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## RESEARCH PAPER

# Negative impact of urban noise on sexual receptivity and clutch size in female domestic canaries

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**Abstract**

In oscines, male song stimulates female reproduction and females are known to adjust both their sexual preferences and their maternal investment according to song quality. Female domestic canaries are especially responsive to wide frequency bandwidth (4 kHz) male songs emitted with a high-repetition syllable rate and low minimal frequencies (1 kHz). We previously showed that low-frequency urban noise decreases female sexual responsiveness for these low-frequency songs (1–5 kHz) through auditory masking. Based on the differential allocation hypothesis, we predicted that urban noise exposure will equally affect female maternal investment. Using a crossover design, we broadcast low-frequency songs to females either in an overlapping noise condition or in an alternating noise condition. Females decreased both their sexual responsiveness and their clutch size in the overlapping noise treatment relative to the alternative noise treatment. No differences were found concerning egg size or egg composition (yolk and albumen mass, testosterone concentration). Due to our experimental design, we can exclude a general impact of noisy conditions and thereby provide evidence for a detrimental effect through masking on avian courtship and reproductive output. These results suggest that noisy conditions may also affect avian communication in outdoor conditions, which may partly explain field reports on noise-dependent breeding success and reduced breeding densities at noisy sites.

**KEYWORDS**

anthropogenic noise, birdsong, clutch size, domestic canary, maternal investment

## 1 | INTRODUCTION

According to the honest signal theory, females select their mates using signals that honestly reveal male overall condition and/or genetic quality (Zahavi, 1975, 1977). Evidence from various taxa shows that female mate choice is often based on signals that are indicators of male quality (Andersson, 1994). The influence of these signals is not limited to mate choice; they also affect females' reproductive effort (Cunningham & Russell, 2000; Horváthová, Nakagawa, & Uller, 2012). The differential allocation hypothesis postulates that female investment in a given reproductive attempt is a direct function of

their mate's attractiveness (Burley, 1988). This allocation pattern can increase offspring survival, growth, or offspring reproductive performance when females are paired with attractive mates (Sheldon, 2000). There is experimental evidence for the differential allocation in insects (Head, Hunt, & Brooks, 2006; Simmons, 1987), fish (Kolm, 2001), frogs (Reyer, Frei, & Som, 1999), reptiles (Olsson, Wapstra, & Uller, 2005), and mammals (Drickamer, Gowaty, & Holmes, 2000), but most support for the differential allocation hypothesis comes from birds. Females adapt their investment in response to male attractiveness in different ways, including faster nest building (Kroodsma, 1976) or increasing clutch size (Horváthová et al., 2012) and resource allocation toward

egg weight (Bonato, Evans, & Cherry, 2009; Christians, 2002; Krist, 2011), egg size (Cunningham & Russell, 2000), or egg content (Gil, 2008).

Male characteristics such as body size, coloration, or vocalizations have been shown to be honest indicators of male quality (Andersson, 1994; Santos, Scheck, & Nakagawa, 2011). Experimental modification of male sexual characters in the field or in the laboratory induces changes in female mate choice and/or their reproductive investment. For example, male long-tailed widowbirds *Euplectes progne* with artificially elongated tails showed higher mating success than males having normal or reduced tails (Andersson, 1982) and female barn swallows *Hirundo rustica* mated to males with experimentally elongated tails increased both their productivity (de Lope & Moller, 1993) as well as the concentration of androgens in their eggs (Gil et al., 2006). In at least two bird species, females laid smaller eggs when their mates' feet were rendered experimentally less attractive by manipulating plumage or foot color (Dentressangle, Boeck, & Torres, 2008; Osorno et al., 2006; Velando, Beamonte-Barrientos, & Torres, 2006). Manipulating vocal cues can also influence female choice in songbirds. Female canaries are particularly responsive to a phrase made of the fast repetition of a two-note syllable with a large frequency bandwidth, known as the A-phrase (Vallet & Kreutzer, 1995), and supernormal stimuli maximizing both syllable repetition rate and frequency bandwidth are preferred by females (Draganoiu, Nagle, & Kreutzer, 2002).

An alternative and more realistic approach to investigating female mate choice and reproductive investment responses to variation in mate attractiveness is provided by the study of animals living in polluted environments. Signal efficiency has been shown to depend on various environmental conditions. Anthropogenic chemicals disrupt mate choice based on olfactory cues in several taxa (Lürling & Scheffer, 2007), water turbidity can hamper mate choice in fish through reduced visibility (Sundin, Berglund, & Rosenqvist, 2010), and background noise can erase female preferences for low-frequency male calls in frogs (Wollerman & Wiley, 2002).

A well-studied example of environmental impact on signal efficiency comes from songbirds communicating under urban noise conditions. Urban anthropogenic noise has most of its energy below 2 kHz, and experimental studies have shown that it differentially affects female response according to the frequency of male song. Singing with low frequencies seems to be important for several songbirds: it has been for instance related to female fidelity in great tits *Parus major* (Halfwerk, Bot, et al., 2011) and to an increase of the number of female sexual responses (Copulation Solicitation Displays, CSD) in domestic canaries *Serinus canaria* (Pasteau, Nagle, & Kreutzer, 2007). In both species mentioned above, urban noise lowered female responses to low-frequency songs but not to high-frequency ones. In a field study, females great tits left their nestboxes less in response to male songs during the egg-laying stage (Halfwerk, Bot, et al., 2011) and this behavior could lead to fewer copulations for males. Female great tits also laid fewer eggs in noisy areas (Halfwerk, Holleman, Lessells, & Slabbekoorn, 2011). This result may be explained through a more general stress-related mechanism (Kight & Swaddle, 2011)—noise disrupting normal hormone release patterns and depleting energy

stores—and/or through a differential allocation caused by lower female responsiveness due to masking of low frequencies by the anthropogenic noise.

Testing these mechanisms needs an experimental approach. In a laboratory study, female domestic canaries performed fewer copulation solicitation displays when songs were partially masked by anthropogenic noise (Huet des Aunay et al., 2014). However, this study did not measure maternal investment. In order to better understand the mechanism by which urban noise impacts on clutch size, we decided to use domestic canaries that provide a well-established model to analyze the maternal investment in experimentally controlled conditions. With this model, previous studies have shown that several characteristics of male song influence maternal investment (Leboucher et al., 2012). For example, females laid larger clutches when exposed to conspecific song with big versus small repertoire size (Kroodsma, 1976). In a different study, females increased egg size when exposed to supernormal songs maximizing syllable rate and frequency bandwidth (Garcia-Fernandez et al., 2013), although this may not be typical for a species with biparental care. Indeed, a recent review paper confirms increased female reproductive investment when paired to attractive males and also reveals a tendency for females of species with biparental care to increase clutch size but not egg size in response to their mates' attractiveness (Horváthová et al., 2012).

Our experiment was designed to assess simultaneously how urban noise affects sexual responsiveness and maternal investment in terms of clutch size and egg characteristics. For this purpose, we exposed females during their reproductive cycle to attractive A-phrases either overlapped or alternated with broadcast urban noise and we measured female sexual responsiveness as well as reproductive investment expressed as clutch size, egg size, and testosterone amount in egg yolk. We predicted (i) that females will show fewer CSDs in the overlapping treatment, as we previously reported in related experimental settings (Huet des Aunay et al., 2014) and (ii) that this inability of the female to accurately assess their mates' attractiveness will equally affect female reproductive investment. Given that the canary is a species with biparental care, we expected females to reduce clutch size rather than egg size during the overlapping noise condition, in response to the inability to accurately assess the attractiveness of their partner (Horváthová et al., 2012) and/or reduce the concentration of the yolk testosterone (Gil, Leboucher, Lacroix, Cue, & Kreutzer, 2004; Tanvez, Béguin, Chastel, Lacroix, & Leboucher, 2004).

## 2 | MATERIAL AND METHODS

### 2.1 | Subjects and housing

The experiment involved a total of 15 domestic canary females from an outbred group of birds of heterogeneous genetic background reared in our own breeding facilities at the University of Paris Nanterre. Females were not previously exposed to any urban noise stimuli. The experimental design was approved under the license number Ce5/2011/041 by the Charles Darwin ethical committee

for animal experimentation, and it was in line with the guidelines of the Association for the Study of Animal Behaviour (ASAB). The experiment was carried out between November 2011 and March 2012.

During the experiment, females were housed in individual cages (35 × 20 cm and 23–25.5 cm high)—placed in individual sound-proof chambers (68 × 51 cm and 51 cm high). The arrangement and nature of sound-proof chambers prevented both visual and acoustic communication between females during the test sessions (2 × 2 hours per day), but the chambers were kept open the rest of the time enabling females to hear each other to avoid social isolation. Birds were provided *ad libitum* with water, food (seeds, mash, and apple), and nest material (cotton lint). In order to start their reproductive cycle and to synchronize periods of receptivity, they were placed on a long-day photoperiod regime: 16-hr light/8-hr dark (Leboucher, Kreutzer, & Dittami, 1994) after being kept for a 10- to 12-month period on a short-day photoperiod regime (8-hr light/16-hr dark).

## 2.2 | Experimental song stimuli and noise spectrum

All the songs used during this experiment were computer-edited using Avisoft SASLab Pro, version 5.0.14 (Raimund Specht, Berlin) and were issued from recordings of captive male canaries made in our aviaries. Songs were not familiar to females and had the following structure: each song lasted 6 s and was organized in three parts: 0.75 s of introductory notes, a 1.50-s trill of a single A-phrase (the target test component), and 3.75 s of final notes. The A-phrases are known to elicit a strong sexual responsiveness in female canaries whereas introductory and final notes are less effective in triggering females' sexual displays (Draganoiu et al., 2002; Pasteau et al., 2007; Vallet & Kreutzer, 1995).

To avoid pseudoreplication, we used 14 different A-phrases issued from different males and composed of two-note syllables emitted at a rhythm of 20 syllables per second with the following spectral characteristics: mean  $\pm$  se frequency bandwidth of 3906 Hz  $\pm$  19 Hz (range = 3700–3980 Hz;  $n$  = 14); minimum frequency of the first note of 1041 Hz  $\pm$  9 Hz, maximum frequency of the first note of 3119  $\pm$  182 Hz; minimum frequency of the second note of 3213  $\pm$  116 Hz, maximum frequency of the second note of 4947  $\pm$  20 Hz (Flat Top window, FFT 512, overlapping 93.75). We chose a frequency bandwidth (4 kHz) close to the average observed and a minimal frequency (1 kHz) corresponding to the extreme low values observed in our population both known to elicit high CSD levels (Draganoiu et al., 2002; Huet des Aunay et al., 2014; Pasteau et al., 2007). Moreover, a previous study reported a negative impact of urban-style noise on the female CSD levels for these low-frequency songs (1–5 kHz) (Huet des Aunay et al., 2014). All phrases were manipulated with Avisoft. Each song stimulus was played back at the standardized level of 65 dB (re. 20  $\mu$ Pa; measured with a Ro-LINE SPL meter 1, using "A" weighting, at the typical position of the test bird, 20 cm from the loudspeaker). This is close to values reported in literature for canary song in laboratory conditions (Hardman et al., 2017).

An artificially generated noise recording was used for the experimental exposure with a spectral energy distribution reflecting

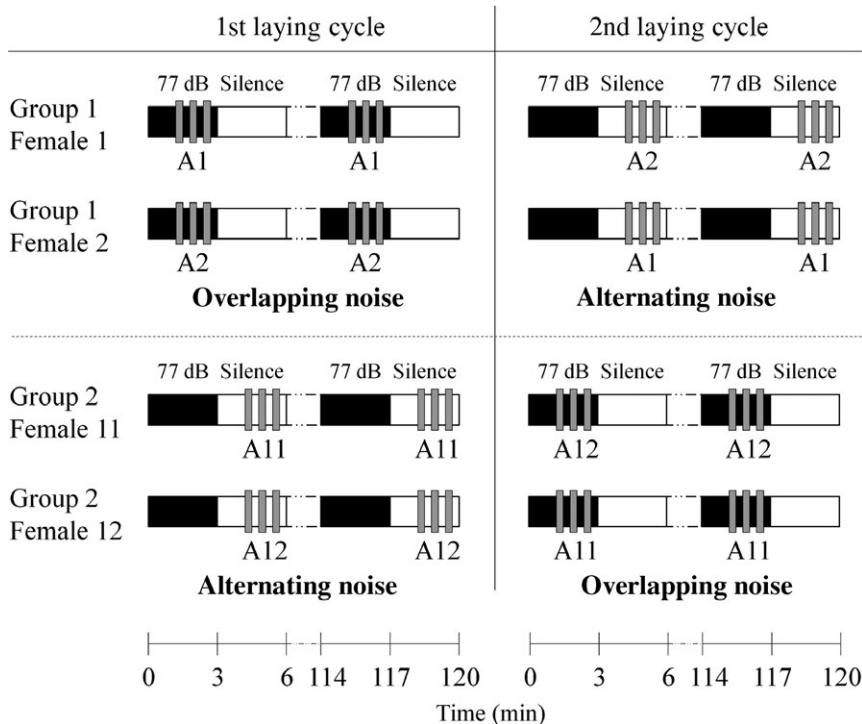
typical urban noise profiles (Lohr, Wright, & Dooling, 2003; Pohl, Slabbekoorn, Klump, & Langemann, 2009). A low-pass filter was applied to a white noise file with a random energy in order to create this urban-style noise recording, using Matlab 7.5 (Mathworks, Inc., Natick, MA, U.S.A). The noise file had a high-pass cut-off frequency at 100 Hz and a spectral energy decrease of 6.5 dB/kHz toward the higher frequencies (Halfwerk & Slabbekoorn, 2009; Halfwerk, Bot, et al., 2011). Based on values of noise levels reported close to the highways (Dooling & Popper, 2007) and in order to be able to compare current research with results from a previous study (Huet des Aunay et al., 2014), we broadcast urban noise with a constant amplitude level of 77 dB (re. 20  $\mu$ Pa; measured with a Ro-LINE SPL meter 1, using "A" weighting, at the typical position of the test bird, 20 cm from the loudspeaker). The constant important urban noise amplitude used in our experiment reflects extreme constraints that can be encountered in areas adjacent to outer rings of big cities (for an example of a French city, Paris, see <http://rumeur.bruitparif.fr>). Most of the energy of our noise stimulus (76%) is concentrated below 2 kHz, where lies on average 20.85% of the energy of our song stimuli (see supporting information). This creates a substantial masking for low frequencies known to elicit high levels of female sexual responses as discussed above (Huet des Aunay et al., 2014).

We played back both song stimuli and noise files from the same 60 watts Mini ELIPSON Horus loudspeaker (frequency response: 80 Hz–20 kHz) placed in the back of the sound-proof chamber at 20 cm distance from the center of the cage. The loudspeaker was connected to a stereo amplifier PIONEERA-209R linked itself to a MARANTZ PMD670 digital recorder (bandwidth: 20 Hz–20 kHz  $\pm$  1 dB).

## 2.3 | Experimental design

We tested whether female preferences for A-phrases and their maternal investment in the eggs were affected by the noise exposure. We used a crossover design: each female was tested during two consecutive breeding cycles (egg laying in response to photoperiod change and song stimulation without exposure to real males) in two different conditions (overlapping vs alternating noise)—each one associated with a breeding cycle. The female noise exposure was the same during the two conditions, but in one case, stimuli were broadcast simultaneously with the urban noise (77 dB), creating an overlapping noise treatment, and in the other case, they were broadcast alternatively with the noise, creating an alternating noise treatment (Figure 1). Seven females were exposed to the overlapping noise treatment for their first breeding cycle and to the alternating noise treatment for their second breeding cycle (Group 1). Eight other females received the treatments in the reverse order (Group 2). A global overview of the design of the study is found in Table 1.

The experimental treatment started the first day after the photoperiod change and stopped 2 days after the laying of the last egg. We defined an egg as the last egg when females did not lay during two consecutive days afterward. Test sessions were carried out twice a day: once in the morning (10:00–12:00) and once in the afternoon



**FIGURE 1** Experimental design: females were tested twice during 2 hrs each day, with attractive A-phrases, during one breeding cycle in an alternating noise condition and during the other breeding cycle in an overlapping noise condition. Black bars represent the noisy periods (77 dB), and white bars represent the silent periods (34 dB). Groups of two females (females 1–2 and females 11–12 in this example) were tested with the same two different A-phrases (A1–A2 shown here as gray stripes), but each one heard a different one associated with the silent period. Only the first and the last 3-min periods of one test session are shown here

(14:00–16:00), separated by at least a two-hour interval. Sessions lasted 2 hrs, and they alternated twenty noisy (77 dB) periods of 3 min with twenty silent (34 dB) periods of 3 min. In each of the twenty noisy periods (overlapping treatment) or twenty silent periods (alternating treatment), song stimuli were presented three times (analyzed as “stimuli order” in the statistical analysis). The first stimulus was emitted after 90 s, and a 24-s period of silence separated the end of one presentation and the start of the following one (Figure 1). Females heard a total of 120 songs daily (60 in the morning and 60 in the afternoon) either alternatively or simultaneously with the urban noise stimulation. Nests were temporarily taken off 2 days after the laying of the last egg, and a period of 2 days without playbacks was allowed before the beginning of the second breeding cycle. For females that did not lay eggs, we changed the noise treatment after 62 days of testing.

To avoid the possible effect of perceptual improvement in hearing something under noisy conditions that was already heard repeatedly in quiet conditions, each female was tested with two different A-phrases, one associated with the alternating noise condition and the other with the overlapping noise condition. Groups of two females were tested with the same two different A-phrases, but each one heard a different one associated with the silent period (Figure 1; Table 1).

The copulation solicitation display (King & West, 1977) was used as a behavioral index for female sexual preferences. During a complete CSD, females crouch and arch their back while bringing their tail forward and tossing their head backward. The response is particularly strong to specific wide-band song types labelled A-phrases (Vallet & Kreutzer, 1995). GHA and MG counted CSDs in real time during the first 3-minute period of each test session (three presentations of an A-phrase) and awarded a score of 0 for no display, 0.5 for an incomplete

display, and 1 for a complete display (Kreutzer & Vallet, 1991). They were not blind regarding the stimuli broadcast.

Nests were inspected daily, and laid eggs were removed and substituted by dummy plastic eggs before incubation. Eggs were weighed with a 0.01 g accuracy, and we separated and weighed the yolk and albumen before storage at  $-20^{\circ}\text{C}$  and subsequent quantification of testosterone concentration in yolk.

## 2.4 | Testosterone assays

Yolk concentrations of testosterone were determined by radioimmunoassay at the Centre d'Etudes Biologiques de Chizé (CNRS, Chizé, France). Yolk samples were homogenized in 1 ml of distilled water. Testosterone was extracted by adding 3 ml of diethyl ether to the entire yolk sample. We took 300  $\mu\text{l}$  of the mixture that we vortexed and centrifuged 5 mins at 2000 rpm, at  $4^{\circ}\text{C}$ . The diethyl ether phase containing steroids was decanted and poured off in an alcohol bath at  $37^{\circ}\text{C}$  after snap-freezing the tube. The ether phase was performed twice for each yolk, and the resultant was then evaporated. The dried extracts were redissolved in 300  $\mu\text{l}$  of phosphate buffer, and each hormone was assayed in duplicate. 100  $\mu\text{l}$  of extract was incubated overnight with 4000 cpm of the appropriate  $^3\text{H}$ -steroid (Perkin Elmer, US) and polyclonal rabbit antiserum. Antitestosterone was provided by Dr. Picaper (CHU La Source, Orléans, France). Bound and free fractions were then separated by dextran-coated charcoal and centrifuged. The activity was counted on a tri-carb 2810 TR scintillation counter (PerkinElmer, US). Tests were performed to validate the testosterone assay on egg yolk samples. The lowest detectable testosterone concentration was 2.07 pg/mg. Two yolk samples were serially diluted in the assay buffer, and their displacement curves were parallel to the standard curve.

**TABLE 1** Overview of the data aggregated by female and breeding cycle

Female	Group/ Cycle <sup>a</sup>	Noise treatment	A-phrases used	Exp.length (d)	1st CSD (d)	CSD (#) <sup>b</sup>	Eggs (#)	Characteristics of eggs (mean ± SD) <sup>c</sup>			
								Total weight (g)	Albumen weight (g)	Yolk weight (g)	Testosterone (pg/mg)
1	G1/C2	Alternating	A2	19	0	31	5	2.04 ± 0.23	1.18 ± 0.15	0.46 ± 0.04	23.63 ± 0.78
	G1/C1	Overlapping	A1	60	36	10	2	1.99	1.18	0.5	11.96
2	G1/C2	Alternating	A1	14	3	2	5	2.30 ± 0.09	1.42 ± 0.11	0.44 ± 0.01	16.69 ± 3.68
	G1/C1	Overlapping	A2	62	49	3	5	2.20 ± 0.01	1.28 ± 0.10	0.41 ± 0.02	17.98 ± 5.91
4	G1/C2	Alternating	A3	12	0	5	5	1.82 ± 0.06	1.09 ± 0.09	0.34 ± 0.03	18.16 ± 3.55
	G1/C1	Overlapping	A4	55	53	1	0	n.a.	n.a.	n.a.	n.a.
5	G1/C2	Alternating	A6	24	0	4	4	2.00 ± 0.06	1.05 ± 0.18	0.5 ± 0.01	7.49 ± 2.52
	G1/C1	Overlapping	A5	55	7	2	0	n.a.	n.a.	n.a.	n.a.
7	G1/C2	Alternating	A8	17	0	27	4	2.14 ± 0.03	1.29 ± 0.04	0.44 ± 0.03	11.83 ± 5.18
	G1/C1	Overlapping	A7	60	29	26	6	2.23 ± 0.05	1.25 ± 0.04	0.42 ± 0.04	8.05 ± 3.38
8	G1/C2	Alternating	A7	24	2	13	0	n.a.	n.a.	n.a.	n.a.
	G1/C1	Overlapping	A8	55	37	8	0	n.a.	n.a.	n.a.	n.a.
11	G2/C1	Alternating	A11	33	12	44	5	2.44 ± 0.05	1.54 ± 0.07	0.47 ± 0.03	14.20 ± 2.51
	G2/C2	Overlapping	A12	20	5	31	1	2.05	1.14	0.52	3.90
12	G2/C1	Alternating	A12	25	20	5	5	2.25 ± 0.03	1.41 ± 0.04	0.46 ± 0.02	14.34 ± 4.17
	G2/C2	Overlapping	A11	20	8	3	5	2.44 ± 0.13	1.47 ± 0.07	0.50 ± 0.04	13.70 ± 2.32
14	G2/C1	Alternating	A14	26	14	7	5	2.20 ± 0.05	1.35 ± 0.04	0.43 ± 0.03	11.31 ± 3.14
	G2/C2	Overlapping	A13	11	5	1	2	2.27 ± 0.13	1.43 ± 0.08	0.46 ± 0.03	9.85 ± 2.98
15	G2/C1	Alternating	A15	23	9	20	5	2.29 ± 0.01	1.41 ± 0.04	0.43 ± 0.03	7.37 ± 2.20
	G2/C2	Overlapping	A16	14	7	4	2	2.36 ± 0.01	1.36 ± 0.02	0.5 ± 0.02	4.03 ± 0.61
16	G2/C1	Alternating	A16	23	4	27	5	2.19 ± 0.14	1.35 ± 0.06	0.42 ± 0.06	17.66 ± 9.48
	G2/C2	Overlapping	A15	21	4	19	4	2.23 ± 0.06	1.39 ± 0.07	0.43 ± 0.03	24.48 ± 6.89

<sup>a</sup>the females were separated in two groups (G1 and G2) and tested during two reproductive cycles (C1 and C2).  
<sup>b</sup>total number including incomplete CSDs (110/320).  
<sup>c</sup>mean and standard deviation of measurements made on unbroken eggs (64 of 75 eggs in total); n.a. stands for not available.



## 2.5 | Statistical analysis

The effects of the treatment (Overlapping versus Alternating Noise) on CSDs and egg parameters were analyzed using the statistical framework of linear mixed-effects models (LMMs) and generalized linear mixed models (GLMMs).

For the CSD analysis (Table 2, second column), we modeled the 0–1 response corresponding to the occurrence of a CSD after a particular stimulus using a Binomial GLMM with a logit link function. We included explanatory variables accounting for “noise treatment” (overlapping vs alternating), “laying cycle” (second vs first), “female group” (second vs first), “stimuli order” (second or third vs the first A-phrase presentation in the 3-min test periods), “advancement in the reproductive cycle” (time since the first CSD), “delay of the first CSD” (the number of days elapsed between the first presentation of the stimuli and the first CSD performed by one female), “egg rank,” and “final clutch size.” The use of a binomial model could not take into account the incomplete displays. Therefore, we performed two analyses, the first one discarding those incomplete displays and the second one considering incomplete displays as complete displays.

The clutch size analysis (Table 2, third column) was realized with a Poisson GLMM with loglink function in which we incorporated three fixed effects as “noise treatment,” “laying cycle,” and “female group.” The analyses of egg mass, the macro-component composition, and yolk testosterone deposition in eggs (Table 2, columns 4–7) relied on Gaussian error distribution and identity link function (i.e., LMMs). We

included five fixed effects in these models: “noise treatment,” “laying cycle,” “female group,” “egg rank,” and “final clutch size.”

To account for differences between females, we introduced two random effects adding to the intercept and to the effect of noise (“noise treatment”). Poisson and binomial models used for the eggs and the CSDs appeared able to fit the variance of the data with these random effects (estimated overdispersion scale parameter close to 1).

These analyses were performed in R version 2.10.1 (the R Foundation for Statistical Computing, Vienna, Austria) with the function *lmer* and *glmer* implemented in package *lme4* for GLMMs. Estimates of the overdispersion with respect of the fitted models were obtained with function “dispersion\_glmer” (package “blmecco”). Estimates of the coefficients accounting for the different fixed effects are reported  $\pm$  SE and derived *p*-values allowed to assess their statistical significance (i.e., non-null coefficients). Sample means are given  $\pm$  SE throughout the results section.

## 3 | RESULTS

Table 1 provides a global overview of the collected data aggregated by female and breeding cycle. Eleven of the 15 tested females displayed CSDs in response to our stimuli (6 of 7 females exposed to overlapping noise during their first breeding cycle—Groups 1 and 5 of eight females exposed to alternating noise during their first breeding cycle—Group 2) and ten of these 11 displaying females also laid eggs.

**TABLE 2** Summary of the statistical results obtained in the mixed-effects model framework

Model Link function	Total CSDs	Clutch size	Characteristics of eggs			
			Total weight	White weight	Yellow weight	Testosterone
			Gaussian identity	Gaussian identity	Gaussian identity	Gaussian identity
Fixed effects <sup>a</sup>						
Intercept	−2.04 ± 1.08	1.27 ± 0.34**	1.81 ± 0.14**	1.03 ± 0.10**	0.47 ± 0.04**	0.52 ± 6.24
Second cycle	1.73 ± 0.74*	0.07 ± 0.32	0.009 ± 0.066	−0.014 ± 0.058	0.015 ± 0.010	3.52 ± 2.10
Second group	1.49 ± 0.83	0.34 ± 0.36	0.19 ± 0.06**	0.18 ± 0.04**	0.017 ± 0.036	1.28 ± 3.79
Overlapping noise	−1.85 ± 0.62**	−0.79 ± 0.35*	0.11 ± 0.07	0.058 ± 0.057	0.0074 ± 0.0099	−0.61 ± 2.12
Egg rank	−0.72 ± 0.10**	–	−0.012 ± 0.008	0.0071 ± 0.0076	−0.015 ± 0.002**	1.97 ± 0.36**
Final clutch size	0.19 ± 0.14	-	0.062 ± 0.023*	0.037 ± 0.017*	0.0000 ± 0.0051	1.05 ± 1.01
Delay of 1st CSD	0.056 ± 0.032	-	-	-	-	-
Second stimulus	−2.00 ± 0.22**	-	-	-	-	-
Third stimulus	−2.35 ± 0.23**	-	-	-	-	-
Time since 1st CSD	0.056 ± 0.020*	-	-	-	-	-
Random-effects modeling variability between females <sup>b</sup>						
Intercept	1.394	0.098	0.145	0.112	0.048	3.882
Overlapping Noise	0.840	0.585	0.174	0.159	0.016	4.149

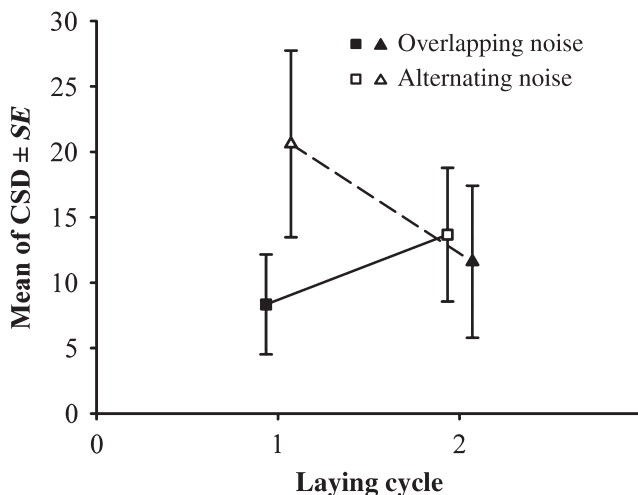
<sup>a</sup>Estimated value and standard error for each model coefficient associated with a fixed effect. Statistically significant effects (i.e. non-null) at levels  $p < 0.05$  and  $p < 0.005$  are highlighted with \* and \*\*, respectively.

<sup>b</sup>Estimated standard deviation of the Gaussian random variable added for each female to the “Intercept” and “Overlapping noise” terms. The correlation coefficient between the two random effects is not reported in this table.

### 3.1 | Copulation solicitation displays (CSD)

The overlapping noise treatment lasted an average of  $39.4 \pm 6.5$  days ( $N = 11$ , range 11–62) whereas the alternating noise treatment lasted an average of  $21.8 \pm 1.8$  days ( $N = 11$ , range 12–33). The mean delay between the onset of the long-day photoperiod, and the first CSD was of  $21.8 \pm 5.8$  days ( $N = 11$ , range 4–53) for the overlapping noise treatment and was of  $5.8 \pm 2.1$  days ( $N = 11$ , range 0–20) for the alternating noise one.

The average CSD rate varied markedly between the different noise treatments with females displaying fewer CSDs in the overlapping noise treatment than in the alternating noise treatment ( $9.6 \pm 3.3$  vs.  $16.8 \pm 4.2$  complete CSDs, see Figure 2). Analysis with the binomial GLMM (Table 2, column “Total CSDs”) confirmed the statistical significance of this observation: the overlapping noise treatment was associated with a negative coefficient and  $p$ -value  $\leq 0.005$ , both when incomplete CSDs were counted as 0 and 1 although only the latter is reported in Table 2. Several factors were taken into account in the model on the noise treatment (Table 2). Females performed fewer CSDs during the second and the third stimulus presentation of the 3-minute test period. No significant group effect and effect of the delay between the onset of the long-day photoperiod and the first CSD were detected. However, there was a significant effect of the breeding cycle with females displaying more CSDs during the second than during the first breeding cycle. Also, the frequency of CSDs increased when advancing in the reproductive cycle toward egg laying but decreased with egg rank after the first egg laid.



**FIGURE 2** Noise impact on female sexual receptivity: mean score  $\pm$  SE of female copulation solicitation displays (CSD; complete + incomplete displays) in response to A-phrases broadcast either in an overlapping noise condition (full symbols) or in an alternating noise condition (empty symbols). Females in Group 1 (shown as squares linked by a continuous line,  $n = 6$ ) received the overlapping noise treatment during their first breeding cycle and the alternating noise treatment during their second breeding cycle. Females in Group 2 (shown as triangles linked by an interrupted line,  $n = 5$ ) received the treatments in the reverse order. This is for an illustrative purpose only, and statistic values were obtained using GLMM

### 3.2 | Clutch size

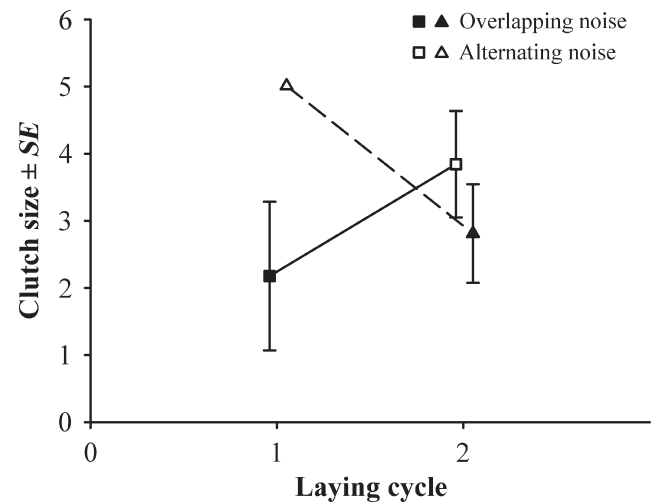
Eight of the 11 females displaying CSDs laid eggs during the overlapping noise treatment, and ten of them laid eggs during the alternating noise treatment. The mean delay between the first CSD and their first egg laid was  $7.6 \pm 1.7$  days ( $N = 8$ , range 1–12) for the overlapping noise treatment and  $7.2 \pm 1.7$  days ( $N = 10$ , range 1–17) for the alternating noise treatment. During the whole duration of the experiment, the females laid a total of 75 eggs.

Analysis with a Poisson GLMM (Table 2, column “Clutch size”) indicates a statistically significant effect of the noise treatment on the clutch size ( $p < 0.05$ ); females laid significantly fewer eggs during the overlapping noise treatment ( $2.5 \pm 0.7$ ,  $N = 11$ , range 0–6, median 2.0) than during the alternating noise treatment ( $4.4 \pm 0.5$ ,  $N = 11$ , range 0–5, median 5.0)—Figure 3. No group or breeding cycle effects were detected (Table 2).

### 3.3 | Egg mass, composition, and testosterone concentration

Eleven of the 75 eggs laid were found cracked or broken, and we could measure the total egg mass, the albumen mass, the yolk mass, and the yolk testosterone concentration for 64 eggs only.

The Gaussian model revealed no significant difference in the egg mass between the two noise exposure treatments (columns “Total weight” in Table 2). However, we detected a group effect with females in Group 2 (Alternating noise in the first cycle) laying bigger eggs and an effect of the final clutch size, females with larger clutches laying



**FIGURE 3** Noise impact on the number of eggs laid: average clutch size  $\pm$  SE of female domestic canaries placed in an overlapping noise condition and in an alternating noise condition. Females in Group 1 (continuous line,  $n = 6$ ) received the overlapping noise treatment during their first breeding cycle and the alternating noise treatment during their second breeding cycle. Females in Group 2 (interrupted line,  $n = 5$ ) received the treatments in the reverse order. This is for an illustrative purpose only, and statistic values were obtained using GLMM



bigger eggs. No statistically significant effects of the breeding cycle or egg rank were detected.

The analysis did not reveal any statistically significant differences in terms of albumen mass, yolk mass, or yolk testosterone concentration between the overlapping and the alternating noise treatment (columns "Albumen weight," "Yolk weight" and "Testosterone" in Table 2). Albumen mass showed the same statistically significant effects as the total egg weight. Yolk mass did not differ between both groups of females but decreased significantly with egg rank. The testosterone concentration showed exactly the opposite pattern of variations with a significant increase with egg rank (Table 2; Figure 4).

## 4 | DISCUSSION

According to our predictions, we found that female domestic canaries (i) showed reduced sexual receptivity and (ii) laid fewer eggs when attractive male songs were partially overlapped by low-frequency noise compared to a condition where the songs were broadcast alternatively with the noise. We did not find any further differences between the egg mass, albumen mass, yolk mass, and testosterone yolk concentration between the two treatments—overlapping versus alternating urban noise. We argue here that urban-style noise reduces female sexual receptivity and maternal investment by masking male–female vocal communication.

### 4.1 | Environmental impact on signal efficiency

On a behavioral level, females reduced their sexual receptivity (measured through the rate of copulation solicitation displays which is a direct invitation for the male to copulate) when the songs were overlapped by low-frequency noise relative to the treatment when noise was presented in alternation with the songs. This result confirms

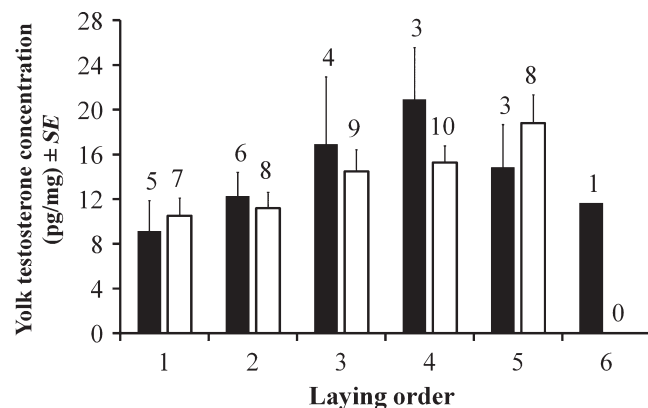
our previous findings (Huet des Aunay et al., 2014) and supports the idea that vocal masking is responsible for this decrease of female responses. Indeed, female canaries prefer songs with a large bandwidth (Draganoiu et al., 2002) and low frequencies (Pasteau et al., 2007). The songs broadcasted in this experiment had a large frequency bandwidth (1–5 kHz) and urban-style noise with most of its energy below 2 kHz overlapped the lower part of this spectrum in the overlapping noise condition only. The most likely mechanism leading to the observed reduction of the CSD score is that females were able to detect neither the low frequencies (around 1 kHz) nor the actual frequency bandwidth of the songs (around 4 kHz) because of signal masking. An accurate assessment of at least two key parameters that determine the attractiveness of the signal is prevented by the urban-like low-frequency noise. Females could either perceive the song as less attractive or they could be unable to accurately assess the attractiveness of the song.

Our results parallel findings obtained in the wild with great tits where females left their nestbox less in response to low-frequency male songs but not to high-frequency songs during the playback of urban noise (Halfwerk, Bot, et al., 2011). More broadly, our findings are in line with the conclusions of recent reviews suggesting that noise interferes with animals' abilities to detect important sounds (Francis & Barber, 2013) in different contexts such as parent–offspring communication (Leonard & Horn, 2012) or prey detection (Senzaki, Yamaura, Francis, & Nakamura, 2016). On a larger scale, the current results bring additional support to the emerging framework of environmental impact on signal efficiency and mate choice, applicable to diverse taxa and sensory modalities (Halfwerk & Slabbekoorn, 2015; Lüring & Scheffer, 2007). Masking of male songs by the noise could also partially explain the lower pairing success of male songbirds in naturally noisy areas (Gross, Pasinelli, & Kunc, 2010; Habib, Bayne, & Boutin, 2007).

### 4.2 | Noise impact on clutch size

Low-frequency noise also affected female reproductive investment: females laid smaller clutches when male songs were overlapped by the urban noise compared to the situation where the urban noise was broadcast in alternation with the male songs. Once more, the best explanation of the observed reduction in the reproductive output is the partial masking of male songs by the low-frequency noise. As the vocal masking most likely prevented females to accurately assess the features that stimulate CSD response, our results are consistent with the differential allocation hypothesis (Burley, 1988) and a reduction of maternal investment in response to an inability to detect mate attractiveness.

On a proximate level, this can be potentially achieved through differential follicular development, as this aspect of maternal investment was already shown to be positively affected by male song in domestic canaries (Bentley, Wingfield, Morton, & Ball, 2000). Our results are in line with two previous studies showing that females lay more eggs according to male attractiveness: female canaries laid larger clutches when listening to rich versus poor song repertoires (Kroodsma, 1976)



**FIGURE 4** Noise impact on egg investment: mean of yolk testosterone concentration (pg/mg) of eggs ( $n = 64$ ) depending on laying order and noise treatment. The overlapping noise treatment ( $n = 8$  clutches) is represented by black bars and the alternating noise treatment ( $n = 10$  clutches) one by empty bars. Above the bars is given the sample size. This is for an illustrative purpose only, and statistic values were obtained using LMM

and female peacocks *Pavo cristatus* equally laid larger clutches when randomly mated to males having larger trains and considered as more attractive (Petrie & Williams, 1993).

A field study reported that urban noise levels close to a highway best explained the observed decrease in clutch size in great tits (Halfwerk, Holleman, et al., 2011). However, our current results bring the experimental proof that urban noise can have a negative impact on clutch size in songbirds and provide support for a proximate mechanism suggested earlier (Halfwerk, Holleman, et al., 2011), namely the interference of noise with the assessment of male quality. Indeed, the observed reduction in the clutch size is most likely explained by the partial masking of the male songs by the noise, which may impede male–female vocal communication.

For other songbird species, the evidence for an urban noise impact on reproduction is contradictory. An experimental study carried out in laboratory conditions reported no impact of urban noise on reproductive output in the zebra finch *Taeniopygia guttata*. However, females in the noisy condition made more nesting attempts and laid more eggs but had a lower hatching success due to higher embryo mortality (Potvin & MacDougall-Shackleton, 2015). In the domestic sparrow *Passer domesticus*, one study failed to find a noise impact either on the clutch size or on the number of fledglings (Meillère, Brischoux, & Angelier, 2015) while a different one has shown experimentally that urban noise had a negative impact on the condition of nestlings and the number of fledged young (Schroeder, Nakagawa, Cleasby, & Burke, 2012). In that study, females showed decreased feeding rates during the noise exposure and one possible explanation of these results is the masking impact on parent–offspring vocal communication. A playback experiment with tree swallows *Tachycineta bicolor* confirmed this impact as chicks begged less in response to calls of their parents during noise exposure than during ambient control conditions (Leonard & Horn, 2012). However, the costs of breeding in noisy conditions can be balanced in certain conditions by the decrease of the predation risk (Francis, Ortega, & Cruz, 2009).

While masking is the most likely explanation of the differences that we observed in terms of sexual responsiveness and clutch size, a stress-related effect (besides the masking effect reported here) cannot be ruled out without a control group with no noise exposure at all. However, the baseline CSD scores from our experiments are comparable and if anything higher than mean values from similar stimuli obtained in previous experiments without noise exposure (Draganoiu et al., 2002; Pasteau et al., 2007). A stress impact of our noise stimuli on the CSD scores reported here seems unlikely to us. However, a possible interaction between female baseline corticosterone and noise impact on reproduction, as was reported in the zebra finch (Potvin & MacDougall-Shackleton, 2015), has yet to be investigated in female canaries.

#### 4.3 | Egg investment

Besides the difference in clutch size, females in our study did not modify the egg mass or the egg composition (measured as albumen mass, yolk mass and yolk testosterone concentration) according to the experimental treatment. However, we found that females that received

the overlapping noise treatment during their first breeding cycle laid lighter eggs than those receiving the overlapping noise treatment during the second breeding cycle. This suggests that a noisy environment early during the breeding season could have long lasting effects, but the observed difference could also be due to other group related differences. Overlapping urban noise induces thus a decrease in both sexual attractiveness of the songs and the number of eggs laid but not into egg size or egg composition.

Previous studies with domestic canaries showed that female canaries could adjust egg size (Garcia-Fernandez et al., 2013; Leitner, Marshall, Leisler, & Catchpole, 2006), yolk weight (Garcia-Fernandez et al., 2013), or testosterone yolk concentration (Gil et al., 2004; Tanvez et al., 2004) to song attractiveness. However, neither of these studies has reported a difference regarding the clutch size. Female canaries seem to have different ways to modify resource allocation according to song attractiveness, increasing the clutch size (Kroodsma, 1976; current study), or modifying the egg size or the egg composition (see studies above). It seems that the system of parental care (biparental versus female care only) cannot explain all the variability observed in the differential allocation patterns as previously suggested (Horváthová et al., 2012).

Our measures of testosterone yolk concentration seem to be reliable as we found the same pattern of increasing concentration with laying order as it has been previously described for the domestic canary (Gil et al., 2004; Schwabl, 1993; Tanvez et al., 2004). This increase of yolk concentration with the laying order was suggested to be a mechanism enabling to counterbalance the development of chicks in species with asynchronous hatching (Müller, Eising, Dijkstra, & Groothuis, 2004; Schwabl, 1993).

## 5 | CONCLUSIONS

Our study reports for the first time a match in the urban-style noise impact on both courtship behavior (fewer female CSDs in response to male song) and reproductive investment (decrease of the clutch size). First, we confirm a noise impact on signal efficiency in an explicit courtship context: the same signal (male song) varied in efficiency across different environmental conditions. Second, we bring evidence for a potential mechanism able to explain the observed decrease in the clutch size: the masking of attractive male songs perturbs male–female vocal communication inducing a lower sexual responsiveness and a lower investment concerning the number of eggs laid. Further work is needed to establish what the effects of urban noise are on the final reproductive success in domestic canaries given the different processes that can be affected as the parental investment, the hatching success, or the nestling growth.

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