Causes and consequences of adaptive seasonal sex ratio variation in house sparrows

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Summary

1. Here we examine how sex ratio variation in house sparrow broods interacts with other demographic traits and parental characteristics to improve the understanding of adaptive significance and demographic effects on variation in sex ratio.

2. The sex ratio in complete broods did not deviate significantly from parity (54·9% males).

3. There was sex-specific seasonal variation in the probability of recruitment. Male nestlings that hatched late in the breeding season had larger probability of surviving than early hatched males.

4. An adaptive adjustment of sex ratio should favour production of an excess of males late in the breeding season. Accordingly, the proportion of male offspring increased throughout the breeding season.

5. A significant nonlinear relationship was present between sex ratio and age of the female. However, there was no relationship between parental phenotype and standardized hatch day that could explain the observed seasonal change in sex ratio.

6. The sex-specific number of offspring recruited by a pair to subsequent generations was closely related to the brood sex ratio.

7. These results indicate an adaptive adjustment of sex ratio to seasonal variation in environmental conditions that affects the offspring fitness of the two sexes differently. Our results also suggest that such a sex ratio variation can strongly influence the demography and structural composition of small passerine populations.

Key-words: adaptive sex ratio variation, demography, house sparrow, population dynamics, sex-specific survival.

Introduction

Fisher (1930) was among the first to realize that selection acts on sex ratio, and stated that frequency-dependent selection will tend to stabilize the sex ratio at equilibrium. Given that the cost of producing each sex is equal, a bias in the sex ratio would favour individuals of the rarer sex as they have a higher probability of finding a mate. Thus, parents should produce an excess of the rarer sex. This will eventually lead to equality in the sex ratio. A mathematical argument was further developed by Shaw & Mohler (1953) who provided an evolutionary stable strategy (ESS) analysis on the theory of sex ratio allocation.

However, Hamilton (1967) showed that relaxation of the assumptions made by Fisher (1930) that sex allocation is controlled by autosomal genes and the presumption of random mating, could produce ESS sex ratios that deviated from parity. Furthermore, when the population is spatially structured, so that kin are more likely to interact with each other, biased sex ratios may also be expected.

Trivers & Willard (1973) extended this theory by showing that biased sex ratio can be expected if individual mothers are able to manipulate primary sex ratio as a conditional strategy. Such an adaptive strategy assumes that: (1) there should be a positive relationship between the phenotypic quality of the mother and the phenotypic quality of the offspring at the end of maternal investment; (2) differences in quality between offspring

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at the end of maternal investment persist into adulthood; and (3) the same difference in phenotypic quality between individuals has a greater effect on male reproductive success than on female reproductive success. Thus, if mothers in good condition produce progeny in better condition than mothers in poor condition, and if sons profit more from good maternal condition than daughters, then mothers in good condition should bias their investment into producing sons, and mothers in poor condition should bias their investment into producing daughters. Consequently, the among individual variance in brood sex ratio should be greater than expected from a binomial distribution (Williams 1979).

Studies on sex ratio variation in birds have until recently been difficult, due to the problem of sexing newly hatched chicks. However, new molecular techniques have made sexing relatively easy in many species (Griffiths *et al*. 1998), resulting in an increase in the number of avian sex ratio studies (e.g. Ellegren, Gustafsson & Sheldon 1996; Sheldon & Ellegren 1996; Bradbury *et al*. 1997; Komdeur *et al*. 1997; Westerdahl *et al*. 1997; Bensch *et al*. 1999; Kölliker *et al*. 1999; Sheldon *et al*. 1999; Leech *et al*. 2001; Albrecht & Johnson 2002; Alonso-Alvarez & Velando 2003; Laaksonen, Lyytinen & Korpimäki 2004). Several studies have found patterns of sex ratio variation consistent with the expectations of theoretical models suggesting adaptive variation in sex ratios (Dijkstra, Daan & Buker 1990; Ellegren *et al*. 1996; Komdeur *et al*. 1997; Sheldon *et al*. 1999; Westerdahl *et al*. 2000; Badyaev *et al*. 2002). In contrast, other studies fail to support theoretical predictions (Radford & Blakey 2000; Leech *et al*. 2001; Westneat *et al*. 2002). Furthermore, different studies on the same species report inconsistent results (Lessells, Mateman & Visser 1996; Kölliker *et al*. 1999; Radford & Blakey 2000). Thus, the evidence for adaptive sex allocation in birds is still scarce (Cockburn, Legge & Double 2002).

Adaptive sex ratio theory commonly assumes that when the relative fitness of male and female offspring differs with environmental conditions, the parents should change the sex ratio accordingly to maximize their fitness (Trivers & Willard 1973; Williams 1979; Frank 1990). In birds, hatch day is an important fitness-related trait (Siikamäki 1996; Reid, Monaghan & Ruxton 2000). Several studies have also shown that environmental effects on offspring fitness can be sex-specific (Dijkstra *et al*. 1990; Laaksonen *et al*. 2004). In some bird species, hatch day may even have long-lasting effects over several years through a differential influence on the age of first breeding of sons and daughters (Dijkstra *et al*. 1990; Smallwood & Smallwood 1998; Cordero *et al*. 2001; Laaksonen *et al*. 2004). For instance, in the common kestrel *Falco tinnunculus* the probability for males to breed as 1 year olds was negatively related to advancing hatch day, but not in females (Dijkstra *et al*. 1990). As a consequence, seasonal variation in sex ratio was found with more

males produced early in the season. Furthermore, a similar pattern of sex-specific variation in the probability of recruitment was later recorded in a different kestrel population (Laaksonen *et al*. 2004), although no seasonal adjustment of sex ratio was present. Although laying-date dependent brood sex ratios have been detected in some bird species, the adaptive significance (i.e. the hatching-date related differential recruitment of the two sexes) has rarely been examined (Dijkstra *et al*. 1990; Smallwood & Smallwood 1998; Cordero *et al*. 2001; Laaksonen *et al*. 2004). Thus, it is still unclear whether the seasonal variation that has been recorded in some species (Korpimäki *et al*. 2000; Cordero *et al*. 2001; Byholm, Brommer & Saurola 2002; Griggio *et al*. 2002; Genovart *et al*. 2003) represents an adaptive adjustment of sex ratio because this requires that there is seasonal variation in the sex-specific fitness return from a given parental investment (Frank 1990).

A problem in studies of adaptive variation in avian sex ratios is that fitness (i.e. number of offspring surviving to the next generation) is difficult to measure because offspring disperse out from the study area and because the number of marked individuals is often small compared with the total number actually present in the study area. This makes it difficult to obtain reliable estimates of the actual number of offspring that the parents are able to recruit into following generations. As a consequence, studies on avian sex ratio variation often consider only one or a few fitness-related traits (Becker & Wink 2003; Ramsay *et al*. 2003), without providing estimates of overall fitness. This makes it difficult to evaluate the presence of interactions between sex ratio and other life-history traits (West & Sheldon 2002). The importance of such interactions for adaptive sex ratio variation was particularly pointed out by Williams (1979) who showed that optimal sex-specific allocation of resources by the parents to offspring may depend on clutch size.

Traditionally, demographic studies of vertebrates consider only the female segment of the population. Some evidence does, however, suggest that variation in sex ratio may have important dynamical consequences for the fluctuations in population size, especially at small population sizes (Engen, Lande & Sæther 2003; Sæther *et al*. 2004). It is therefore important to understand how changes in brood sex ratio affect the sex ratio among the new individuals that recruit into the population.

The purpose of the present study was to examine the fitness consequences of sex ratio variation in a house sparrow *Passer domesticus* population in northern Norway, in which a large proportion of all birds is individually recognizable. Our aim was to analyse how the fitness effect of variation in the brood sex ratio was dependent on other life-history traits. Previous studies of this population (Ringsby, Sæther & Solberg 1998; Ringsby *et al*. 2002) have demonstrated that hatch date is an important determinant of fitness, and here we will extend these analyses to include the effects of offspring

sex on these relationships. Similarly, several studies have shown that there are sex-specific differences in the body growth at early ontogenetic stages (Teather & Weatherhead 1994; DeKogel 1997; Nager *et al.* 1999; Badyaev, Whittingham & Hill 2001) that may cause sex-specific variation in age-dependent differences in mortality rates. The presence of such relationships requires that the survival rate during the whole juvenile period is considered when assessing the fitness-consequences of variation in sex ratio. Finally, we examined whether variation in brood sex ratio affects the sex-specific rate of recruitment of new individuals into the following generations.

Methods

STUDY POPULATION

This study was carried out during 1993–2002 on six islands (Hestmannøy, Gjærøy, Indre Kvarøy, Ytre Kvarøy, Nesøy and Aldra) in an archipelago off the coast of Helgeland in northern Norway (66°N 13°E, see map in Ringsby *et al.* 2002). On these islands the house sparrows live in close proximity to human settlements, and usually nest inside barns on dairy farms.

FIELD PROCEDURES

Fieldwork was conducted during the breeding season from early May to the middle of August. In the study area, each house sparrow pair lays one to three clutches per season. Every island was thoroughly searched every fifth or sixth day for new nests and clutches. Just prior to fledging (8–12 days old), fledglings in occupied nests were individually marked with a numbered metal ring and a unique combination of colour rings. A large proportion of the adult birds and fledged juveniles on the study islands was captured by mist netting and was also individually colour-banded.

A fledgling was defined as a recruit if it was recaptured or observed on one of the main study islands, on a neighbouring island in the archipelago or on the mainland adjoining the archipelago after 1 April the following year. The recapture rate in this population was high (Ringsby *et al.* 1999), indicating that the probability of detecting a recruit, given that it was alive and present, was high.

A small (*c.* 25 µL) blood sample was taken from the brachial vein of all adults and nestlings during banding for sex-determination and parenthood analysis by molecular genetic methods (see below). For further description of the study area and field procedures, see Sæther *et al.* (1999), Ringsby *et al.* (1999) and Jensen *et al.* (2003, 2004).

At each capture of an adult bird we measured its tarsus length, bill depth and bill length (to the nearest 0·1 mm) using slide callipers, wing length to the nearest mm (method 3, Svensson 1992) using a ruler, and body mass (to the nearest 0·1 g), using a 100 g Pesola spring

balance. Measurements of badge size in males was defined as the area covered by black feathers and feathers with black base and grey tips on the throat and chest when the bird was held with its bill pointing at a right angle to its body. The area of the badge was then calculated according to Møller (1987) as badge size = $166·67 + (0·45 \cdot l \cdot w)$, where l is badge length and w is badge width.

Measurements of fledglings included tarsus length, wing length and weight. Morphological measurements of fledglings were standardized to the age of 11 days by use of quadratic regressions relating individual size and mass to age (Ringsby *et al.* 1998).

Body condition index (BCI) of birds was defined as the unstandardized residuals from a linear regression of individual body mass on tarsus length. The body condition of adult males and females were estimated separately (males: regression coefficient $b = 1·067 \pm 0·136$ (1 SE), $F_{1,203} = 61·57$, $P < 0·001$; females: $b = 1·101 \pm 0·219$ (1 SE), $F_{1,194} = 25·40$, $P < 0·001$). Furthermore, for fledglings, the body condition index was estimated from a model with both male and female fledglings ($n = 895$ for males and $n = 753$ for females). This model also included sex as a fixed factor ($P = 0·028$), and the interaction between sex and tarsus length ($P = 0·020$) to account for differences between the sexes in the relationship between tarsus length and body mass at the time of fledging (male fledglings: $b = 2·477 \pm 0·097$ (1 SE); female fledglings: $b = 2·253 \pm 0·074$ (1 SE), $P < 0·001$).

As various fieldworkers measured the birds, differences in measurement technique were accounted for using linear regression methods to standardize measurements for all morphological traits in adults. Measurements of tarsus length, bill length, bill height and wing length were standardized to measurements taken by Thor Harald Ringsby (T.H.R), and measurements of badge size were standardized within each year by adding the mean difference between measurements taken by each fieldworker and T.H.R., to the fieldworkers measurements (see further description of standardization procedures in Jensen *et al.* in press).

A large proportion of the birds on the study islands was ringed, and recapture rates were high (Ringsby *et al.* 1999). Birds that were captured as unringed adults in a given year were thus assumed to have hatched the previous year, and their age if alive in subsequent years were then estimated accordingly. The exception was birds captured in the initial year 1993 when no adult birds had previously been caught. For most birds, however, the age of the bird was known, as the bird was ringed as a chick in a nest or as a fledged juvenile during the summer or autumn of the year of hatching.

The sizes of some morphological traits in adults are known to change with age (Jensen *et al.* 2004). To correct for age effects, age-dependent trait sizes were calculated according to the procedure described in Jensen *et al.* (in press). Thus, separate generalized linear models (GLM; SPSS Inc 1997) were run within

each sex in which the models included individual number as fixed factor, age and age[2] as covariates, and the focal morphological trait as response variable. For each individual the size at a given age was estimated for each of the age-dependent traits by summing up its individual intercept, the intercept of the total model, and the individual's age in a specific breeding season multiplied by the parameter estimates of age and age[2], respectively. This estimation procedure was used in those cases for which the effects of age or age[2] was significant or nearly significant ($P < 0.1$). Furthermore, badge size measurements were square root transformed to normalize its distribution. We used the appropriate age-adjusted traits in all analyses.

The day of hatching was either recorded directly or assessed from length of the incubation period combined with a subjective judgement of the age of the nestlings at first visit after hatching. The onset of breeding differed significantly among the island populations (Ringsby *et al.* 2002). Thus, in order to control for this variation in the further analyses, we standardized the hatching day at each island by creating *z*-scores (Sokal & Rohlf 1995), i.e. dividing the difference between the hatch day of each nest and the mean hatch day (within year and island) by the standard deviation of the hatch day.

MOLECULAR METHODS

Over 10 years a total of 1778 offspring from 611 broods were sexed (177 offspring in 1993, 246 offspring in 1994, 197 offspring in 1995, 173 offspring in 1996, 173 offspring in 1997, 173 offspring in 1998, 133 offspring in 1999, 129 offspring in 2000, 152 offspring in 2001, and 225 offspring in 2002). A Chelex (Biorad, Hercules, CA, USA) resin-based extraction procedure (Walsh, Metzger & Higuchi 1991) was used to make DNA available for polymerase chain reaction (PCR) amplification of two homologous genes (CHD1-W and CHD1-Z) using primers P2 and P8 (Griffiths *et al.* 1998). PCR was carried out in 10 µL volume containing 0·5 units of Taq DNA polymerase (AH Diagnostics), 20 mM $(NH_4)_2SO_4$, 75 mM Tris–HCl pH 8·8, 0·15 mg mL^{-1} DNAse free BSA, 10 mM β-mercaptoethanol, 2·5 mM $MgCl_2$, 0·14 mM dNTPs (AH Diagnostics Aarhus, Denmark), 0·6 µM of each primer and approximately 20 ng of genomic DNA. PCR reactions started at 94 °C for 4 min, followed by 30 cycles of denaturing at 94 °C for 30 s, annealing at 51 °C for 45 s and elongation at 72 °C for 45 s. Then final annealing followed at 51 °C for 1 min and final elongation at 72 °C for 7 min. The PCR products were then stored at 4 °C until further analysis. The PCR products were separated by electrophoresis on 6% denaturing polyacrylamide gels and visualized by silver staining (Bassam, Caetanoanolles & Gresshoff 1991).

Females are the heterogametic sex in birds and carry copies of CHD1-W and CHD1-Z, whereas males carry only the smaller CHD1-Z. CHD1-W and CHD1-Z are easily separated because they differ in size by approximately 50 base pairs in the house sparrow. Therefore, individuals with two distinct bands were females and those with just one band were males.

To validate our procedures, PCR products for 1312 birds of known phenotypic sex (determined when a bird was captured or observed in the field) were scored for their genetic sex. These results agreed with the gender observed in the field in 98·1% (1287 of 1312) of the cases. The disagreement found was probably due to mislabelling of the blood samples in the field or misidentified observation of sex in the field. In cases where the phenotypic sex seemed unreliable, we used the genetically determined sex in the analyses. In those cases in which the phenotypic sex was reliable (i.e. multiple observations or captures of adult birds where it always was assigned the same sex), we used the phenotypic sex in the analyses.

In order to examine if parental morphology influenced on the brood sex ratio, we needed to know the genetic parents of different nests and clutches. To get this information, potential parents were genotyped on up to nine highly polymorphic microsatellite loci. The software Cervus 2·0 was then used to determine genetic parenthood, and thus link males and females to their respective nests and clutches. For further details on the parenthood analyses, see Jensen *et al.* (2003, 2004).

STATISTICAL ANALYSES

The sex ratio of the brood was expressed as the proportion of sexed individuals that were male. The nestlings were sexed at age 8–12 days, and to avoid any effects of sex-biased mortality that might have occurred before sexing, we only included nests in which number of nestlings sexed was equal to the total clutch size. This selection reduced our sample size considerably (from $n = 1778$ to $n = 363$ nestlings). Maximum recorded number of eggs was used as an estimate of total clutch size. However, in cases in which the number of young in the nest was larger than the previously determined clutch size, we used the total number of young at the first visit after hatching as total clutch size. This could be the case if, for example, nests were visited early in the incubation period and the clutch was not complete at that time. Accordingly, the total number of young counted at the first visit was used as total clutch size in 55 nests. The sex ratio in this sample was 0·534 ± 0·247. We compared this with the sex ratio in 24 nests where the clutch size was estimated from maximum recorded number of eggs. In this sample the sex ratio was 0·522 ± 0·2. Consequently, based on the slight differences in average sex ratios and standard deviations among the two groups there is little evidence that any sex-biased mortality occurred before the total number of young was determined. Thus, this conservative selection criterion excludes any potential confounding effects of sex-specific mortality during early nestling stages (Røskaft & Slagsvold 1985; Martins 2004) that may

cause deviation from the primary sex ratio at the time of sexing. Furthermore, we also restricted the analyses to clutch sizes between four and six (mean clutch size in this population is 4·55 (SD = 1·29), own unpublished data) to reduce number of nests that had suffered egg loss due to partial predation or other accidental causes.

To examine whether the primary sex ratio deviated from $P = 0·5$ (i.e. equal number of male and female nestlings in the brood), we applied binomial tests (Sokal & Rohlf 1995; Wilson & Hardy 2002). Correspondingly, the deviance between the variance in primary sex ratios within each brood size and binomial variance, was examined by applying a GLM (binomial family) (Venables & Ripley 2002) using R (R Development Core Team 2004) with the number of male and female nestlings, within each brood, as response variables, including only an intercept as explanatory variable (Wilson & Hardy 2002). Accordingly, if the sex-determination of offspring within a nest is a random process, one should not expect the variance to deviate significantly from the binomial variance. Furthermore, under binomial variance the residual deviance is expected to follow a chi-square distribution with degrees of freedom equal to the number parameters, corresponding to a test for over-dispersion (McCullagh & Nelder 1989).

To examine whether the probability of recruitment differed among male and female fledglings, we fitted a generalized linear mixed model (GLMM) using the lme4 (Bates & Sarkar 2006) and Matrix (Bates & Maechler 2006) package in R in which the identity of the mother was included as a random factor because nestlings within the same brood share a common growth environment and are not independent of each other (Krackow & Tkadlec 2001). In our mixed models we excluded nests where the identity of the mother was unknown (i.e. 14 nests). Furthermore, in the analyses where hatch day was included one nest was excluded because of unknown hatch day for that nest. We used the Laplace approximation method in the lmer function (lme4 package). In the analyses of the proportion of sons in a brood (i.e. the brood sex ratio), the same analysis was applied only including number of sons in the brood as the dependent variable and brood size as the binomial denominator, thus following the general procedure described by Hardy (2002). In analyses of the influence of parental phenotype on the brood sex ratio the identity of the mother or father was included as a random factor respectively.

The relationship between absolute fitness of parents in relation to sex ratio and hatch day was analysed using GLMM with Poisson family models (Venables & Ripley 2002). In order to see if the sex ratio among recruits changed in relation to hatch day we used GLM correcting for overdispersion (i.e. using the quasi-binomial family argument).

In general, we initially fitted a global model containing all explanatory variables as well as the two-way interactions. A final model was then determined by step-wise exclusion of the least significant terms, starting with nonsignificant two-way interactions ($P > 0·1$), and then nonsignificant main effects not included in the interactions. The significance of terms in the models was assessed by the use of Wald test statistics (Sokal & Rohlf 1995).

Results

DISTRIBUTION OF SEX RATIOS

A binomial test revealed that the overall sex ratio (P) was male biased, although not significantly different from equality there was a strong tendency for male biased sex ratio ($P = 0·549$, $P = 0·06$, d.f. = 364). Furthermore, there was no significant ($P > 0·2$, $n = 79$ broods) difference in sex ratio among clutch sizes (GLM with clutch size as factor, dispersion parameter = 0·965; clutch size 4: $P = 0·506$, $n = 40$, clutch size 5: $P = 0·593$, $n = 30$, clutch size 6: $P = 0·555$, $n = 9$). Similarly, a GLM also revealed that the sex ratio did not differ significantly ($P > 0·7$, dispersion parameter = 0·989) between the first, second and third clutches within a season ($P = 0·54$, $n = 61$, $P = 0·56$, $n = 15$ and $P = 0·57$, $n = 3$ for the first, second and third clutch within a season, respectively).

Despite large variation in sex ratios, ranging from nests with exclusively males to nests with exclusively females (Fig. 1), there was no significant deviation from binomial variance for either clutch size (clutch size 4: $\chi^2 = 1·18$, $P = 0·19$ d.f. = 40, clutch size 5: $\chi^2 = 1·15$, $P = 0·27$, d.f. = 30, clutch size 6: $\chi^2 = 0·70$, $P = 0·68$, d.f. = 9) using all clutches.

SEX-SPECIFIC SURVIVAL IN RELATION TO HATCH DAY

Hatch day is an important trait closely associated with offspring fitness in house sparrows (Ringsby *et al.* 1998, 2002). To examine whether the effect of hatch day on the probability of survival was sex-specific, we included the probability of survival as a response variable in a GLMM (binomial distribution, logit link function, Laplace optimization) with offspring sex, standardized hatch day and the interaction term as independent variables as well as the identity of the mother as a random factor (see Methods for further description).

The probability of recruitment increased significantly with standardized hatch day for male fledglings ($b = 0·49$, SE = 0·23, $z = 2·13$, $P = 0·033$, $n = 291$) (Fig. 2). Males also survived significantly better after fledging than females ($P = 0·047$, $n = 291$). In contrast, for female fledglings there was a negative, but non-significant ($P > 0·059$) relationship between standardized hatch day and the probability of survival (Fig. 2), resulting in a significant interaction term between sex and hatch day ($P = 0·004$, $n = 291$). Thus, the probability of males and females to recruit was differently influenced by the relative hatching date (Fig. 2).
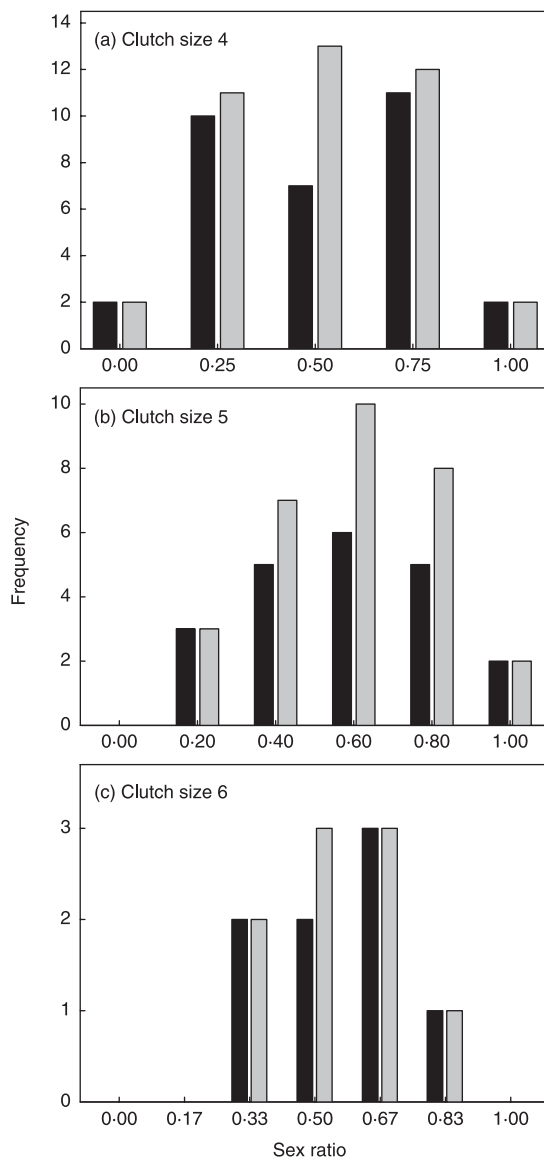
Fig. 1. The distribution of sex ratios (proportion of males) of house sparrow broods in relation to clutch size and clutch number (black columns: first clutch of the season, grey columns: all clutches).

When including nests from the first clutch only, the probability of male recruitment was still positively related to hatch day, although the relationship was nonsignificant ($b = 0.55$, SE = 0.29, $z = 1.9$, $P = 0.057$, $n = 223$). Males had again a higher probability of surviving after fledging than females ($P = 0.044$, $n = 223$). For females there was still a negative, but nonsignificant ($P > 0.059$) relationship with standardized hatch day, resulting in a significant interaction term between sex and hatch day ($P = 0.006$, $n = 223$).

ADAPTIVE ADJUSTMENT OF SEX RATIO

The sex-specific seasonal variation in the probability of recruitment suggests a possible way that females may adaptively adjust the sex ratio of their clutch, and produce predominantly males late in the breeding season when
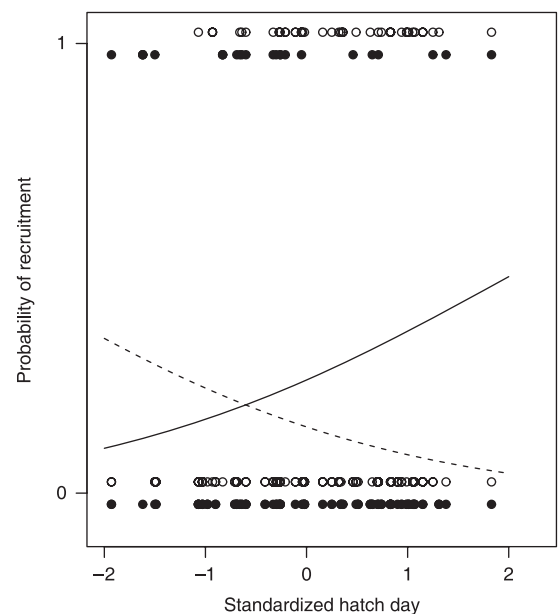
Fig. 2. The probability of recruitment of male (solid line) and female (dashed line) house sparrow offspring in relation to standardized hatch day. The curve was fitted using the logistic equation from the mixed model. The equations were for males:

$$\frac{\exp(-0.96141+0.49349*\text{standardized hatch day})}{1 + \exp(-0.96141+0.49349*\text{standardized hatch day})}$$ and for

females: $$\frac{\exp(-1.56967-0.5168*\text{standardized hatch day})}{1 + \exp(-1.56967-0.5168*\text{standardized hatch day})}.$$

Hatch day was standardized by creating z-scores, i.e. dividing the difference of each nest from the mean hatch day (within year and island) by the standard deviation of the hatch day.

their probability of survival was highest. Accordingly, the sex ratio showed a significant increase with standardized hatch day ($b = 0.24$, SE = 0.12, $z = 2.04$, $P = 0.04$, $n = 64$ (all clutches); Fig. 3). When repeating the analysis including only nests from the first clutch, a similar relationship was still present although not significant ($b = 0.26$, SE = 0.14, $z = 1.89$, $P = 0.058$, $n = 49$). Thus, female house sparrows adjusted the sex ratio according to the increased probability of recruitment that males experience late in the breeding season.

When we extended these analyses to a model that also included standardized hatch day, clutch size and their interactions, we found no significant effect of clutch size on the sex ratio. Thus, the seasonal variation in sex ratio was independent of clutch size.

PARENTAL MORPHOLOGY AND SEX RATIO

The variation in primary sex ratio observed during the breeding season in this house sparrow population could potentially be explained by seasonal variation in parental quality, i.e. if mothers in good condition breed late in the season, and if good quality mothers were more likely to produce sons (Trivers & Willard 1973). Similarly, females might also adjust the sex ratio according to the characteristics of the mate. If male attractiveness is related to male reproductive success,
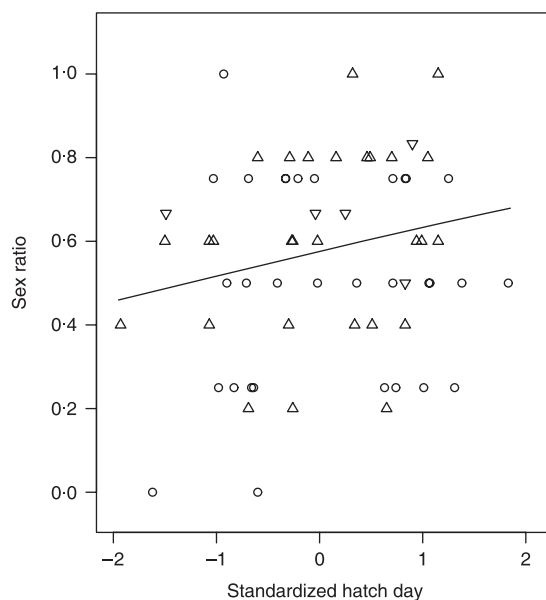
Fig. 3. Seasonal variation (relative to the mean hatch day, see legend to Fig. 2) in brood sex ratio of house sparrows for different clutch sizes (clutch size 4: circle, clutch size 5: triangle and clutch size 6: downward triangles). The curve was fitted using the logistic equation from the mixed model. The equation was:

$$\frac{\exp(0.30596+0.23987*\text{standardized hatch day})}{1 + \exp(0.30596+0.23987*\text{standardized hatch day})}.$$

and if such traits are inherited by sons, male offspring of such fathers may have higher reproductive value than the daughters of those fathers. Females are therefore expected to bias the brood sex ratio toward males if mated with a high quality male.

These hypotheses were examined by including sex ratio as a response variable in a GLMM in which parental phenotypic traits (bill length, bill height, body mass, tarsus length, wing length, age, and the second order term of age in both sexes, and badge size in males) were included as explanatory variables in separate univariate models as the global model did not converge due to low sample size. Furthermore, because the age structure of our sample of birds in the beginning of the study period was strongly skewed towards young individuals (see Methods), we carried out the analyses only for the years 1996–2002 (i.e. $n = 17$ broods were excluded from the analyses), to control for any confounding relationships due to age-dependency, e.g. in morphological variation (Jensen *et al*. in press). In order to avoid decrease in body condition during the season to confound our results we only used the first clutch in these analyses (i.e. excluded $n = 12$ broods). Furthermore, we also excluded nests where parental morphological measurements were unavailable. In the analyses of the effects of paternal morphology on the sex ratio, we excluded nests (18 of 33 nests, 45·45%) in which more than one male had progeny in the same nest (i.e. in broods with multiple paternities).

For females, there was a nonlinear effect of age on the sex ratio ($b = 1.87$, SE = 0.94, $z = 2.00$, $P = 0.04$; $b_2 = -0.44$, SE = 0.18, $z = -2.48$, $P = 0.013$, $n = 27$)
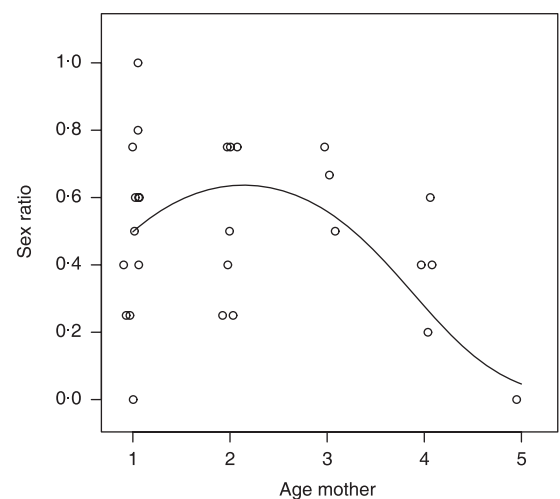
Fig. 4. Brood sex ratio of house sparrows in relation to maternal age. The curve was fitted using the logistic equation from the mixed model. The equation for females were:

$$\frac{\exp(-1.4415+1.7463*\text{age}-0.43817*(\text{age}^2))}{1 + \exp(-1.4415+1.87463*\text{age}-0.43817*(\text{age}^2))}.$$

(Fig. 4). However, no other phenotypic traits of females were significantly related to the brood sex ratio ($P > 0.25$, $n = 27$). Furthermore, there were no significant correlations between female morphological traits and hatch day ($P > 0.17$, $n = 27$). Hence, although female age influenced brood sex ratio, this relationship can not explain the observed seasonal change in sex ratio. Finally, when repeating the same analyses for males we found no significant effect of any of the morphological traits ($P > 0.13$, $n = 15$).

PROBABILITY OF RECRUITMENT IN RELATION TO SEX RATIO

To further examine how variation in sex ratio within clutches influenced fledgling survival, we examined whether the probability of a fledgling recruiting was related to the sex ratio among its siblings within the nest. The analyses were carried out in two steps. First, we analysed whether the probability of recruitment was related to the brood sex ratio, including all nests. Each individual fledgling was categorized as either a recruit or nonrecruit (see Methods) and was included as response variable in a GLMM in which sex ratio in the brood, nestling sex and the interaction between the two terms were included as explanatory variables. In addition, the identity of the mother was included as a random factor. The probability of recruitment to the next breeding season was not related to the sex ratio in the brood ($P > 0.5$, $n = 296$), and there was no significant interaction term between nestling sex and brood sex ratio ($P > 0.4$, $n = 296$). This indicated that the sex ratio in the brood did not influence the post-fledging probability of recruitment of male and female fledglings differently.

Second, to analyse if the relative survival between the sexes was dependent on the sex ratio in the brood, we

included into the second analysis only nests in which at least one fledgling recruited. However, excluding nests where no fledglings survived to recruitment gave a truncated binomial distribution and violates the assumption for the use of traditional GLMMs (McCullagh & Nelder 1989). Hence, to test whether the probability of recruitment to the next breeding season was different for male and female fledglings in relation to the brood sex ratio, we included the sex ratio among recruits as the response variable in a logistic regression in which the log of the sex ratio was included as the explanatory variable. In this model, deviation from a slope of one indicates whether the probability of recruiting to the next breeding season is dependent on the sex ratio in the brood. In these analyses nests with no recruits as well as nests in which the brood consisted exclusively of males or females, i.e. sex ratio was either 0 or 1, were excluded because such nests do not provide information about the relative survival between males and females. The sex ratio among recruits from a nest was positively related to the brood sex ratio in the nest ($r_s = 0.43$, $P = 0.002$, $n = 45$ broods). However, the slope of the regression line did not differ significantly from one ($b = 0.813$, $P > 0.5$, dispersion parameter $= 1.003$, $n = 45$ broods). Thus, there was again no indication that the brood sex ratio differently influenced the post-fledging survival of the two sexes.

ABSOLUTE FITNESS AND SEX RATIO

The next step was to examine whether sex ratio in the brood affected fitness of the parents, i.e. the number of recruits produced. Poisson regression analysis (see Methods) revealed that there was no relationship between the brood sex ratio and number of nestlings that recruited to the next breeding season ($b = 0.04$, $SE = 0.49$, $z = 0.09$, $P = 0.92$, $n = 65$, Fig. 5), suggesting that overall parental fitness was not related to the sex ratio in the nest. Moreover, the number of male nestlings recruiting was positively related to brood sex ratio ($b = 1.82$, $SE = 0.67$, $z = 2.73$, $P = 0.006$, $n = 65$, Fig. 5), whereas the number of female nestlings recruiting was negatively related to brood sex ratio ($b = -3.03$, $SE = 0.84$, $z = -3.59$, $P = 0.0003$, $n = 65$, Fig. 5). Including clutch size as a covariate into the respective models did not change the result for any of the analyses. Furthermore, repeating the analyses when nests where no fledglings had survived to recruitment were excluded gave similar results as above. Thus, sex ratio among recruits was closely related to sex ratio in the brood.

As expected from the sex-specific seasonal variation in the probability of survival (Fig. 2), the number of male fledglings that recruited to the next breeding season was positively, although marginally nonsignificantly, related to standardized hatch day ($b = 0.32$, $SE = 0.17$, $z = 1.86$, $P = 0.062$, $n = 64$). This positive relationship remained also when including absolute hatch day ($b = 0.014$, $SE = 0.0074$, $z = 1.94$, $P = 0.052$, $n = 64$) in
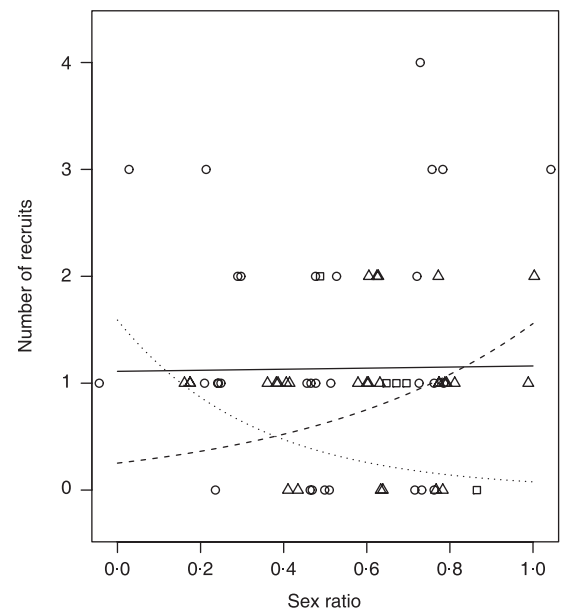
Fig. 5. The total number of recruits (solid line), male recruits (dashed line) and female recruits (spotted line) of house sparrows in relation to the brood sex ratio for different clutch sizes (clutch size 4: circle, clutch size 5: triangle and clutch size 6: square).

the analysis. Thus, there was a tendency that number of male recruits produced was higher in clutches that were initiated late in the season compared with early. Similarly, there was a negative relationship between the number of female recruits and standardized hatch day ($b = -0.54$, $SE = 0.25$, $z = -2.14$, $P = 0.03$, $n = 64$), but not with absolute hatch day ($P > 0.18$, $n = 64$). Furthermore, the total number of recruits produced was not related to standardized hatch day ($P > 0.8$, $n = 64$) or absolute hatch day ($P > 0.4$, $n = 64$). As a consequence, there was seasonal variation in the sex ratio among recruits (GLM with quasi-binomial argument, $b = 0.78$, $SE = 0.38$, $z = 2.04$, $P = 0.047$, dispersion parameter $= 1.073$, $n = 45$ broods), i.e. more male recruits were produced late in the breeding season (Fig. 6).

Discussion

Here we demonstrate that male house sparrow offspring survived significantly better when born late in the season than females (Fig. 2). Accordingly, this was associated with a seasonal change in the primary sex ratio (Fig. 3), where the proportion of males in the brood increased with advancing laying date. This indicates that the house sparrow is able to adjust the sex ratio in relation to changes in the environment that affect sexual differences in the relative fitness of the offspring. However, because the sex-specific probability of post-fledging survival was independent of brood sex ratio, the sex-specific recruitment rate was closely related to the sex ratio of the brood (Fig. 5). Thus, sex ratio variation in the broods affected the sex ratio
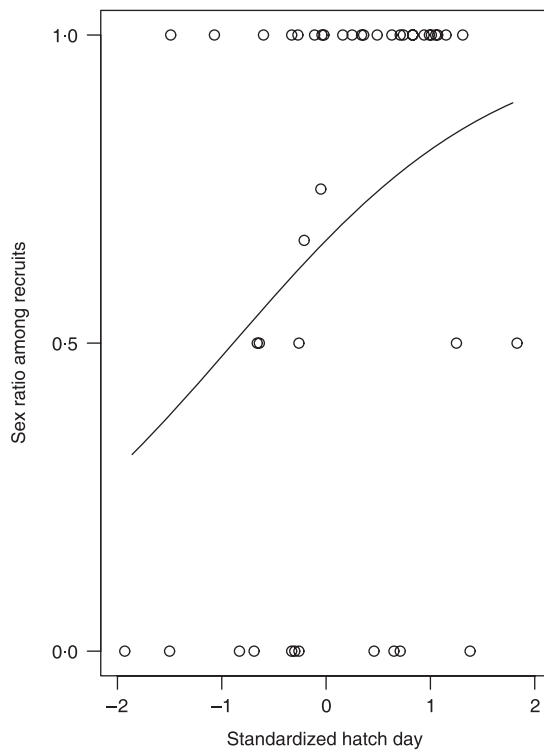
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Fig. 6. Seasonal variation (relative to the mean hatch day, see legend to Fig. 2) in sex ratio among recruits in house sparrows. The curve was fitted using a logistic distribution function. The equation was:
$$\frac{\exp(0.6938 + 0.7804 * \text{standardized hatch day})}{1 + \exp(0.6938 + 0.7804 * \text{standardized hatch day})}.$$

among recruits 1 year later (Fig. 6) that may influence the population dynamics of house sparrow populations.

The observed tendency for production of slightly more males than females (Fig. 1) has also been found in earlier studies of sex ratio variation in house sparrows (Summers-Smith 1988; Cordero *et al.* 2000; Westneat *et al.* 2002). This is in contrast with the general pattern in passerines to produce female-biased broods (Gowaty 1993). However, the deviation from parity (Fig. 1) was not significantly larger than could be expected by chance alone, neither in this study nor in the study by Westneat *et al.* (2002). Furthermore, Cordero *et al.* (2000) did not find any evidence that the sex ratio in a sample of eggs was significantly different from equality. Thus, despite a strong tendency towards male bias we found no indication that house sparrows significantly bias the sex ratio among offspring. The variance in brood sex ratios was, however, large (Fig. 1). Such large variation has also been found in great tits *Parus major* (Verboven, Kakela & Orell 2002), suggesting that sufficient variation is present for an adaptive sex ratio adjustment.

The probability of male recruitment was positively related to hatch day (Fig. 2), i.e. males had larger chances of recruiting to the next breeding season when they hatched late in the breeding season. However, no such seasonal variation was present in females (Fig. 2). Although most studies have found a negative relationship between hatching date and recruitment (Spear &

Nur 1994; Arroyo 2002; Cooch 2002; Reed *et al.* 2003), a positive relationship between hatching date and juvenile survival has often been demonstrated especially in multibrooded species (Klomp 1970; Brinkhof *et al.* 1993). Increased probability of survival among offspring that hatch late has previously been demonstrated in the house sparrow (Ringsby *et al.* 1998, 2002) as well. However, sex-specific differences in the seasonal variation in recruitment probability have previously only been reported in a few studies of sexual size dimorphic raptors (Dijkstra *et al.* 1990; Smallwood & Smallwood 1998; Laaksonen *et al.* 2004), and in the spotless starling *Sturnus unicolor* (Cordero *et al.* 2001).

One explanation for sex-specific variation in survival was provided by Lack (1954). Based on analysis of sexually size dimorphic birds, he suggested that nestlings of the larger sex survive better because of a competitive advantage in sibling competition. This prediction has been supported for some species (Lessells *et al.* 1996; Oddie 2000; Arroyo 2002; Hipkiss *et al.* 2002), but more often it has been found that the larger sex is more prone to die because of unmet energetic demands during periods of extreme environmental stress and/or faster growth rate (Slagsvold, Røskaft & Engen 1986; Teather & Weatherhead 1989; Griffiths 1992). In house sparrows, eggs containing male embryos are significantly larger than eggs containing female embryos (Cordero *et al.* 2000), and male nestlings are heavier than their female siblings (Westneat *et al.* 2002). Furthermore, adult males are approximately 6% larger than adult females (Summers-Smith 1988; Cramp & Perrins 1994), hence males are the larger and more costly sex to raise. Thus, the increased mortality of males observed early in the breeding season in this study corresponds well with the general pattern emerging from other studies that mortality is higher among males than females in sexually size dimorphic species, particularly early in the season when environmental conditions are harsh (Ringsby *et al.* 2002).

Current sex ratio theory (Trivers & Willard 1973; Frank 1990) states that if the reproductive value of sons and daughters differs, parents should adjust offspring sex accordingly to maximize their own fitness. As expected from the sex-specific seasonal change in the probability to recruit (Fig. 2), female house sparrows biased the brood sex ratio towards males late in the breeding season (Fig. 3). Such seasonal change in sex ratio has also been found in a number of other species (Dijkstra *et al.* 1990; Lessells *et al.* 1996; Cordero *et al.* 2001; Byholm *et al.* 2002; Genovart *et al.* 2003). This may suggest that birds are able to adjust their sex ratio adaptively to seasonal variation in the environment that causes sex-specific variation in offspring fitness (Dijkstra *et al.* 1990; West & Sheldon 2002). Another explanation for this seasonal pattern in sex ratio (Fig. 3) may be that the onset of breeding is dependent on some parental characteristics. For instance, if mothers in good condition breed late in the breeding season (Gustafsson *et al.* 1994; Verhulst, Vanbalen &

Tinbergen 1995; Hipfner 1997) and according to Trivers & Willard (1973), assuming that male offspring are more costly to produce than females, we would expect a higher proportion of male offspring produced by mothers of high quality late than early in the season. Accordingly, sex ratio in our population was related to age (Fig. 4), i.e. a male-biased sex ratio was found predominantly among females in intermediate age classes. Such age effects on sex ratio have also been found in other bird species, e.g.: barn swallow *Hirundo rustica* (Saino *et al.* 2002), Eurasian oystercatcher *Haematopus ostralegus* (Heg *et al.* 2000) and red-winged blackbird *Agelaius phoniceus* (Blank & Nolan 1983). In small passerines, age strongly influences the timing of breeding (Perrins 1970; Sæther 1990). Accordingly, there was an inverse correlation between hatching date and male age in our population ($r_s = -0.62$, $P = 0.014$, $n = 15$). Such a relationship between age and hatching date could induce a seasonal variation in sex ratio. However, our analyses show that a seasonal variation in sex ratio is present even after accounting for age and phenotypic characteristics. This indicates that the seasonal variation in sex ratio (Fig. 3) represents an adjustment to factors in the environment affecting the fitness of the two sexes differently, which is a prerequisite for an adaptive sex ratio variation (West & Sheldon 2002).

The number of recruits produced was not related to the brood sex ratio (Fig. 5). Furthermore, the total number of recruits produced to the next breeding season was independent of hatching date. As a consequence, the proportion of male recruits increased throughout the breeding season because of the seasonal increase in the sex ratio of the broods (Fig. 6). This temporal variation in sex ratio among recruits can have potentially large effects on the population dynamics. Engen *et al.* (2003) showed that changes in the sex ratio affected the population growth rate (λ), especially at small population sizes in which sex ratio strongly contributed to a stochastic Allee effect (Lande 1998) that even could drive the population to extinction (Sæther *et al.* 2004). This suggests that variation in the brood sex ratio may have important dynamical consequences especially at small population sizes and should be carefully considered when modelling fluctuations of such populations.

Acknowledgements

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