PATTERNS OF SEX RATIO VARIATION IN HOUSE SPARROWS

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Abstract. PCR amplification of a sex-linked gene was used to assay the sex ratio of nestling House Sparrows (Passer domesticus) from five consecutive breeding seasons. We tested several predictions from sex ratio theory, including that at the population level, sparrows should produce a 1:1 sex ratio. Of 1162 nestlings, 53% were male, which is not significantly different from 50%. We did find a significant skew toward males in two of the five years, and significant heterogeneity in sex ratio among seasons. There was no evidence that brood sex ratios were skewed from a binomial distribution, despite a modest excess of all male broods. We found that male nestlings weighed significantly more (0.5 g) than their female siblings. We tested the possibility that females produce males when conditions are good. Sex ratio was not associated with nest attempt, despite some evidence that conditions varied seasonally. Clutch size was negatively associated with date of first egg, but neither nestling weight nor sex ratio showed any correlation with date. We also tested an array of female characteristics; sex ratio was not associated with female body size, condition, or age. Females that hatched a larger proportion of eggs produced more males, a consistent pattern in all five seasons. However, the female’s mate’s characteristics (size, condition, age, or size of throat patch) did not influence sex ratio. These data contribute to a growing number of studies that provide an inconsistent picture of sex ratio variation in birds.

Key words: birds, CHD gene, conditional strategy, sex allocation, sexual selection.

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Patrones de Variación en la Proporción de Sexos de Passer domesticus

Resumen. Un gen ligado al sexo, amplificado por PCR, fue usado para examinar la proporción de sexos de pichones de Passer domesticus provenientes de cinco temporadas de apareamiento consecutivas. Se probaron varias predicciones de la teoría de proporción de sexos, incluyendo que a nivel poblacional, los gorriones deberían producir una proporción de sexos 1:1. De 1162 pichones, 53% fueron machos, lo cual no difiere significativamente de 50%. Se encontró un sesgo significativo hacia machos en dos de los cinco años y una heterogeneidad significativa en la proporción de sexos entre estaciones. No hubo evidencia de que la proporción de sexos de la camada se desviera de una distribución binomial, a pesar de un modesto exceso de crías macho. Se encontró que los pichones machos pesaron significativamente más (0.5 g) que sus hermanas. Se examinó la posibilidad de que las hembras producen machos cuando las condiciones son benignas. La proporción de sexos no estuvo asociado con el momento de anidación dentro de la temporada, a pesar de que algunas evidencias sugieren que las condiciones variaron estacionalmente. El tamaño de la camada estuvo negativamente asociado con la fecha de puesta del primer huevo, pero no el peso del pichón ni la proporción de sexos mostró correlación con dicha fecha. Se examinaron además un serie de características de la hembra; la proporción de sexos no estuvo asociada con el tamaño del cuerpo, la condición o la edad de la hembra. Las hembras que empollaron una mayor cantidad de huevos produjeron más machos, un patrón consistente en las cinco temporadas. Las características de las parejas de las hembras (tamaño, condición o tamaño de la mancha del cuello) no influyeron la proporción de sexos. Estos datos contribuyen al
INTRODUCTION

In anisogamous organisms, whether an offspring is male or female has major implications for its development, morphology, behavior, and fitness. Fisher (1930) suggested that offspring gender might be under control of the parent and evolve through frequency-dependent selection. Whether an offspring is male or female is not just a by-product of random segregation of sex genes or chromosomes during meiosis, but is a result of a parental strategy influencing the sex of offspring that is shaped by selective forces.

Fisher’s original focus was on the population sex ratio. He described frequency dependent selection on a genetically determined parental strategy affecting sex ratio. Selection on mechanisms that would skew sex ratios toward one sex would be influenced by the cost of producing that sex and the expected fitness of that sex. The sexes could differ in costs of production, such as might occur when they differ in body size. Differences in the fitness value of one sex could occur if that sex were less frequent than the other. In either case, selection would favor biasing investment toward the less costly or the rarer sex, which on average would stabilize investment in the sexes.

Trivers and Willard (1973) and Charanov (1982) expanded these ideas to include more flexible mechanisms. Some factors that favor biases in the ratio of male and female offspring might vary from one situation to the next. Thus individuals might have a strategy that depends on some variable factor (a conditional strategy). For example, Trivers and Willard (1973) predicted that if males have a higher variance in reproductive success than females, producing a high quality male would leave more grandoffspring than producing a high quality female. Parents that can produce high quality offspring should therefore produce more sons whereas those who cannot should produce more daughters. Factors potentially contributing to a parent’s ability to produce high quality offspring include the presence of abundant resources in a patchy environment, ability of parents to provide for the offspring, or the attractiveness of the parent of the more strongly sexually selected sex.

Studies of a variety of taxa have generally supported these predictions (e.g., Frank 1990, Sheldon 1998). But in some (e.g., birds), evidence of adaptive sex ratio has been scarce (Gowaty 1991), perhaps in part because gender is hard to identify when offspring are still associated with their parents. The recent development of molecular techniques that allow quick and easy identification of offspring gender (Ellegren 1996, Griffiths et al. 1996) has dramatically increased the opportunity to study sex ratio in birds. However, the results of these studies create a puzzling picture of sex ratio adjustment as a parental strategy. In Seychelles Warblers (Acrocephalus sechellensis), females produce substantially more female offspring when ecological conditions favor helpers at the nest, which are typically female (Komdeur et al. 1997). Female Blue Tits (Parus caeruleus) produce more sons when their mates have more UV reflectance in their plumage as shown both by correlation analyses and by experimental manipulation of UV reflectance (Sheldon et al. 1999). These results and a few others like them (Ellegren et al. 1996, Nager et al. 1999, Westerdahl et al. 2000) strongly support the idea that sex ratios are under flexible control.

However, some other species predicted to have flexible sex ratios show little evidence of such plasticity. For example, although males of the polygynous Corn Bunting (Miliaria calandra) are potentially under much stronger sexual selection than females and are considerably larger in size, brood sex ratios did not differ from 1:1, and none of a suite of factors predicted to influence sex ratio was found to do so (Hartley et al. 1999). A similar lack of covariates with sex ratio was found in the Yellowhammer (Emberiza citrinella; Pagliani et al. 1999), Bluethroat (Luscinia svecica; Questiau et al. 2000), and Barn Swallow (Hirundo rustica; Saino et al. 1999), even though males in all three species are under sexual selection and in Yellowhammers, are larger than females. Many other species show little evidence of facultative sex ratio adjustment (Clutton-Brock 1986, Gowaty 1991, Koenig and Dickinson 1996, Sheldon 1998).

Such variation is intriguing, and demands further investigation. The purpose of this study was...
to explore the patterns of sex ratio variation in a predominantly monogamous yet sexually dimorphic species, the House Sparrow (*Passer domesticus*). House Sparrows are a common species on several continents, typically commensal with humans. Adult males are slightly larger (about 2%) than females and have conspicuously different plumage traits that appear several months after independence from the parents (Summers-Smith 1988). Most individuals form monogamous pairs during breeding, but males can occasionally attract a second mate (Veiga 1993) or sire offspring through extra-pair copulations (Wetton and Parkin 1991, Cordero et al. 1999, Whitekiller et al. 2000). The prevailing evidence indicates that male reproductive success is more variable than female success (Müller 1989). Thus, producing a high quality male could be more valuable to parents than producing a high quality female, and a low quality male might be worse than a low quality female. Unfortunately, what traits contribute to variance in male success and hence might be associated with biases in sex ratio are unclear. Male plumage traits such as the black throat patch (badge) may be involved in female mate choice (Müller 1988, Veiga 1993) and male-male interactions (Møller 1987). A female paired to a male with a large badge might therefore benefit from producing sons. Variation in badge size can be influenced by natal environment (Griffith et al. 1999a), so females in particular environments might benefit by producing sons. Interestingly, Cordero et al. (2000) found that House Sparrow eggs containing male embryos were larger than eggs containing females. Given that this result hints that females can at least assess the sex of particular zygotes and differentially invest in them very early, we concluded that they might also show the ability to manipulate offspring sex ratio in response to variable conditions.

Trivers’ and Willard’s (1973) hypothesis is not the only one suggesting that sex ratio might be part of an adaptive strategy, but some key conditions for other hypotheses are lacking in House Sparrows. House Sparrows do not have helpers at the nest, and so the possibility that parents produce the sex that helps (Gowaty and Lennartz 1985, Emlen et al. 1986) does not exist. Clark (1978) suggested that local resource competition could influence optimal sex ratio. Indeed, Gowaty (1993) found suggestive evidence for effects of resource competition on sex ratios in birds, and noted that even subtle biases in dispersal timing could influence sex ratio. Female House Sparrows have greater natal dispersal than males in a Kansas population (Fleischer et al. 1984), but data from the present population reveals little difference between the sexes (DFW, unpubl. data). Because we have limited ability to test aspects of the resource competition hypothesis, we do not focus on it here. However, we will discuss our results with respect to the general idea and the limited data we have.

Using a PCR technique that amplified the CHD gene on the avian sex chromosomes (Ellegren 1996, Griffiths et al. 1996), we examined sex ratio variation in broods of House Sparrows and tested the following predictions arising from Fisher (1930) and Trivers and Willard (1973):

1. Population sex ratios would be close to 1:1 because male and female nestlings and fledglings differ little in size and hence in apparent cost, adult sex ratios appear close to 1:1, and juvenile dispersal is not biased by sex;
2. Seasonal patterns of the proportion of males within broods would match seasonal patterns of brood success;
3. Higher quality females (those that are larger, older, and nest earlier) would produce more males; and
4. Females paired to high quality males (those that are larger, older, and have larger sexual ornaments) would produce more males.

**METHODS**

**STUDY POPULATION**

We studied House Sparrows at the University of Kentucky’s Agricultural Experiment Station, located on the northern outskirts of Lexington, Kentucky (38°0′N, 84°30′W). The station is a tract of farms covering approximately 5 km² and containing scattered buildings used for storage and livestock. House Sparrows breed throughout the area; we have focused since 1992 on those breeding in nest boxes on the sides of four barns, and in isolated boxes erected along fencelines between the barns. Birds at these barns are only partially isolated from other sparrows. Dispersal almost certainly means the birds under study are part of a larger population that includes birds at other buildings within the experiment station and those in the north edge of a continuous suburban/urban population of sparrows in the city of Lexington. The data reported here are from
the breeding seasons of 1995–1999. We monitored between 45 and 60 nest boxes for breeding sparrows in each season. This effort covered from 1–5 nesting attempts by each female.

FIELD PROCEDURES
Throughout each year, adult sparrows were caught in seed-baited treadle traps or mist nets and were banded with a numbered USFWS metal band and a unique combination of colored plastic leg bands for field identification. Measurements were taken of each bird’s weight, wing length, tarsus length, bill depth and bill width. We measured the black throat patch of males in two ways: we took the length and width of the area of feathers that were completely black, and length and width of the whole patch (including black feathers with white tips). A small (ca. 50 μL) blood sample was taken from the brachial vein of all adults and 10-day-old nestlings during banding. We froze samples at −20°C for later genetic analysis.

During the breeding season, nest boxes were visited 2–3 times per week to determine date of first egg and date of hatching, and observed to identify adults associated with each brood. Adults were considered to be associated with a brood if consistently seen entering and exiting the box during any stages of nest development (building, incubation, or nestling feeding) or defending the box over multiple observations.

SEX DETERMINATION
We used two sets of PCR primers known to amplify the CHD gene in chickens (Ellegren 1996, Griffiths et al. 1996). This gene is located on the sex chromosomes and has two forms differing in length, one on the W and another on the Z chromosome. In birds, males are the homogamic sex (ZZ) and females are heterogamic (WZ). The two sets of primers both amplify the relevant section on both chromosomes, but these areas typically differ in length between the chromosomes. Thus, females produce a two-banded pattern and males a single band.

DNA was extracted from each sample using Chelex® extraction (Walsh et al. 1991). DNA from families was run on the same gel, and at least two adults of known sex were included on every gel. Photographs were taken of each gel and then sex was scored immediately so that the gel could be consulted in case of ambiguities on the photograph.

We used primers 2917F and 3088R from Ellegren (1996) to sex about two-thirds of the samples (all those from 1997–1999). Primers P2 and P8 (Griffiths et al. 1998) were used to sex the offspring from the 1995 and 1996 seasons. PCRs were carried out in 20 μL volume containing 25 ng of sparrow DNA, 0.5 mM forward and reverse primer, 1× PCR buffer, 0.2 mM dNTPs, 4 mM MgCl2, 10 ng bovine serum albumin, and 0.5 units of Taq polymerase. PCR reactions were hot-started at 94°C for 3 min, followed by one round of annealing at 55°C for 30 sec, and extension at 72°C for 1 min, then followed by 34 cycles of 94°C for 30 sec, 50°C for 30 sec, and 72°C for 45 sec. Early on, we end-labeled the forward primer (2917F) with 32P ATP and used autoradiography to visualize the products following electrophoresis through a 6% polyacrylamide gel. Later, most samples were electrophoresed through 2% agarose gels and stained with ethidium bromide. Samples analyzed using the P2 and P8 primers were either visualized from agarose gels stained with ethidium bromide or silver-stained polyacrylamide gels (Bassam et al. 1991).

We tested the CHD primers using DNA from 30 adult House Sparrows of known sex. The banding pattern for each sample matched that expected for that bird; males showed one band and females two bands. In addition, 30 nestlings were later recaptured after molting into adult plumage; only one had been incorrectly sexed (identified as female when it was actually a male). We attribute this to an error in bookkeeping or labeling of the sample. We therefore consider our approach to be a satisfactory means of identifying the sex of nestling House Sparrows.

STATISTICAL ANALYSES
Sex ratio is a binomially distributed variable. To test if the sex ratio of nestlings was significantly skewed from the 50:50 ratio expected, we used a binomial with \( P = 0.50 \) treating each nestling as an independent event. This is appropriate because the most basic null hypothesis about sex ratios, that offspring gender is determined merely by Mendel’s law of segregation, explicitly posits that each offspring is an independent event. For more detailed analyses of the distribution of sex ratios among broods, we performed a randomization test using each brood as an independent event. To do this, we used the observed number of broods containing 2–5
TABLE 1. The number of females represented, the number of nestlings analyzed, the proportion of nestlings that were male and the probability it deviated from 0.5, for House Sparrows nesting on the University Agricultural Experiment Station in Lexington, Kentucky, in each of five seasons.

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of adult females</th>
<th>Number of broods</th>
<th>Number of nestlings</th>
<th>Proportion male</th>
<th>Probability of observed, given expected proportion of 0.5</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>33</td>
<td>59</td>
<td>193</td>
<td>0.49</td>
<td>( P = 0.36^a; t = 0.4; P = 0.66^b )</td>
</tr>
<tr>
<td>1996</td>
<td>49</td>
<td>75</td>
<td>287</td>
<td>0.45</td>
<td>( P = 0.09^a; t = -1.8; P = 0.08^b )</td>
</tr>
<tr>
<td>1997</td>
<td>57</td>
<td>95</td>
<td>335</td>
<td>0.57</td>
<td>( P &lt; 0.02^a; t = 2.4; P &lt; 0.02^b )</td>
</tr>
<tr>
<td>1998</td>
<td>20</td>
<td>33</td>
<td>115</td>
<td>0.52</td>
<td>( P = 0.32^a; t = 0.3; P = 0.74^b )</td>
</tr>
<tr>
<td>1999</td>
<td>52</td>
<td>68</td>
<td>232</td>
<td>0.60</td>
<td>( P &lt; 0.01^a; t = 2.0; P &lt; 0.05^b )</td>
</tr>
<tr>
<td>Total</td>
<td>211</td>
<td>330</td>
<td>1162</td>
<td>0.53</td>
<td>( P = 0.06^a; t = 1.5; P = 0.14^b )</td>
</tr>
</tbody>
</table>

*a* Binomial probability using nestlings as independent observations.

*b* From a one-sample *t*-test using transformed sex ratios for all offspring of each female within a season (see methods).

chicks and created a null distribution \((n = 1000)\) of deviances from the expected proportions of broods having each possible mixture of the two sexes, assuming a binomial with \( P = 0.50 \). For tests of factors potentially correlated with sex ratio we used PROC GENMOD in SAS (SAS Institute Inc. 1990) with a logit link and the distribution identified as a binomial. The number of male nestlings was used as the EVENT variable and the number of nestlings per observation (female or male) as the TRIALS variable. For phenotypic factors linked to the female or her mate, we used the total number of nestlings sexed within a season as the unit of analysis. We treated the few cases in which the same adult bird appeared in two or more seasons as independent events.

For tests of effects of seasonal timing, we used a repeated measures ANOVA because we often collected data on more than one nesting attempt by a particular female in a season. Because only a fraction of the females had more than three nesting attempts within a season, we restricted repeated measures tests to the first 3 nests.

We used principal components analysis (PCA) to reduce the number of independent variables in some analyses. Tarsus and wing length were positively correlated, and so reduced to one variable, size, corresponding to the first principal component. The four bib measures were positively correlated as well, and reduced to one variable, bib size, corresponding also to the first principal component in a PCA of those four variables. This variable is correlated with actual measures of bib area (DFW, unpubl. data).

RESULTS

SEX RATIO WITHIN AND AMONG YEARS

The primers were used to sex 1162 nestlings from the nests of 211 females over the five study years. The overall sex ratio was not significantly skewed from 50:50 (Table 1). Significantly more males than females were produced in two of the five years (Table 1).

As might be expected from the data in Table 1, an analysis of the effect of year on the proportion of males produced by females within a season revealed significant between-year heterogeneity (overall deviance = 253.2, effect of year, \( \chi^2_4 = 16.5, P < 0.01 \)). This effect persisted in analyses of the effect of barn on sex ratio (total deviance = 246.9, effect of year, \( \chi^2_4 = 9.9, P < 0.04 \)). Proportion male was not significantly different between barns (\( \chi^2_3 = 6.3, P > 0.1 \)).

We tested brood sex ratios for deviations from the pattern expected if the probability of a nestling being a male was 0.50 and independent from nestling to nestling within a brood. A chi-square test on the categories all male, all female, and mixed genders, weighting expected values by the relative number of broods of a given size, was not significant (\( \chi^2_2 = 3.0, P > 0.2 \)), indicating all male and all female broods were distributed as expected by chance alone. Similarly, a randomization test of the pattern of brood sex ratios indicated that the observed deviation from 50:50 was not significantly larger than expected by chance (\( \chi^2_2 = 47.3, P > 0.8 \)).

One possible source of bias after eggs have been laid is differential mortality of eggs or young nestlings from one sex before we sampled them. Indeed, last-laid eggs hatched later than...
the rest of the clutch, and the nestlings from these eggs were more likely to die before we sampled them (Stewart 1999). We tested for this and found no significant difference in proportion male between intact broods and those that lost at least one chick, either in 124 first broods (overall deviance = 169.7, effect of dichotomous nestling mortality variable, \( \chi^2 = 2.1, P > 0.1 \)) or for 119 second broods (overall deviance = 161.1, effect of dichotomous nestling mortality variable, \( \chi^2 = 0.1, P > 0.7 \)).

**WITHIN-SEASON PATTERNS**

If certain times of year are better for raising young, then the sex ratio might be biased toward males at those times, assuming that male offspring would benefit more from good conditions. We therefore tested for times in the season that were more favorable for producing offspring. We did so by analyzing the influence of nest order and date of first egg on clutch success.

Clutch size showed a significant polynomial relationship with clutch order for the first 4 clutches (repeated measures ANOVA, polynomial contrast quadratic, \( F_{1,102} = 11.6, P < 0.01 \); Fig. 1). We also examined patterns of nestling mass. Average within-brood nestling mass showed significant variation between nest attempts (repeated measures ANOVA on first 3 nests only, polynomial contrast-quadratic, \( F_{1,55} = 7.2, P < 0.01 \)), but the pattern was opposite from that of clutch size (with early and late broods having higher weights; Fig. 1) and was somewhat inconsistent between years (repeated measures ANOVA, quadratic contrast of brood by year interaction, \( F_{4,55} = 2.6, P < 0.05 \)) with 1997 featuring midseason broods with higher weights.

Brood mass may be biased if male nestlings are heavier than female nestlings. We analyzed the mass of male versus female nestlings via a matched test within broods using broods that had at least one of each using a matched test within broods. We found that males were significantly heavier than their female siblings (paired t-test, mean difference = 0.52 g, \( t_{206} = 2.8, P < 0.01 \)). This difference between the sexes was not affected by time in the season or year, as neither factor had a significant effect on the within-nest difference in mass (year: \( F_{2,203} = 1.1, P > 0.4 \); month: \( F_{4,202} = 0.5, P > 0.7 \)).

We controlled for differences between the sexes in nestling mass by standardizing each nestling’s mass within year and sex, and then averaging the standardized measures within broods. We tested if some broods within the season did better than others using this relative measure. We found no effect of brood order on relative nestling mass (repeated measures ANOVA on first 3 broods, \( F_{3,52} = 0.7, P > 0.5 \); polynomial test of order quadratic, \( F_{1,26} = 1.2, P > 0.3 \)).
The data on clutch size and nestling mass did not provide a clear prediction about when would be a good time to produce males as opposed to females. The clutch size data suggested that midseason was the best time to lay eggs, whereas the majority of the data on nestling mass was equivocal. Analyses of the sex ratio data (using arcsine transforms of the proportion of males) revealed no significant relationship between nest order and sex ratio (repeated measures ANOVA on first 3 nests, $F_{2.56} = 1.4, P > 0.2$, Fig. 1).

Within each round of nesting in a season, females varied in the time at which they started egg laying, and this could have affected offspring quality. Analyses of clutch size with date of first egg within attempts revealed a consistent negative relationship across the four attempts in the season (Fig. 2). That is, females laying eggs early within each attempt produced larger broods. However, nestling mass showed no consistent relationship with date of first egg across attempts (Fig. 2). Similarly, the proportion of males showed no consistent relationship with date of first egg within each attempt (Fig. 2).}

**FEMALE CHARACTERISTICS AND SEX RATIO**

We determined sex ratios from multiple broods of the same female within the season for 200 females summed over the 5 years (counting returning females as independent cases). For those females with more than two broods, we tested for consistency of offspring sex ratio. We found no association between the proportion of males in one brood with that in another of the same female (Pearson correlation on arcsine-transformed ratios: broods 1 and 2, $r = -0.14, F_{1.66} = 1.2, P > 0.3$; broods 2 and 3, $r = 0.07, F_{1.46} = 0.2, P > 0.6$). Nevertheless, we proceeded to analyze the possible effect of female characteristics by calculating the sex ratio of all of the sampled chicks produced by each female over the season. We found no significant associations between the proportion of males the female produced and the date of her first egg of the season ($\chi^2_1 = 0.3, P > 0.6, n = 198$), her minimum age ($\chi^2_4 = 1.8, P > 0.8, n = 105$), her body size ($\chi^2_1 = 1.2, P > 0.3, n = 47$), or her body condition (weight scaled to size) at capture in the same season ($\chi^2_1 = 0.2, P > 0.6, n = 41$).

If higher quality females lay more eggs, hatch a greater proportion of the eggs they lay, or produce heavier offspring, we might expect them to also produce more males. To measure relative clutch size, we controlled for the effect of nest order on clutch size and the effect of date of first egg within nest order by averaging residuals from the regressions (Fig. 2) of clutch size on date of first egg over all four nesting attempts. We found no association between proportion of males and relative clutch size ($\chi^2_1 = 1.4, P > 0.2, n = 194$). To control for the larger mass of male nestlings, we averaged the standardized value of nestling mass within each sex and year over all attempts in that year. We found no association between standardized nestling mass and proportion of males ($\chi^2_1 = 0.2, P > 0.6, n = 197$). Finally, we calculated hatching success as the number of hatchlings produced in a season divided by the number of eggs laid. Females that hatched a larger proportion of eggs also produced more males ($\chi^2_1 = 7.0, P = 0.008, n = 197$). If we assume all seven female variables tested are independent, then the Dunn-Šidák correction for multiple tests (Sokal and Rohlf 1995) gives an alpha of 0.007, making hatching proportion marginally nonsignificant. Nevertheless, we think this result reflects an actual relationship. First, the seven factors are not independent (female age influences first egg date and nestling mass, DFW, unpubl. data), making even the Dunn-Šidák correction conservative. Moreover, the relationship between hatching success and sex ratio remained significant when year was included in the model (proportion of eggs hatching: $\chi^2_1 = 5.3, P < 0.02$) and the interaction term was not significant (proportion of eggs hatching by year: $\chi^2_1 = 3.5, P > 0.5$). Indeed, the relationship between sex ratio and hatching proportion showed a consistently positive relationship in each of the five years, an unlikely event if the overall relationship was spurious.

**SEX RATIO AND MALE CHARACTERISTICS**

We tested for biases in the sex ratio produced by females mated to particular males based on male characteristics. We found no relationship between the proportion of males and male minimum age ($\chi^2_4 = 1.2, P > 0.3, n = 142$), body size (principal component 1 of tarsus and wing length; $\chi^2_1 = 1.2, P > 0.3, n = 98$), bib size (principal component 1 from four measures of bib dimensions; $\chi^2_1 = 0.05, P > 0.8, n = 98$), body condition (mass scaled to size) at the time when the male was captured in the same season ($\chi^2_1 = 0.9, P > 0.6, n = 93$), and date in the
FIGURE 2. Relationship between date of first egg and clutch size (top row), residual of nestling mass controlling for number of hatchlings (middle row), and the proportion of males (bottom row) for each of four sequential nest attempts by House Sparrows within a season. Solid lines represent the best-fit line. Proportion of males was arcsine transformed before analysis.
season when the male’s mate laid her first egg ($\chi^2_1 = 1.3, P > 0.3, n = 200$).

DISCUSSION
Sex ratio could be an interesting evolutionary trait in three distinctly different ways. First, it could fluctuate in evolutionary time due to selection pressures arising out of variation in adult sex ratios and the relative costs of producing each sex (Fisher 1930). Under Fisher’s view, sex ratio variation could evolve, but individual females could not adjust sex ratios as part of a conditional strategy. A second possibility is that females might assess adult sex ratio or the relative costs of producing either sex (or both), and facultatively adjust the sex ratio of their own offspring. Finally, Trivers and Willard (1973) and Charnov (1982) extended this idea to other factors that might influence female conditional strategies. The optimal sex ratio for a given female might vary depending on her quality, the quality of her mate, or the relative amount of resources available to her. Our results bear on each of these possibilities either directly or indirectly.

We initially predicted that the proportion of males in nestling House Sparrows would be close to 0.5. The overall sex ratio from the 5 years of study was indeed close to that (0.53). In contrast to Schifferli (1980), we found that male House Sparrows weighed significantly more than females when they were banded at 10 days of age. This suggests that males might be costlier to produce than females, although the difference in mass is only about 2%. We also found substantial year-to-year variation in sex ratio, with some years significantly biased toward males, and others nearly significantly biased toward females. Such fluctuation could arise if there was yearly variation in either adult sex ratio or the differential cost of each sex, and a subsequent balancing evolutionary response. Our data show no indication of variation in costs between years (males were consistently larger than females in each season). The sex ratio of adult birds consistently inhabiting boxes is slightly male biased, with some males at boxes remaining unpaired for significant periods of time. However, we do not know the sex ratio of floaters, although we suspect there are few female floaters. Data on sex ratio of captures during the winter revealed a male bias in 5 of the 6 seasons between 1992 and 2001 with sufficient data, but unfortunately only two estimates were available during the 5 years of this study (1995–1996: 26 of 49 winter captures were male; 1998–1999: 71 of 113 captures were male).

These data do not support the Fisherian mechanism of adaptive sex ratio because conditions are such that House Sparrows ought to produce more females. Moreover, the pattern of variation from year to year does not suggest a purely evolutionary response of a non-facultative setting of sex ratio. The changes occur too quickly (within one year, equal to one generation). Instead, the year-to-year pattern suggests that females may assess adult sex ratio each season and adopt a conditional strategy of response (Trivers and Willard 1973). Our data on adult sex ratios are also inadequate to test this hypothesis. We note here that either the Fisherian evolutionary response or the facultative response to adult sex ratio require that juveniles end up in the population that is skewed. Juvenile sparrows from our study site probably disperse to a nearby site supporting House Sparrows. However, if conditions on our study site fluctuate in parallel with those at other sites, then either mechanism for adaptive sex ratio adjustment could work. Experimental manipulation of adult sex ratio combined with surveys of neighboring clusters of sparrows seems the most powerful way to test these ideas in House Sparrows.

The tendency for House Sparrows to produce more males is counter to the general tendency of passerine birds to produce more females (Gowaty 1993). The skew toward females could be due to local resource competition with male offspring, since females tend to disperse more than males in passerines (Gowaty 1993). Although Fleischer et al. (1984) found female House Sparrows dispersed more than males, we have not found a similar skew in this population (DFW, unpubl. data). Gowaty (1993) suggested that even subtle differences in the timing of dispersal could influence local resource competition and hence the sex ratio. Good estimates of the timing of dispersal of juveniles require data that we have not collected in our population. However, we did examine this indirectly by testing if the delay to recapture depends on sex. If one sex disperses before another, then they should be under-represented in trapping sessions occurring long after fledging. We found no such relationship between the delay to recapture and sex (logistic regression, $\chi^2_1 = 0.6, P > 0.4, n = 161$).
Thus, on one hand, our data reveal that the population we studied may be unusual in having less of a bias in dispersal than most passerines and less of a skew toward females as well, supporting Gowaty’s (1993) conclusions. On the other hand, our data also indicate that local resource competition cannot explain the tendency of this population to produce males.

We explored a variety of factors that could influence a more fine-tuned flexible strategy of sex ratio adjustment. We found that other factors predicted to influence the sex ratio, such as the apparent condition of the female or her mate’s apparent sexual attractiveness, did not affect sex ratio. These results could mean that either females are not under selection to adjust the sex ratio, that they are under selection but are physically incapable of adjustment, or that we have measured the wrong variables. Because House Sparrows are socially monogamous and have relatively low frequencies of extra-pair paternity (ca. 12% of young, Wetton and Parkin 1991, Cordero et al. 1999, Stewart 1999, Whitekiller et al. 2000), the difference in variance in reproductive success between the sexes is slight. Hence, producing a high quality male might not be better than producing a high quality female. Research from a variety of House Sparrow populations indicates some level of sexual selection on males (e.g., Möller 1989, Veiga 1993), but the magnitude and target of that selection appears variable (Griffith et al. 1999b) and is not conspicuous in the present population (Westneat et al., unpubl. data). If the benefits of producing a high quality male are weak, then strategies for achieving a bias in sex ratio may not have evolved.

Finally, female House Sparrows may benefit from manipulating sex ratios in some circumstances, but we may have measured the wrong factors. For example, it is possible that a female’s size, body condition, or age do not influence the quality of a female’s offspring. We did find that the proportion of eggs that hatched was correlated with brood sex ratio. We have no evidence to suggest that this relationship is a consequence of male eggs being more likely to hatch. Rather, this result suggests that some females were less able to incubate and protect their eggs, and that when these females succeeded, they tended to produce female offspring. We do not know what aspect of female quality contributes to this. One possibility may be female social status: socially subordinate females may suffer from conspecific disruptions near the nest during incubation or nestling care. We know that social interactions between females can influence egg or nestling mortality via infanticide (Veiga 1990), but less intense interactions might also influence the timing of incubation patterns and hence hatching success when eggs are not destroyed. Why this would affect sex ratios is not known, but if female social status also influences the quality of offspring produced and females can assess their own social status, hatching success may be an indicator of an aspect of female condition important to sex ratio. Data on female social status and its effects on reproduction will be needed to assess this idea.

In general, our study adds to a growing body of findings on sex ratios that present a confusing picture of how well theory explains patterns of sex ratio variation. Some birds clearly are capable of manipulating sex ratio (e.g., Seychelles Warbler, Komdeur et al. 1997). Evidence that eggs containing male embryos are larger than those with female embryos hints that adult female House Sparrows can differentially invest in one sex (Cordero et al. 2000). However, we found little evidence that female manipulation affects sex ratio at 10 days of age. Our data suggest female quality may influence sex ratio, but we found no evidence that the characteristics of the female’s mate have any effect. So, like a number of other studies, we found slight yet incomplete evidence of such manipulation despite some suggestions that adjusting sex ratios might be beneficial. Our results are also consistent with a recent study of Great Tits (Parus major) that found substantial year-to-year variation in sex ratio and its correlates (Radford and Blakey 2000). Sex ratios and the factors that influence them thus vary considerably within and among species. These differences will require some reassessment of theory and considerably more empirical work. Eventually, we think it likely that the clearest explanations will arise from experimental and comparative empirical studies that directly confront the array of possible reasons for such differences among populations.

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LITERATURE CITED


