The effects of rearing conditions on sexual traits and preferences in zebra finches

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Citation

Holveck, M. J. (2008, February 28). *The effects of rearing conditions on sexual traits and preferences in zebra finches*. Retrieved from https://hdl.handle.net/1887/12621

Chapter 5

Low quality females avoid high quality males when choosing a mate

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ABSTRACT

Sexual selection studies generally assume that all females prefer to mate with the highest-quality male. However, female sexual preferences vary in many species including humans but what causes and maintains this variation remains an enigma (Badyaev and Qvarnström, 2002; Cotton et al., 2006; Jennions and Petrie, 1997). Here we show experimentally in a songbird that unfavourable developmental conditions modify partner preference such that females actively avoid high-quality males in favour of low-quality males. We manipulated brood size of captive zebra finches *Taeniopygia guttata* to rear low- and high-quality individuals, those from large and small brood sizes respectively (Alonso-Alvarez et al., 2006; de Kogel, 1997; de Kogel and Prijs, 1996; Naguib et al., 2004). When choosing between male songs (Chapter 2 of this thesis), high-quality females preferred the songs of high-quality males, in agreement with general expectations. In contrast, low-quality females significantly preferred songs of low-quality males over high-quality males. This pattern was confirmed during reproduction: latency until laying the first egg was shorter when birds were paired assortatively with respect to rearing brood size (quality). This suggests males with similar developmental background were accepted faster as partners, in agreement with the song choice results. Females invested more in egg mass if paired with high-quality males, regardless of their own quality. This form of differential allocation (Burley, 1986) indicates that female perception of male quality (other than their choices) was independent of their own quality. These results demonstrate that the direction of female mating preferences can be based on self-assessed phenotypic quality, a phenomenon previously only reported for humans (Little et al., 2001; Todd et al., 2007). We suggest that the assortative mating preferences of low-quality females may be an adaptive strategy (Fawcett and Johnstone, 2003; Härdling and Kokko, 2005; Johnstone, 1997; McNamara et al., 1999; Real, 1991) to avoid costs of intra-sexual competition over high-quality males, and increased risk of desertion by higher-quality males.

Studies of sexual selection generally assume that females prefer to mate with the highest-quality male available. Consequently, variation in female preferences has often been considered an empirical nuisance rather than a salient feature of sexual selection. However, rather than being entirely stochastic, the variation in female preference is often stable (Bakker et al., 1999; Qvarnström et al., 2000; Riebel, 2000), and a full understanding of sexual selection has to take the causes and consequences of such variation into account.

In addition to genetic influences on female preferences, phenotypic aspects such as females' condition (Cotton et al., 2006) or learned preferences (Riebel, 2000; Riebel, 2003a) are potential sources of preference variation. Female songbirds, for example, display large and repeatable variation in song preference that are in part the result of their early experiences (Riebel, 2000). The developmental stress hypothesis (Buchanan et al., 2003; Nowicki et al., 2002a) proposed that nutrition and social environment during early development affect male song learning and, as a consequence, song quality (Spencer et al., 2003; Spencer et al., 2005b, but see Gil et al., 2006). We extend this hypothesis, and investigated whether female song preference learning and mating behaviour are also modulated by developmental conditions. We used brood size manipulation, to manipulate the early social environment and to induce long-term phenotypic changes within an ecological meaningful range (Alonso-Alvarez et al., 2006; de Kogel, 1997; de Kogel and Prijs, 1996; Naguib et al., 2004).

In our experiment, subjects were raised by unrelated foster parents in either small or large broods (Fig. 1). We refer to these as HIGH and LOW condition treatments respectively. As expected (Alonso-Alvarez et al., 2006; de Kogel, 1997; de Kogel and Prijs, 1996; Naguib et al., 2004), the brood size manipulations affected offspring condition. As fledglings, birds from small broods had larger body sizes than those from large broods (day 35: mean tarsus length ± 1 s.e. small broods = 15.48 ± 0.07 mm, $n = 48$; large broods = 15.15 ± 0.07 mm, $n = 57$; $F_{1,27} = 10.92$, $P = 0.0015$), and this effect persisted into adulthood (day 180: mean ± 1 s.e. small broods = 15.50 ± 0.05 mm, $n = 47$; large broods = 15.13 ± 0.07 mm, $n = 53$; $F_{1,27} = 20.60$, $P < 0.0001$). As juveniles during the sensitive phase for song learning (Slater et al., 1988) birds were in mixed-treatment mixed-sex groups of four individuals with an unfamiliar unrelated mated adult male that acted as 'song tutor' (Gil et al., 2006, Fig. 1).

After females reached adulthood their song preferences were tested

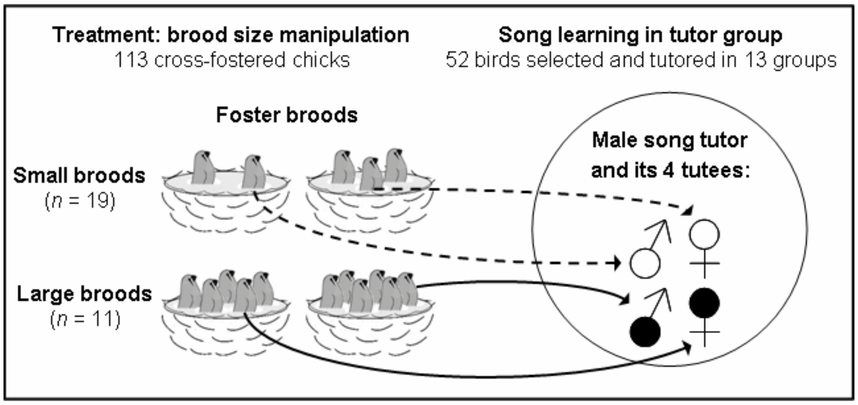


Figure 1. Experimental procedure. Chicks (n = 113) of 30 pairs (14 in 2004; 16 in 2005; Table S1) were cross-fostered at 3 ± 1.7 days post-hatching in either small (2-3 chicks, n = 19 broods) or large broods (5-6 chicks, n = 11 broods), until nutritional independence. During the subsequent sensitive period for song learning, 13 groups (6 in 2004, 7 in 2005) of four genetically and fosterly unrelated chicks (one of each sex and treatment) were housed each with an unrelated tutor and his mate from 33.5 ± 3.3 to 69.4 ± 3.3 days post-hatching (n = 52 tutees). Afterwards and between experiments, tutees were housed in single-sex groups of 4-5 birds.

in an operant conditioning set-up (Chapter 2 of this thesis). Preference measured in this way predicts real mate choice in zebra finches (Chapter 2 of this thesis). In the tests the females were offered the choice between the songs of a HIGH and a LOW condition male that had learned their songs simultaneously in one of the other tutor groups (unfamiliar to the choosing female). Females were tested twice with different song pairs, and showed strong assortative preferences by rearing environment in both tests (Fig. 2; $F_{1,22} = 140.9$, $P < 0.0001$), despite having no prior experience with the test songs and in absence of other cues on male quality. They thus preferred the song of males that were reared in the same environment as themselves. This effect was symmetrical, in the sense that HIGH condition females significantly preferred songs of HIGH condition males (one-sample $t_{11} = 10.8$, $P < 0.0001$), and LOW condition females significantly preferred the songs of LOW condition males ($t_{11} = -5.7$, $P < 0.001$). Every single female preferred a male of matching background. This effect was absent when

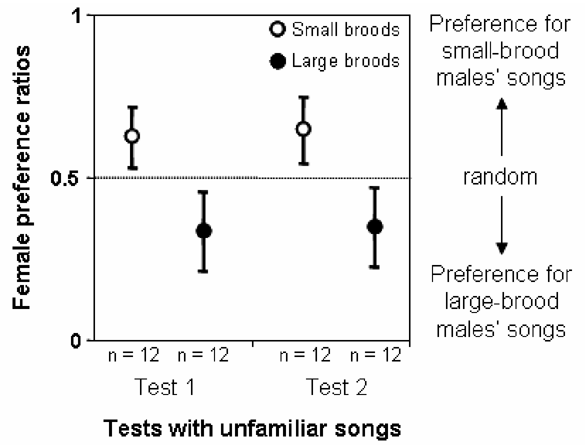


Figure 2. Preference ratios for unfamiliar songs of small- versus large-brood males. Females (12 from small broods and 12 from large broods; one female died eliminating a set) were tested twice with two different sets of unfamiliar songs (Tests 1 and 2). Male songs were considered unfamiliar to females when individuals were not from the same birth nest, foster brood or tutor group. Shown are means ± 1 s.d..

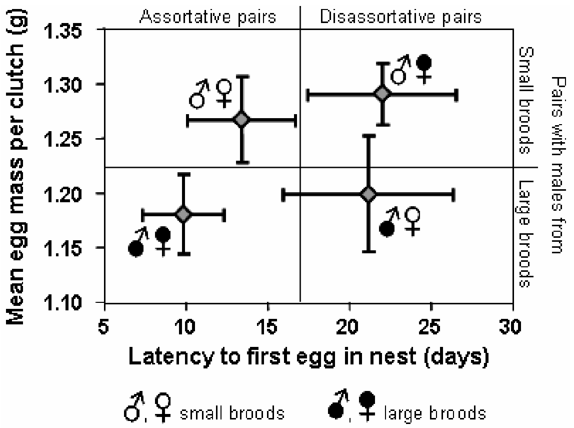


Figure 3. Mean egg mass per clutch in relation to latency to first egg in nest for females paired assortatively or disassortatively with respect to brood size. Females had not been exposed to the song of their mate in the earlier preference tests. Shown are means ± 1 s.e.m.; *n* = 6 for every pair category except for the one with birds from small broods where *n* = 5 (1 female had still not laid any eggs after 67 days). Clutch size did not differ significantly between groups (Table S5).

females chose between the songs of the HIGH and LOW condition males that were their social companions during the tutoring phase (HIGH-females: $t_{11} = 0.05$, $P = 0.97$; LOW-females: $t_{11} = -0.15$, $P = 0.9$; $F_{1,22} = 0.0001$, $P = 0.99$). Thus, early familiarity appears to interfere with the judgement of male quality (Riebel, 2000).

To investigate the reproductive consequences of the assortative mating preferences we paired females with unfamiliar males either assortatively (HIGH/HIGH or LOW/LOW) or disassortively (HIGH/LOW or LOW/HIGH) and allowed the birds to breed. Females in assortative pairs advanced the time of their first breeding in comparison to females in disassortative pairs (Fig.3; $F_{1,21} = 8.08$, $P < 0.01$), while there was no effect of the developmental background of the female per se ($F_{1,20} = 0.12$, $P = 0.7$). This indicates that females accepted males sooner as a mate when he had the same developmental background, which is consistent with the song preferences. However, the perception that LOW condition females had of male condition was not impaired since females made a larger reproductive investment, as measured by the mean egg mass per clutch, when mated to a HIGH condition male (Fig.3; $F_{1,21} = 6.64$, $P < 0.02$), regardless of their own developmental background ($F_{1,15} = 1.15$, $P = 0.7$). This result is important, because it demonstrates that females from HIGH and LOW condition treatments did in fact agree on the phenotypic quality of the males they were paired to, despite showing different preferences. Thus the results of the mate choice and breeding experiments both revealed rearing conditions as a source of variation in female mating behaviour.

To our knowledge, we provide the first demonstration that rearing conditions can change the *direction* of female mating preferences towards low-quality males (Cotton et al., 2006) in the absence of competition over access to mates (Fawcett and Johnstone, 2003; Härdling and Kokko, 2005) and without any evidence that low condition affected female choosiness (Burley and Foster, 2006; Cotton et al., 2006). Female motivation to hear songs was independent of the rearing treatment (comparing total number of key pecks; Table S3) and they showed striking discrimination abilities. They were able to extract information on unfamiliar males' developmental background from differences in song quality only (Fig. 2).

This begs the question of why low-quality females opted for low-quality males. Such a preference for low-quality individuals could arise 1) in competition over access to mates: females in lower condition are likely to loose out (Fawcett and Johnstone, 2003; Härdling and Kokko, 2005), thus they will save time and energy by preferring lower-quality mates; 2) in species with mutual mate choice: if low-condition individuals face higher rejection or divorce rates (Johnstone, 1997; McNamara et al., 1999; Real, 1991), it could pay them to go for lower-quality individuals straight away. These theoretical assumptions are met: Zebra finches show mutual mate choice and biparental care (Jones et al., 2001b). Advancing the time of first breeding increases lifetime reproductive success in zebra finches (Alonso-Alvarez et al., 2006) and producing heavier eggs increases hatchling survival (Christians, 2002). Low-quality females will thus increase their fitness if they save time (Alonso-Alvarez et al., 2006) by actively preferring low- instead of high-quality individuals for which they are likely to be out-competed by higher-quality females (Jones et al., 2001b) or because males might desert them for high-quality females once the opportunity arises (McNamara et al., 1999). This illustrates how and why the assortative mating preferences of low-quality females might be an adaptive strategy. However it remains to be demonstrated that a preference for low-quality males indeed allows low-quality females to avoid the costs of female-female competition over mate access and/or guarding and to improve their fitness.

Our experiments clearly revealed state-dependent behaviour: Both low- and high-quality females determined their level of investment (the timing and mass of the laid eggs, two important fitness related parameters: Christians, 2002) strategically based on whether a male matched their (condition-dependent) preferences but also on his absolute quality. Whereas earlier studies reported as foremost effect of low condition reduced female choosiness in zebra finches (Burley and Foster, 2006) and other animal species (Cotton et al., 2006), the finding that females prefer males who match their own quality is highly reminiscent of what so far has only been reported for human mating preferences where self-perceived attractiveness has been found to influence a woman’s preference function (Little et al., 2001; Todd et al., 2007). Our experiment has demonstrated that developmental conditions can be at the heart of such rightly so perceived differences. This lends empirical support to the increasing theoretical appeals to investigate mate choice as state-dependent behaviour and to integrate individual developmental trajectories (Badyaev and Qvarnström, 2002; Cotton et al., 2006; McNamara and Houston, 1996) into sexual selection studies. As demonstrated here it has been rightly advocated earlier that this might prove extremely fruitful in addressing as yet unexplained variation in female mating preferences (Badyaev and Qvarnström, 2002; Cotton et al., 2006; Jennions and Petrie, 1997).

METHODS

Housing

Birds were housed in standard laboratory cages (80 x 40 x 40 cm) on a 13.5:10.5 hour light:dark schedule (lights on: 07:00 C.E.T.) at 20-22°C and 35–50% humidity with *ad libitum* access to a commercial tropical seed mixture (Tijssen goed voor dieren, Hazerswoude, Holland), drinking water and cuttlebone supplemented thrice weekly with egg food (Witte Molen, B.V., Meeuwen, Holland), twice with millet branches and once with germinated seeds.

Song preference tests

Starting at 164 ± 15 days post-hatching, the three tests per female each lasted two days with 8.1 ± 1.4 intermittent days in the home cage. Tests, one with songs of familiar males from females' own tutor groups and two with unfamiliar males' songs, were conducted blind with regard to treatment in eight identical binary-choice operant set-ups (Chapter 2 of this thesis). Presentation of stimulus songs was fully balanced with regard to potential side preference effects (Chapter 2 of this thesis). Preference ratios were the number of key pecks for HIGH song divided by total number of key pecks.

Stimulus songs

We recorded non-directed song of each male tutee (*n* = 26) at 141 ± 13 days post-hatching in a cage (70 x 30 x 45 cm) in a sound attenuation chamber (Sennheiser MKH40 microphone and MZN16 P48 power supply) using Ishmael software (version 1.0.2, http://cetus.pmel.noaa.gov/cgi-bin/MobySoft.pl; automatic energy detection settings for 2000-10000 Hz, detection threshold 1, detection limits 0.2-100 s, buffer 3 s). Stimulus preparation was conducted blind with regard to male treatment. For each song stimulus, we chose one four-motif song per male, digitally deleted introductory elements, highpass filtered the songs at 500 Hz (smoothing = 100 Hz) to remove low-frequency background noise and RMS-equalized amplitudes (peak digitally scaled to 1) with Praat software (4.2.07 for Windows, http://www.praat.org).

Body size measurements

Tarsus length, a good correlate of structural size in birds, is the distance from the right tibiotarsus-tarsometatarsal joint to the point of the tarsometatarsal joint at the base of the right middle anterior toe (Baumel et al., 1979). It was measured with callipers to the nearest 0.05 mm at days 35 and 180 (mean age of brood). Measures taken three times were highly repeatable (Becker, 1984; Lessells and Boag, 1987): day 35: $F_{(104,210)} = 96.7$, $P < 0.001$, $R = 0.97 \pm 0.005$; day 180: $F_{(99,200)} = 142.5$, $P < 0.001$, $R = 0.98 \pm 0.004$.

Breeding experiment

For their first breeding attempt (one female died and was replaced by a tape-tutored, instead of live-tutored, one reared in a corresponding manipulated brood), six pairs for each of the four possible brood size*sex combinations were formed between unfamiliar and genetically unrelated birds, resulting in 12 assortative or disassortative pairs (2004: 554 ± 12 days, 11 pairs; 2005: 431 ± 11 days, 13 pairs). Nest boxes (20 x 10 x 10 cm) were provided with hay as nesting material and checked once daily after 10:00 hours. New eggs were weighed to the nearest 0.1g (Sartorius BL600 scale) and marked with indelible pen on the day of laying. A clutch was considered complete if no new eggs were laid over four days.

All procedures followed Dutch laws and were approved by Leiden University committee for animal experimentation.

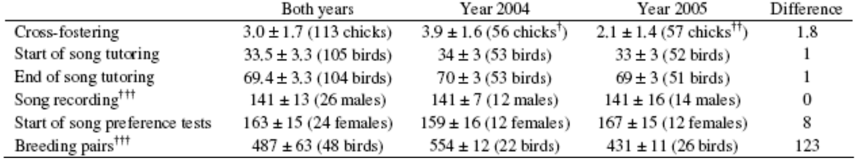
Statistical analysis

Data were analyzed with linear models (generalized and/or mixed; two-tailed, $\alpha = 0.05$) in R software (2.4.1 for Windows, http://www.r-project.org). Birth nest and foster brood were crossed random effects in models with the response variables preference ratios, key pecks and tarsus size at day 35 and 180. We sequentially deleted random factors explaining less than 0.2 % variance, higher order interactions and then factors with $P > 0.05$ until reaching the minimal adequate model. The analyses of the breeding experiment (on latency to first egg in the nest, clutch size and mean egg mass per clutch) gave identical outcomes if run with or without the pair with the replacement female. For full details see Tables S2-S5. All means are quoted ± 1 s.d. except where stated otherwise.

ACKNOWLEDGMENTS
We thank Carel ten Cate, Simon Verhulst, Peter Slater, Tim Fawcett, Jeff Graves, Hans Slabbekoorn, Machteld Verzijden, Cerisse Allen and Diego Gil for comments on the manuscript and Simon Verhulst for critical discussion and suggestions regarding the breeding experiment. We also thank Pauline Manhes, Peter Snelderwaard, Paula den Hartog, Erwin Ripmeester, Robert Lachlan, Hans Slabbekoorn, Padu Franco and Ardie den Boer-Visser for assisting in collecting data and Henny Koolmoes for assistance with animal care.

SUPPLEMENTARY INFORMATION

Table S1. Age (days ± 1 s.d.) and sample sizes of birds



	Both years	Year 2004	Year 2005	Difference
Cross-fostering	3.0 ± 1.7 (113 chicks)	3.9 ± 1.6 (56 chicks[†])	2.1 ± 1.4 (57 chicks[††])	1.8
Start of song tutoring	33.5 ± 3.3 (105 birds)	34 ± 3 (53 birds)	33 ± 3 (52 birds)	1
End of song tutoring	69.4 ± 3.3 (104 birds)	70 ± 3 (53 birds)	69 ± 3 (51 birds)	1
Song recording[†††]	141 ± 13 (26 males)	141 ± 7 (12 males)	141 ± 16 (14 males)	0
Start of song preference tests	163 ± 15 (24 females)	159 ± 16 (12 females)	167 ± 15 (12 females)	8
Breeding pairs[†††]	487 ± 63 (48 birds)	554 ± 12 (22 birds)	431 ± 11 (26 birds)	123

8 birds died before the start of song tutoring (6 HIGH and 2 LOW); 1 (LOW) died between the start and the end of the song tutoring.

[†] 24 chicks from 8 small broods (HIGH condition treatment) and 32 chicks from 6 large broods (LOW condition treatment).

[††] 30 chicks from 11 small broods and 27 chicks from 5 large broods.

[†††] In each year, 1 female (HIGH) died before the pair formation. To replace the missing pair, we formed an extra pair in 2005 with a tape-tutored, instead of live-tutored, female (HIGH). We therefore formed 11 pairs in 2004 (male/female: 2 HIGH/HIGH, 3 LOW/LOW, 3 HIGH/LOW and 3 LOW/HIGH) and 13 pairs in 2005 (male/female: 4 HIGH/HIGH, 3 LOW/LOW, 3 HIGH/LOW and 3 LOW/HIGH).

Table S2. Results of the two linear mixed-model analyses of tarsus size (mm) of the study population

	Day 35			Day 180		
	Effect size (s.e.)	*F* (d.f.)	*P*	Effect size (s.e.)	*F* (d.f.)	*P*
Final model						
BS	-0.14 (0.04)	10.92 (1,27)	**0.0015**	-0.18 (0.04)	20.60 (1,27)	**<0.0001**
Rejected terms						
Year	-0.00004 (0.13)	0.00 (1,26)	0.99	-0.07 (0.12)	0.42 (1,26)	0.5
Sex	-0.05 (0.10)	0.32 (1,25)	0.6	-0.05 (0.09)	0.38 (1,25)	0.5
Age	0.01 (0.03)	0.04 (1,24)	0.8	-0.01 (0.05)	0.05 (1,24)	0.8
BS x year	-0.05 (0.09)	0.34 (1,23)	0.6	0.03 (0.08)	0.13 (1,23)	0.7
BS x sex	0.06 (0.07)	0.70 (1,22)	0.4	0.06 (0.07)	0.74 (1,22)	0.4
Year x sex	-0.03 (0.20)	0.03 (1,21)	0.9	-0.23 (0.17)	1.83 (1,21)	0.2
BS x age	0.01 (0.02)	0.24 (1,20)	0.6	0.03 (0.04)	0.52 (1,20)	0.5
Year x age	-0.08 (0.10)	0.68 (1,19)	0.4	-0.05 (0.09)	0.27 (1,19)	0.6
Sex x age	0.004 (0.05)	0.10 (1,18)	0.9	0.03 (0.09)	0.14 (1,18)	0.7
BS x year x sex	-0.26 (0.16)	2.81 (1,17)	0.1	-0.07 (0.14)	0.27 (1,17)	0.6
BS x year x age	0.07 (0.07)	1.00 (1,16)	0.3	0.02 (0.07)	0.10 (1,16)	0.7
BS x sex x age	-0.04 (0.05)	0.06 (1,15)	0.4	0.02 (0.07)	0.08 (1,15)	0.8
Year x sex x age	-0.05 (0.18)	0.06 (1,14)	0.8	-0.07 (0.19)	0.15 (1,14)	0.7
BS x year x sex x age	-0.10 (0.15)	0.43 (1,13)	0.5	-0.18 (0.16)	1.37 (1,13)	0.2
$n^{\dagger}$		105			100	

BS: brood size.

Five chicks (3 HIGH, 2 LOW) died before day 10 (mean age of brood). Therefore, we used brood size at day 10 to characterize the rearing conditions. “Brood size” was 2, 3, 5 or 6. “Year” is a binary variable (2004 or 2005) as is “sex” (male or female). “Age” is the individual age in days at the time of measurement (individual age at day 180 is included in the analyses of the study population for comparability although tarsus does not grow any more at that time).

Full model: brood size x year x sex x age + birth nest + foster brood, with a Gaussian distribution. “Rejected terms” are the parameters that were not significant when added to the final model. The random factor “foster brood” was not retained in either of the two models (its explained variance in full models was less than 0.2 %). The random factor “birth nest” was retained in the two models (its explained variance in full models was 25.6% for day 35 and 27.9% for day 180). The degrees of freedom (d.f.) for linear mixed models in R 2.4.1 are inherently approximated. We could deduce the d.f. values given here since the models did not have crossed random effects, but had a single random factor “birth nest” of sample size 29.

†Sample sizes were different for different ages because of mortality: five birds died between day 35 and day 180 (1 HIGH, 4 LOW).

Table S3. Results of the generalized linear model analyses of preference ratio and total number of key pecks

	Test 1			Tests 2 and 3[†]		
	Effect size (s.e.)	F (d.f.)	P	Effect size (s.e.)	F (d.f.)	P
Preference ratio						
Final model						
BS	0.003 (0.23)	0.0001 (1,22)	0.99	1.47 (0.13)	140.91 (1,22)	**<0.0001**
Rejected terms						
Tarsus	-4.47 (4.50)	0.99 (1,21)	0.3	-2.29 (2.90)	0.62 (1,21)	0.4
Year	0.39 (0.24)	2.59 (1,20)	0.1	-0.18 (0.12)	2.22 (1,20)	0.2
BS x tarsus	8.32 (15.07)	0.30 (1,19)	0.6	6.66 (7.89)	0.71 (1,19)	0.4
Tarsus x year	-0.67 (9.78)	0.005 (1,18)	0.9	-9.28 (4.80)	3.77 (1,18)	0.1
BS x year	-0.52 (0.62)	0.53 (1,18)	0.5	0.40 (0.29)	0.0025 (1,18)	0.96
BS x tarsus x year	20.96 (33.87)	0.38 (1,16)	0.5	24.58 (14.49)	2.88 (1,16)	0.1
Key pecks						
Final model						
BS	-0.26 (0.38)	0.45 (1,22)	0.5	0.47 (0.34)	1.93 (1,22)	0.2
Rejected terms						
Tarsus	6.36 (6.56)	0.95 (1,21)	0.3	0.93 (7.18)	0.02 (1,21)	0.9
Year	-0.30 (0.35)	0.74 (1,20)	0.4	0.12 (0.35)	0.11 (1,20)	0.7
BS x tarsus	-23.04 (21.38)	1.22 (1,19)	0.3	-8.99 (19.16)	0.22 (1,19)	0.6
Tarsus x year	-20.42 (12.94)	2.61 (1,18)	0.1	-4.18 (14.04)	0.09 (1,18)	0.8
BS x year	1.26 (0.80)	0.48 (1,18)	0.5	-0.31 (0.90)	0.19 (1,18)	0.7
BS x tarsus x year	-28.03 (41.80)	0.46 (1,16)	0.5	-40.16 (39.11)	1.05 (1,16)	0.3

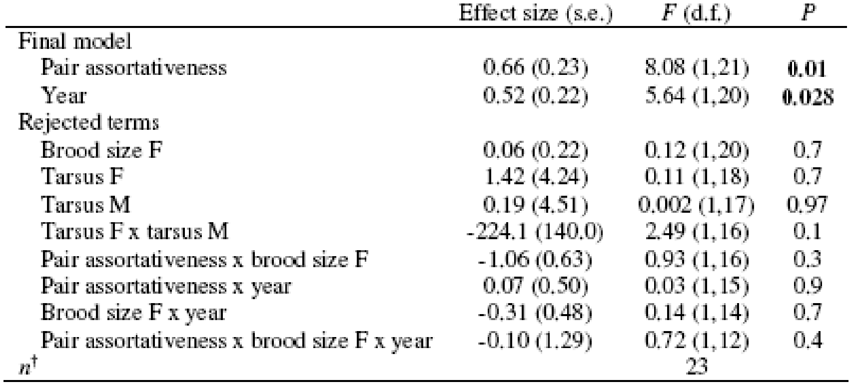
BS: brood size.

“Brood size” and “year” are binary variables (HIGH or LOW and 2004 or 2005 respectively). Here, brood size at day 10 could not be used to characterize the rearing conditions due to low sample size. “Tarsus” is the adult tarsus size measured after the preference tests at day 180 (mean age of brood). We used its log transformation in the model analyses.

Full model: brood size x tarsus x year + birth nest + foster brood, with a quasi-binomial distribution for “preference ratio” and a quasi-Poisson distribution for “key pecks”. “Rejected terms” are the parameters that were not significant when added to the final model. The random factors “birth nest” and “foster brood” were not retained in any of the 4 models (their explained variances in full models were less than 0.2%).

[†] Tests 2 and 3 were repeated measures of the same females and were combined in a single analysis by summing the number of pecks over the two tests. We obtained identical outcomes with generalized linear mixed models where female identity was entered as random effect and always kept in the models to account for repeated measures per individual in Tests 2 and 3.

Table S4. Result of the generalized linear model analysis of latency to first egg in the nest (i.e. time between pairing and laying)



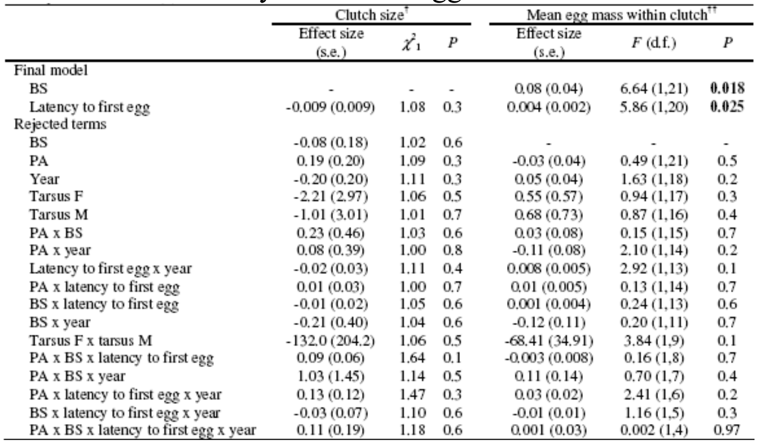
	Effect size (s.e.)	*F* (d.f.)	*P*
Final model			
Pair assortativeness	0.66 (0.23)	8.08 (1,21)	**0.01**
Year	0.52 (0.22)	5.64 (1,20)	**0.028**
Rejected terms			
Brood size F	0.06 (0.22)	0.12 (1,20)	0.7
Tarsus F	1.42 (4.24)	0.11 (1,18)	0.7
Tarsus M	0.19 (4.51)	0.002 (1,17)	0.97
Tarsus F x tarsus M	-224.1 (140.0)	2.49 (1,16)	0.1
Pair assortativeness x brood size F	-1.06 (0.63)	0.93 (1,16)	0.3
Pair assortativeness x year	0.07 (0.50)	0.03 (1,15)	0.9
Brood size F x year	-0.31 (0.48)	0.14 (1,14)	0.7
Pair assortativeness x brood size F x year	-0.10 (1.29)	0.72 (1,12)	0.4
n[†]		23	

“F” stands for female and “M” for male. “Pair assortativeness”, “brood size F” and “year” are binary variables (assortative or disassortative, HIGH or LOW and 2004 or 2005 respectively). Here, brood size at day 10 could not be used to characterize the rearing conditions due to low sample size. “Tarsus” is the adult tarsus size measured after the preference tests at day 180 (mean age of brood). We used its log transformation in the model analyses.

Full model: pair assortativeness x brood size F x year + tarsus F x tarsus M, with a quasi-Poisson distribution. “Rejected terms” are the parameters that were not significant when added to the final model. We could not test for the random effects “birth nest” and “foster brood” since they were different for the two mates of each pair. A significant effect of “brood size M” would have appeared as a significant effect of the interaction “pair assortativeness x brood size F”.

[†] Sample size is not 24 because one female from a HIGH/HIGH pair had still not laid an egg in the nest 67 days after pairing (the last female to lay her first egg in the nest did so 36 days after pairing).

Table S5. Results of the generalized linear model analysis of clutch size and linear model analysis of mean egg mass of an individual clutch



	Clutch size[†]			Mean egg mass within clutch[††]		
	Effect size (s.e.)	χ^2_1	*P*	Effect size (s.e.)	*F* (d.f.)	*P*
Final model						
BS	-	-	-	0.08 (0.04)	6.64 (1,21)	**0.018**
Latency to first egg	-0.009 (0.009)	1.08	0.3	0.004 (0.002)	5.86 (1,20)	**0.025**
Rejected terms						
BS	-0.08 (0.18)	1.02	0.6	-	-	-
PA	0.19 (0.20)	1.09	0.3	-0.03 (0.04)	0.49 (1,21)	0.5
Year	-0.20 (0.20)	1.11	0.3	0.05 (0.04)	1.63 (1,18)	0.2
Tarsus F	-2.21 (2.97)	1.06	0.5	0.55 (0.57)	0.94 (1,17)	0.3
Tarsus M	-1.01 (3.01)	1.01	0.7	0.68 (0.73)	0.87 (1,16)	0.4
PA x BS	0.23 (0.46)	1.03	0.6	0.03 (0.08)	0.15 (1,15)	0.7
PA x year	0.08 (0.39)	1.00	0.8	-0.11 (0.08)	2.10 (1,14)	0.2
Latency to first egg x year	-0.02 (0.03)	1.11	0.4	0.008 (0.005)	2.92 (1,13)	0.1
PA x latency to first egg	0.01 (0.03)	1.00	0.7	0.01 (0.005)	0.13 (1,14)	0.7
BS x latency to first egg	-0.01 (0.02)	1.05	0.6	0.001 (0.004)	0.24 (1,13)	0.6
BS x year	-0.21 (0.40)	1.04	0.6	-0.12 (0.11)	0.20 (1,11)	0.7
Tarsus F x tarsus M	-132.0 (204.2)	1.06	0.5	-68.41 (34.91)	3.84 (1,9)	0.1
PA x BS x latency to first egg	0.09 (0.06)	1.64	0.1	-0.003 (0.008)	0.16 (1,8)	0.7
PA x BS x year	1.03 (1.45)	1.14	0.5	0.11 (0.14)	0.70 (1,7)	0.4
PA x latency to first egg x year	0.13 (0.12)	1.47	0.3	0.03 (0.02)	2.41 (1,6)	0.2
BS x latency to first egg x year	-0.03 (0.07)	1.10	0.6	-0.01 (0.01)	1.16 (1,5)	0.3
PA x BS x latency to first egg x year	0.11 (0.19)	1.18	0.6	0.001 (0.03)	0.002 (1,4)	0.97

BS: brood size; PA: pair assortativeness.

"Pair assortativeness", "brood size" and "year" are binary variables (assortative or disassortative, HIGH or LOW and 2004 or 2005 respectively). Here, brood size at day 10 could not be used to characterize the rearing conditions due to low sample size. "Latency to first egg" refers to the time between pairing and the first egg laid in the nest. "Tarsus" is the adult tarsus size measured after the preference tests at day 180 (mean age of brood). We used its log transformation in the model analyses.

Full model: pair assortativeness x brood size x latency to first egg x year + tarsus F x tarsus M, with a Poisson distribution for "clutch size" and a Gaussian distribution for "mean egg mass". "Rejected terms" are the parameters that were not significant when added to the final model. We could not test for the random effects "birth nest" and "foster brood" since they were different for the two mates of each pair.

[†] "Brood size" is the female brood size. A significant effect of male brood size would have appeared as a significant effect of the interaction "pair assortativeness x brood size". Since *F* tests are inappropriate with a Poisson distribution, we used chi-square tests for which the values were calculated by dividing the residual deviance of the model omitting the tested parameter by the one of the model including the tested parameter. The degrees of freedom therefore reflect the comparison of the models with and without the tested parameter.

[††] "Brood size" is the male brood size. A significant effect of female brood size would have appeared as a significant effect of the interaction "pair assortativeness x brood size". We safely discarded the factor "clutch size" after checking for its non-significant effect on "mean egg mass". This was done in a previous analysis since we could not add another factor to the full model due to the loss of degrees of freedom. We did not find an effect of "clutch size" nor of its interaction with other factors on "mean egg mass" in the following model: clutch size x brood size x latency to first egg + tarsus F x tarsus M. The effect of "clutch size" was also not significant when entered as a single factor ($F_{(1,21)}$=2.68, P=0.12).