

Parental effort and response to nestling begging in the house sparrow: repeatability, heritability and parent–offspring co-evolution

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Abstract

Parental effort has a direct impact on individual fitness. Theoretical models exploring how parental effort evolves to cope with offspring demand and sexual conflicts may differ in the assumptions they make in respect to the genetic heritability of parental behaviours. Only a few attempts, however, have been made to estimate the heritability of parental behaviours and their possible co-evolution with offspring solicitation behaviour. Analysing parent and offspring behaviours in four generations of cross-fostered broods of house sparrows, we found that parental effort (food delivery rate) was repeatable across consecutive broods and heritable across generations. In contrast, parental response to experimentally induced changes in nestling begging was neither repeatable across broods nor heritable across generations or correlated to nestling begging. Thus, the results give no indication for genetic covariance between begging intensity and parental response, but provide the first cross-fostering-based evidence for the heritability of parental investment levels across generations.

Introduction

Parental care is a fundamental life history trait that affects individual fitness through its impact on offspring survival and quality (Clutton-Brock, 1991). The level of parental care may be shaped by two main conflicts. The first is the genetic conflict between parents and offspring over the required amount of parental care (Trivers, 1974). The second is the conflict between two providing parents (in species with bi-parental care), where each parent can benefit from minimal investment at the expense of the other parent (Trivers, 1972).

It is well agreed that the resolution of parent–offspring conflict over the amount of parental care is mediated through offspring begging and the parental response to this begging (Godfray, 1995; Budden & Wright, 2001; Wright & Leonard, 2002; Hinde *et al.*, 2010). While theoretical interpretations of this resolution are still being

debated (see Mock & Parker, 1997; Royle *et al.*, 2002; Smiseth *et al.*, 2008), at the behavioural level, it is clear that parents usually increase provisioning in response to begging (reviewed by Kilner & Johnstone, 1997; Budden & Wright, 2001) and that such response is probably adaptive (Grodzinski & Lotem, 2007; Grodzinski *et al.*, 2009). It is less clear, however, to what extent parental effort and parental response to begging are genetically variable. Evolutionary ‘resolution’ models of parent–offspring conflict implicitly assume that offspring begging and parental response to it are genetically variable (Parker & Macnair, 1979; Godfray, 1991, 1995; Rodríguez-Gironés *et al.*, 1996; Mock & Parker, 1997; Godfray & Johnstone, 2000) or even correlated (Feldman & Eshel, 1982). This genetic variability may be maintained if parent and offspring strategies are continuously (or even antagonistically) co-evolving (Kölliker *et al.*, 2010), but may be reduced if they reach an evolutionarily stable state.

As mentioned above, the second conflict that affects the level of parental care is that between two providing parents. In this case too, alternative models may suggest

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different predictions in respect to the genetic variability of parental effort. Nakagawa *et al.* (2007) suggested that the 'Sealed-bid' model, according to which parents do not respond to changes in their partner's investment, predicts higher levels of repeatability and heritability of parental effort levels than 'Negotiation-rule' models that involve flexible adjustment of parental effort (McNamara *et al.*, 1999; Johnstone & Hinde, 2006). Thus, empirical data on the repeatability and heritability of parental effort levels may be of interest both to the study of parent-offspring conflict and parent-parent conflict.

An active area of research on parental investment and parent-offspring conflict is that of the provisioning of bird nestlings by their parents. In addition to extensive research on nestling begging (see Wright & Leonard, 2002), much work has also been carried out on the environmental and social factors that determine the level of parental provisioning. These factors include food availability (Boland *et al.*, 1997), offspring number (Nur, 1984; Ruusila & Poysa, 1998), their age and condition (Whittingham & Robertson, 1993), male relatedness to the offspring (Lifjeld *et al.*, 1998; Sheldon & Ellegren, 1998), and the chance for male future reproduction (Smith, 1995). The genetic basis of variation in parental provisioning rate or in parental responsiveness to begging, however, has rarely been studied.

Genetic variation in a behavioural trait is usually estimated by its heritability (Falconer & Mackay, 1996). However, in avian species, heritability estimations can be difficult because of dispersal and death of individuals; therefore, some studies have used repeatability measurements (the proportion of variance in a character that occurs among individuals) as an upper limit estimation for heritability (Freeman-Gallant & Rothstein, 1999; MacColl & Hatchwell, 2003; Schwagmeyer & Mock, 2003; Gray *et al.*, 2005; Nakagawa *et al.*, 2007). These studies reported that parental effort (feeding rate at the nest) is highly repeatable, and in most cases more so for males. Only a few studies have measured the heritability of parental effort across generations (Freeman-Gallant & Rothstein, 1999; MacColl & Hatchwell, 2003), and these have reported significant heritability estimates. However, in obtaining measurements without cross-fostering of nestlings between broods, these studies cannot preclude possible parental effects or interaction between parents and their biological offspring as factors that could inflate their heritability estimates.

The heritability of parental effort or parental response to begging can be inferred indirectly from the existence of genetic covariation between offspring begging levels and parental behaviour (Kölliker *et al.*, 2000; Agrawal *et al.*, 2001; Kölliker & Richner, 2001; Kölliker *et al.*, 2005). Such genetic covariation was found to be positive in one of two insect species examined (Lock *et al.*, 2004) and negative in the other (Agrawal *et al.*, 2001). One attempt to assess this correlation in birds reported a positive correlation between begging inten-

sity and maternal response to playback calls in cross-fostered great tits, *Parus major* (Kölliker *et al.*, 2000). Thus far, this indirect evidence (but from a carefully controlled cross-fostering study) provides the only indication for the heritability of parental response to nestling begging.

To study the repeatability, heritability, and genetic covariation of parental behaviour and nestling begging, we used a large captive-breeding colony of house sparrows (*Passer domesticus*). Previously, we reported on the heritability of nestling begging intensity in our house sparrow population (Dor & Lotem, 2009). Here, we focus on parental behaviour. Analysing parent and offspring behaviours across four generations of cross-fostered broods, we estimated for the first time the repeatability and heritability of both parental effort (average provisioning rate) and parental response to changes in nestling begging across generations and examined possible genetic correlation between parental behaviours and begging intensity.

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 from 2003 to 2007. The sparrow population was housed in five adjacent aviaries (8–12 nesting pairs/aviary). The sparrows nested in wooden nest boxes with one compartment for the nest and another, separated by a glass plate that held an infrared video camera. The sparrows were fed *ad lib* with a combination of commercial birds' mixture, boiled eggs, Dora seeds, and fly larvae. All individuals were banded with an aluminium ring and three coloured rings to enable individual recognition. Breeding season lasted from March to August of each year, allowing many of the same pairs to have up to three successive broods per season. Nests were monitored for egg laying and hatching (= day 0), and the identity of nesting pairs was determined. Before each breeding season, the sparrows were captured using mist nets. We released all breeders from the previous year (into the zoo area), and yearlings were relocated to a breeding aviary for their first breeding season (see more detailed description in Dor & Lotem, 2009).

Experimental set up

All clutches in the colony were cross-fostered 2–3 days before the expected day of hatching, resulting in a random allocation of foster clutches to foster parents. Cross-fostering was vital to our study as it controls for parental effects and for possible dynamic interactions between parents and their biological offspring that may confound heritability estimates. Cross-fostering also

provided the possibility to detect genetic covariance between begging and parental behaviour. Possible bias in our findings as a consequence of extra-pair paternity (EPP) are discussed in detail in Dor & Lotem (2009), and their effect is likely to be small (see Discussion).

Parental behaviour was video recorded when the nestlings were 3 days old. 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 by a 30-m cable to a video in a surveillance room. On the morning of the video recording, the nestlings were weighed (using OHAUS scales to the nearest 0.1 g), measured for wing length (with a caliper to the nearest 0.1 mm), and individually marked using nontoxic colour paints (Tulip[®], Duncan Enterprises, Fresno, CA, USA).

Video recording began between 09:00 and 10:00 am, at least 30 min after we had completed taking measurements and after nestling and parental behaviours appeared normal (*i.e.* free from the effects of human disturbance). After 1 h of video recording ('premanipulation' session), the two heaviest nestlings were removed and taken to an incubator in the laboratory for 1 h ('chick removal' session), during which they were food-deprived. Video recording continued for an additional 1 h after the food-deprived nestlings were returned to the nest ('nestling return' session), totalling 3 h of video recording per nest. The last session, with the two heaviest nestlings having been food-deprived, was aimed at creating a marked increase in begging behaviour compared with the first, premanipulation, session, to enable measurement of parental response to such an increase (see Results). These two sessions ('premanipulation' and 'nestling return' sessions) comprised a similar number of nestlings present in the nest, thus being suitable to assess any changes in parental behaviour because of changes in begging intensity.

Measuring parental effort and parental response

We analysed all parental visits from the video recordings. For each visit, we recorded the time, parental sex, and the size of each meal (three meal sizes estimated relative to the parent's beak size, see a similar method in Schwagmeyer & Mock, 2008). We also analysed the nestlings' begging intensity (see next section) during the 'premanipulation' session and 'nestling return' session (1 h each). From these data, we calculated two parental behaviours: (1) Parental effort – the rate of parental feeding visits (number of visits per hour) during the 'premanipulation' session and (2) Parental response – the change in parental effort from the 'premanipulation' session to the 'nestling return' session. Parental response was further standardized according to the actual change in begging intensity that occurred in each nest following our manipulation (see 'Statistical analysis').

Measuring nestling begging intensity

Begging intensity was used: (1) to measure the actual changes in begging as a result of our manipulation (*i.e.* the removal of the two heaviest nestlings), as well as to control for variation in the magnitude of changes in begging across different broods (see Statistical analysis) and (2) to assess the correlation between the parents' behaviour (parental effort and response to changes in begging) and the begging intensity of their biological offspring (measured in a foster nest), as well as the correlation with the parents' own begging intensity measured when they themselves had been nestlings during the previous year.

We analysed begging intensity during parental visits throughout the 'premanipulation' and 'nestling return' sessions (1 h of video recording each). To assess begging intensity, we scored the begging posture of all nestlings at one video frame sample per second during the first 10 s of the visit (or until a nestling was fed), using a graphic scale from 0 (no begging) to 3 (erect position of begging) (for details see Dor & Lotem, 2009). For each nestling, we then calculated a mean begging posture score for each visit and an average score across all visits. These average begging scores were later standardized to control for variation in food deprivation and body size (see a detailed description in Dor & Lotem, 2009).

Measuring the repeatability and heritability of parental behaviours

Repeatability was calculated from repeated measurements of the same individuals during successive breeding efforts throughout the same breeding season. These calculations were made only for pairs that were stable throughout the entire breeding season (*i.e.* the same male and female remained together). Repeatability (r) was calculated from the variance components of One-way ANOVA (Lessells & Boag, 1987) based on the expression:

$$r = S_A^2 / (S^2 + S_A^2),$$

where S_A^2 is the variance among individuals and S^2 is the variance within individuals. Standard errors for repeatability were calculated according to Becker (1984).

Heritability was estimated from the regression of brood-mean (or mean per offspring sex) on mid-parent trait values, giving the slope as the heritability estimate (Falconer & Mackay, 1996). Six females and five males in our sample provided data for both the offspring mean values (analysed in relation to that of the biological parents) and the parent mean values (analysed in relation to that of the biological offspring). The inclusion of such data is unlikely to bias our heritability estimates unless heritability itself is heritable, which is unlikely (*i.e.* that some family lines have higher parent-offspring similarity than others so that including three

generations of such a family would bias our population estimate). Removing those data that contributed to offspring mean values from individuals that had already contributed data as parents did not qualitatively change the results.

Statistical analysis

Parental feeding visit rate is known to be affected by the number of nestlings in the nest, and this was indeed the case for both parents in our study (males: $r = 0.48$, $P = 0.002$, $n = 37$; females: $r = 0.39$, $P = 0.020$, $n = 35$). To control for this effect, we calculated standardized parental effort as the residuals from a regression model, using the rate of parental feeding visits as a dependent variable (square-root-transformed) and the number of nestlings as the predictor. We used these standardized values to calculate repeatability and heritability of parental effort.

The change in begging intensity as a result of the nestling manipulation (the temporary removal of the two heaviest nestlings) varied between nests. To examine parental response to changes in begging intensity, we had to control statistically for this variation and express the change in parental feeding rate relative to the change expected from the actual change in nestling begging that occurred in each nest. This was done by using standardized parental response values taken as the residuals from a regression model of parental response and changes in begging intensity. We used these standardized values to calculate repeatability and heritability of parental response to begging. However, similar analyses without controlling for changes in begging intensity generated similar results (not presented). Statistical analyses were performed using Statistica 7.0 (Statsoft, Inc., Tulsa, OK, USA). Power analysis for correlation was performed using G*Power 3.1.2 (Faul *et al.*, 2009). We report means \pm standard error unless otherwise specified.

Results

Parental response to experimental manipulation of begging calls

Experimental manipulation of the nestlings within the nest was successful in increasing the level of begging intensity in the nest by an average of $33.4 \pm 5.4\%$ (from 0.96 ± 0.05 to 1.27 ± 0.05), when comparing the period before nestling removal to the period after they were returned. In accordance with the increased level of begging intensity, which occurred in most of the nests (43 of 48; Binomial test $P < 0.001$), parents in most cases increased their feeding visit rate (32/36 for females, 32/37 for males; Binomial test $P < 0.001$ for both cases), and on average from 20.3 ± 1.5 to 31.7 ± 1.7 visits per h (for both sexes combined).

Repeatability of parental effort and parental response to begging

Repeatability of parental effort and parental response was calculated separately for females and males (Table 1). We found a significant repeatability for parental effort for both females (0.57 ± 0.16 , $P = 0.004$) and males (0.51 ± 0.17 , $P = 0.007$). However, no significant repeatability for parental response to changes in begging intensity was found for either females or males (see Table 1).

Heritability of parental effort and parental response to begging

Heritability was calculated from the slope of mid-offspring over mid-parent regression using either all offspring, sons only, or daughters only (Table 2, Fig. 1). We found evidence for heritability for parental effort (ranging from 0.12 to 0.50), but only the heritability between mid-parents and sons was significant ($h^2 = 0.50 \pm 0.22$, $P = 0.049$). It should be noted, however, that a single female offspring that, as a parent, had demonstrated an unusually low visit rate during the premanipulation session (only 10 visits per h to a brood of six nestlings) resulted in the lowest standardized data point in Fig. 1a,c (bottom right hand side of each of these graphs), which clearly deviates from the main correlation. If this data point is removed, the heritability calculated from mid-parents and mid-offspring data (Fig. 1a) is significant ($r = 0.57$, $h^2 = 0.49 \pm 0.21$, $P = 0.042$, $n = 13$). In contrast to the positive heritability estimates of parental effort, the heritability estimates of parental response to begging were all negative and not significant (Table 2).

Genetic correlation between parental behaviours and begging intensity

The genetic correlation between begging intensity and the two parental traits (parental effort and parental response) was assessed using two different correlations calculated from our data set: (1) the correlation between the parental traits and the standardized begging intensity of their biological brood (parental and biological-offspring traits were measured in two different nests because of cross-fostering) and (2) the correlation

Table 1 Within-year repeatability of parental effort and parental response to begging.

	<i>n</i>	<i>N</i> ₀	<i>R</i> (SE)	<i>F</i>	<i>P</i>
Parental effort					
Female	15	2.11	0.57 (0.16)	3.84	0.004
Male	16	2.24	0.51 (0.17)	3.31	0.007
Parental response					
Female	15	2.11	0.14 (0.23)	1.35	0.266
Male	16	2.24	-0.32 (0.19)	0.49	0.921

Table 2 Heritability estimates of parental effort and parental response to begging, calculated from parents–offspring regressions.

	<i>n</i>	<i>r</i>	<i>h</i> ² (SE)	<i>P</i>
Parental effort				
Parents–offspring	14	0.286	0.30 (0.30)	0.322
Parents–sons	10	0.634	0.50 (0.22)	0.049
Parents–daughters	8	0.084	0.12 (0.60)	0.843
Parental response				
Parents–offspring	14	−0.116	−0.18 (0.44)	0.692
Parents–sons	10	−0.053	−0.09 (0.61)	0.884
Parents–daughters	8	−0.317	−0.36 (0.43)	0.444

between standardized begging intensity as nestlings and the parental effort and response of the same individuals as parents (measured in the consecutive breeding season). We found no significant correlations between begging intensity and parental response from parent–offspring correlation (Fig. 2a: $r = -0.08$, $P = 0.74$, $n = 19$) or from within-individual correlation ($r = -0.25$, $P = 0.213$, $n = 27$). Similarly, no significant correlations were found between begging intensity and parental effort, using either of these two methods (parent–offspring correlation: $r = 0.28$, $P = 0.25$, $n = 19$, Fig. 2b; Within-individual correlation: $r = -0.01$, $P = 0.95$, $n = 27$). Separate analyses of the mother's and father's behaviours in relation to the begging of their offspring gave similar nonsignificant results.

Discussion

In this study, we used cross-fostering experiments in four generations of captive house sparrows to estimate the repeatability and heritability of parental effort and parental response to nestling begging and to assess possible genetic covariance between parental behaviours and nestling begging. We found no evidence for heritability (or even repeatability) in parental response to begging. We also did not find origin-related covariation between parental response and begging intensity, which could have provided indirect evidence for the genetic heritability of parental response. Similarly, we found no evidence for genetic covariance between parental effort (nest visitation rate) and nestling begging. In contrast, our direct assessment shows that parental effort was repeatable across consecutive broods and heritable across generations, especially so for males. This finding provides the first cross-fostering-based evidence for the heritability of parental effort, thus corroborating previous field studies (without the use of cross-fostering) that indicated heritable variation in parental effort (Freeman-Gallant & Rothstein, 1999; MacColl & Hatchwell, 2003).

Before discussing further the implications of our results, we should consider their strength and robustness. Several possible biases that could affect the results from our captive colony are discussed in detail by Dor & Lotem

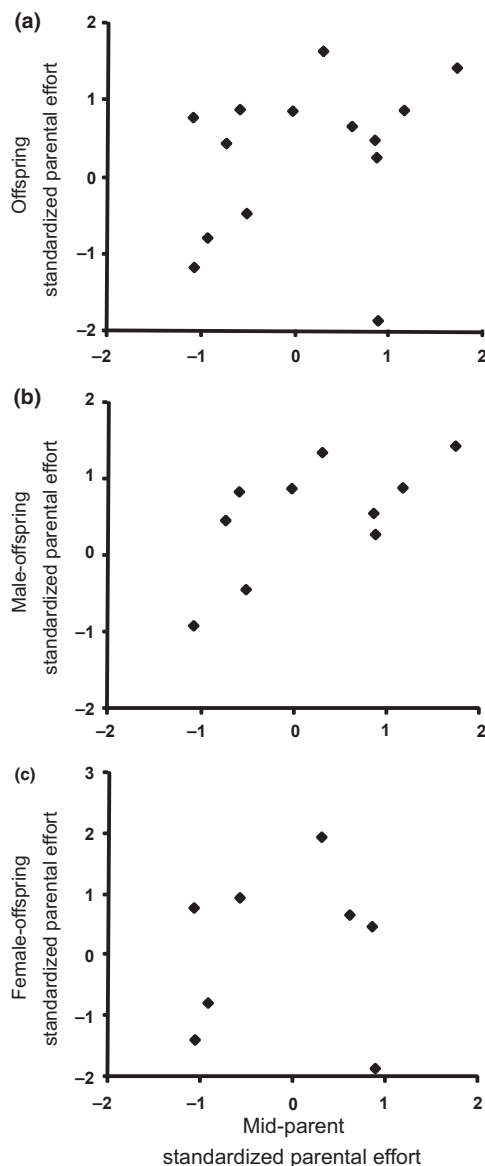


Fig. 1 Standardized parental effort for parents and their biological offspring: (a) mid-parent on mean offspring regression, (b) mid-parent on mean male offspring regression, and (c) mid-parent on mean female offspring regression. Slope of the regression represents the heritability (h^2) of parental effort.

(2009). Briefly, we showed that nestling begging behaviour and the conditions in our captive-breeding colony were similar to that of wild populations, that the method of measuring begging behaviour was sufficiently accurate to detect significant variation in relation to various environmental factors, and that the possible effect of extra-pair paternity (ranges from 1% to 20% in natural populations; Griffith *et al.*, 1999; Whitekiller *et al.*, 2000; Stewart *et al.*, 2006; Edly-Wright *et al.*, 2007) was negligible, as indicated by our heritability levels of

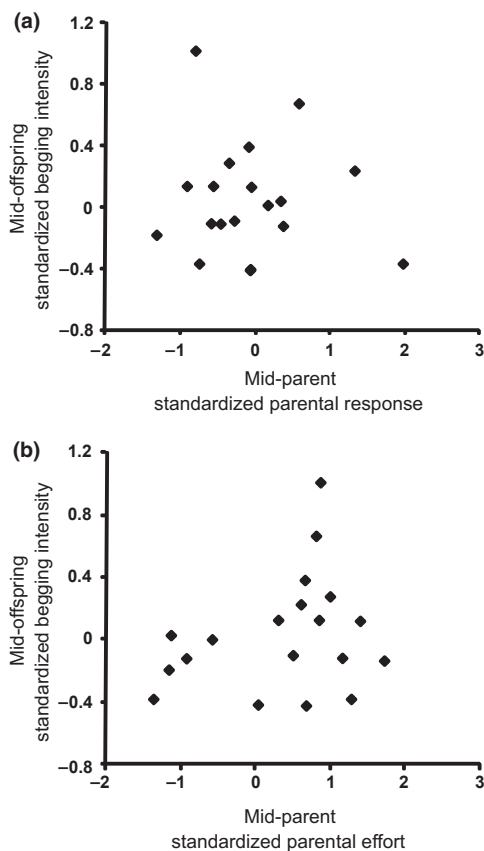


Fig. 2 The genetic correlation between parental behaviours and begging intensity of their biological offspring (measured in two different nests because of cross-fostering): (a) genetic correlation between parental response and begging intensity and (b) genetic correlation between parental effort and begging intensity.

morphological traits (see Dor & Lotem, 2009), as well as by the significant heritability of parental effort found in this study.

Another problem to address is related to statistical power and nonsignificant results. Clearly, the lack of significant heritable component in parental response to begging may be attributed to a small sample size. However, the degree of heritability that might remain undetected by our analysis was unlikely to be high, as suggested by the fact that our data were sufficiently powerful to detect significant repeatability and heritability in parental effort. The low repeatability of parental response to changes in begging suggests that this trait may simply be too variable at the behavioural level to allow the detection of a possible heritable component. Further work on this aspect would certainly be useful, but we may conclude tentatively that according to the first cross-fostering-based measurements of the heritability of parental response to begging, the heritability of this trait is low.

Although the lack of significant parent–offspring genetic covariance may also be attributed to low statistical power, we were unlikely to have missed strong relationships had they existed in our population. First, the strong positive relationship between begging and parental response to begging that was found in great tits was based on a similar sample size (see Kölliker *et al.*, 2000; Fig. 2). A power analysis suggests that the probability of not detecting a positive correlation of the magnitude reported by Kölliker *et al.* (2000) in our data was below 0.14 ($n = 19$, in this study; $n = 24$, $r = 0.676$, in Kölliker *et al.* (2000); Power $(1 - \beta) = 0.86$); and the probability of not detecting either a positive or negative correlation of that magnitude was below 0.28 ($n = 19$, in this study; $n = 24$, $r = 0.676$, in Kölliker *et al.* (2000); Power $(1 - \beta) = 0.72$). Second, the lack of relationship in our study was based not only on a parent–offspring correlation ($n = 19$) but also on a within-individual correlation ($n = 27$). In both cases, there was no indication for a positive (or negative) relationship between begging and parental effort or between begging and parental response. Finally, the lack of genetic covariance with begging behaviour is not surprising given that the heritability of begging behaviour in our house sparrow population was relatively low (Dor & Lotem, 2009). All things considered, there is no evidence in our data to suggest that parent and offspring strategies are continuously (or antagonistically) co-evolving in a process that maintains their genetic variation (Kölliker *et al.*, 2010). However, such a process may occur on a much finer scale that could not be detected by our study or that is masked by different patterns of selection on parents and offspring that act simultaneously and practically cancel one another (Kölliker *et al.*, 2005; Hinde *et al.*, 2010). Alternatively, begging levels and parental response to begging are based on some uniform genetic rules that are evolutionarily stable, but generate considerable variation at the phenotypic level (c.f. Godfray, 1991, 1995; Johnstone, 2004).

The most significant findings of our study are those of the repeatability and heritability of parental investment levels, measured by nest visitation rate. Although we found similar repeatability for males and females, field studies of house sparrows (Schwagmeyer & Mock, 2003; Nakagawa *et al.*, 2007) and of other passerines (Freeman-Gallant & Rothstein, 1999; MacColl & Hatchwell, 2003) reported higher repeatability values for males. It is possible that in captivity, females were more protected from environmental changes and physiological stress and could thus maintain their ‘intended’ level of parental effort more easily. In the field, on the other hand, parental care may be more costly for females than for males, which makes females less resilient to environmental changes and consequently less consistent in their parental effort. This may also explain why field measurements of the heritability of parental effort showed higher heritability levels for males than for females

(Freeman-Gallant & Rothstein, 1999; MacColl & Hatchwell, 2003).

In the field, parental visit rate depends on many factors and may therefore be related to overall individual quality or foraging ability. Field data on the heritability of parental visit rate can therefore be attributed to the heritability of a wide range of traits. On the other hand, parental effort in our captive colony was less likely to be dependent on foraging ability or on individual quality because food was easily accessible. Thus, parental effort in our study was more likely to represent individual motivation to invest in parental care or, in other words, to represent more closely the genetic component of parental effort. Accordingly, the heritability found in our captive colony, and possibly also in previous field studies, may indeed reflect genetic variation in the preprogrammed baseline level of parental effort.

It has been suggested that the existence of genetic variation in parental effort may be more consistent with the 'Sealed-bid' model of parent–parent conflict than with the 'Negotiation-rules' models (Nakagawa *et al.*, 2007). However, intermediate levels of heritability may be consistent with both models. The heritability (and repeatability) of parental investment observed in our study was clearly below 1, which leaves much room for behavioural plasticity that may be expressed during negotiation (McNamara *et al.*, 1999; Johnstone & Hinde, 2006; Lendvai *et al.*, 2009).

Finally, an important question to consider is that of what maintains genetic variation in parental effort within populations? Although our data do not support the parent–offspring co-evolutionary scenario (see above), antagonistic co-evolution between males and females and negatively frequency-dependent selection are interesting possibilities for future exploration. As high parental effort tends to reduce longevity in the parent (Clutton-Brock, 1991; Owens & Bennett, 1994), environmental fluctuations in the probability of survival may generate oscillating selection for high and low levels of parental effort that may covary with longevity and perhaps with other traits as well (see Wolf *et al.*, 2007). Such ideas gain increasing relevance in light of the evidence for genetic variation in the level of parental effort that was found in this study.

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References

- Agrawal, A.F., Brodie, E.D. & Brown, J. 2001. Parent-offspring coadaptation and the dual genetic control of maternal care. *Science* **292**: 1710–1712.
- Becker, W.A. 1984. *Manual of Quantitative Genetics*, 4th edn. Academic Enterprises, Pullman, WA.
- Boland, C.R.J., Heinsohn, R. & Cockburn, A. 1997. Experimental manipulation of brood reduction and parental care in cooperatively breeding white-winged choughs. *J. Anim. Ecol.* **66**: 683–691.
- Budden, A.E. & Wright, J. 2001. Begging in nestling birds. *Curr. Ornithol.* **16**: 83–118.
- Clutton-Brock, T.H. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton.
- Dor, R. & Lotem, A. 2009. Heritability of nestling begging intensity in the house sparrow (*Passer domesticus*). *Evolution* **63**: 738–748.
- Edly-Wright, C., Schwagmeyer, P.L., Parker, P.G. & Mock, D.W. 2007. Genetic similarity of mates, offspring health and extrapair fertilization in house sparrows. *Anim. Behav.* **73**: 367–378.
- Falconer, D.S. & Mackay, T.F.C. 1996. *Introduction to Quantitative Genetics*, 4th edn. Longman, New York.
- Faul, F., Erdfelder, E., Buchner, A. & Lang, A.-G. 2009. Statistical power analyses using G*Power 3.1: tests for correlation and regression analyses. *Behav. Res. Methods* **41**: 1149–1160.
- Feldman, M.W. & Eshel, I. 1982. On the theory of parent-offspring conflict: a two locus genetic model. *Am. Nat.* **119**: 285–292.
- Freeman-Gallant, C.R. & Rothstein, M.D. 1999. Apparent heritability of parental care in savannah sparrows. *Auk* **116**: 1132–1136.
- Godfray, H.C.J. 1991. Signaling of need by offspring to their parents. *Nature* **352**: 328–330.
- Godfray, H.C.J. 1995. Signaling of need between parents and young – parent-offspring conflict and sibling rivalry. *Am. Nat.* **146**: 1–24.
- Godfray, H.C.J. & Johnstone, R.A. 2000. Begging and bleating: the evolution of parent-offspring signalling. *Philos. Trans. R. Soc. B* **355**: 1581–1591.
- Gray, C.M., Brooke, M.D.L. & Hamer, K.C. 2005. Repeatability of chick growth and food provisioning in Manx shearwaters *Puffinus puffinus*. *J. Avian Biol.* **36**: 374–379.
- Griffith, S.C., Stewart, I.R.K., Dawson, D.A., Owens, I.P.F. & Burke, T. 1999. Contrasting levels of extra-pair paternity in mainland and island populations of the house sparrow (*Passer domesticus*): is there an 'island effect'? *Biol. J. Linn. Soc.* **68**: 303–316.
- Grodzinski, U. & Lotem, A. 2007. The adaptive value of parental responsiveness to nestling begging. *Proc. R. Soc. B Biol. Sci.* **274**: 2449–2456.
- Grodzinski, U., Hauber, M.E. & Lotem, A. 2009. The role of feeding regularity and nestling digestive efficiency in parent-offspring communication: an experimental test. *Funct. Ecol.* **23**: 569–577.

- Hinde, C.A., Johnstone, R.A. & Kilner, R.M. 2010. Parent-offspring conflict and coadaptation. *Science* **327**: 1373–1376.
- Johnstone, R.A. 2004. Begging and sibling competition: how should offspring respond to their rivals? *Am. Nat.* **163**: E388–E406.
- Johnstone, R.A. & Hinde, C.A. 2006. Negotiation over offspring care – how should parents respond to each other's efforts? *Behav. Ecol.* **17**: 818–827.
- Kilner, R. & Johnstone, R.A. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol. Evol.* **12**: 11–15.
- Kölliker, M. & Richner, H. 2001. Parent-offspring conflict and the genetics of offspring solicitation and parental response. *Anim. Behav.* **62**: 395–407.
- Kölliker, M., Brinkhof, M.W.G., Heeb, P., Fitze, P.S. & Richner, H. 2000. The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care. *Proc. R. Soc. B Biol. Sci.* **267**: 2127–2132.
- Kölliker, M., Brodie, E.D. & Moore, A.J. 2005. The coadaptation of parental supply and offspring demand. *Am. Nat.* **166**: 506–516.
- Kölliker, M., Ridenhour, B.J. & Gaba, S. 2010. Antagonistic parent-offspring co-adaptation. *PLoS ONE* **5**: e8606. doi: 10.1371/journal.pone.0008606.
- Lendvai, A.Z., Barta, Z. & Chastel, O. 2009. Conflict over parental care in house sparrows: do females use a negotiation rule? *Behav. Ecol.* **20**: 651–656.
- Lessells, C.M. & Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* **104**: 116–121.
- Lifjeld, J.T., Slagsvold, T. & Ellegren, H. 1998. Experimentally reduced paternity affects paternal effort and reproductive success in pied flycatchers. *Anim. Behav.* **55**: 319–329.
- Lock, J.E., Smiseth, P.T. & Moore, A.J. 2004. Selection, inheritance, and the evolution of parent-offspring interactions. *Am. Nat.* **164**: 13–24.
- MacColl, A.D.C. & Hatchwell, B.J. 2003. Heritability of parental effort in a passerine bird. *Evolution* **57**: 2191–2195.
- McNamara, J.M., Gasson, C.E. & Houston, A.I. 1999. Incorporating rules for responding into evolutionary games. *Nature* **401**: 368–371.
- Mock, D.W. & Parker, G.A. 1997. *The Evolution of Sibling Rivalry*. Oxford University Press, Oxford.
- Nakagawa, S., Gillespie, D.O.S., Hatchwell, B.J. & Burke, T. 2007. Predictable males and unpredictable females: sex difference in repeatability of parental care in a wild bird population. *J. Evol. Biol.* **20**: 1674–1681.
- Nur, N. 1984. Feeding frequencies of nestling blue tits (*Parus caeruleus*) costs, benefits and a model of optimal feeding frequency. *Oecologia* **65**: 125–137.
- Owens, I.P.F. & Bennett, P.M. 1994. Mortality costs of parental care and sexual dimorphism in Birds. *Proc. R. Soc. B Biol. Sci.* **257**: 1–8.
- Parker, G.A. & Macnair, M.R. 1979. Models of parent-offspring conflict. IV. Suppression: evolutionary retaliation by the parent. *Anim. Behav.* **27**: 1210–1235.
- Rodríguez-Gironés, M.A., Cotton, P.A. & Kacelnik, A. 1996. The evolution of begging: signaling and sibling competition. *Proc. Natl. Acad. Sci.* **93**: 14637–14641.
- Royle, N.J., Hartley, I.R. & Parker, G.A. 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends Ecol. Evol.* **17**: 434–440.
- Ruusila, V. & Poysa, H. 1998. Shared and unshared parental investment in the precocial goldeneye (Aves : Anatidae). *Anim. Behav.* **55**: 307–312.
- Schwagmeyer, P.L. & Mock, D.W. 2003. How consistently are good parents good parents? Repeatability of parental care in the house sparrow, *Passer domesticus*. *Ethology* **109**: 303–313.
- Schwagmeyer, P.L. & Mock, D.W. 2008. Parental provisioning and offspring fitness: size matters. *Anim. Behav.* **75**: 291–298.
- Sheldon, B.C. & Ellegren, H. 1998. Paternal effort related to experimentally manipulated paternity of male collared flycatchers. *Proc. R. Soc. B Biol. Sci.* **265**: 1737–1742.
- Smiseth, P.T., Wright, J. & Kölliker, M. 2008. Parent-offspring conflict and coadaptation: behavioural ecology meets quantitative genetics. *Proc. R. Soc. B Biol. Sci.* **275**: 1823–1830.
- Smith, H.G. 1995. Experimental demonstration of a trade-off between mate attraction and paternal care. *Proc. R. Soc. B Biol. Sci.* **260**: 45–51.
- Stewart, I.R.K., Hanschu, R.D., Burke, T. & Westneat, D.F. 2006. Tests of ecological, phenotypic, and genetic correlates of extra-pair paternity in the house sparrow. *Condor* **108**: 399–413.
- Trivers, R.L. 1972. Parental and investment and sexual selection. In: *Sexual Selection and the Decent of Man* (B. Campbell, ed.), pp. 136–179. Aldine, Chicago, IL.
- Trivers, R.L. 1974. Parent-offspring conflict. *Am. Zool.* **14**: 249–264.
- Whitekiller, R.R., Westneat, D.F., Schwagmeyer, P.L. & Mock, D.W. 2000. Badge size and extra-par fertilizations in the house sparrow. *Condor* **102**: 342–348.
- Whittingham, L.A. & Robertson, R.J. 1993. Nestling hunger and parental care in red-winged blackbirds. *Auk* **110**: 240–246.
- Wolf, M., van Doorn, G.S., Leimar, O. & Weissing, F.J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature* **447**: 581–584.
- Wright, J. & Leonard, M.L. 2002. *The Evolution of Begging: Competition, Cooperation and Communication*. Kluwer, Dordrecht.

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