

Reproductive success and individual variation in feeding frequency of House Sparrows (*Passer domesticus*)

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Abstract Parental care is assumed to be closely associated with individual differences in reproductive success. We investigated how feeding frequencies varied among parents and how this affected the subsequent reproductive success in insular populations of House Sparrows *Passer domesticus* in northern Norway. Female parents fed their offspring more than male parents did, and the feeding rates were positively related to the feeding rates of the partner. A positive relationship between feeding rates and bill depth was present in females. In males, the feeding rates were negatively related to total badge size and positively related to visible badge size, after the effect of other variables had been taken into account. A non-linear convex relationship between feeding frequency and hatch day was present in males, which could reflect either the seasonal change in weather conditions or the seasonal variation in food availability. For both sexes, feeding frequencies increased with increasing brood size, but at the same time the average feeding rate per nestling decreased with increased brood sizes. Finally, our results indicate that the amount of parental investment, measured as feeding rates during the nestling stage, may have a positive long-term influence both on the number of fledglings that recruit as well as the probability that fledglings survive until recruitment.

Keywords Feeding rate · House sparrow · Micro transponder · *Passer domesticus* · Parental care · Reproductive success

Introduction

Parental care, which is defined as any form of parental behaviour that appears likely to increase the fitness of the offspring (Trivers 1972), is expected to be closely associated with individual variation in reproductive success. Variation in parental care has been found to explain substantial components of the variation in individual fitness in several species (Clutton-Brock 1991). However, although parental care clearly must affect offspring fitness, little is known about the quantitative relationship between parental investment and the fitness of offspring, and how this varies with environmental conditions (Clutton-Brock 1991; Lewis et al. 2006).

The physical condition of individuals is often shown to be correlated with life-history traits; as such, the former may function as a proxy for fitness (e.g. Kacelnik and Cuthill 1990; Blums et al. 2005). It has been found that parents in good body condition may allocate more resources to the current breeding attempt than those in poor body condition (e.g. Drent and Daan 1980; Ankney et al. 1991; Erikstad et al. 1993; O'Dwyer et al. 2006). The results of several bird studies have revealed that parents with high body mass, large body size or in good body condition raise chicks which grow faster and survive better than chicks of smaller parents (e.g. Perrins and Moss 1975; Högstedt 1980; Mills 1989; Sæther et al. 1993; Weimerskirch et al. 1995; Wendeln and Becker 1999). For example, the body condition of male Antarctic Petrels *Thalassoica antarctica* correlated significantly with the growth rate of the chick,

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suggesting that “good” parents were better at finding food of higher energetic quality than “poor” parents (Lorentsen 1995, 1996; Varpe et al. 2004; for Snow Petrel *Pagodroma nivea*, see Tveraa and Christensen 2002). Parental care, when measured for example as feeding frequency, may also involve a heritable element, as indicated by Nakagawa et al. (2007) who found that within- and between-year repeatabilities in the feeding rate were high in males but moderate to low in females.

Elaborate ornaments are found mainly among males within several taxa, such as insects, fish, birds and mammals. These are believed to be under the influence of both natural and sexual selection, such that individuals with larger ornaments generally have higher reproductive success (Andersson 1994; Jensen et al. 2004; Andersson and Simmons 2006). However, different routes lead to such a pattern (Badyaev and Qvarnström 2002; Fueller et al. 2005; Kokko et al. 2006). Some models for sexual selection assume a positive relationship between ornament size and the male’s general genetic quality or condition (Zahavi 1975; Schlüter and Price 1993; Andersson 1994; Iwasa and Pomiankowski 1994; Rowe and Houle 1996; Iwasa and Pomiankowski 1999). Thus, if a secondary sexual trait has a function as a quality indicator of individuals, the signal should be “honest” and therefore costly to bear (Zahavi 1975, 1977; Kodric-Brown and Brown 1984; Grafen 1990; Borgia 1993; Griffith et al. 1999a).

The ornamental black breast badge in male House Sparrows (*Passer domesticus*) has been found to be under sexual selection, playing a role in both intra- and intersexual selection (Møller 1987a, b, 1988, 1989, 1990; Veiga 1993, 1995, 1996; Solberg and Ringsby 1997; Griffith et al. 1999b, Voltura et al. 2002; Jensen et al. 2008). This black badge is positively related to age (Jensen et al. 2004, 2006; Anderson 2006), and it has been shown to be costly to produce and influenced by nutritional constraints (Veiga and Puerta 1996; Buchanan et al. 2001), being induced by such variables as environmental variation. Jensen et al. (2006) found that a positive effect of temperature during moult explained close to 40% of the variance in size of the visible badge of 1-year-old House Sparrow males. In an experimental study, Griffith (2000) demonstrated that individual birds that invested highly into current reproduction (i.e. by experimentally enlarging clutch size and thus increasing expected energy expenditure) developed a smaller total badge size the subsequent breeding season. These results suggest that the badge size in male House Sparrows is the consequence of energetic trade-offs in which nutritional resources are allocated either into enlargement of the size of the breast badge or towards other energy-demanding processes, such as parental care. The badge can therefore be considered as an “honest” signal of male quality, including male age (Anderson 2006).

Accordingly, Griffith et al. (1999a) found that males that invested more in current reproduction were more attractive to females, as they showed a preference for males with smaller badges. However, other studies have shown that males with intermediate badge size invested most into parental care (Vaclav and Hoi 2002). Equivocal relationships between an ornament and parental investment (i.e. direct benefits) are also common in other species (Hadfield et al. 2006). Thus, the link between paternal care and size of the ornament is still not fully understood (Anderson 2006).

Season and climate may affect food availability as well as the energetic demands of both parents and offspring (Royama 1966; van Balen 1973; Siikamäki 1998; Bradbury et al. 2003; Visser et al. 2004) by, for example, affecting prey size and abundance (e.g. Curio 1959; Royama 1966; van Balen 1973; Kuitunen et al. 1996; Freitag et al. 2001). The relative feeding frequency of the sexes can also vary within the season due to variations in food supply (Kuitunen et al. 1996). Studies of the Great Tit (*Parus major*) and Blue Tit (*Parus caeruleus*) have demonstrated that the feeding frequency increases with increasing food abundance and size of prey, resulting in a higher growth rate and fledgling mass due to the higher rate of food delivery to the nest (Naef-Daenzer and Keller 1999). However, both Royama (1966) and van Balen (1973) recorded an inverse relationship between feeding frequency and prey size, indicating that the parents increased the feeding rate to compensate for smaller prey (see also Grieco 2002; Kohler et al. 2006). In contrast, based on a study of House Finch *Carpodacus mexicanus*, Nolan et al. (2001) suggested that the number of feeding visits to the nest was a reasonable predictor of the mass of food provided to the nestlings. In terms of the House Sparrow, another factor that has been shown to influence feeding rates in passerines is the number of nestlings in a brood and their age (e.g. Gibb 1955; Royama 1966; Clark 1984). Large broods are expected to have higher total energetic demands than small broods, as well as lower demands for brooding due to more efficient heat conservation (Gibb 1955; Royama 1966; Dunn 1976; Krystofkova et al. 2006). Accordingly, several adaptive mechanisms have been described that influence parental feeding frequencies, which ultimately increases the reproductive output of the parents.

In the study reported here, we have examined factors that influence individual variation in parental care, using the parental visiting rate to nestlings as a proxy that presumably reflects the feeding rate per hour in insular House Sparrow populations in northern Norway, and studied whether variation in feeding rate can explain components of variation in reproductive success. More specifically, we first examined whether parental feeding frequency was influenced by reproductive characteristics, such as brood size and age of nestlings. In a series of analyses we then related variation in climate conditions and hatch day to the

parental feeding frequencies and studied whether individual variation in feeding frequencies were related to phenotypic traits of the mother and the social father. We also examined whether variation in feeding rates influenced the body mass of the nestlings at 5 and 10 days of age as well as the number of fledglings and recruits produced.

Materials and methods

Study area

The fieldwork was conducted in 1996 on five islands (Hestmannøy, Indre Kvarøy, Ytre Kvarøy, Nesøy and Gjerøy) in an archipelago off the coast of Helgeland in northern Norway (66°30'N to 66°40'N, 13°E) (see map in Ringsby et al. 2002). The inhabited islands, varying from approximately 2 to 16 km² in area, have small populations of House Sparrows. The House Sparrows generally live in the vicinity of farms, where they breed in nest sites inside barns and silos, commonly underneath the ceiling or, if outside, underneath the roof. At the time of the study, the breeding population sizes varied between the islands, from a minimum of 16 birds on Nesøy to a maximum of 65 individuals on Hestmannøy (for further details see Sæther et al. 1999). Adult birds were captured by mist-nets, measured for phenotypic traits (see below) and ringed with an individually numbered metal ring (supplied by Stavanger Museum, Norway). Unique combinations of coloured plastic rings were attached to the tarsi, which allowed for individual recognition of the birds in the field.

Feeding frequencies

A microtransponder (Trovan ID 100; <http://www.trovan.com>) with an individual specific code was placed within a soft plastic tube (1 cm long, 2.5 mm in diameter), which was sealed with glue at both ends and then glued to the plastic rings on one leg. This microtransponder-unit was attached only to adult birds.

Recording feeding frequencies

Antennae were installed in the nest entrances. Their rectangular size (8.5 × 5.5 cm) and their registering distance (approx. 4.0 cm around the antenna) covered a volume of approximately 330 cm³ over the antenna when placed on the floor of the nest entrance. Thus, the possibility that a bird would not be registered while visiting the nest was close to zero. By using a stationary data logger, we recorded the timing of the visits by each individual parent to the nest. In order to avoid registrations in which the birds were not bringing any food, but were sitting on the antenna

and transmitting signals continuously, we programmed a 30-s time lag between successive registrations for the same individual. This enabled use to ignore registrations within an interval of less than 30 s.

The use of the microtransponder technique to collect individual feeding frequencies enabled the number of nest visits to be registered with high accuracy. We therefore assume here that the feeding frequency is a proxy for the amount of parental effort provided in a nest as well as the amount of food provided to the offspring.

Measuring phenotypic traits

Body mass was measured using a 50-g Pesola spring balance (to the nearest 0.1 g). Wing length was measured using a ruler with an accuracy of 0.5 mm (Svensson 1992). Tarsus length, bill length and bill depth were all measured to the nearest 0.1 mm using a Vernier slide calliper (Svensson 1992; Solberg and Ringsby 1997). For adult males, two types of badge measurements were taken. The first was total badge size, which was the area covered with black feathers and with feathers with black bases and light-grey feather tips. The area was estimated using the regression equation developed by Møller (1987a, b): badge size (mm²) = 166.7 + 0.45 [badge length (mm) × badge width (mm)]. The second was visible badge size, which was the area covered with black feathers without light tips. The size of this area was estimated using the same equation as for total badge size (Møller and Erritzøe 1992; Solberg and Ringsby 1997; Jensen et al. 2004). Both measurements of badge size were adjusted by taking the square root in order to transform the values towards the same mean and variance as the other phenotypic traits.

All measurements used in the analyses were taken during the period May–August 1996. Individuals captured more than once were measured each time they were caught, and the average of all measurements were used in the analyses. We accounted for individual variation in measurement techniques among fieldworkers by using linear regression techniques (see Jensen et al. 2004, 2006).

For nestlings, we recorded hatching day, where 1 May was set to day 1 in the breeding season. Morphological traits (i.e. tarsus length, wing length and body mass) of nestlings were measured twice, first at the age of approximately 5 days and, secondly, at the age of approximately 10 days. All nestling measurements were taken between the age of 3 and 13 days. Based on the predicted age-specific relationship of individual morphological nestling traits, we adjusted the sizes to the age of 5 and 10 days, respectively, using regression techniques. At the first visit, the nestlings were ringed with an individually numbered metal ring, and at the last visit, the fledglings were individually marked with coloured plastic rings.

Table 1 Pearson correlation coefficients (r_P) between phenotypic traits within social fathers (above the diagonal, $n = 24$) and social mothers (below the diagonal, $n = 21$) of House Sparrows in northern Norway

	Body mass	Tarsus length	Wing length	Bill length	Bill depth	Total badge size	Visible badge size
Body Mass		0.298	0.507*	-0.098	0.317	-0.010	0.113
Tarsus length	0.192		0.215	-0.081	0.393	-0.120	0.127
Wing length	0.141	-0.045		0.256	0.481*	0.374	0.212
Bill length	-0.265	0.007	-0.323		0.449***	0.196	0.426*
Bill depth	0.024	0.122	-0.117	-0.114		0.252	0.216
Total badge size							0.668***

Asterisks indicate significant correlations: * $P < 0.05$, *** $P < 0.001$

Fledglings produced during the 1996 season that were recaptured or resighted later than 1 April 1997 were defined as recruits. In addition to the five study islands, the search for recruits also included 13 surrounding islands where the arrival of immigrants was closely monitored during the years following the study (see Altwegg et al. 2000).

Significant positive correlations were present between several morphological traits in males, with the strongest relationships between total badge size and visible badge size, and between bill length and bill depth. No significant relationships were present between female traits (Table 1).

In all clutches where the social mother was known, the female was the genetic mother (Jensen et al. 2003, 2004).

Climate data

We used the average climate data from two weather stations run by the Norwegian Meteorological Institute within a radius of 20 km from the study area (see Fig. 1 in Ringsby et al. 2002). These data included average temperature ($^{\circ}\text{C}$), maximum wind strength (m/s) and the total amount of precipitation (mm) per day. The different climatic factors were strongly inter-correlated and were also significantly related to the seasonal day number. Thus, there was an increase with season in temperature ($r_P = 0.734$, $n = 102$, $P < 0.001$) and a decrease in the amount of rainfall as the season progressed ($r_P = -0.286$, $n = 102$, $P < 0.05$). In addition, there was a negative correlation between temperature and precipitation ($r_P = -0.401$, $n = 102$, $P < 0.001$). Note that these correlations are based on climate data from the 102 days during the breeding season in 1996 when feeding frequencies were recorded.

Statistical analyses

Sample sizes

As feeding frequency can differ diurnally (e.g. Gibb 1955; von Haartman 1969), we included data collected between

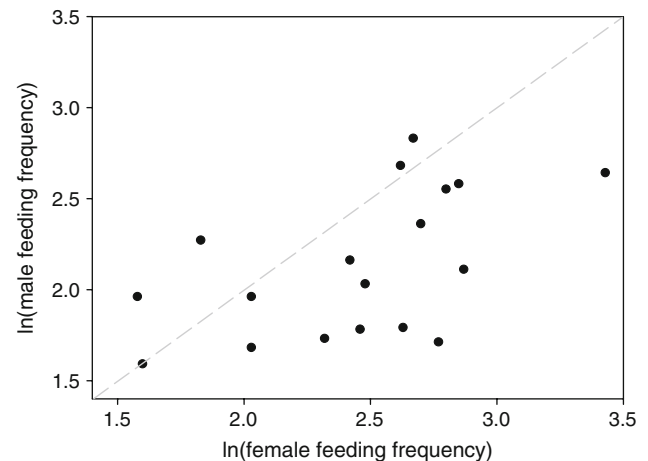


Fig. 1 The relation between the logarithm of the feeding frequencies (number of feedings per hour) of social parents in House Sparrow populations in northern Norway. The dotted line represents a regression line with a rate of increase equal to one. Accordingly, as most data points are below the dotted line, this indicates that the female mate feed on average more than males

6:00 a.m. and 12:00 a.m. For most nests, the recordings of feeding frequencies were initiated when the nestlings were at the age of 5 days and lasted until the nestlings were about 10 days of age. However, in some nests, the recording period was initiated earlier than 5 days of age, and in a number of nests, the recording period was prolonged for some days after 10 days of age, depending on practical limitations and the technical capacity. On average, feeding rates were recorded for 3.96 (SD = 1.90) days per nest ($n = 25$). Correspondingly, each nest was on average recorded for 4.40 (SD = 1.62) h per day between 6:00 a.m. and 12:00 a.m. Feeding rates were recorded in 25 clutches. Data on daily average feeding rate from the social male were obtained from 24 clutches for an average of 4 days (see above) from the period where nestlings were between 5 and 10 days of age. As such, data on feeding rates from the social female were obtained from 19 clutches. A few parents had two clutches during the breeding season, and the absolute number of social males and social females recorded was 19 and 16, respectively.

We based the analyses on balanced data—i.e. that no missing values are present for any of the variables under examination. Accordingly, we recorded the analyses of daily variation in male feeding frequencies, which included 24 clutches and involved 96 daily means of recorded feeding frequency. Correspondingly, for females, there were 18 clutches, with a total of 75 daily means of feeding frequency. By including nest identity as a random factor, we accounted for the dependency generated within the data due to repeated daily sampling within a nest during the 5-day period from 5 to 10 days of age. However, we did not account for the potential bias due to five male parents and two female parents, respectively, who were represented with two clutches each during the breeding season. The reason for this was that our aim was to reduce the number of parameters present in the statistical models (Burnham and Anderson 2002). In addition, because the number of second clutches was limited in this data set and the second clutch typically was laid 4–6 weeks later in the season than the first clutch, we assumed that the bias due to this dependency was of minor importance.

Variation in male and female feeding rates

To examine which factors were affecting variation in male and female feeding rates, we applied generalized linear mixed models [lmer procedure, REML, R 2.4.0; R Development Core Team (2007)] in which feeding rates [transformed to natural logarithms (ln)] were included as the response variable. Unbiased parameter estimates and uncertainties in cases where mixed models were applied were obtained using restricted maximum likelihood methods (REML, R 2.4.0, lmer procedure). To evaluate the significance of the explanatory variables in generalized linear mixed models (lmer, R 2.4.0), we applied the procedure “mcmcsm” (R 2.4.0). This is a generic function that generates a sample from the posterior distribution of the parameters of a fitted model using Markov Chain Monte Carlo methods. Then, based on the 95% quantiles, we extracted a lower (LCL) and an upper (UCL) 95% confidence limit (CL), respectively. In this report, the LCL and UCL are given in parenthesis (i.e. LCL, UCL). If the CL of a parameter does not include zero, the parameter estimate is regarded as being significantly different from zero (i.e. $P < 0.05$).

Tests of normality of the residuals of male and female feeding rates (ln-transformed) showed no deviance from normality in a Kolmogorov–Smirnov test ($P > 0.1$ for both sexes). Accordingly, we applied a Gaussian error distribution for these models.

Size and growth of nestlings between age 5 and 10 days

The relationship between the nestling size and feeding rate was examined by focusing on nestling body mass at the age

5 and 10 days, respectively, as this parameter is known to be largely influenced by the current food supply (e.g. Gibb 1955; Royama 1966; Clark 1984) and to affect future fledgling survival (e.g. Ringsby et al. 1998, 1999, 2002).

We obtained data on both male and female feeding frequencies as well as nestling sizes in 18 clutches. However, in five of these clutches some of the nestlings died during the period for which feeding rates were recorded (i.e. between age 5 days and 10 days). We tested whether there was a relationship between feeding rate and mean body mass as well as the change in mean body mass from age 5 to 10 days. Kolmogorov–Smirnov tests revealed that the residuals of all variables expressing variation in nestling body mass did not deviate from normality ($P > 0.1$).

Measuring reproductive success

We investigated whether the sum of both parents' feeding visits per hour could explain the reproductive success, estimated as the number of fledglings recorded at day 10 of age. Here we applied generalized linear models [glm() procedure, Poisson error term, R 2.4.0] and included only nests where no loss of nestlings had occurred. This reduced the data set from 18 clutches to 13 clutches. Correspondingly, we also tested whether the feeding frequency of the social parents influenced the probability of survival during the period from 5 to 10 days of age (glm, binomial error term, R 2.4.0). For this latter study, we included 18 clutches in the sample.

As a last step, we analysed whether the sum of the feeding effort of both parents could explain the number of fledglings that recruited into the breeding population of the natal or a neighbouring island 1 year later (glm, Poisson error term, R 2.4.0) and, correspondingly, the probability that a fledgling survived until recruitment 1 year later (glm, binomial error term, R 2.4.0). Due to low sample sizes and the urge to minimize the number of model parameters, we did not account for differences in sampling effort among islands in the analyses.

Results

The average recorded feeding rate was 9.98 (SD = 5.95) visits/h for males ($n = 24$) and 13.64 (SD = 5.95) visits/h for females ($n = 19$). The estimates were based on all recorded visits of males and females, respectively, between 6:00 a.m. and 12:00 a.m. during the time period when chicks were 5–10 days old. Thus, females had a significantly higher feeding rate per hour than males, both within pairs (paired Wilcoxon signed rank test $Z = -2.504$, $P = 0.012$) as well as in general (Mann–Whitney $U = 140.0$, $P = 0.031$). The Levene test of homogeneity

of variances confirmed that the variance in feeding frequencies (ln-transformed) did not differ among sexes ($P > 0.1$). There was also a positive correlation between male and female feeding frequencies within pairs ($r_p = 0.544$, $n = 18$, $P = 0.02$, Fig. 1)—females with high feeding rates had therefore paired with social male partners who were also good feeders.

The influence of number of nestlings, nestling age and seasonality on feeding rate

We first examined whether the feeding rates of the parents were influenced by the age and number of nestlings in a clutch. The model that we used included both the first and the second order terms of nestling age and number of nestlings, respectively. Because we had recorded feeding frequencies over several days within the same nests, and collected data from five islands, we accounted for this potential bias in sampling variance by including both nest identity and island as random factors.

For females, there was a significant convex relationship between feeding frequency and the number of nestlings in the clutch. This result indicated that intermediate brood sizes of three nestlings had the highest maternal food provisioning rate [$b_1 = 0.759$, $SE = 0.245$, $t = 3.099$, $CL (0.273, 1.247)$; $b_2 = -0.117$, $SE = 0.041$, $t = -2.849$, $CL (-0.200, -0.035)$], where b_1 and b_2 denote the regression coefficients of the first and second order terms of the explanative variable, respectively. However, there was no significant effect ($P > 0.1$) of the age of the nestlings on the mothers' feeding rate.

Correspondingly, for males, there was a positive linear relationship between the number of nestlings and their feeding frequency [$b_1 = 0.153$, $SE = 0.068$, $t = 2.249$, $CL (0.009, 0.300)$], whereas no such relationship existed between the feeding frequency of males and the age of nestlings.

We then explored the influence of climatic and seasonal variables on the variation in feeding frequencies by including climatic variables (daily mean temperature, precipitation and wind strength) as well as hatch day and (hatch day)² in the generalized linear mixed models (lmer, Gaussian error term, R 2.4.0). When analysing the seasonal effects on male and female feeding frequencies, we accounted for the non-linear effect of the number of nestlings in females as well as for the linear effect of the number of nestlings in males, respectively. For both males and females, we accounted for nest identity and island identity, which were included as random effects.

In both females and males, there was a non-linear convex effect of hatch day on feeding frequencies, suggesting that the feeding frequencies of both sexes were higher in the middle of the breeding season compared to earlier or

later in the season [females $b_1 = 0.095$, $SE = 0.031$, $t = 3.000$, $CL (0.030, 0.163)$ and $b_2 = -0.001$, $SE = 0.0002$, $t = -3.176$, $CL (-0.001, -0.0003)$; males $b_1 = 0.083$, $SE = 0.033$, $t = 2.469$, $CL (0.003, 0.156)$ and $b_2 = -0.0008$, $SE = 0.0003$, $t = -2.570$, $CL (-0.001, -0.00001)$].

There were no significant relationships between any of the climatic variables (temperature, wind strength and precipitation) and the recorded feeding rates.

Parental morphology and feeding frequency

To evaluate the effect of the mother's morphological characteristics on her feeding rate, we evaluated the linear effect of each trait in separate models. Here also we accounted for the non-linear effects of the number of nestlings and hatch day (according to the findings above) in addition to including nest identity and island as random factors. The results suggested that females with deep bills had the highest food provisioning rate (Table 2). No significant relationships were found between either tarsus length, body mass, wing length, bill length and the females' feeding rate, respectively.

For males, we evaluated the effect of the social male's morphological characteristics on their feeding rate by examining the linear effect of each male trait in separate models. The models accounted for the linear effects of the number of nestlings and the non-linear effect of hatch day (according to the findings above) in addition to including nest identity and island identity as random factors. The results revealed that there was no significant linear effect of any of the male traits on the male parent's feeding frequency. However, when both total and visible badge size were included in the model, the results suggested a substantial positive effect of visible badge size in addition to a negative significant effect of the total badge size (Table 2). Based on this result, the best male-feeders had small but distinct black badges.

The effects of feeding frequency on nestling body mass and growth

For the following analyses we included only nests ($n = 13$) in which no mortality was recorded during the study period (i.e. 5–10 days of age) to exclude variation in feeding rates caused by change in brood size due to mortality.

Positive, but non-significant relationships were present between the average body mass of nestlings (both at 5 and 10 days of age) and the total (i.e. the sum of) feeding rates of their parents [Table 3, (a) and (b)]. In contrast, there was no effect of the feeding rates of both parents on the change in mean body mass from age 5 to age 10 days [Table 3, (c)]. Although not significant, there was also a tendency

Table 2 Parameter estimates (*b*) for morphological traits influencing female and male feeding rates^a in House Sparrows in northern Norway

Response variable	Explanative variables	<i>b</i>	SE	<i>t</i>	LCL	UCL
Female feeding rate	Intercept	−6.155	2.280	−2.699	−10.779	−1.572
	Bill depth	0.972	0.284	3.411	0.400	1.546
	Number of nestlings	0.455	0.174	2.605	0.109	0.820
	(Number of nestlings) ²	−0.063	0.029	−2.151	−0.126	−0.005
Male feeding rate	Intercept	3.996	2.072	1.928	0.043	7.462
	Total badge size	−0.424	0.139	−2.042	−0.655	−0.162
	Visible badge size	0.299	0.099	3.008	0.119	0.472
	Hatch day	0.062	0.029	2.095	0.009	0.117
	(Hatch day) ²	−0.0006	0.0003	−2.271	−0.001	−0.0001
	Number of nestlings	0.207	0.062	3.315	0.089	0.314

The table includes the standard error (SE) and *t* values of the parameter estimates. Lower and upper 95% confidence limits for each estimate are given (LCL and UCL, respectively). When the confidence interval of the parameter does not include zero this indicates that the factor differs significantly from zero at the 5% level

Sample size: females *n* = 75; males, *n* = 96

^a Feeding rates were recorded per hour and log-transformed

Table 3 Parameter estimates (*b*) for the relationship between the total feeding rate (explanative variable) within pairs on six different measures (denoted a to f) of nestling size and growth (response variable) of house sparrows in northern Norway

Model	Response variable	<i>b</i>	SE	<i>t</i>
(a)	Mean body mass (age 5 days)	6.356	3.295	1.929 [#]
(b)	Mean body mass (age 10 days)	5.076	3.314	1.620
(c)	Change in mean body mass	−1.280	2.916	−0.439
(d)	Change in total nestling mass in clutch	23.34	11.96	1.952 [#]
(e)	Total nestling mass in clutch (age 5 days)	66.46	15.75	4.220 ^{**}
(f)	Total nestling mass in clutch (age 10 days)	89.80	20.94	4.289 ^{**}

The size of nestlings was measured as the individual mean body mass at age 5 and 10 days as well as the total sum of the nestling mass within a clutch, both at age 5 and age 10 days. Nestling growth was measured as the mean of the individual change in body mass and as changes in total nestling mass within a clutch. All feeding rates were ln-transformed

Only clutches where no nestling mortality occurred were included, i.e. *n* = 13. We applied simple generalized linear models with normal error distribution

***P* < 0.01, [#]*P* < 0.1

that the change in total nestling mass in a clutch from age 5 to age 10 days was positively influenced by the sum of the parental feeding rates [Table 3, (d)]. There was also a positive relationship between the sum of parental feeding and the total nestling mass, both at age 5 and 10 days, respectively [Table 3, (e) and (f)].

The absolute number of feeding visits paid by the parents increased for larger broods (*r_P* = 0.700, *P* < 0.01, *n* = 13; see also Fig. 2a; Table 3). However, when we divided the total number of feedings per hour by the number of nestlings present in a brood, the per capita feeding rate was strongly negatively related to the number of fledglings (*r_P* = −0.862, *P* < 0.001, *n* = 13; Fig. 2b). Thus, the larger the clutch, the lower the average feeding rate per nestling. In light of this result, one could expect the mean fledgling size to be smaller in large broods than in

small broods, due to fewer feeding visits per nestling in larger broods. However, no such negative relationship was found for body mass at 5 or 10 days of age, respectively (*P* > 0.1, *n* = 18, glm, Gaussian error-distribution, R 2.4.0 for both analyses).

The influence of feeding rate on nestling survival from age 5 to age 10 days

The results revealed that there was no significant linear relationship between the total parental feeding rates and the number of fledglings produced (*P* > 0.1, *n* = 18, glm, Poisson error distribution, R 2.4.0). However, one influential data point (marked with an arrow in Fig. 3a) seemed to mask a positive relationship. A reanalysis of the data without this data point revealed a tendency that

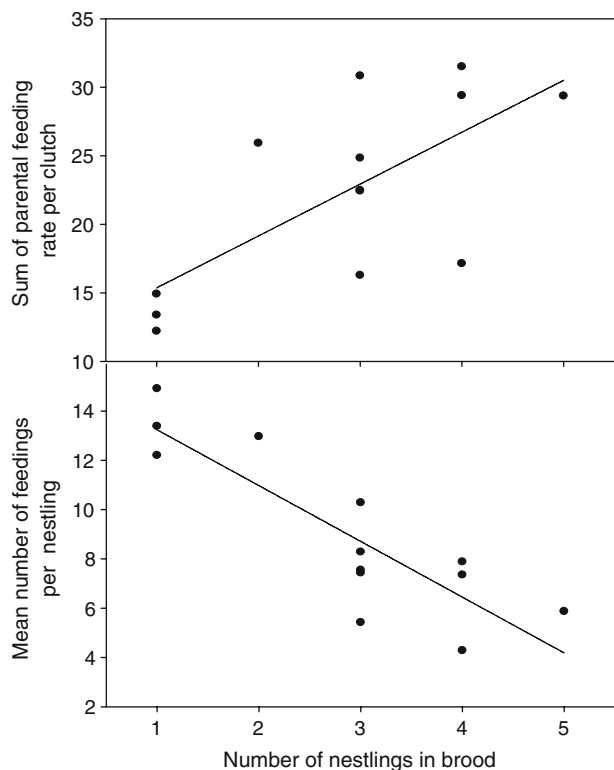


Fig. 2 **a** Sum of the feeding rates of House Sparrow parents in northern Norway (measured as the sum of visits per hour) in relation to the number of nestlings in broods, **b** relation between the feeding rates of the parents per nestling (i.e. the sum of feedings/brood size) and the size of the brood

the number of nestlings in a nest that survived to fledging increased with the sum of the parental feeding rates ($b = 0.784$, $SE = 0.432$, $Z = 1.816$, $P = 0.069$, $n = 17$).

The influence of feeding rate on recruitment

There was a positive relationship between the number of recruits produced in a brood and the sum of the parental feeding rates ($b = 3.103$, $SE = 1.406$, $Z = 2.207$, $P = 0.027$, $n = 18$, glm, Poisson error distribution, R 2.4.0, in a model including island as a random factor; Fig. 3b).

We also found a positive, but non-significant tendency that the sum of the parental feeding rates influenced the probability of recruitment ($b = 3.579$, $SE = 1.859$, $Z = 1.925$, $P = 0.054$, glm, binomial error distribution, R 2.4.0, including island as a random factor). Accordingly, our results suggest that the amount of parental investment, measured as feeding rates during the nestling stage, may have a positive long-term influence both on the number of fledglings recruited and the probability of fledgling survival until recruitment.

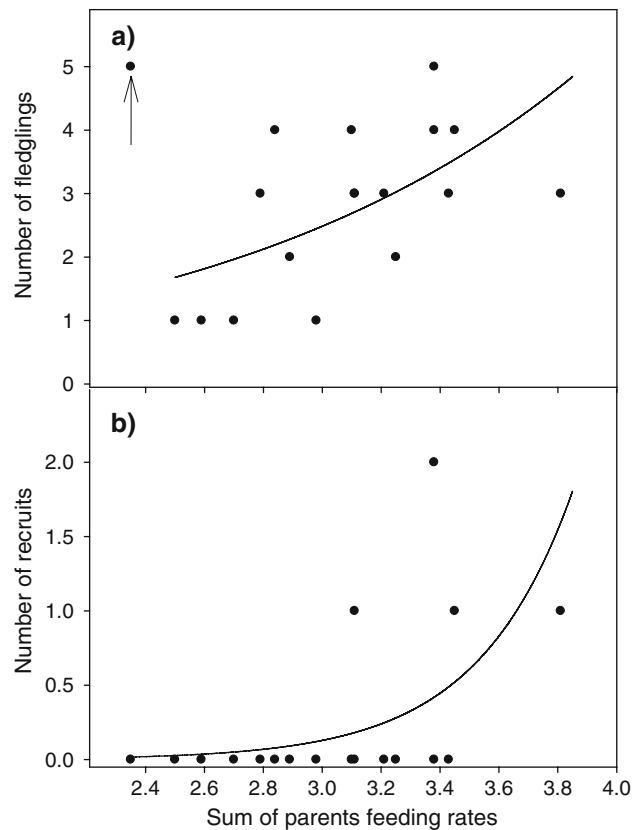


Fig. 3 The number of fledglings (**a**) and the number of recruits to the following year (**b**) in relation to the parents feeding effort in House Sparrows in northern Norway. The regression lines were generated by Poisson regression analyses. The graph in **a** reveals a strong tendency for a positive rate of increase ($P = 0.069$) between the sum of the parents feeding rate and the number of fledglings in the brood. Note that the arrow in **a** denotes an outlier that was omitted when estimating the parameters of the regression line. A corresponding significantly positive rate of increase was present in (**b**) ($P = 0.027$)

Discussion

We have demonstrated that it is possible to predict one important component of parental investment, the feeding rate of the social parents, on the basis of their morphological characteristics. Mothers with deep bills and social fathers with a relatively small total badge and a relatively large visible badge were feeding their nestlings more frequently (Table 2). Furthermore, the mean feeding frequency per hour among both parents was positively related to the number of nestlings in the clutch (Table 2) and there was a strong tendency (but not significant) that the probability of survival for a fledgling until recruitment was positively affected by the total parental feeding rate per hour. However, there was a positive relationship between the summed feeding rates of a pair and the number of recruits they produced. Thus, the results of our study suggest that the feeding frequency of House Sparrow

parents may function as a proxy of parental care closely related to female morphology and sexually selected traits in males.

Male feeding rate and badge size

Our results suggest that the male feeding rate was affected negatively by the total badge size per se and positively by the visible badge size per se (Table 2). As the overall phenotypic correlation between visible and total badge size was positive (Table 1), this result suggests that the relative size of the visible badge size, given the size of the total badge, and vice versa, can be important predictors of a male's food provisioning rate to nestlings. A similar pattern was reported by Voltura et al. (2002) who showed that male visible badge size (measured from photographs) was associated with a tendency to bring a relatively larger proportion of the total food provisions to the nestlings.

Interestingly, the visible badge size is to a large extent determined by each male's activity level, in terms of abrasion of the grey feather tips and preening behaviour in the spring and early summer, resulting in exposure of the underlying black feathers (Møller and Erritzøe 1992). This suggests that if the badge size of males have a function as an honest signal to females about the male's ability to invest in current reproduction, one should expect the badge to be costly to produce or carry (Andersson 1994; Getty 1998). This is supported by the study of Veiga and Puerta (1996) who found the reduction of blood proteins during moult to be negatively correlated with badge size after moult in juveniles.

We have previously reported that lifetime reproductive success is positively correlated with total badge size in males in the same study population (Jensen et al. 2004). Similarly, based on a 10-year study of the same population in northern Norway, Jensen et al. (2008) found that there was generally positive selection on total badge size of males—to a large extent because males with larger badges had a higher number of mates. All though our results may at first sight seem to contradict those of Jensen et al. (2004, 2008), they could rather be looked upon as complementary because the individual variation in feeding frequency is only one fitness-related component of the parents. In support of this latter hypothesis, Jensen et al. (2008) did not find any significant selection acting on badge size using annual production of recruits as the fitness measure. Furthermore, other individual properties, such as the variance in longevity, dominance in winter flocks (Møller 1987b; Solberg and Ringsby 1997) or properties enhancing the probability of achieving extra-pair paternity (unpublished data), have also been shown to correlate with male badge size. These results suggest that the component of variation addressed in our study—the relationship between feeding

frequency, badge size and reproductive success—may be concealed by these overall long-term patterns involving other components of fitness, which are positively correlated to male badge size. Nevertheless, our results indicate that the sexually selected ornament of the House Sparrow male is a complex trait that signals direct benefits in terms of parental care, as measured in terms of feeding rates (e.g. Hadfield et al. 2006).

Female feeding rate and bill depth

We found the feeding frequency in females to be positively linked to bill depth (Table 2). Some bird studies have reported bill shape to be closely adapted to an efficient handling of specific food items. In particular, the well-documented examples of *Geospiza* finches from the Galapagos demonstrate how strong natural selection may act on bill shape (e.g. Grant 1986, 2003; Grant and Grant 1989). House Sparrow nestlings are mainly fed an insect diet by their parents (Summers-Smith 1988). The efficiency at which such food items are caught and handled is not unlikely to be related to the positive relationship found between bill depth and feeding rate (Table 2).

A 10-year study carried out by our group on these same island populations documented that positive selection is acting on female bill length via an effect on the production of recruits, but we found no significant positive selection on bill depth (Jensen et al. 2008). This result suggests that the positive relationship between feeding rate and female bill depth found in the study reported here is likely to be linked to a different component of the variation in the production of recruits than that found in the selection study by Jensen et al. (2008).

Feeding rate and reproductive success

All though we found a close positive relationship between the parental feeding rate and the number of nestlings present in the clutch (Table 3, Fig. 2a), the average feeding rate per nestling was dramatically reduced in larger broods (Fig. 2b). Thus, the net increase of parental feeding rate in larger clutches did in no way compensate for the increase in number of nestlings. One could also hypothesize that the mean body mass should decrease in large clutches in comparison to small clutches. This was not confirmed by our data—neither for body mass at 5 days of age nor body mass at 10 days of age ($P > 0.1$). Other mechanisms may possibly explain the lack of a negative relationship between mean body mass of nestlings and brood size, such as the parents of large broods compensating for a reduced feeding rate per nestling by increasing the amount and/or the energetic content of food delivered per nestling (e.g. Royama 1966; van Balen 1973; Grieco 2002; Krystofkova

et al. 2006). Such a strategy has been described in Blue Tits and starlings (*Sturnus vulgaris*) and would contribute to maintaining the amount of food per nestling, despite reduced feeding rates (Grieco 2002 and Tinbergen 1981, respectively). As we did not sample for variation in the quality or quantity of the food delivered to the nestlings, we were not able to test this hypothesis in our study. Alternatively, as altricial bird species begin their life as ectothermic–poikilothermic organisms and then undergo a rapid physiological transition to the endothermic–homeothermic condition, nestlings raised in larger broods have been shown to have an advantage due to achieving a given level of homeothermic capacity earlier than nestlings raised in smaller broods, thereby reducing their needs for food per time unit (Dunn 1976; Clark 1984; Chastel and Kersten 2002). Thus, nestlings raised in large broods can presumably maintain their body mass at a lower energetic cost compared to nestlings raised in smaller broods; in this way, they may reduce their need for a high provisioning rate (Fig. 2b).

The positive correlation between feeding rate and both brood size and total nestling mass (Table 3) is consistent with the hypothesis that parents adjust their rate of food provision according to brood size. However, we were not able to account for the variation in feeding rates and the variation in searching time due to seasonal variation in food availability in our analyses. This hypothesis therefore assumes a positive correlation between the amount of food delivered and the food provisioning rate, as documented by, for example, Naef-Daenzer and Keller (1999). A positive relationship between food provisioning rate and the number of nestlings in a clutch has been known since the 1950s when Gibb (1950, 1955) found that parents of both Great Tits and Blue Tits feed more larger broods more frequently than smaller ones (see also Lack 1966; Moreau 1947). This relationship was subsequently found in several other studies (Hussell 1972; Best 1977; Bryant and Gardner 1979; Cronmiller and Thompson 1980), but exceptions to this general pattern have been reported (Pinkowski 1978; Bearman and Sealy 1982; Bedard and Meunier 1983).

We also found a positive relationship between the food provision rate of the parents and the number of recruits recorded 1 year later (Fig. 3b). However, this pattern may well have been generated as a consequence of the positive relationship between parental feeding rate and the number of fledglings in the clutch. Nevertheless, we found the sum of the parental feeding rates to be positively related to the probability of recruitment. However, the general validity of these analyses must be interpreted with great care because of the small sample size. Alternatively, offspring raised by parents with high feeding rates may possess some advantageous biological characteristics transferred from their parents, either as a quality genetically correlated to the

parental feeding rates or as a quality transferred as a non-genetic maternal or paternal effect. A positive relationship between feeding effort and recruitment rate has previously been found in the Long-tailed Tit (MacColl and Hatchwell 2003).

The influence of seasonality

We found a concave nonlinear relationship between hatch day and feeding frequency (e.g. Table 2). Because hatch day was positively correlated to temperature and negatively correlated to precipitation (see **Materials and methods**), a component of the variation in hatch day may in fact reflect changes in climatic conditions during the breeding season. In addition, it is plausible that the explanatory effect of hatch day on feeding frequencies reflected the seasonal dynamics of food availability—i.e. if the abundance and the size of prey varies as the season progresses (Schwagmeyer and Mock 2003).

Conclusions

We have presented results from House Sparrow populations in northern Norway which suggest that social mothers with deep bills and social fathers with relatively small total badges and large visible badge sizes had the highest feeding frequency [Tables 2 and 3, (a) and (b)]. These results indicate that the feeding rate can be a trait genetically correlated with these traits (Lande and Arnold 1983). The ornament also may be informative of the direct benefits of mate choice through an effect on feeding frequency. However, further research is needed to fully understand the direct and indirect benefits of mating with a male carrying an ornament of a given size. Due to spatial and temporal variation in selection regimes, such mechanisms may have significant impact on population dynamics as well as the genetic variance in the population.

Zusammenfassung

Reproduktionserfolg und individuelle Unterschiede in der Fütterungshäufigkeit beim Haussperling

Es wird angenommen, dass elterliche Fürsorge eng verbunden ist mit individuellen Unterschieden im Reproduktionserfolg. Wir untersuchten an Inselpopulationen des Haussperlings (*Passer domesticus*) in Nord-Norwegen, inwieweit sich Fütterungshäufigkeiten zwischen Eltern unterschieden und wie sich dies auf den folgenden Reproduktionserfolg auswirkte. Weibchen fütterten ihre Nachkommen häufiger als Männchen und die Fütterungsraten waren positiv korreliert zu denen des

Partners. Bei Weibchen fand sich eine positive Korrelation zwischen Schnabeltiefe und Fütterungsrate. Bei Männchen waren die Fütterungsraten negativ korreliert zur gesamten Größe des Kehlflecks und positiv korreliert zur sichtbaren Größe des Kehlflecks nach Korrektur für Effekte anderer Variablen. Eine nicht-lineare konvexe Beziehung bestand bei Männchen zwischen Fütterungshäufigkeit und Schlupftag, was entweder die saisonale Änderung der Witterungsbedingungen oder die saisonal veränderte Verfügbarkeit von Futter widerspiegeln könnte. In beiden Geschlechtern stieg die Fütterungshäufigkeit mit steigender Anzahl von Jungtieren, wobei gleichzeitig die mittlere Fütterungshäufigkeit pro Nestling sank. Schließlich zeigen unsere Ergebnisse, dass der elterliche Aufwand, gemessen als Fütterungsrate während der Nestlingszeit, langfristig sowohl die Anzahl rekrutierender Flügglinge wie die Wahrscheinlichkeit, dass Flügglinge bis zur Rekrutierung überleben, positiv beeinflusst.

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