Begging intensity is known to be influenced by nestling size and the duration of food deprivation (see introduction). To control for these effects we used standardized begging values taken as the residuals from a multiple regression model carried out on the data of each year (using Statistica 7.0, Statsoft, Inc., Tulsa, OK). We used the first breeding season data to select the appropriate model through a process of backward elimination (we already required standardized begging measurements after the first year to obtain a selection criterion). The dependent variable was the average begging posture of a nestling in all nest visits during the 1-h video recording (see above), and the predictors included in the model were mass ($P < 0.01$), average meal size ($P < 0.01$), and total food received ($P < 0.01$). Relative ranks within the nest ($P > 0.05$) and clutch size ($P > 0.05$) were removed from the model. For consistency, in all subsequent years we used the same set of predictors on the relevant year's data. We applied a similar procedure to standardize the acoustic energy of begging for variation in nestling mass (time of food deprivation was standardized through the experimental procedure, see above). Finally, to double check, we also carried out all the analyses with nonstandardized begging measurements and the results were not

qualitatively different to those presented in the article. Standardized begging could not be used to calculate heritability from response to selection, and in this case the average begging posture during the 1-h video was taken as a typical representation of begging intensity.

We used parametric statistics after checking for normality and homogeneity of variances (or used nonparametric tests if necessary). Data are presented as mean ± SE unless otherwise specified. Statistical analyses were performed using Statistica for Windows; version 7.0, Statsoft, Inc.

Results

BREEDING BIOLOGY AND HERITABILITY OF MORPHOLOGICAL TRAITS

Growth and development of nestlings in the breeding colony were similar to those of free-living house sparrows studied in Israel (Singer 1984; Kedar 2003). Although the sparrows in the aviaries received ad lib food supply, a process of brood reduction, similar to that observed in natural nests, was clearly indicated: a clear size hierarchy was maintained during the nestling stage (Fig. 1A) and the probability of surviving to day 9 was directly related to this rank (determined by mass at day 3, Fig. 1B). Overall, only 66.5% of the nestlings in our study survived from day 3 to day 9 (465/699), which is similar to average fledging success of sparrows from North America and Europe (66.1–67.5%, Anderson 2006) and close to fledging success found in free-living population in Israel (74.6%, Singer and Yom-Tov 1988). These results show that ad lib food supply to the parents did not diminish sibling competition for food.

Adult body mass and wing length are known to be heritable in wild populations of house sparrows with known genetic pedigrees (Jensen et al. 2003: heritability estimates of 0.175 and 0.406, respectively). Our results confirm that this is also the case in our captive sparrow population: Body mass and wing length (at 8–10 months of age) of two randomly selected siblings from subsequent broods of the same genetic parents were significantly correlated (Fig. 2, body mass: $n = 49$, $r = 0.474$, $P < 0.001$; wing length: $n = 50$, $r = 0.349$, $P = 0.013$). These results suggest that possible paternity errors due to extra-pair mating did not greatly confound our heritability estimates. Additional analysis based on parent–offspring data pairs failed to show significant correlation in body mass ($n = 41$, $P = 0.622$, $r = 0.079$, $h^2 = 0.09$), but showed a significant correlation in wing length ($n = 41$, $P = 0.042$, $r = 0.319$, $h^2 = 0.49$). Jensen et al. (2003) also found that the heritability of wing length was higher than that of body mass (0.406 vs. 0.175). It is possible that in our sibling analysis the correlation in body size was somewhat inflated by common environmental conditions at the time of capturing the birds (siblings were captured and measured on the same
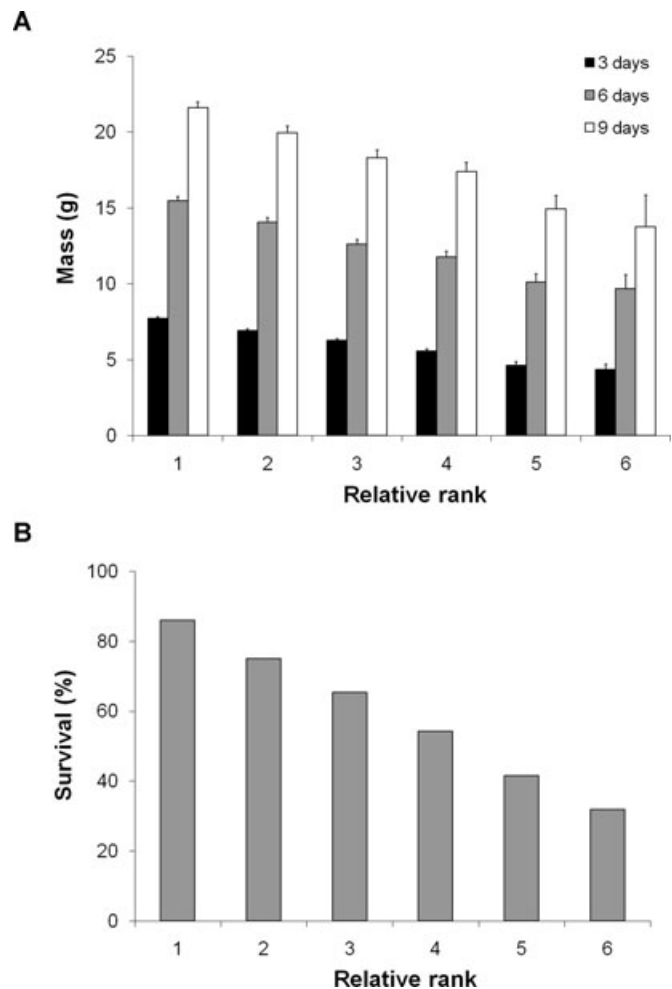
Figure 1. Nestling hierarchy (relative rank was determined by mass at day 3) and differential survival in the sparrow colony as indicated by (A) nestling mass (±SE) at day 3, 6, and 9 ($N = 137$, 119, 105, 66, 29, 8, for ranks 1 to 6, respectively), and (B) nestling survival rate from day 3 to day 9 ($N = 156$, 156, 156, 116, 65, 23, for ranks 1 to 6, respectively). Data include all broods of 2004 to 2007, consisting of brood sizes of 6 ($n = 23$), 5 ($n = 42$), 4 ($n = 51$), and 3 ($n = 40$).

day whereas parents and offspring were measured in different years).

ARTIFICIAL SELECTION FOR BEGGING INTENSITY

The results of the bidirectional selection regime generated in 2005 and 2006 are summarized in Table 1. The differences between the average level of begging intensity of offspring from the "High" and "Low" groups were not statistically significant (Table 1: t-test; $t_{13} = 1.331$, $P = 0.206$, and $t_{16} = 0.117$, $P = 0.908$, for 2005 and 2006, respectively). However, they are all in the direction expected by the existence of heritable component to begging intensity. It is quite possible that our limited sample size (31 offspring broods in total) was not large enough to detect a relatively small heritable component of nestling begging. Calculating realized heritability
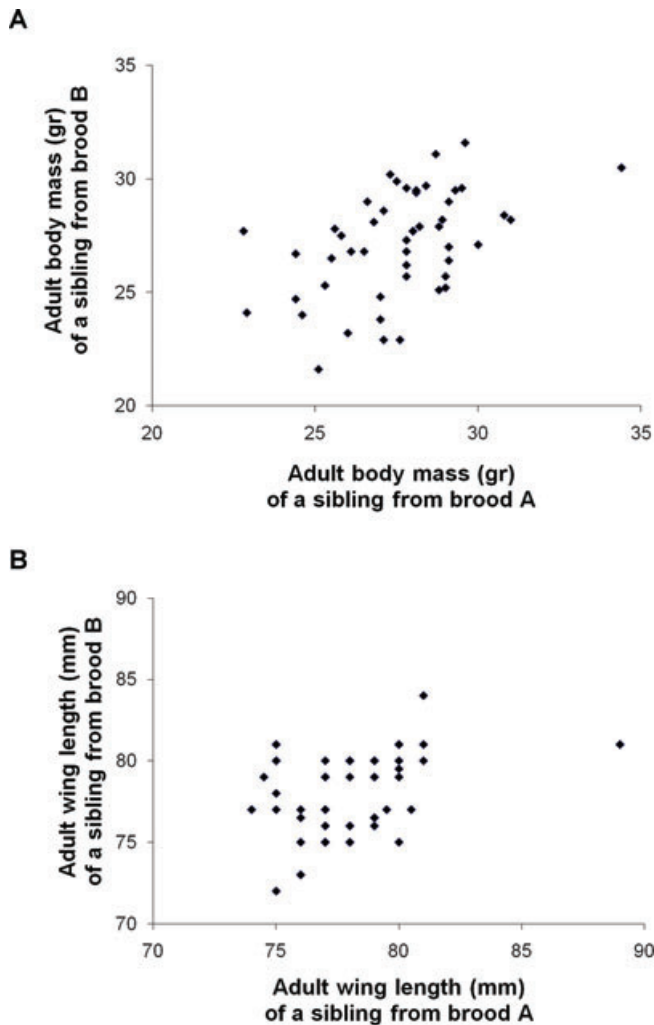
A

B

Figure 2. Measurements of (A) adult body mass and (B) adult wing length of two randomly selected siblings from consecutive broods of the same genetic parents.

based on these data (see Table 1) suggests that begging heritability may be low to moderate (around 0.3 in 2005 but below 0.1 in 2006).

PARENT–OFFSPRING ANALYSIS OF BEGGING INTENSITY

The slopes of parent–offspring regressions were all found to be positive, representing heritability estimations of 0.27 ± 0.24, 0.35 ± 0.32, and 0.17 ± 0.32 for midparent–offspring, mother–offspring, and father–offspring relations, respectively (Table 2). All these regressions were not statistically significant, but this might be expected given the effect size and sample size.

SIBLING ANALYSIS OF BEGGING INTENSITY

Standardized begging intensity between two siblings sampled at random (from consecutive broods of the same genetic parents) was not associated (Fig. 3A, $n = 44$, $r = -0.101$, $P = 0.513$), nor

was the average begging (of all nestlings) of these consecutive broods ($n = 44$, $r = -0.101$, $P = 0.863$). On the other hand, when comparing the begging of two randomly selected siblings from the same brood (within the first of the consecutive broods that took part in the above analysis) we found that their begging was significantly correlated (Fig. 3B: $n = 44$, $r = 0.514$, $P < 0.001$). Note that these nestlings were not only from the same genetic parents, but were also raised at the same nest, by the same foster parents, and their begging was measured during the same 1-h video session. Analyzing the above data using a nested ANOVA model (Table 3) showed that most of the variance in begging is explained by the common environment of the nest of rearing (51%) or by variation within the nest (49%), but not by parental origin (0%).

The lack of evidence from the sibling analysis for begging heritability (compared to that for morphology, Fig. 2), led us to analyze 20 sibling pairs for which we had data for both their begging as nestlings, and their body mass and wing length as adults. Despite the smaller sample size, the 20 pairs were still significantly correlated in wing length ($r = 0.466$, $P = 0.038$), nonsignificantly but reasonably correlated in body mass ($r = 0.307$, $P = 0.187$), but not correlated in standardized begging ($r = -0.086$, $P = 0.717$). Thus, this conservative analysis is consistent with the results from the larger datasets presented in Figures 2 and 3 and in Table 3.

HERITABILITY OF THE ACOUSTIC ENERGY OF BEGGING CALLS

The analyses of the acoustic energy of begging calls revealed similar results to those based on begging posture and described above. The correlation between siblings from consecutive broods of the same genetic parents was relatively weak ($n = 18$, $r = 0.117$, $P = 0.644$), but there was a strong correlation between siblings raised together at the same brood ($n = 18$, $r = 0.769$, $P < 0.001$). This was also indicated by using a nested ANOVA model (Table 4), showing that most of the variance in begging acoustic energy is explained by the common environment of the nest of rearing (57%) or by variation within the nest (39%), but not by parental origin (4%). We also had a small sample size to test parent–offspring correlations for acoustic energy of begging calls; however, all of them were weak and nonsignificant (midparent and offspring: $n = 7$, $r = 0.004$, $P = 0.994$; female and offspring: $n = 9$, $r = -0.289$, $P = 0.452$; male and offspring: $n = 11$, $r = 0.133$, $P = 0.697$).

Discussion

We used three different methods for estimating the heritability of nestling begging. Comparing these various estimates (Table 5), it can be seen that two methods, bidirectional selection and

Table 1. Realized heritability of begging intensity calculated from two cycles of bidirectional selection for "High" and "Low" begging intensities. Heritability was calculated from the equation $h^2=R/S$ (Falconer and Mackay 1996). Begging values are mean±SE of average begging during a 1-h video session. For each parent, begging was measured when it was a nestling during the previous year (see methods). Offspring begging is based on mean standardized begging of each brood (i.e., brood means are the independent data points).

Year	Begging of Parental population	Selection group	Begging of Parents	Begging of offspring	Selection differential (*S*)	Response to selection (*R*)	Realized Heritability (h^2)
2005	0.723±0.04	High	1.04±0.06	0.83±0.05	0.315	0.108	0.34
	(*n*=69)		(*n*=24)	(*n*=9)			
		Low	0.43±0.02	0.64±0.16	0.289	0.078	0.27
			(*n*=24)	(*n*=6)			
2006	0.863±0.05	High	1.09±0.06	0.88±0.07	0.230	0.015	0.07
	(*n*=61)		(*n*=29)	(*n*=11)			
		Low	0.62±0.04	0.86±0.15	0.247	0.002	0.01
			(*n*=27)	(*n*=7)			

parent–offspring regressions, gave similar positive heritability estimates at the range of 0.1 to 0.3, suggesting low to moderate heritability In the selection experiment, the differences among selection groups were in the expected direction, and resulted in realized heritability estimates that vary from 0.34 to 0.01 (Table 1), and with an average value of 0.17. It is interesting to note that the response to selection was higher in 2005 when the selection differentials were slightly higher (see Table 1). This is also consistent with the existence of heritable component. A low-to-moderate degree of heritability is also suggested by our parent–offspring analyses, where all the slopes were positive (Table 2). Our sibling analysis, on the other hand, indicates lower heritability estimates, for both begging posture and acoustic energy (see Tables 3 and 4, respectively). These latter results favor a "low heritability" interpretation over a "moderate heritability" interpretation, especially when Table 3 is considered (where the variance component of parental origin was virtually zero despite reasonable sample size and highly significant common rearing effect). Overall, our results are consistent with heritability studies of other behavioral traits that typically exhibit low-to-moderate degree of heritability and require large sample sizes to yield significant effects (Mousseau and Roff 1987).

The above heritability estimates for nestling begging in the house sparrow were consistently lower than the 0.40 to 0.52 figure reported from great tits (Kölliker et al. 2000; Kölliker and Richner 2001). Such high values were unlikely to be missed by

our study because they correspond to the heritability estimations of morphological traits or to the effect of rearing environment; all of which were found to be statistically significant in our analysis.
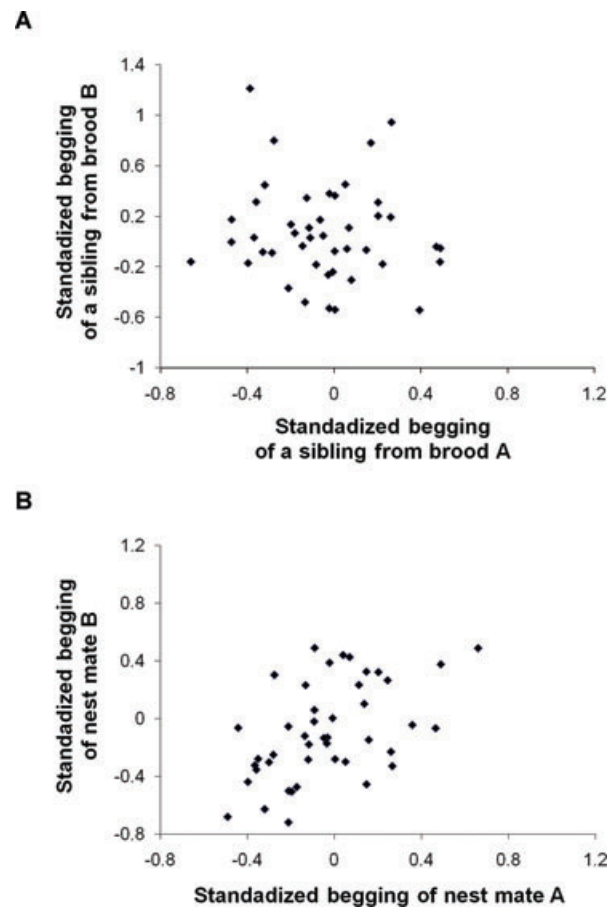
Figure 3. Standardized begging levels of (A) two randomly selected siblings from two consecutive broods of the same genetic parents, and (B) two randomly selected siblings raised together in the same brood.

Table 2. Heritability estimations for standardized begging intensity from parent–offspring regressions.

	n	*r*	h^2 (±SE)	*P* value
Midparent–offspring	27	0.219	0.27 (±0.24)	0.273
Mother–offspring	42	0.168	0.35 (±0.32)	0.288
Father–offspring	35	0.093	0.17 (±0.32)	0.595

Table 3. Estimation of the genetic component of standardized begging posture from sibling analysis by applying nested ANOVA model with consecutive broods' data nested within parental origin.[1]

Source	F value	P	Variance component (%)
Parental origin	$F_{43,44}=1.01$	0.483	0
Between broods (nested within parental origin)	$F_{44,281}=5.26$	<0.0001	51
Within broods			49

[1]Data include all nestlings from each of the two consecutive broods of the same parents ($n=44$ parent pairs).

Table 4. Estimation of the genetic component of standardized acoustic energy of nestling begging from sibling analysis by applying a nested ANOVA model with consecutive broods' data nested within parental origin[1].

Source	F value	P	Variance component (%)
Parental origin	$F_{17,18}=1.10$	0.419	4
Between broods (nested within parental origin)	$F_{18,36}=3.96$	0.0002	57
Within broods			39

[1]Data include two nestlings taken from each of the two consecutive broods of the same parents to be tested in the laboratory (see methods, $n=18$ parent pairs, 4 nestlings for each pair).

Before discussing the implications of these results, we should carefully consider possible biases related to our experimental setup:

(1) Conditions at the nest. We have no reason to suspect that begging behavior of nestlings in our captive population was abnormal or fundamentally different than that of nestlings in the wild in a way that could tamper with our heritability data. As we show at the beginning of the "Results" section, sparrow nestlings in our breeding colony experienced competitive brood reduction conditions similar to those in natural populations. Regardless of the possible causes for this interesting result (see below), the existence of sibling competition suggests that begging behavior in captivity was as meaningful as in natural populations. We also know that begging levels measured in this study were in the same range as those measured in our outdoor breeding colony (Yedvab 1999; Kedar et al. 2000, Figure 3; Kedar 2003), and that the acoustic energy of begging calls was correlated with begging posture measured at the nest (R. Dor, unpubl. data). Furthermore, additional data from our captive colony (R. Dor and A. Lotem, unpubl. ms.) show that as expected from current knowledge in the field of nestling begging (Kilner and Johnstone 1997; Budden and Wright 2001; Leonard and Horn 2001), nestlings in our colony were more likely to receive food when begging at higher levels, and introducing hungry nestlings (that beg intensely) into the nest, increases parental food delivery. Thus, begging behavior of nestlings in our captive population does not seem to be different than that of nestlings in the wild in a way that can bias our results. If anything, heritability is expected to be higher in captive populations due to lower environmental variation (Riska et al. 1989). This would make our claim for low heritability a rather conservative one. A recent review suggests, however, that heritability measurements in captivity and in the wild tend to give similar results (Weigensberg and Roff 1996).

The reasons for a typical brood reduction process in the captive colony despite ad lib food supply to the parents should be studied further. Interestingly, it suggests that parents adjust their investment in the brood using a mechanism that merely satisfies brood demand to some degree, irrespective of the ease of obtaining more food (which was always available in the dish nearby).

(2) Extra-pair paternity. Extra-pair paternity (EPP) could introduce errors into our parent–offspring and sibling analysis, causing us to underestimate the degree of heritability. Although we do not have data on extra-pair paternity in our dataset, we can

Table 5. Comparison of the heritability (h^2) estimations for begging intensity (posture and acoustic energy) using the different methods described in Tables 1–4 and in the text. Sample sizes are presented in parentheses.

Analysis method		Heritability (h^2) estimations	
		Begging posture	Acoustic energy
Bidirectional selection	First year (2005)	0.27 (6), 0.34 (9)	
	Second year (2006)	0.01 (7), 0.07 (11)	
Parent–offspring regression	Midparent–offspring	0.27 (27)	0.01 (7)
	Mother–offspring	0.35 (42)	–0.55 (9)
	Father–offspring	0.17 (35)	0.17 (11)
Sibling analysis	Full siblings (different broods)	0 (44)[1]	0.08 (18)[1]

[1]Based on the variance component of parental origin in Tables 3 and 4, multiplied by two (see Kölliker and Richner 2001).

control for this bias in two ways. First, extra-pair paternity could not bias the results of the selection experiment because mating (including extra-pair ones) could only take place within each selection group (located in separate aviaries). The finding that this analysis gave low-to-moderate heritability estimates, similar to our parent–offspring analysis, suggests that EPP did not bias our analysis in any meaningful way. Second, despite being subject to the same errors caused by EPP, the heritability of adult wing length and body mass was significant and similar to that found by Jensen et al. (2003), which controlled for EPP, giving yet another indication that the possible bias due to EPP must have been small. Moreover, a conservative analysis based on a subset of 20 sibling pairs for which we had data on both adult wing length and body mass, as well as on their begging intensity as nestlings, confirmed that the first two were heritable as expected, whereas the heritability of begging was much lower (see Results). Because in this case the effect of EPP (i.e., of including in the analysis some pairs that are not true siblings) is exactly the same for all traits, one should conclude that the heritability of begging is considerably lower than that of adult wing length and body mass.

(3) Methods of measuring begging intensity. Begging measurements that were based on body posture gave similar results to those that were based on the acoustic energy of begging calls (Tables 3 and 4). However, because in both cases heritability was low, it could be argued that, in both cases our methods were simply unreliable or too noisy to detect consistent patterns. We can refute this argument because begging levels of siblings raised together at the same nest were significantly correlated (Fig. 3B). These results could not have been achieved if our measurements of begging had been unreliable or with a low degree of repeatability (note that in the case of acoustic energy the similarity in begging levels among siblings was maintained despite being tested in isolated chambers). Finally, all our begging measurements were based on averaging many repeated begging events for each nestling, and in parent–offspring and sibling analysis we further standardized those averages by statistically controlling for variation in hunger and body mass (see Methods). Thus, these begging measurements represented a nestling's typical begging intensity after removing much of the temporal variation caused by hunger, size, or age.

The main implication of our results is that nestlings begging may be heritable to some degree, but probably to a lower degree than the current estimate of 40–52%, measured in great tits by Kölliker et al. (2000). One possible reason for the differences between the two studies is that the heritability of begging in great tits is really higher than in house sparrows. Another possible reason is that the heritability estimate in the great tits study could have been inflated by maternal effects to a greater degree than in our study. Kölliker et al. based their heritability estimate on comparing begging intensity of crossed-fostered siblings originating from the same brood. Our sibling analysis, on the other hand, was based

on siblings from consecutive broods. It is quite possible that maternal conditions of siblings originating from the same clutch are more similar to those for siblings produced separately at different times during the breeding season. A well-studied maternal effect is that of hormone secretion to the egg yolk during egg formation (Schwabl 1993, 1996; Lipar and Ketterson 2000; Safran et al. 2008), which is also known to affect begging behavior (Schwabl 1996; Eising and Groothuis 2003; Goodship and Buchanan 2006). If hormonal secretion is affected by physiological state during egg production, it is quite likely to be more similar for eggs within a clutch than for eggs from different clutches (Schwabl 1997; Pilz et al. 2003). Moreover, maternal effects of this kind are less likely to bias our mother–offspring analysis or artificial selection experiments. For such a bias to occur, the maternal effect has to be passed from mother to grandchildren (through her daughter) or to be heritable by itself (e.g., the tendency to secrete more testosterone to egg yolk may be heritable). Finally, maternal effects should not bias heritability estimates that are based on father–offspring analysis (Falconer and Mackay 1996). In our study, father–offspring analysis was based on 35 father–offspring pairs (Table 2), and gave a moderate slope of 0.085 (which may indicate heritability of $2 \times 0.085 = 0.17$).

Given that genetic origin can explain only part of the variation in our begging data, what are the remaining factors that can explain this variation? Recall that in our begging measurements we already reduced much of the variation due to hunger, age, or mass differences. Thus, the remaining variation cannot be explained simply as different points along a begging reaction norm in which begging is plotted against state or condition. It is more likely to represent variation in the attributes of such reaction norms (such as their intercept, slope, or shape; see Smiseth et al. 2008). We also found that some of this variation can be explained by a common rearing environment. This suggests that a combination of environmental and social conditions can cause the reaction norm of begging to develop in different ways, or even to change dynamically over time. In this light, the evolution of begging may be best viewed as the evolution of the mechanisms that adjust begging responses to environmental and social conditions. These mechanisms may be based on rules for responding to physiological stress or parasites (Christe et al. 1996; Saino and Møller 2002), and to sibling competition (Smith and Montgomerie 1991; Roulin et al. 2000; Roulin 2001, 2004), as well as on learning rules that adjust begging behavior in relation to its effectiveness (Kedar et al. 2000; Rodriguez-Girones et al. 2002; Grodzinski et al. 2008). From a parent–offspring coevolutionary perspective it would be highly interesting to determine whether these mechanisms themselves are genetically variable and continue to coevolve with parental behavior. Alternatively, if parent–offspring conflict is resolved and the population is at evolutionary equilibrium (Parker and Macnair 1979; Godfray 1991, 1995) these

mechanisms may not be genetically variable and therefore their heritability may be low.

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