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## Article

### Females are more determinant than males in reproductive performance in the house sparrow *Passer domesticus*

Juan Manuel Peralta-Sánchez, Jose Colmenero, Sandra Redondo-Sánchez, Juan Ontanilla and Manuel Soler

J. M. Peralta-Sánchez, Depto de Microbiología, Facultad de Ciencias, Univ. de Granada, Granada, Spain and Dept of Integrative Ecology, Estación Biológica de Doñana, C.S.I.C., Seville, Spain. – J. Colmenero, S. Redondo-Sánchez, J. Ontanilla and M. Soler (<https://orcid.org/0000-0002-6451-0793>) ✉ ([msoler@ugr.es](mailto:msoler@ugr.es)), Depto de Zoología, Facultad de Ciencias, Univ. de Granada, Granada, Spain. MS also at: Grupo Coevolución, Unidad Asociada al CSIC, Univ. de Granada, Granada, Spain.

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Which sex has a more determinant role in reproductive performance? This is a long standing question in evolutionary ecology. Theory predicts and several pieces of evidence have indicated that females are more determinant than males. However, a direct test of this hypothesis has never been made. Here we perform such a direct test by using an alternative analytical approach, controlling for age and/or individual experience, and a captive population of the house sparrow *Passer domesticus*, a monogamous bi-parental dimorphic species in which both sexes contribute with approximately equal amounts of parental care. In this species, it has been demonstrated that contribution by males to offspring parental care is crucial to maximize reproductive success. Captive conditions with absence of predators and availability of food ad libitum allow us to control several important factors that may affect reproductive performance, such as environmental fluctuations in resource availability and differences in territory quality, without affecting reproductive performance. We consider four types of pairs, and our main prediction derived from the hypothesis is that mixed pairs involving an experienced female (FBM × EF) should present better reproductive performance than mixed pairs involving a first-time breeder female (EM × FBF). Our results confirm the general pattern reported in other bird species that older or more experienced individuals enjoy a higher reproductive success than first-time breeders. In addition, in agreement with our main prediction, we found that FBM × EF produced significantly more fledglings and had higher fledging success than EM × FBF. Our results, for the first time demonstrate the broadly accepted statement that females have a more determinant role than males in reproductive performance.

Keywords: male and female relative investment, parental care, *Passer domesticus*, reproductive performance

## Introduction

The relative contribution of both sexes toward rearing offspring is a key factor driving sexual selection and the evolution of mating systems. There exists a conflict of interest



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between the sexes over levels of parental investment because each individual of the pair gains fitness benefits from the reproductive investment of both, but pays only the costs of its own care (Trivers 1972). The most common scenario is that females invest more than males in most vertebrates. However, among birds, social monogamy and bi-parental care is the norm (81% of all bird species; Cockburn 2006), and the traditional explanation for this higher male investment is that the effort of both parents are necessary to adequately care for their offspring (Lack 1968).

In bi-parental socially monogamous altricial bird species, the relative proportion of parental care investment by the two mates could substantially vary among species in kind and amount of parental care investment. In most species both males and females invest equally in parental care, but in others, parental care investment may be either male or female biased (reviewed by Woodard and Murphy 1999). Usually, males invest more in defending territories while females invest more in building nests, incubating and brooding (Winkler 2016). In feeding the young, the most expensive parental care in altricial birds, males and females contribute about equally (Davies et al. 2012).

A long standing question in evolutionary ecology is which sex has a more determinant role in reproductive performance. The most broadly accepted response is that females are more determinant of reproductive performance (Davies et al. 2012). Although males and females usually contribute roughly equally in feeding their offspring, especially in monogamous species (reviewed in Woodard and Murphy 1999), sexual conflict theory predicts less food provisioning effort by males (Davies et al. 2012). These differences are more drastic in sexually dimorphic species (Mizuta 2005), as a consequence of male paternity uncertainty and/or the existence of additional

reproductive opportunities for males (Dixon et al. 1994, Dunn and Cockburn 1996). There are two pieces of evidence showing that females are more determinant than males. First, experiments exploring the response of a parent to a reduction in parental care by its partner or to an increase in brood size, showed that mainly males increase their parental investment (Harrison et al. 2009, Santos and Nakagawa 2012). The suggested explanation for these results is that females cannot increase their investment because in natural conditions they are working close to their maximum capacity while males are not (MacGregor and Cockburn 2002, Low et al. 2011, Santos and Nakagawa 2012). And second, by quantifying energy expenditure during feeding young in both males and females, it was found that maternal effort has more of an effect on offspring fitness than paternal effort on both nestling size (Moreno et al. 1997) and nestling health (Merino et al. 1996).

The two pieces of evidence described above do not directly test the hypothesis that females have a more determinant role than males in offspring fitness, a hypothesis that, as far as we know, has never been appropriately tested. This lack of direct test may lay in the difficulty of addressing this question directly, probably due to two major reasons. First, the experimental manipulation needed to perform such tests, i.e. reduce male or female working capacity to make care provisioning more energetically demanding in one of the two sexes, usually fail because each parent usually compensates, at least partially, for reduction in the feeding effort of the other parent (reviewed in Harrison et al. 2009). Secondly, multiple factors influence provisioning behaviour including: nestling age, brood size, mate quality, male uncertainty of paternity status, intersexual differences in foraging behaviour, existence of other reproductive opportunities and individual ability or experience in rearing offspring.

Table 1. Generalized linear mixed-effect models of the reproductive parameters of first clutches taking into account the four considered groups in relation with the age of each member of the breeding pair (both adults: EM×EF, both first time breeders: FBM×FBF, adult male and a young female: EM×FBF, and young male with an adult female: FBM×EF). Significant p-values in bold.

Dependent variable	Model Adjusted r <sup>2</sup>	Model p	Independent variables		df	F	p	
Julian laying date	0.25	< <b>0.001</b>	Breeding pair	Fixed	3	159	7.06	< <b>0.001</b>
			Experimental site	Random	1	159	1.89	0.171
			Year	Random	1	159	26.14	< <b>0.001</b>
Clutch size	0.01	0.234	Breeding pair	Fixed	3	159	1.87	0.136
			Experimental site	Random	1	159	0.17	0.681
			Year	Random	1	159	0.28	0.597
Brood size	0.04	<b>0.032</b>	Breeding pair	Fixed	3	159	2.77	<b>0.043</b>
			Experimental site	Random	1	159	1.22	0.271
			Year	Random	1	159	1.83	0.178
Number of fledglings	0.13	< <b>0.001</b>	Breeding pair	Fixed	3	159	6.81	< <b>0.001</b>
			Experimental site	Random	1	159	7.84	<b>0.006</b>
			Year	Random	1	159	1.94	0.166
Arcsine hatching success	0.05	<b>0.023</b>	Breeding pair	Fixed	3	159	1.69	0.172
			Experimental site	Random	1	159	3.95	<b>0.049</b>
			Year	Random	1	159	1.42	0.236
Arcsine fledging success	0.10	<b>0.001</b>	Breeding pair	Fixed	3	139	4.72	<b>0.004</b>
			Experimental site	Random	1	139	9.93	<b>0.002</b>
			Year	Random	1	139	1.04	0.310

The objective of this paper is to perform such a direct test by using an alternative analytical approach and the house sparrow *Passer domesticus* as model species. The house sparrow is an appropriate model species because it is a monogamous, bi-parental, dimorphic species in which both sexes contribute with approximately equal amounts of parental care (Summers-Smith 1963). Both males and females participate in all forms of parental care: nest building, incubation, brooding and nestling provisioning (Anderson 2006). However, important differences between sexes exist in parental care provided in each phase of the nestling cycle. Nest building and nest guarding is performed predominantly by males, incubation and nestling brooding is performed mainly by females and investment in nestling provisioning does not differ significantly between partners (Anderson 2006). This relevant contribution by males to offspring parental care is considered to be essential to maximize reproductive success. It has been demonstrated that male assistance is crucial to increase reproductive success in house sparrows, indeed it has been found that male feeding rate explains variation in fledging numbers and fledging success (Hoi et al. 2003).

Our analytical approach allows to control for age and/or individual experience because these parameters, which are directly related, have a positive effect on reproductive success (Saether 1990, Forslund and Pärt 1995, Fowler 1995). In birds, more experienced individuals (i.e. those that have previously reproduced for one or more breeding attempts) usually start breeding earlier, have larger clutches and/or fledge

more young than first-time breeders (Nol and Smith 1987, Komdeur 1996, Woodard and Murphy 1999, Robertson and Rendell 2001). This general pattern has also been reported in house sparrows (Hatch and Westneat 2007). Therefore, if we have the possibility of making comparisons between types of pairs of different age-category groups can help test the hypothesis that older females have a more determinant reproductive performance than males. To test our hypothesis, we consider four types of pairs: experienced male  $\times$  experienced female (EM  $\times$  EF); first-time breeder male  $\times$  first-time breeder female (FBM  $\times$  FBF); experienced male  $\times$  first-time breeder female (EM  $\times$  FBF); and first-time breeder male  $\times$  experienced female (FBM  $\times$  EF). Our prediction is that mixed pairs involving an experienced female (FBM  $\times$  EF) should present better reproductive performance than mixed pairs involving an experienced male (EM  $\times$  FBF) both when considering only first clutches and when considering total reproductive outputs.

## Material and methods

The house sparrow is a small passerine around 15 cm in length belonging to the family Passeridae. Several traits make this species an excellent candidate to study reproductive performance: it shows a clear sexual dimorphism, it uses a monogamous reproductive system, breeds in colonies and acclimates easily to captivity (Moreno-Rueda and Soler 2002, Anderson 2006).

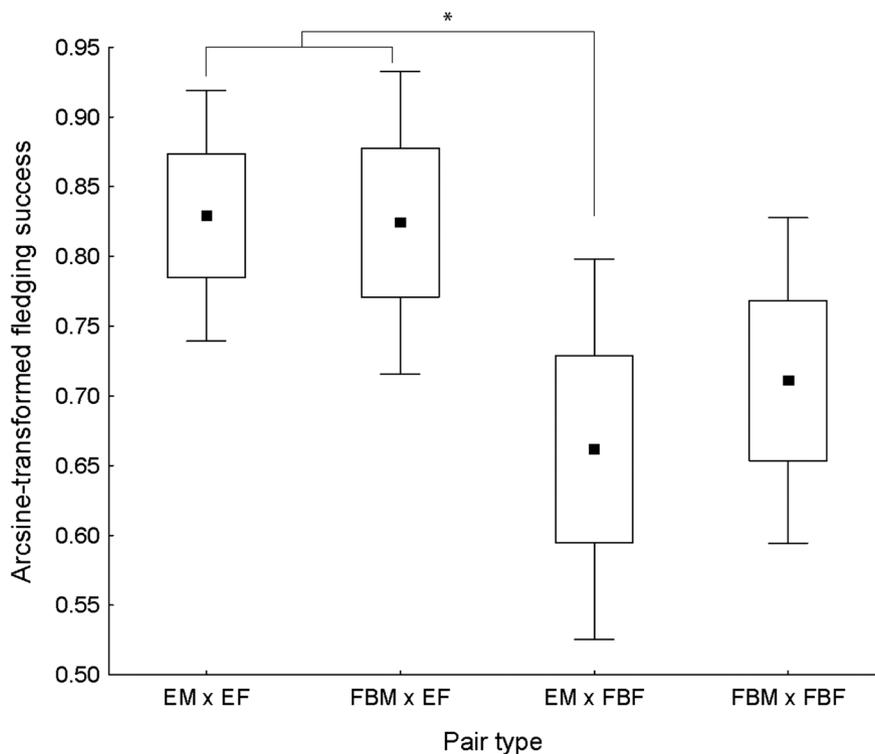


Figure 1. Arcsine-transformed of fledging success in the first clutch of the breeding season in relation with the age of each member of the breeding pair (both experienced: EM  $\times$  EF, both first-time breeders: FBM  $\times$  FBF, experienced male and a first-time breeder female: EM  $\times$  FBF, and first-time breeder male with an experienced female: FBM  $\times$  EF). Boxes represent standard error of the mean, while whiskers represent 95% confidence interval.

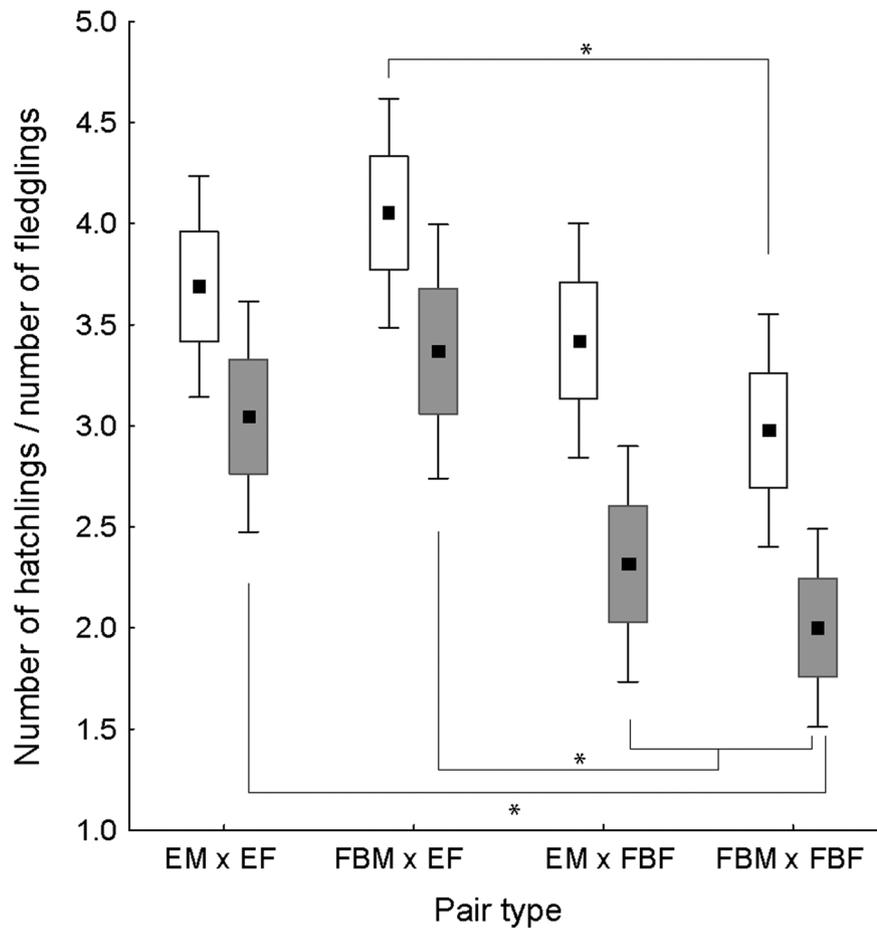


Figure 2. Brood size (white boxes) and number of fledglings (grey boxes) in the first clutch of the breeding season in relation with the age of each member of the breeding pair (both experienced: EM×EF, both first-time breeders: FBM×FBF, experienced male and a first-time breeder female: EM×FBF, and first-time breeder male with an experienced female: FBM×EF). Boxes represent standard error of the mean, while whiskers represent 95% confidence interval. Significant differences between groups are showed with asterisks.

Table 2. Generalized linear mixed-effect models of the reproductive parameters of first clutches considering the two mixed groups in relation with the age of each member of the breeding pair (adult male with a young female: EM×FBF, and young male with an adult female: FBM×EF). Significant p-values in bold.

Dependent variable	Model adjusted r <sup>2</sup>	Model p	Independent variables		df	F	p	
Julian laying date	0.12	<b>0.007</b>	Breeding pair	Fixed	1	72	1.06	0.306
			Experimental site	Random	1	72	2.61	0.111
			Year	Random	1	72	11.71	<b>0.001</b>
Clutch size	-0.01	0.597	Breeding pair	Fixed	1	72	1.67	0.200
			Experimental site	Random	1	72	0.17	0.679
			Year	Random	1	72	0.02	0.894
Brood size	0.05	0.080	Breeding pair	Fixed	1	72	2.69	0.105
			Experimental site	Random	1	72	1.03	0.313
			Year	Random	1	72	1.98	0.164
Number of fledglings	0.16	<b>0.001</b>	Breeding pair	Fixed	1	72	7.34	<b>0.008</b>
			Experimental site	Random	1	72	4.93	<b>0.030</b>
			Year	Random	1	72	2.13	0.149
Arcsine hatching success	0.08	<b>0.030</b>	Breeding pair	Fixed	1	72	1.47	0.229
			Experimental site	Random	1	72	2.77	0.100
			Year	Random	1	72	2.65	0.108
Arcsine fledging success	0.18	<b>0.001</b>	Breeding pair	Fixed	1	72	5.47	<b>0.022</b>
			Experimental site	Random	1	72	8.62	<b>0.005</b>
			Year	Random	1	72	2.04	0.158

Table 3. Generalized linear mixed-effect models of the total reproductive output in a single breeding season taking into account the four considered groups in relation with the age of each member of the breeding pair (both adults: EM×EF, both first time breeders: FBM×FBF, adult male and a young female: EM×FBF, and young male with an adult female: FBM×EF). Significant p-values in bold.

Dependent variable	Model adjusted r <sup>2</sup>	Model p	Independent variables		df	F	p	
Number of clutches	0.03	0.091	Breeding pair	Fixed	3	159	2.13	0.098
			Experimental site	Random	1	159	0.98	0.324
			Year	Random	1	159	4.24	<b>0.041</b>
Clutch size average	0.08	<b>0.003</b>	Breeding pair	Fixed	3	159	3.26	<b>0.023</b>
			Experimental site	Random	1	159	0.21	0.647
			Year	Random	1	159	5.82	<b>0.017</b>
Total number of eggs	0.07	<b>0.005</b>	Breeding pair	Fixed	3	159	5.30	<b>0.002</b>
			Experimental site	Random	1	159	0.19	0.667
			Year	Random	1	159	0.14	0.713
Hatching success average	0.03	0.074	Breeding pair	Fixed	3	159	1.46	0.227
			Experimental site	Random	1	159	0.01	0.903
			Year	Random	1	159	4.52	<b>0.035</b>
Total number of hatchlings	0.00	0.433	Breeding pair	Fixed	3	159	1.08	0.359
			Experimental site	Random	1	159	1.22	0.271
			Year	Random	1	159	0.02	0.890
Brood size average	−0.01	0.547	Breeding pair	Fixed	3	159	0.32	0.812
			Experimental site	Random	1	159	0.35	0.555
			Year	Random	1	159	1.42	0.234
Total number of fledglings	0.12	<b>&lt; 0.001</b>	Breeding pair	Fixed	3	159	8.40	<b>&lt; 0.001</b>
			Experimental site	Random	1	159	0.37	0.544
			Year	Random	1	159	0.02	0.880
Fledglings average per clutch	0.09	<b>&lt; 0.001</b>	Breeding pair	Fixed	3	159	6.01	<b>0.001</b>
			Experimental site	Random	1	159	0.84	0.360
			Year	Random	1	159	1.77	0.185
Fledgling success average	0.03	0.088	Breeding pair	Fixed	3	159	3.24	<b>0.024</b>
			Experimental site	Random	1	159	0.58	0.448
			Year	Random	1	159	0.04	0.841

### Captivity conditions and implications

This study was performed during 2014–2015 in installations of Univ. of Granada in the Faculty of Sciences (Granada, Spain) and in Hernan Valle field station (Guadix, Spain) using a total of 165 breeding pairs. The aviary in the Faculty of Sciences measured around 375 m<sup>3</sup>. In Hernan Valle, we used 17 cages (15 × 50 m; 2 × 40 m). In all aviaries we adjusted population density around 0.20 bird m<sup>−3</sup> and established sex ratio to 1:1. All birds were banded with unique numeric rings as well as colour rings for individual identification.

House sparrows were fed at libitum with a mixture of commercial seeds for canaries, and nestling food (egg-food with fruits, Bogená), cracked grains of wheat and rice, fly maggots, apple, lettuce and sand. Food and water were spaced across the aviaries to ensure that all birds had easy access (Soler et al. 2011).

In all aviaries, nest-boxes (21 × 24 × 16 cm, hole diameter: 5 cm) were placed in higher density than the number of potential pairs (about 25% more), so birds could choose between different nest-boxes. No preference was observed for nest-box selection (personal observation). Vegetable material, mainly grass and some straw, for nest construction was provided ad libitum during the breeding season. Nest-boxes were out of the aviary located in the faculty, in an adjacent laboratory, which allowed nest examination (and experimental manipulation when needed) from the laboratory, which minimize the stress suffered by the captive population.

Our analytical approach requires knowing the sex and the age of each individual, information which is rarely available in wild populations. It is especially challenging to measure age-specific reproductive performance in natural conditions because of logistical requirements of monitoring recognizable individuals of known age (Clutton-Brock and Sheldon 2010). Captive populations provide individual information on age-specific reproductive performance of both males and females. In addition, reproductive performance in natural conditions may be affected by several factors such as environmental fluctuations in resource availability and differences in territory quality, which would make it more difficult to obtain strong conclusions. In captive conditions, the absence of predators and the availability of food (large abundance and easy to find) allowed us to collect a sufficiently large sample size for meaningful analyses. Furthermore, it is worth noting that pairs in captivity have similar or slightly higher reproductive performance than wild pairs (Nichols et al. 2010; this paper). Thus, captive populations provide a magnificent opportunity for testing hypotheses because many factors that negatively affect data collection are controlled for without affecting breeding parameters.

### Analytical procedure

During the breeding seasons of 2014 and 2015, all breeding pairs were identified and assigned to one of the following groups: EM × EF, FBM × FBF, EM × FBF and FBM × EF

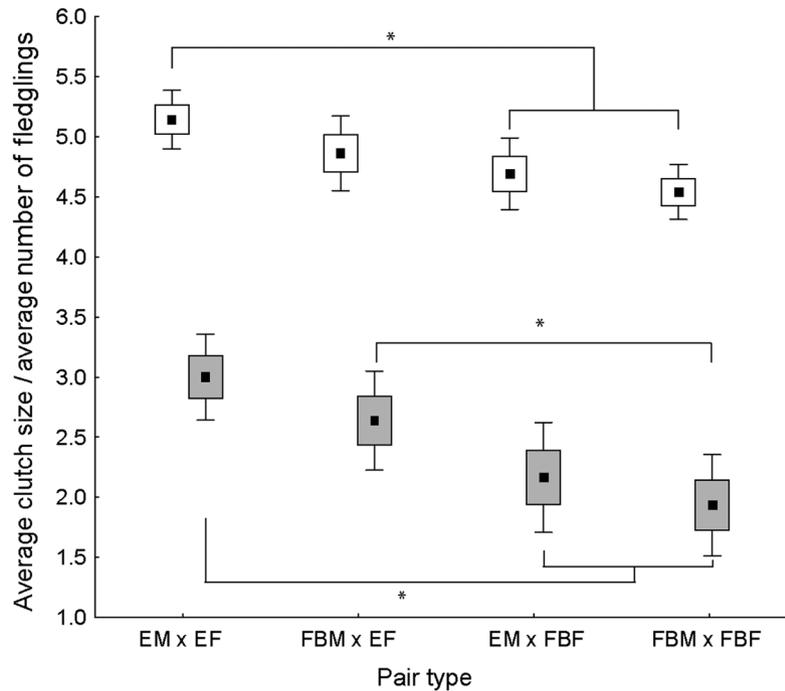


Figure 3. Average clutch size (white boxes) and average number of fledglings (grey boxes) during the breeding season in relation with the age of each member of the breeding pair (both experienced: EM×EF, both first-time breeders: FBM×FBF, experienced male and a first-time breeder female: EM×FBF, and first-time breeder male with an experienced female: FBM×EF). Boxes represent standard error of the mean, while whiskers represent 95% confidence interval.

(see above). Mixed pairs (experienced×first-time breeder) were scarcer than equal age pairs (experienced×experienced, first-time breeder×first-time breeder). In order to obtain a balanced sample size of each group, we randomly chose 45 EM×EF, 44 FBM×FBF, 38 EM×FBF and 38 FBM×EF pairs. These 165 breeding pairs performed a total of 467 breeding attempts: 165 breeding pairs attempted a first clutch, 155 performed a second clutch, 111 a third clutch and 32 a fourth clutch. We did not include fifth ( $n=3$ ) and sixth breeding attempts ( $n=1$ ) in the analyses.

Reproductive parameters were recorded for each clutch: Julian laying date, clutch size (number of eggs), hatching success (ratio hatchlings/eggs), brood size (number of hatchlings), number of fledglings and fledging success (ratio fledgling/hatchlings). For total breeding output, we calculated number of clutches, average clutch size, total number of eggs, total number of hatchlings, average brood size, average hatching success, total number of fledglings, fledgling average per clutch and average fledgling success (Supplementary material Appendix 1 Table A1).

## Statistics

We explored reproductive performance at first clutch and total reproductive output for the breeding season between pair type by means of generalized mixed-effect models (GLMM). In these models, we used breeding parameters as dependent variables, breeding pair as fixed factor and year and experimental site as random factors. We performed

Fisher LSD Tests in order to explore significant differences between pairs of breeding pair types. For first clutches, 20 first clutches did not hatch, so it was not possible to calculate fledging success for these breeding pairs. Hence, sample size in analyses related to number of fledglings and fledging success was 145. For those dependent variables that differed significantly between breeding pair types, we performed additional GLMM by only including mixed pairs, i.e. FBM×EF and EM×FBF.

The residuals of most of the reproductive variables followed a normal distribution (Kolmogorov–Smirnov,  $p>0.10$ ). However, residuals of total number of clutches, hatching success in the first clutch and fledging success in the first clutch did not reach normality. The log<sub>10</sub>-transformed total number of clutches as well as the arcsine-transformed hatching and arcsine-transformed fledging success (both in the first clutch) were homoscedastic (Levene’s tests,  $p>0.219$ ), justifying the use of parametric tests.

Statistical analyses were performed in Statistica 10.0 and significant  $p$ -values were set at 0.05.

## Results

### First clutches

Laying date, brood size, number of fledglings and fledging success differed significantly between breeding pair types (Table 1). EM×FBF pairs showed significantly lower fledgling success

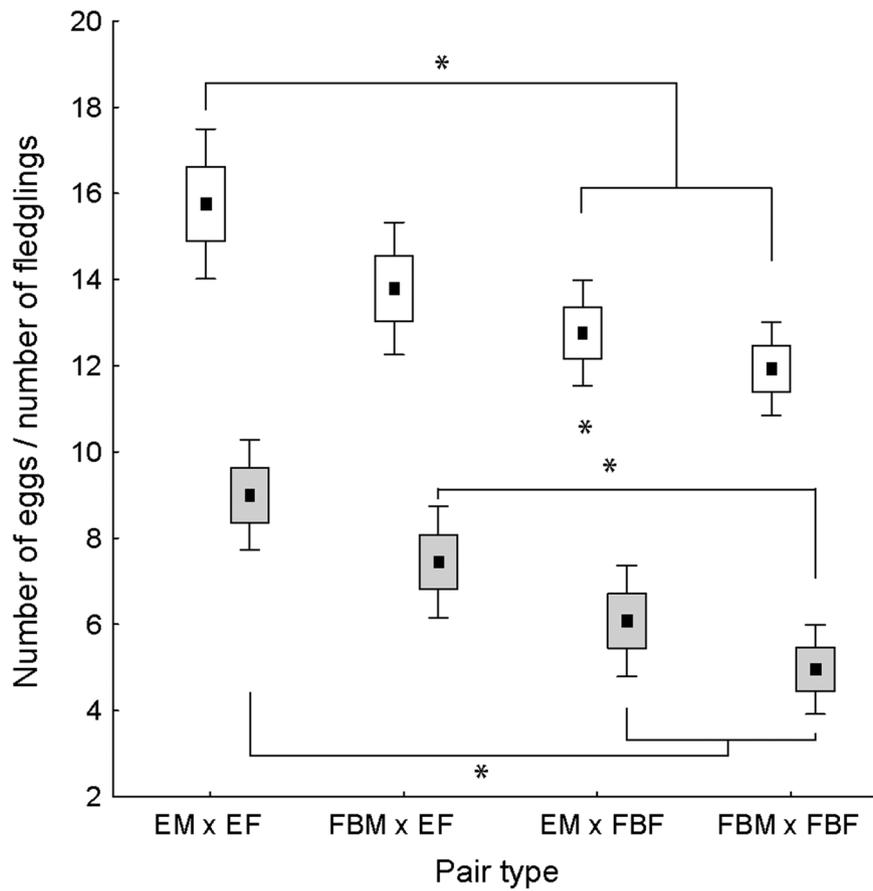


Figure 4. Total number of eggs (white boxes) and total number of fledgling (grey boxes) produced during the breeding season in relation with the age of each member of the breeding pair (both experienced: EM×EF, both first-time breeders: FBM×FBF, experienced male and a first-time breeder female: EM×FBF, and first-time breeder male with an experienced female: FBM×EF). Boxes represent standard error of the mean, while whiskers represent 95% confidence interval. Significant differences between groups are showed with asterisks.

than pairs with an experienced female (EM×EF and FBM×EF) (Fig. 1; Fisher LSD post-hoc tests,  $p < 0.036$ ). We found that FBM×EF produced significantly more fledglings and had higher fledging success than EM×FBF (Fig. 1, 2, Table 2).

Experienced pairs (EM×EF) started laying eggs significantly earlier than pairs with first breeder pairs (FBF×EF, EM×FBF and FBM×FBF) (Supplementary material Appendix 1 Fig. A1; Fisher LSD post-hoc test,  $p > 0.001$ ). Significant differences in brood size between breeding pair types (Table 1) were due to differences between FBM×EF and FBM×FBF (Fisher LSD post-hoc tests,  $p < 0.001$ ).

### Total reproductive outputs

Breeding pair type significantly explain variation in average clutch size, total number of eggs, total number of fledglings, average number of fledglings and average fledging success (Table 3).

EM×EF had larger average clutch size (Fig. 3) and produced more eggs (Fig. 4) than pairs with first-time breeder females (EM×FBF and FBM×FBF; Fisher LSD post-hoc tests,  $p < 0.016$ ). Pairs with first-time breeder females did not show differences between them in these variables (Table 4).

EM×EF had larger average number of fledglings per clutch (Table 3, Fig. 4) produced more fledglings in the breeding season (Table 3, Fig. 4), and experienced higher average fledging success per clutch (Table 3, Fig. 5) than pairs with first-time breeders females (EM×FBF and FBM×FBF; Fisher LSD post-hoc tests,  $p < 0.038$ ). Moreover, FBM×EF experienced significantly higher averages in these variables than FBM×FBF (Fig. 3–5; Fisher LSD post-hoc tests,  $p < 0.040$ ).

When we considered only mixed pairs (FBM×EF and EM×FBF), no significant differences were found in any of the variables of the total breeding output (Table 4).

### Discussion

Our results confirm that more experienced house sparrows have higher reproductive success than first-time breeders (Fig. 1–5, Table 1, 3), a general pattern that has been reported in many bird species (Nol and Smith 1987, Saether 1990, Fowler 1995, Komdeur 1996, Newton and Rothery 1997, Woodard and Murphy 1999, Espie et al. 2000, Robertson and Rendell 2001, Wiklander et al. 2001, Laaksonen et al. 2002), including the house sparrow (Hatch and Westneat

Table 4. Generalized linear mixed-effect models of the total reproductive output in a single breeding season considering the two mixed groups in relation with the age of each member of the breeding pair (adult male with a young female: EM×FBF, and young male with an adult female: FBM×EF). Significant p-values in bold.

Dependent variable	Model adjusted r <sup>2</sup>	Model p	Independent variables	df	F	p		
Number of clutches	0.04	0.109	Breeding pair	Fixed	1	72	0.10	0.750
			Experimental site	Random	1	72	4.58	<b>0.036</b>
			Year	Random	1	72	3.69	0.059
Clutch size average	0.03	0.153	Breeding pair	Fixed	1	72	0.70	0.406
			Experimental site	Random	1	72	0.22	0.643
			Year	Random	1	72	3.43	0.068
Total number of eggs	0.00	0.373	Breeding pair	Fixed	1	72	1.24	0.269
			Experimental site	Random	1	72	2.03	0.158
			Year	Random	1	72	0.33	0.566
Hatching success average	0.13	<b>0.005</b>	Breeding pair	Fixed	1	72	0.54	0.463
			Experimental site	Random	1	72	0.23	0.634
			Year	Random	1	72	10.78	<b>0.002</b>
Total number of hatchlings	0.03	0.143	Breeding pair	Fixed	1	72	2.79	0.099
			Experimental site	Random	1	72	2.60	0.111
			Year	Random	1	72	0.26	0.615
Brood size average	-0.02	0.645	Breeding pair	Fixed	1	72	0.35	0.556
			Experimental site	Random	1	72	0.91	0.344
			Year	Random	1	72	0.10	0.755
Total number of fledglings	0.05	0.091	Breeding pair	Fixed	1	72	2.53	0.116
			Experimental site	Random	1	72	1.73	0.192
			Year	Random	1	72	1.17	0.283
Fledglings average per clutch	0.10	<b>0.013</b>	Breeding pair	Fixed	1	72	2.77	0.100
			Experimental site	Random	1	72	1.16	0.284
			Year	Random	1	72	5.17	<b>0.026</b>
Fledgling success average	0.02	0.212	Breeding pair	Fixed	1	72	2.79	0.099
			Experimental site	Random	1	72	1.39	0.242
			Year	Random	1	72	0.07	0.793

2007). Hatch and Westneat (2007) found that more experienced house sparrows breeding in natural conditions initiated breeding earlier and fledged more nestlings than yearlings; results that coincide with those obtained in this study in a captive population.

In bi-parental monogamous bird species, males strongly influence reproductive performance (Woodard and Murphy 1999), and this is also the case of the house sparrow (Hoi et al. 2003). Our prediction based on the sexual conflict theory that mixed pairs involving an experienced female should present better reproductive performance than mixed pairs involving a first-time breeder female is supported when considering only first clutches (Fig. 1, 2, Table 2). The fact that mixed pairs in which the experienced sex is the female (FBM×EF) produced more fledglings and had higher fledging success than mixed pairs in which the experienced sex is the male (EM×FBF) supports the idea that females are more determinant than males in reproductive performance. However, our prediction is not supported when considering total reproductive outputs.

Other results indicate that females are more important than males in reproductive performance. Specifically, pairs with experienced males and first-time breeder females (EM×FBF) do not have better reproductive performance than pairs with first-time breeder males and first-time breeder females (FBM×FBF). This means that the role of

males in reproductive performance is less important than that of females because mixed pairs with experienced females (FBM×EF) have a better reproductive performance than pairs with first-time breeder males and first-time breeder females (FBM×FBF). Interestingly, however, these results could be the consequence of females increasing their fitness as they age more than males do, not necessarily implying that females are influencing reproductive performance more than males.

In agreement with our results, a study of parental behaviour in eastern kingbirds *Tyrannus tyrannus* found that experience of females was the main factor responsible for differences in reproductive success (Woodard and Murphy 1999). However, pairs with an experienced male also had higher reproductive success than first-time breeder pairs, which has not been confirmed in our study with house sparrows. Woodard and Murphy (1999) also found that the poor reproductive performance of inexperienced pairs was mainly due to differences in territory quality, which cannot apply to our study in captive conditions.

The broadly reported (see references above) fact that more experienced individuals have a better reproductive performance than younger ones has been attributed to improved feeding efficiency, more efficient predator avoidance strategies, or higher territory quality (Crawford 1977, Holmes et al. 1996, Woodard and Murphy 1999), factors that cannot have an effect in our captive population.

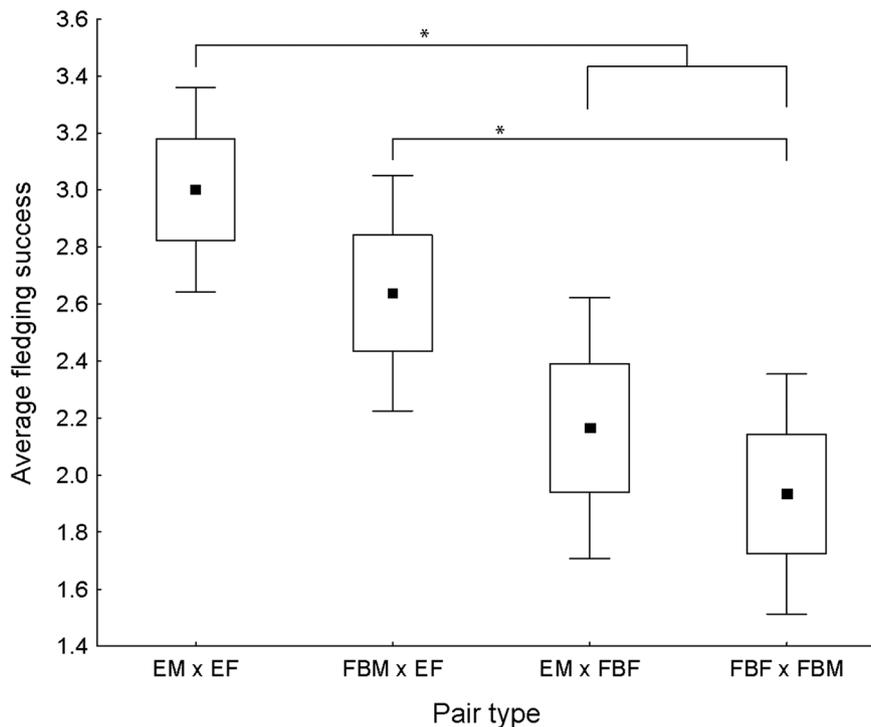


Figure 5. Average fledgling success during the breeding season in relation with the age of each member of the breeding pair (both experienced: EM×EF, both first-time breeders: FBM×FBF, experienced male and a first-time breeder female: EM×FBF, and first-time breeder male with an experienced female: FBM×EF). Boxes represent standard error of the mean, while whiskers represent 95% confidence interval.

First-year female house sparrows lay smaller clutches than more experienced females (Dawson 1972, Krentz and Ankney 1986, Anderson 2006), although in our population, experienced females' clutch size (4.8 eggs) is not significantly higher than first-year females' clutch size (4.4 eggs) (Supplementary material Appendix 1 Table A1). In our study the significant difference between EM×FBF pairs and FBM×EF pairs were found in the number of fledglings produced, which was higher when the experienced female is involved. Perhaps this is influenced by the crucial role of females feeding nestlings during the last days of the nestling period in the house sparrow. In this species males contribute half or more of the feeds during the first week of the nestling period, but during the last five days his contributions drop dramatically, while females increase their feeding rates (Seel 1969, Hegner and Wingfield 1986, Anderson 2006).

In conclusion, although our new analytical approach does not allow us to explore the reasons, it shows that mixed experienced–unexperienced pairs in which the experienced individual is the female produce more fledglings than those in which the experienced individual is the male. This demonstrates the broadly accepted statement that females have a more determinant role than males in reproductive performance.

#### Data availability statement

Data available from the Digibug Digital Repository: <<http://hdl.handle.net/10481/58538>> (Peralta-Sánchez et al. 2020).

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Supplementary material (available online as Appendix jav-02240 at <[www.avianbiology.org/appendix/jav-02240](http://www.avianbiology.org/appendix/jav-02240)>). Appendix 1.