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Social and genetic benefits of parental investment suggest sex differences in selection pressures

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Provisioning behavior in altricial birds is often used to measure parental investment and is assumed to have fitness consequences to the parents providing it, with the benefits outweighing the costs. Here we investigate the fitness costs and benefits (parent survival and offspring recruitment) of provisioning behavior in wild house sparrows *Passer domesticus*, using long-term data from a pedigreed isolated population. We disentangled the long-term fitness consequences in terms of number of recruits, of provisioning behavior from those of other parental investments and individual quality through a cross-foster design. We accounted for extra-pair offspring in all analyses. Provisioning behavior confers social fitness benefits in terms of the number of recruits to both parents. Only in females we detected an influence individual quality: female sparrows with high provisioning frequencies were associated with more genetic recruits than those who provided food less frequently to their young, even though foster parents reared the offspring. We detected a relationship between annual survival probability and provisioning behavior only in males, but not in females. This finding, together with indirect benefits differing by sex, indicates that different selection pressures are acting on the sexes. Our study can show that it is justified to use provisioning behavior as a form of parental investment sensu Trivers, since we show that this behavior is costly to parents and that the genetic fitness benefits exceed the costs.

Parental investment is any investment 'by the parent in […] offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring' (Trivers 1972). The resources parents can allocate to providing care are limited, they cannot be allocated to self-maintenance, therefore it is commonly assumed that caring for offspring reduces survival (Clutton-Brock 1991, Stearns 1992). This trade-off between current reproduction and residual fitness is central in life-history theory, and has received considerable attention in evolutionary ecology (Nur 1984, Godfray 1995, Wagner and Williams 2007).

Parental investment in the form of parental provisioning behavior has been studied extensively in altricial bird species with biparental provisioning behavior, quantified as the frequency with which a parent brings a certain amount of food to their dependent offspring (Nolan et al. 2001). The frequency of provisioning is frequently used because it is easily measurable and because of the evidently severe consequences if parents do not feed their young. However, in order to study provisioning behavior as a form of parental investment one has to show 1) that provisioning behavior invokes costs to the parent's future (or residual) reproductive success and 2) that it amplifies the chances of the young to recruit and so benefits the fitness of the parent, where the fitness benefits should exceed the costs (Williams 1966, Clutton-Brock 1991, Owens and Bennett 1994).

1) Since food brought to the young is not eaten by the parent, costs in terms of self-maintenance are likely to occur to parents. Such costs can lead to a reduction in the physiological condition of the parent, potentially harming their future breeding success (Williams 1966). Furthermore, frequent foraging trips may result in an increased risk of predation (Martin et al. 2000, Raihani et al. 2010). Indeed, there is empirical support from experimental brood size manipulations (Nur 1984, Dijkstra et al. 1990) and from comparative meta-analyses of such studies for apparent costs of provisioning behavior in terms of survival, reduced parental body condition and future fecundity (Reznick 1985, Ketterson and Nolan 1994, Owens and Bennett 1994, Liker and Székely 2005). However, there are several inherent problems that make measuring the actual costs of provisioning behavior difficult and problematic to interpret. Studies directly manipulating the workload of parents by removing one parent, manipulating brood size or manipulating flight abilities of parents have produced ambiguous results (Wright and Cuthill 1989, 1990, Dijkstra et al. 1990, Wright et al. 1998, Sanz et al. 2000, Schwagmeyer et al. 2002). It was suggested that some individuals flexibly adjust costs, by reallocating energy

resources, i.e. making fewer trips and bringing larger food items (Bautista et al. 1998, Deerenberg et al. 1998). Therefore it is difficult to experimentally modify and measure the costs of provisioning behavior. Equally, it is difficult to separate the costs of provisioning behavior from those of other components of reproduction such as gamete production and incubation (Clutton-Brock 1991).

2) The measurement of the benefits of provisioning behavior is often done in a two-step approach, where fitness benefits are only indirectly measured. Often, the consequences of provisioning behavior for hatchling and fledgling growth and morphology are measured instead of recruitment to the breeding population. In a second step, often as results from different studies, the link between offspring morphology and fitness is established (Magrath 1991, Voltura et al. 2002). It is preferable to measure the association between provisioning behavior and fitness directly, in the same population and study (Evans 1990, Schwagmeyer and Mock 2008, Ringsby et al. 2009). Another complication is that it is inherently difficult to disentangle the nutritional consequences of provisioning behavior to the chicks (Wright and Cuthill 1989, 1990) from possible genetic benefits of individual quality of the parents (Cornwallis and Uller 2010) to offspring from high-quality parents. These high-quality parents may display much provisioning behavior, but this may not necessarily be the reason for why their offspring have a higher probability to recruit. The reason may instead be that the carry genes that are beneficial and lead to higher fitness. Such effects can only be disentangled with a cross-foster approach (e.g. as was done by Hinde et al. 2010). In the following, we use the term ‘genetic benefits’ for genetic fitness consequences of individuals with high provisioning rates, and ‘social benefits’ for the nutritional benefits of the actual provisioning received.

Here, we exploit a long-term study of an island population of house sparrows *Passer domesticus* that allows us to accurately estimate both fitness components: survival and reproduction. The main objectives of this work are to estimate the costs of provisioning behavior in terms of survival and to estimate the social and genetic fitness consequences of provisioning behavior provided by parents. We hypothesize that 1) provisioning behavior is costly to parents in terms of survival. We further expect that 2) high quality individuals, those with high quality provisioning behavior, will recruit more offspring than individuals with low quality provisioning behavior. We test whether this relationship is true even if the offspring is not receiving the high quality provisioning behavior and fostered by a randomly assigned parent, due to genetic or epigenetic effects of individual quality. Our house sparrow population is an excellent study system because we can measure fitness costs and benefits for the providing parent directly as annual and lifetime reproductive success and annual survival probability.

Methods

Data set

Our population of wild house sparrows is located on Lundy Island, in the Bristol Channel 19 km off the southwest coast of England (51°10′N, 4°40′W, Cleasby et al. 2010), which is studied continuously since 2000. The remote location ensures very low dispersal from or to the island, because house sparrows are sedentary by nature and not well suited for long-distance flight over large bodies of water (Bengtson et al. 2004). Therefore we assume that dispersal to and from Lundy is essentially non-existent. Additionally, the small size of the area frequented by sparrows (< 1 km^2) allows for high annual resighting probabilities (Schroeder et al. 2011). We, as a routine of our annual fieldwork, carried out cross-fostering of chicks at an age of two days in the years 2004–2007 (but not in 2008), between broods that were laid on the same day and had the same clutch size (Schroeder et al. 2011). The cross-fostering was done with the intention to be able to distinguish between genetic and environmental effects, and not for a specific experiment (see also Schroeder et al. 2011, 2012a). Therefore, we did not affect original brood size. In some instances, this resulted in partial cross-fostering where only a part of one brood was swapped with all chicks of another brood.

Provisioning behavior – methods

We used data collected from 2004 to 2008. Provisioning behavior was quantified at nest boxes since 2004 using camcorders when nestlings were seven days old (Nakagawa et al. 2007). A video camera was set up in such way that a bird that entered and left the nest box could be individually identified and provisioning visits quantified. The individual color ring combinations on tape identified individual birds. Recording was carried out in the morning (between 5:00 am and 12:00 pm, noon) of day 7 (with day 1 being the day the first chick hatched), or, if weather forbid this, on the following day. On the resulting videos (average length 90 min), we scored an entry and following exit of the nest box as a feeding visit. As total observation time, we used the time from the first visit until the end of the tape, which allowed the birds to habituate to the presence of the video camera (for more details on methodology we refer to Nakagawa et al. 2007). In our analyses, we use feeding frequency (visits h^{-1}) for all analyses (Schroeder et al. 2012a). We found no effect of time of day on provisioning frequency in our data (Cleasby et al. 2010). We have provisioning behavior available for 344 observations over four years.

For more details on our methodology, the validity of our provisioning scores and our study site, we refer to: (Nakagawa et al. 2007, Ockendon et al. 2009, Cleasby et al. 2010, Schroeder et al. 2012a).

Genetic pedigree

We had DNA samples available for nearly all individuals, often repeated samples, either as blood or feather samples. We used genotyping data from 13 microsatellite markers: Ase 18 (Richardson et al. 2000), Pdo 1, Pdo 3 (Neumann and Wetton 1996), Pdo 5, Pdo 6 (Griffith et al. 1999), Pdo 9, Pdo 10 (Griffith et al. 2007), and Pdo 16, Pdo 17, Pdo 19, Pdo 22, Pdo 27, and Pdo 40 (Dawson et al. 2012). We used the software packages CERVUS 3.0 and MasterBayes (Hadfield et al. 2006, Walling et al. 2010) to assign extra-pair fathers to offspring. An extended version of our pedigree is presented in detail in Schroeder et al. (2012b). Of the data presented here, 12% ± 5 of all genotyped nestlings annually were sired by a male other than the social father.

Statistical analyses

To assess the survival costs of provisioning behavior, we modeled the binary annual survival in a generalized linear mixed model (GLMM) with a binomial error distribution, one for each sex. Survival was modeled as binomial response variable. Annual provisioning behavior (per hour, averaged per individual over all its broods per year) and its square term were modeled as explanatory variables. Individual identity and year were modeled as random effects. We added age as a continuous covariate to our model. To account for the possibility that parents that survive better may be birds of high quality with both high provisioning behavior and reproductive output (Results), we added genetic recruits as a covariate. All covariates were centered prior to the analysis. We found different results for males and females, and to test whether those sexual differences were significant, we modeled annual survival probability as a function of provisioning behavior and squared provisioning behavior and their respective interaction with sex. We were interested in the absolute costs and benefits of total parental investment for individuals, and therefore, did not correct for the number of hatchlings, for the number of annual broods and also not for the investment of the social mate in this analysis; we simply used feeding visits per hour. However, in additional analyses (not presented) where we used the mean annual provisioning behavior per hatchling instead, or added clutch size as a covariate; the results led to the same conclusions.

To assess the fitness consequences of provisioning behavior in terms of fecundity, we used the number of offspring that were recruited into the breeding population. We restricted our data only to broods that were cross-fostered to distinguish between the effects of individual quality and provisioning behavior. These criteria resulted in 298 observations of 115 pedigreed females and 290 observations of 112 pedigreed males in 4 yr. We used two measurements of reproductive success: First, to assess genetic benefits, we used genetic fecundity. This measure is the number of genetic recruits sired by an individual, including extra-pair offspring per brood for females; and also for males for life-time reproductive success per individual bird. As a second measure, to assess social benefits, we used social fecundity, as the number of social recruits an individual actually reared and provided care for.

We investigated the effect of individual provisioning behavior (feeds h^{-1}) on day 7 on recruits produced in the focal brood in four separate models, two for each sex. Of these two models per sex, we ran one with genetic recruits and the other one with social recruits as the response variable. We modeled the number of recruits as a function of provisioning behavior in GLMMs with Poisson error distribution.

The incremental benefit of more food brought to chicks will be larger for hungry chicks than for those chicks that are well fed. Therefore, we expected that the relationship between provisioning behavior and the number of recruits would reach a plateau at a certain investment, and we therefore tested for a squared effect of provisioning behavior (see also Cleasby et al. 2010). We added bird age and date of egg laying to all our models because it is known that older individuals often have higher reproductive output (Delhey et al. 2003), as do earlier broods (Ringsby et al. 1998). Another study on our population revealed that loud noise from a power generator in one barn affects provisioning behavior and subsequent reproductive output of nestboxes located there, but not parental or territory quality (Schroeder et al. 2012a). We tested a two-level fixed factor for this location (or not) of the nestbox of each brood in all our models, however, it had no effect on top of the effect of provisioning behavior, and we here present results of models without this factor. We modeled bird identity, year and cohort (birth year of the adult) as random effects to account for repeated measures and annual variation.

With a model including bird identity as random effect and repeated measures, we were also able to distinguish between within- and between-individual effects. To estimate the difference between any within- and between subject effects, we added the within-individual mean of provisioning behavior as an explanatory covariate (van de Pol and Wright 2009). This parameter now estimates the difference between within- and between-individual effects, – if it differs significantly from zero, the slopes of both effects are significantly different. In such a model, the estimate of provisioning behavior itself now represents the within-individual effect (van de Pol and Wright 2009). Since we were interested in the absolute effect of provisioning behavior on individual fitness, we chose not to include the number of nestlings in any of our models. It must be noted that our results stayed qualitatively the same when we used the number of hatchlings or, respectively, the number of eggs as additional covariates.

We acknowledge that data on the number of recruits per brood are overdispersed, zero-inflated with a very low mean. However, our justification to use overdispersed Poisson instead of zero-inflated, is that Bayesian methods can accommodate considerably large amounts of overdispersion, not necessarily affecting parameter estimates. To increase confidence in our results, we have also run similar models with zero-inflated Poisson error structures, and the results have remained qualitatively similar, leading to the same conclusions (can be presented on request). Still, the results should be considered with these limitations in mind.

In an additional analysis, we used data containing only sparrows known to be dead, which were either birds found dead, or those assumed to be dead because they were not registered for more than two years. We calculated life-time genetic number of recruits (sum of all genetic recruits, accounting for extra-pair offspring in both sexes) and life-time social number of recruits (sum of all socially reared offspring) of 213 individual birds with known life-history and measured provisioning behavior. We ran two GLMMs each with social and genetic life-time reproductive success parameters as response variables respectively, and life-time provisioning behavior per hour, averaged over all years and broods, and age as covariates. We tested for sex effects and all two-way interactions. We modeled cohort as random effect.

We used Bayesian Markov chain Monte Carlo methods to fit mixed models, which accounts well for overdispersion of count data (Hadfield 2010). We report parameter estimates as the peak of the posterior distribution (posterior mode) and the region of 95% credibility as the interval with the highest posterior density (95% CI) for each fixed effect. We used DIC to decide on the inclusion of random effects, and considered a fixed effect significant if its 95% probability credibility interval (95% CI) did not include zero. We used the R 2.12.1 (R Development Core Team) environment and the package MCMCglmm for our analyses (Hadfield 2010). To increase confidence in our results, we additionally fitted all models again using restricted maximum likelihood methods (REML, not presented) in R with the lme4 package. In all cases, conclusions drawn from the results were identical.

Results

Provisioning behavior

There was no difference in provisioning behavior between the sexes (females: 8.42 ± 3.88 SD visits h^{-1}, males: 8.70 ± 4.59 SD, n = 344). There was no relationship of age with provisioning behavior in either sex (Spearman rank correlation: males: $\rho = 0.01$, $p = 0.86$, females: $\rho = 0.03$, $p = 0.51$, $n = 213$), neither within nor between individuals (linear mixed model, LMM with provisioning behavior as dependent, age as a covariate, bird identity as random: fixed parameter estimates (95% CI): $b_{[mean\ age]} = -0.56$ (-1.46 to 0.18), $b_{[age]} = 0.37$ (-0.05 to 0.93)). Provisioning behavior of males and females of a pair was significantly positively associated (Pearson correlation: 0.31, $p < 0.001$), however, variability was high ($R^2 = 0.10$). We found no association between provisioning behavior and day of season, neither within nor between individuals (linear mixed model explaining provisioning behavior with day of season per bird as covariate and with bird identity and year as random effects: fixed parameter estimates (95% CI): $b_{[day\ of\ season]} = -0.008$ (-0.04 to 0.02), $b_{[day\ of\ season]} = 0.01$ (-0.002 to 0.02)). In the same population, feeding frequency was repeatable, and more so in males ($0.44 < R < 0.66$) than in females ($0.19 < R < 0.35$, Nakagawa et al. 2007).

Life-history traits

On average, birds produced 2.36 ± 1.05 broods yr^{-1} and individuals sired 0.70 ± 0.99 SD genetic recruits yr^{-1}, with no differences between the sexes (Wilcoxon signed-rank test: W = 80325, p = 0.80, n = 213). The average annual mortality probability was similar for both sexes (Chi-square test: $\chi^2 = 0.66$, $p = 0.42$, $n = 213$). Survival probability decreased significantly with age of individual birds (GLMM fixed parameter estimates (95% CI): survival as binary dependent, individual as random effect: $b_{[age]} = -0.28$ (-1.25 to -0.13)), with no difference between the sexes ($b_{[sex]} = 0.36$ (-0.15 to 0.87)).

Costs of provisioning behavior

Annual survival probability was highest for males that fed their brood with an intermediate frequency, and lowest for males that fed their broods more frequently, or not at all (Fig. 1). We found no association between annual survival and provisioning behavior in females (Table 1). We then proceeded and tested for a significant difference between the sexes, by modeling both sexes together with a GLMM, and modeling the interaction of sex with provisioning behavior and squared provisioning behavior as covariates. We found that indeed, the interaction between provisioning behavior square and sex was statistically significant ($b_{[Pb2 \times sex]} = -0.29$ (-0.68 to -0.01)).

Genetic benefits of provisioning behavior – genetic recruits

In females, we found an association of individual quality with provisioning behavior (Table 2): females with higher provisioning behavior had more genetic recruits, despite them being reared by foster parents. While this relationship was apparent at both, the within- and between-individual levels, the difference between both slopes was not significant (Table 2). The quadratic term was negative and statistically

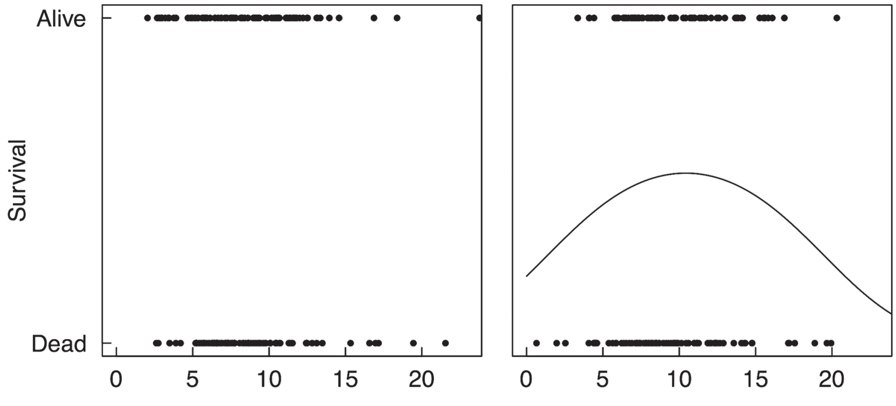

Figure 1. Annual survival of Lundy Island house sparrows in relationship to their average annual provisioning frequency (feeds h^{-1}) on day 7. For males, the line represents model predictions.

Table 1. Binomial GLMM explaining annual survival with parental investment, measured as annual average feeding visit frequency to broods in male and female house sparrows breeding on Lundy Island. Statistically significant effects are indicated in bold.

	Females		Males	
Fixed effects	Estimate	95% CI	Estimate	95% CI
Intercept	1.66	−1.77–24.68	0.07	−0.88–2.42
Provisioning rate	−0.10	−1.19–0.65	0.11	−0.27–0.11
Provisioning rate^2	0.00	−0.30–0.05	**−0.27**	**−0.56–0.01**
Genetic recruits	0.15	−0.30–2.62	0.35	−0.04–0.76
Age	−0.92	−11.27–0.03	−0.16	−2.22–0.11

significant. We found no significant association of provisioning behavior with the number of genetic recruits for males (Table 2).

Social benefits of provisioning behavior – social (reared) recruits

In both sexes the individuals providing more provisioning behavior had more social recruits (Table 3). There was a small, negative significant squared association, which is likely due to the fact that birds can only produce a limited number of offspring (see also methods).

Life-time reproductive success

Genetic life time reproductive success was not related to average annual provisioning behavior of individuals (Fig. 2, posterior mode (95% CI) of effect when in model: $b_{[PB]} = 0.05$ (−3.29 to 2.78); $b_{[sex]} = -0.26$ (−0.54 to 0.09); $b_{[PI2]} = -2.87$ (−40.0 to 32.10), n = 213). No second-order interaction was significant, so we removed those from our final model. Only maximum age was significantly positively associated with life time genetic fecundity (global model, posterior mode (95% CI) $b_{[maximum\ age]} = 0.51$ (0.34 to 0.65)).

However, social life-time fecundity was positively associated with provisioning behavior in both sexes (Fig. 2). Birds of both sexes that provided more provisioning behavior had higher life-time social fecundity, and the beneficial effects of provisioning behavior got less important with a longer life span (posterior mode (95% CI) $b_{[PB]} = 7.21$ (1.55 to 12.20); $b_{[maximum\ age]} = 0.59$ (0.23 to 0.88), $b_{[PB \times maximum\ age]} = -1.68$ (−3.33 to −0.12). Sex had no effect ($b_{[sex]} = -0.11$ (−0.46 to 0.14)).

Table 2. Genetic benefits of provisioning rate in male and female house sparrows breeding on Lundy Island. Results of a Poisson GLMM explaining number of sired recruits with provisioning behavior measured as average feeding visit frequency. Statistically significant effects are indicated in bold.

	Females		Males	
Fixed effects	Estimate	95% CI	Estimate	95% CI
Intercept	**−2.00**	**−3.37–0.79**	**−2.08**	**−3.56–1.07**
Individual mean provisioning rate	−0.04	−0.50–0.08	0.06	−0.36–0.43
Provisioning rate	**0.67**	**0.05–2.77**	0.17	−0.53–1.14
Provisioning rate^2	**−1.06**	**−2.77–0.08**	−0.17	−1.04–0.52
Date	0.11	−0.18–0.39	0.09	−0.16–0.44
Time of day	−0.25	−0.52–0.05	−0.21	−0.58–0.11
Age	0.34	−0.30–0.77	0.16	−0.31–0.59

Table 3. GLMM explaining the number reared recruits of with parental investment, measured as annual average feeding visit frequency to broods in female and male house sparrows breeding on Lundy Island. Statistically significant effects are indicated in bold.

	Females		Males	
Fixed effects	Estimate	95% CI	Estimate	95% CI
Intercept	**−1.64**	**−2.06–1.17**	**−1.51**	**−1.66–1.38**
Individual mean provisioning behavior	−0.23	−0.47–0.08	0.13	−0.04–0.25
Provisioning rate	**2.47**	**1.01–2.66**	**1.05**	**0.94–1.53**
Provisioning rate^2	**−1.66**	**−2.22–0.06**	**−0.85**	**−1.38–0.66**
Date	0.30	−0.08–0.40	0.05	−0.01–0.16
Time of day	−0.06	−0.32–0.15	−0.005	−0.11–0.04
Age	0.22	−0.04–0.43	0.14	−0.10–0.18

Discussion

We show that in a species with bi-parental care, provisioning behavior to altricial young appears to be costly for male parents in terms of survival, while this was not the case in females. Thanks to the cross-foster experiment, we could disentangle genetic fitness benefits from a high quality-providing parent from the social benefit for fitness of the actual provisioning behavior of the parent. Parents who provided their own chicks with high provisioning behavior had higher life-time reproductive success (social recruits), and the direct fitness benefits of provisioning behavior (social benefits) outweighed its costs. It is therefore justified to assume that provisioning behavior in house sparrows is a form of parental investment; that it is costly to parents but the genetic fitness benefits exceed the costs (Williams 1966, Trivers 1972).

We further distinguished between genetic benefits (high-quality parents providing high-quality provisioning behavior, but having high fitness due to their genetic make up not due to the high quality provisioning behavior) and social benefits of provisioning behavior (chicks experiencing high-frequency provisioning behavior being more likely to recruit into the population). We found evidence for genetic benefits in female birds; females that invested more in their current brood had more genetic recruits, even if these young themselves did not receive the parental investment from their genetic mother. There was a significant negative quadratic relationship between female provisioning frequency and genetic recruits. This is likely to be due to the fact that birds cannot increase provisioning frequency unlimitedly, and therefore provisioning frequency will level off at high values. This effect will cause a negative quadratic relationship to appear, where however the right-hand side of the squared effect does not represent biologically meaningful values. Therefore it is reasonable to interpret this relationship as genetic benefits for females, that level off at a certain high provisioning rate.

Offspring of females that showed high provisioning behavior were in some way better equipped to survive until recruitment. This suggests that provisioning behavior is not

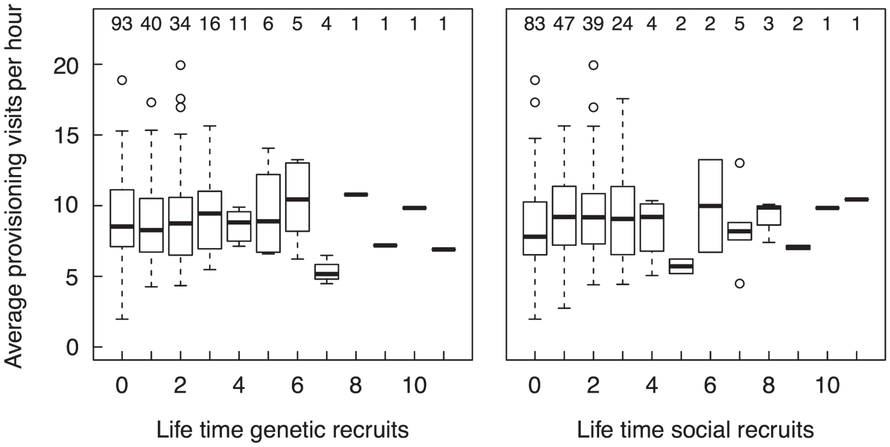

Figure 2. Number of total genetic recruits sired and social recruits reared over the lifespan of Lundy Island house sparrows of both sexes in relation to average provisioning behavior frequency per brood and per hour. Number above the boxplots represent sample sizes of the corresponding bin.

the only component of female house sparrow parental investment, and that a female can pass on benefits to her offspring by other means. However, this ability to do so is apparently correlated with a female's ability to provide care. Such benefits may be direct and/or indirect genetic effects, which could act via nutrient or hormone composition of eggs or incubation behavior (Mousseau and Fox 1998, Cornwallis and Uller 2010). Another option is that this represents an effect of early common environment. Chicks were only cross-fostered on day 2 after hatching, and it may be that the provisioning behavior provided during the first 24–48 h of a bird's life affects fitness prospects of offspring. However, the number of recruits of a male was not significantly associated with his provisioning behavior. If we assume that the importance of provisioning behavior to offspring does not differ relative to the sex of the adult providing it between day 1 and later, then it is unlikely that the provisioning behavior during the first day of a chick's life affected recruitment prospects. We therefore suggest that female house sparrows providing more provisioning behavior are of higher individual quality.

As expected, offspring that experienced more frequent provisioning behavior from their foster parents were more likely to recruit into the population (Cleasby et al. 2010). Given that our cross-foster regime led to a randomized distribution of nestlings to parents, this is likely due to the nutritional effect of differential provisioning of offspring. Our study provides additional evidence for the suggestion that the relationship between provisioning behavior and offspring performance is, at least partly, influenced by the frequency of provisioning (Wright and Cuthill 1989, 1990). A positive association between offspring recruitment and provisioning behavior has been reported previously in the house sparrow (Schwagmeyer and Mock 2008), yet without distinguishing between direct and indirect effects.

It is intrinsically difficult to demonstrate experimentally the costs of provisioning behavior. We found a quadratic relationship between male survival and provisioning behavior, which is likely due to few males, who were in a low body condition (for instance, due to a disease or an injury) and therefore more likely to die, but also not being able to provide frequently to their young.

Our results make use of a cross-foster regime and therewith support the idea that male provisioning behavior is costly in terms of increased mortality in males. Specifically, each extra provisioning visit per hour reduced a male's annual survival probability (by ca 0.036%, Table 1). One explanation may be that provisioning behavior might incur costs through increased exposure to predators (Martin et al. 2000, Tilgar et al. 2011). An individual that makes frequent foraging and feeding trips runs a higher risk of being detected and caught by a predator than does an individual with less exposure time (Eggers et al. 2005). House sparrow males have been shown to be more repeatable in their provisioning behavior than females (Nakagawa et al. 2007). Females are perhaps better able to adjust their provisioning behavior to predator presence than males, and can flexibly avoid predators, while males may take higher survival risks. Such flexibility by females could conceivably involve less frequent provisioning but with larger, and higher quality food items, a strategy that has been shown to exist in house sparrows (Schwagmeyer and Mock 2008). Examining whether such flexibility in provisioning can result in predator avoidance is an interesting avenue for future research.

One study demonstrated previously the survival costs of provisioning behavior in the wild; male, but not female, long-tailed tits *Aegithalos caudatus* that provided less provisioning behavior had subsequently increased survival (Meade et al. 2010). Sex-specific differences in the costs of provisioning behavior have previously been suggested in passerines. Male great tits *Parus major* with clipped wings decreased their feeding, while females continued feeding at the same frequency but lost more body mass (Sanz et al. 2000). This suggests, not only in house sparrows, the costs of provisioning behavior may be greater for males than for females. A difference in the costs of provisioning behavior can lead to differential selection pressures between the sexes (Owens and Bennett 1994). If the costs are more persistent for males, and if males are more predictable carers than females (Nakagawa et al. 2007), then females could use provisioning behavior at a previous occasion as an honest signal of male quality when choosing mates (Schuett et al. 2010). Some behavioural traits in passerines have been recently shown to display moderate heritability, allowing for the possibility that such behaviour can be under selection (van Oers et al. 2004, Charmantier et al. 2007). Therefore, it is possible that provisioning behavior, and any correlate of it, may influence female choice (Wolf et al. 1998, Schuett et al. 2010). If this would be the case, females choosing mates that provide high-quality care can assure social fitness benefits for both her intra- and extra-pair offspring. Males would benefit from honest signaling of their provisioning behavior qualities because they may be better able to compete for high quality females, who confer genetic benefits. Obviously, more research should be done, – it is for instance, necessary to account for the behavior or the partner, its mate choice and parental investment, and to determine the amount of such variation caused by direct and indirect additive genetic effects (Dor and Lotem 2009).

Individual quality can confound measures of trade-offs of parental investment, and the results of our study highlight that such complexities should not be ignored (van Noordwijk and de Jong 1986). Our study provides support for the idea that provisioning behavior can indeed be seen as a form of parental investment sensu Trivers (1972), and that it can act as an honest signal of mate quality. The strength of our work is that it provides estimates for the benefits and potential costs of provisioning behavior without manipulating workload, which can be problematic in wild populations. Furthermore, since genetic fitness benefits differ by sex, selection pressures on parental investment may act antagonistically on both sexes, which allows for the evolution of sexual dimorphism in parental investment behavior in the context of sex-dependent selection.

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