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Water restriction influences intra-pair vocal behavior and the acoustic structure of vocalisations in the opportunistically breeding zebra finch (*Taeniopygia guttata*)

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ABSTRACT

Seasonally-breeding species experience significant and predictable shifts in vocal behaviour; however, it is unclear to what extent this is true for species that breed opportunistically. The Australian zebra finch is an opportunistically breeding species, which means individuals must time breeding bouts based on many environmental factors. Here we tested the effect of experimental water restriction, which suppresses reproductive readiness in zebra finches, on vocal behaviour of males and females. More specifically, we quantified the effect of water restriction on three parameters of vocal behaviour in pair-bonded zebra finches: vocal activity, patterns of vocal exchanges, and the acoustic structure of vocalisations (calls and male song). We found that water restriction caused a decrease in vocal output (both song and call rate). Additionally, water restriction affected the composition of male songs. However, there was no effect of water restriction on the patterns of calling exchanges for monogamous partners (temporal coordination and turn taking). Finally, water restriction had vocalisation- and sex-specific effects on the acoustic structure of song syllables and calls. Because the direction of these effects were vocalisation- and sex- specific, there may be different mechanisms underlying the effects of water restriction on acoustic structure depending on context. These results contribute to the growing body of research highlighting the rich communicative potential of bird calls. Our current results raise the hypothesis that zebra finches may use changes in vocal behaviour and/or the structure of vocalisations of their conspecifics when making breeding decisions.

1. Introduction

Temperate seasonally-breeding songbirds experience profound fluctuations in singing associated with the changing seasons (Slagsvold, 1977; Catchpole and Slater, 2008). More broadly, there is growing evidence from many species which suggests there are widespread changes to auditory-vocal communication systems throughout the year, including variation in the type and composition of songs and calls (Marler, 1956; Brenowitz, 2004; Marler, 2004; Maddison et al., 2012; Lohr et al., 2013), acoustic structure of song syllables (Maddison et al., 2012), and auditory perception (Lucas et al., 2007; Bass et al., 2016; Caras and Remage-Healey, 2016). Whereas, a higher amount of courtship song during breeding seasons can easily be described as an example of breeding behavior coupled to the appropriate environmental context, the functional significance of these other changes in auditory-vocal communication systems remain largely unknown.

For opportunistically breeding species, it is unclear to what extent environmental condition induces changes in auditory-vocal communication systems, such as is seen in seasonally-breeding species. The Australian zebra finch is an opportunistically breeding species. Zebra finches time breeding bouts based on many environmental factors such as food and water availability, the presence of green grasses, humidity and day length (Perfito, 2010). However, zebra finches within the same population, under good environmental conditions, are not all in the same breeding state (Perfito, 2010). Furthermore, in the wild, zebra finch pairs do not always breed synchronously (Zann, 1996). In the laboratory, experimental water restriction has reliably been used as a method for manipulating male and female breeding readiness (Perfito

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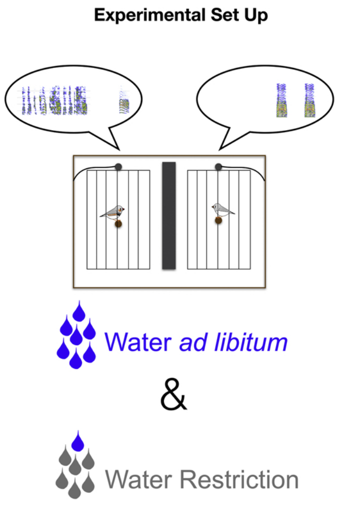

Summary of Dependent Variables and Analyses

Type	Dependent Variable	Notes on Analyses
Vocal Output	Song Rate	All songs were used.
	Call Rate	All calls were used.
	Burst Rate	Partner-directed calling appears to predominately occur during elevated calling events which we have termed bursts.
	Call Rate in Bursts	
Global Song Elements/ Composition	Duration of Full Motifs	All songs were used to quantify the proportion of song bouts composed of the global song elements (introductory note sequence, full motifs and partial motifs).
	Proportion of Song Full Motifs	
	Inter-Sequence Interval	
	Proportion Introductory Notes	
Quality of Calling Exchanges	Male-Female Calling Delay	All calls, within bursts, were used to calculate the cross-correlation M-F calling delay.
	Male-Female Turn Taking	All calls, within bursts, were used to calculate % Markov Fit.
Acoustic Structure	Male and Female Calls	All song and a subset of good quality calls were used. Acoustic structure was assessed with two methods. First, all the data points of the spectrogram were used as raw measures in a PCA. Second, traditionally defined acoustic features (RMS, median freq, standard deviation and interquartile range of the spectral envelope) were quantified.
	Global Song Elements	
	4 Individual Notes Extracted from Song	

Fig. 1. Schematic of our general experimental paradigm. The vocal behavior of established zebra finch pairs was recorded under two environmental conditions, water *ad lib* (Control) and water restricted (WR). Experimental water restriction is known to reduce breeding readiness in zebra finches. In order to focus on vocal behavior specifically, independent of other communication channels, recordings were made while pairs were visually isolated. The table summarizes the parameters of vocal behavior we used as dependent variables and the analyses conducted. Briefly, timestamped calls and male song were extracted, and we used these vocalisations to quantify three characteristics of vocal activity (male song rate, burst rate, and call rate). Additionally, we quantified the effect of water restriction on the composition of male song (e.g. global song elements such as introductory note sequence, full motifs and partial motifs) and on the quality of the partners' calling exchanges (cross-correlation of male-female calls, and % Markov Fit of patterns of turn taking). Finally, we used two methods (full spectrum analysis and pre-defined acoustic features) to assess the effects of water restriction on the acoustic structure of vocalisations.

et al., 2006; Prior et al., 2013; Prior and Soma, 2015). The physiological effects of water restriction on males and females are somewhat varied; however, both sexes do experience similar shifts in neuroendocrine state as has been described for seasonally-breeding species (e.g. brain and circulating steroid levels) (Perfito, 2010; Prior et al., 2013; Perfito et al., 2015; Prior and Soma, 2015).

While zebra finches will engage in courtship behaviors throughout the year, the fact that they coordinate breeding bouts at the level of the pair raises the question of whether shifts in vocal dynamics, that preceed breeding, could be used to coordinate breeding attempts. Indeed there is evidence that zebra finch vocal behavior shifts with environmental condition, and that there are season-like shifts in neuroendocrine state which could mediate this shift in behavior (Prior and Soma, 2015; Perfito et al., 2015). For wild zebra finches, there is evidence that undirected song is more common during non-breeding periods (Dunn and Zann, 1996a,b). Additionally, during periods of active nesting zebra finches produce a synchronized vocal exchange (duet) that is used to coordinate bi-parental care (Elie et al., 2010; Boucaud et al., 2016, 2017). More broadly, there is a shift in call types used during nesting (Gill et al., 2015), with some call types used almost exclusively during nesting (Elie et al., 2010; Gill et al., 2015).

Here we tested the effect of water restriction, an environmental manipulation that impacts breeding, on three aspects of zebra finch vocal behavior: (1) overall vocal activity, (2) patterns of vocal exchanges, and (3) the acoustic structure of vocalizations. We manipulated breeding readiness using established experimental water restriction paradigms. In order to compare the effect of water restriction to previous studies, we quantified circulating testosterone in males and circulating corticosterone levels in males and females. Despite that zebra finches are gregarious, they appear to spend the majority of their life with their pair bonded mate (Zann, 1996; McCowan et al., 2015); thus, we chose to focus on describing the effects of water restriction on the vocal behavior of well-established zebra finch pairs. Additionally, in order to control for social condition during recordings, we recorded vocal behavior while pairs were visually isolated (Perez et al., 2015b). This forced all intra-pair communication to be through the vocal-acoustic domain and not visual or tactile.

2. Materials and methods

2.1. Subjects

Twenty-eight paired adult domesticated zebra finches (> 120 days old) were used for this study. All pairs were bonded for > 1 year and had been allowed to breed together for several breeding cycles. Thus, only successfully-bonded pairs were used. Each pair was housed in their own cage (dimensions 50.8 × 40.5 × 30.5 cm). The colony was maintained on a 14:10 h light:dark cycle with temperatures between ˜24-26 °C. All individuals had *ad libitum* access to seed, cuttlefish bone, and grit in addition to supplemental green vegetables once per week. Note that over the course of the study one individual died; therefore, fifteen pairs were recorded in the control condition (CON), while only fourteen of these pairs were also recorded in the water restricted condition (WR).

2.2. Experimental design

Water availability was manipulated in order to influence reproductive condition. Pairs were slowly water restricted over the course of six weeks from 5 mL down to 1 mL per individual per week. This protocol is similar to what has previously been published (Prior et al., 2013, 2014). Briefly, at the start of water restriction, two empty water towers were placed on each cage. Initially, 2 mL of water was administered via pipette into each water tower five days a week. The amount of water administered was gradually decreased to .5 mL twice a week in each water tower.

Vocal behavior of each pair was recorded three times during Water Restriction (WR) and three times during Water *ad libitum* (CON) resulting in six recordings/pair (each recording ˜4 h). From these recordings, we quantified the overall vocal activity (song and call rate), the quality of vocal exchanges (male song composition and patterns of intra-pair calling exchanges), and the acoustic structure of vocalisations (Fig. 1). To control for potential confounds of habituation to the recording session, the order of water restriction was counterbalanced across pairs: nine pairs were recorded first under the CON and then under the WR condition (Cohort 1), and six pairs were recorded first under the WR and then under the CON condition (Cohort 2). For both cohorts there was a break (37 days for cohort 1 and 16 days for cohort 2) between conditions. Importantly, this amount of time (> 2 weeks) has previously been shown to allow recovery from water restriction (Vleck and Priedkalns, 1985). In order to assess the effect of water restriction on systemic hormone levels, we collected blood samples from the brachial vein and quantified circulating corticosterone and testosterone levels 0–3 days following the completion of recordings for each condition (CON and WR). Thus, there were at least 2 weeks between blood sample collection and the subsequent acoustic recordings.

2.3. Recording vocal behavior

To identify effects of water restriction on acoustic communication, we recorded intra-pair vocal behavior while the male and female of each pair were visually isolated. Since the only means of contact between partners during visual separation is acoustic, this paradigm allowed us to disentangle effects of our environmental manipulation on acoustic communication from more general pairing behaviors. Previous research has shown that intra-pair vocal dynamics are more stereotyped while visually isolated (Perez et al., 2015b). While visually-isolating pairs introduces a perturbation that could itself impact behavior, this isolation removes confounds that could result from effects of water restriction on other sensory systems involved in communication dynamics.

Each pair was moved from their home cage to a sound attenuation chamber (cage dimensions 63.5 × 33.0 × 30.5 cm) the day before recordings (~14:00 h). The male and female were physically separated in the testing chamber by placing each bird in individual but adjacent cages. Each cage contained two perches, a seed cup and a water tower, which was either filled or empty depending on water condition. Initially pairs remained in visual contact to facilitate habituation to the testing chamber. After ~ 3 h, an opaque partition was placed between the two cages (Fig. 1). Behavior was not recorded until the following day which ensured behavior was not recorded immediately after the stress of handling and moving. In total pairs had at least 15 h to habituate to the testing set up.

The following morning, passive recordings of each pair were made using a digital recorder (SongMeters SM2, 16-bit, 44 kHz sampling rate; Wildlife Acoustics Inc., Concord, MA, U.S.A.) with omnidirectional microphones (SMX-II, Wildlife Acoustics Inc.; omnidirectional, flat frequency response 20 Hz-20 kHz, sensitivity 36 ± 4 dB, 0 dB 1/4 1 V/pa at 1 kHz). One microphone was positioned above each partner's cage. More specifically, the microphone was positioned downwards above the cage in order to minimize amplitude variations due to the position of the bird. Each recording was ~4 h long from ~08:00-12:00, the period starting at lights on. There were six recordings in total (Recording number (Nb), 1–6), with ~12 h of recordings/pair/water condition.

2.4. Scoring vocal behavior

All vocalisations were extracted from recordings using in-house software, as previously described (Elie et al., 2011; Perez et al., 2015b) (*see supplemental information*).

2.4.1. Songs

Songs were identified manually (see supplemental information). In total we recorded 205 songs from 13 males during CON and 28 songs from 8 males during WR. Characteristics of each song were manually scored (N.H.P.) using Praat (V 5.3.56, 2014) (Boersma and Weenik, 1996). Song bouts were defined as a single rendition of song, separated by at least 1 s. Because there were drastically fewer WR songs and most males did not sing on each recording date, we analyzed song rate by calculating a single song rate per male for each water condition (CON and WR).

In order to determine the effect of water restriction on the composition and acoustic structure of song, we further processed song in two ways. First, global song elements were extracted manually, as concise sequences, in Praat. More specifically, the following sequences were extracted: an introductory note sequence as well as every full and partial motif (Fig. 2A). Any additional inserted elements (e.g. distance calls) were not extracted for analysis. Second, the following four individual notes were extracted: the first and last introductory notes, as well as two song syllables: one from the first half of the motif (early syllable) and one from the second half of the motif (late syllable) For a given male, the same two song syllables were extracted from each song bout. We preferentially selected harmonic, 'stacked' syllables to facilitate consistent labeling of the note boundaries.

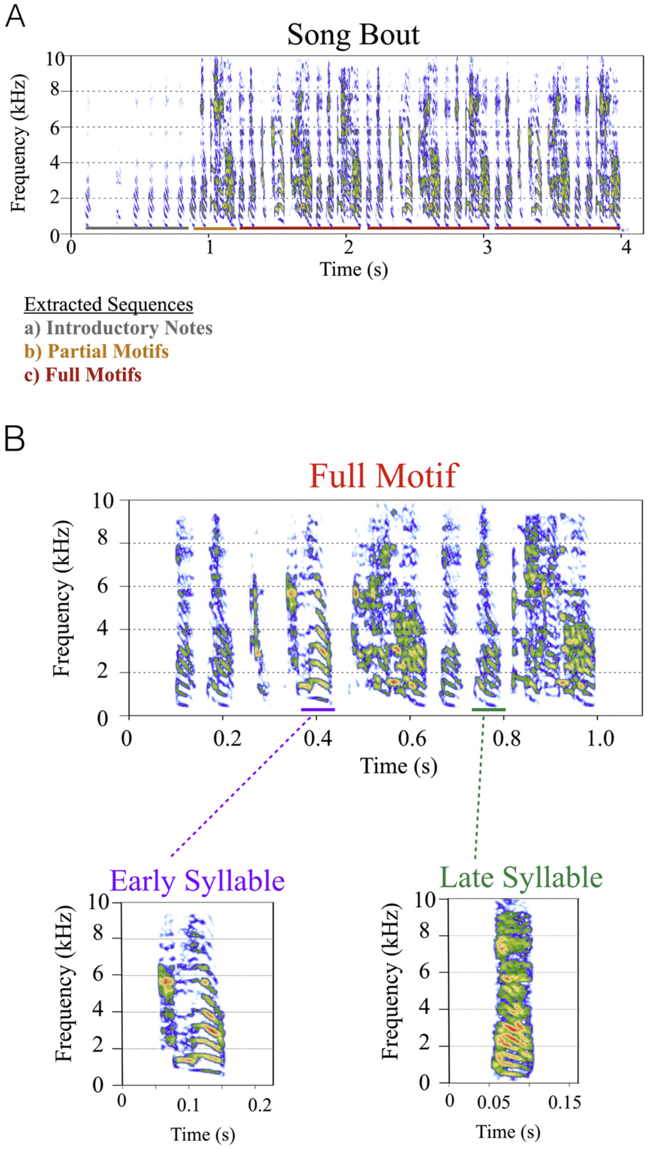

Fig. 2. Spectrogram of a male song bout. Examples of extracted song elements are labeled: (A) global song elements, and (B) individual syllables.

We used the extracted global song elements to generate four characteristics of song: (1) mean duration of full motifs, (2) the ratio of the duration of full motifs to the duration of the total song bouts, (3) the mean inter-sequence interval (between the introductory note sequence of first motif and subsequent motifs) and (4) the ratio of the duration of the introductory note sequence to the total duration of motifs in the corresponding song bout. Additionally, acoustic structure analyses were performed on the full and partial motifs (*see supplemental information*). The extracted introductory notes and song syllables were used for acoustic structure analysis (*see supplemental information*).

2.4.2. Calls

In addition to song, we extracted all the calls during a recording. Our initial observations suggested that pairs engaged in call and response periodically throughout the recordings and that during quieter periods there was typically only one individual calling. Thus, in order to focus on intra-pair calling, we defined calling 'bursts', where calling activity was elevated (overall call rate per pair was > 10% above the average for the recording) (*see supplemental information*). By isolating bursts specifically for analysis, we increased the likelihood that we were examining parameters of true vocal exchanges. We quantified burst rate (# bursts/ hour) and call rate per individual (for the full recording and within bursts specifically), as well as two parameters of calling exchanges: (1) temporal coordination (cross-correlation), and (2) the predictability in the pattern of turn-taking (% Markov fit), independent of the timing (*see supplemental information*).

In highly coordinated pairs, we expected that the delay of the male's (M) response to his female (F) partner would be the same as that F's response to the M (comparison of M-F and F-M calling delay). Furthermore, we expected higher consistency in the delay times between calls (delay times of the M answer to the F, and the F answer to the M). These would be examples of increased temporal coordination.

Previous work has shown visually isolated pairs are more Markovian in their alternation of calls (Perez et al., 2015b). More Markovian patterns mean that the identity of a given caller depends on the identity of the previous caller. In this way, the pattern of turn taking is assessed independently of the calling delays. This phenomenon may be analogous to how speech patterns in humans change between talkers when they are face-to-face in contrast to when they are on the phone. More Markovian exchanges are likely a result of the birds' increased attention to the acoustic channel (Perez et al., 2015b). Together, the cross-correlation and % Markov fit provide a description of the pattern of intra-pair vocal dynamics.

Additionally, for each individual, we randomly selected a subset of 50 calls from each recording to use for the acoustic structure analyses (function: "random", a uniform random selection in python). These calls were then manually examined, and only cleanly recorded calls were kept for further analysis (calls that did not include noises from wing/body movements, the cage, or other vocalizations from the partner). On average there were 121 ± 32 (Mean ± SD) calls per individual per condition. Final sample sizes are: N = 1991, Female CON; N = 1608, Female WR; N = 1683, Male CON; and N = 1670, Male WR. The majority of calls were 'stack' calls (Ter Maat et al., 2014; Gill et al., 2015) *(see supplemental information)*.

This subset of extracted calls was used to quantify the effect of water condition on the acoustic structure of calls. We used two complementary methods of analysis: (1) full-spectrum analysis (Mouterde et al., 2014a; Elie and Theunissen, 2016), and (2) quantification of predefined parameters (Seewave package (Sueur et al., 2008)) implemented in R software (v. 3.2.3, 2015, R Foundation for Statistical computing).

2.5. Analysis of acoustic structure

We used a standard two-tier approach (full spectrum analysis and pre-defined acoustic features) to describe the effects of water restriction on the acoustic structure of vocalisations. The two approaches we used answer slightly different questions. First, we asked whether water condition affected the acoustic structure of vocalisations in any way, i.e. "Is there any difference?". In order to comprehensively analyze the spectrogram, we used an in-house program (written in R) to summarize all the information in the entire spectrogram by using all the data points of the spectrograms as raw measures in a PCA (Mouterde et al., 2014b; Elie and Theunissen, 2016) (*see supplemental information*). The full spectrum analysis allows for an unbiased assessment of how WR affected the spectrogram (there is no *a priori* selection of specific acoustic elements); however, the principal components cannot be easily related back to specific acoustic features. Thus, we also asked "are there acoustic differences in traditionally defined parameters?". For this analysis we used Seewave package in R (Sueur et al., 2008) to quantify the effect of water condition on four pre-defined acoustic features: an estimate of call loudness (root-mean-square RMS of the temporal envelope) and three parameters of the spectral envelope (median freq (kHz), SD (kHz), and IQR (kHz)) (*see supplemental information*).

2.6. Circulating testosterone and corticosterone levels

For each individual, blood samples were collected during both treatments after acoustic recordings were taken. Note that this means there was a minimum of 2 weeks between blood sample collection and a subsequent recording. Both partners of a pair were bled at the same time by two experimenters (M.A.S.F and N.H.P). All blood samples were collected between 11:00-13:00 h and within 3 min of opening the cage door to catch individuals (Mean ± SEM: 55 ± 6 s). Blood samples were centrifuged to obtain plasma (10 min at 10,000 x g), which was stored at −20 °C until further processing. Circulating concentrations of steroids were assayed using enzyme immunoassay kits (Cayman Chemical Co., Ann Arbor, MI: Testosterone, 582701; Corticosterone, 500655) (*see supplemental information*).

2.7. Statistics

All statistical analyses were carried out in R (v. 3.2.3, 2015, R Foundation for Statistical computing). We used generalized linear-mixed models (LMMs; function lmer from the Package). The design of our study included three potential factors, Water Condition (WR and CON), Recording Nb (1-6: indicating the order recordings were made in), and Cohort (Cohort 1, CON first and Cohort 2, WR first). We used Recording Nb as a continuous variable in our models. We did not include Cohort as a factor. For pair-level dependent variables, Pair was included as a random factor. For individual-level dependent variables, Individual was included as a random factor, and Sex was included as a between-subjects factor. Prior to interpretation, we checked the validity of each model by plotting the distribution of the residuals. Data were transformed as necessary. Model summaries are provided in Supplementary Table 1-7.

3. Results

3.1. WR does not affect circulating corticosterone and testosterone

Consistent with prior research, water restriction had no effect on circulating corticosterone levels in males or females (*Males*, mean ± SEM, CON: 1.64 ± 0.43 ng/mL; WR: 1.17 ± 0.14 ng/mL; $\chi^2(1) < 0.01$, P = 0.987; *Females*, mean ± SEM, CON: 1.34 ± 0.23 ng/mL; WR: 1.43 ± 0.35 ng/mL; $\chi^2(1) = 1.48$, P = 0.225). Additionally, circulating testosterone levels were low for males regardless of water condition and there was no main effect of water restriction on circulating testosterone (mean ± SEM, CON: 0.41 ± 0.10 ng/mL; WR: 0.47 ± 0.15 ng/mL; $\chi^2(1) = 0.40$, P = 0.527). The low circulating level of testosterone for males in both treatment groups suggests that the effect of water restriction was smaller in the current study than what has been previously reported (Prior et al., 2013).

3.2. WR decreases overall vocal activity

Overall, in response to water restriction, zebra finches vocalized less. This effect was clearest on male song rate during water restriction ($\chi^2(1) = 6.70$, P = 0.009) (Fig. 3A). In addition, there was a small, but statistically significant decrease in call rate (calculated from the entire recordings) for both males and females in response to water restriction (*Females*, mean ± SEM, CON: 3.03 ± 0.43 calls/min; WR: 2.67 ± 0.29 calls/min. *Males*, mean ± SEM, CON: 3.56 ± 0.57 calls/min; WR: 2.92 ± 0.34 calls/min) (Water Condition $\chi^2(1) = 6.66$, P = 0.010. Sex $\chi^2(1) = 0.87$, P = 0.350. Recording nb $\chi^2(1) = 0.09$, P = 0.763. Water Condition × Sex $\chi^2(1) = 0.24$, P = 0.877).

As we were primarily interested in intra-pair calling behavior, we also quantified the effect of water restriction on calling during 'bursts', periods of elevated calling activity. There was no main effect of water restriction on burst rate (number of bursts/hour of recording) (Water

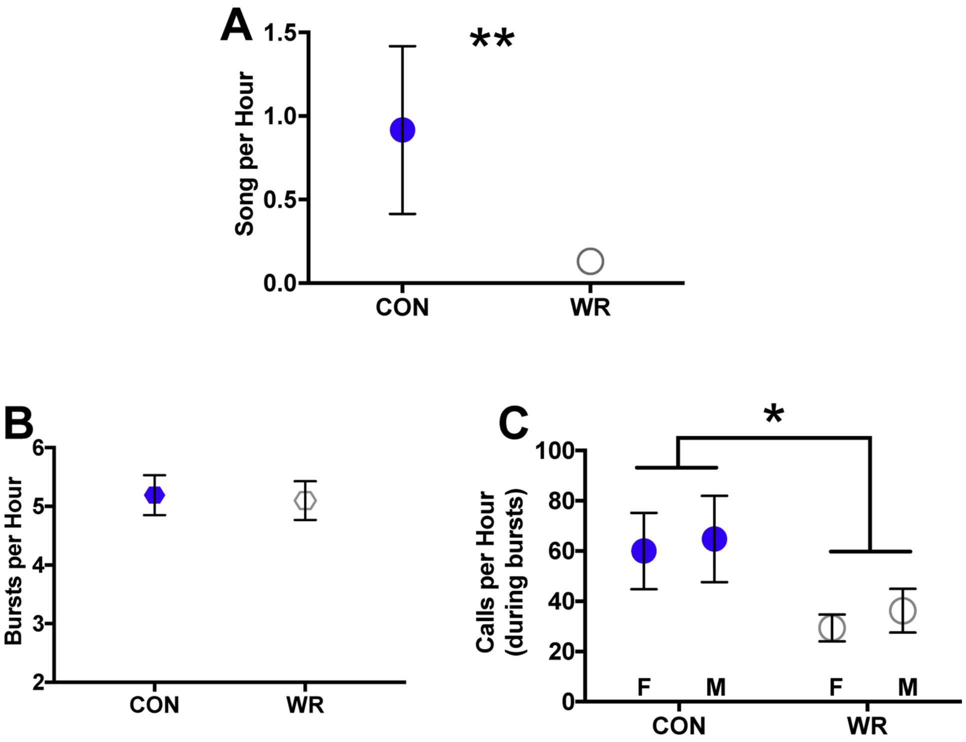

Fig. 3. Effect of water restriction on vocal activity. (A) Song rate (per hour). Note that only singing males are shown here. (B) Burst rate (per hour). Bursts are periods of elevated calling activity. (C) Individual call rate within bursts (per hour). Call rate is plotted per hour to be consistent with panels A and B. Call rates per min are as follows: *Females*, mean ± SEM, CON: 1.00 ± 0.25 calls/min; WR: 0.49 ± 0.09 calls/min. *Males*, mean ± SEM, CON: 1.08 ± 0.29 calls/min; WR: 0.60 ± 0.15 calls/min). Mean ± SEM. * $P < 0.05$, ** $P < 0.01$, CON = control (*blue circles)*, WR = water restricted (*gray circles)*. Circle = individual level parameter; Hexagon = pair level parameter. Note that in Panel A, the height of the standard error bars is equal to the height of the symbol for WR, therefore Prism does not include error bars in this instance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

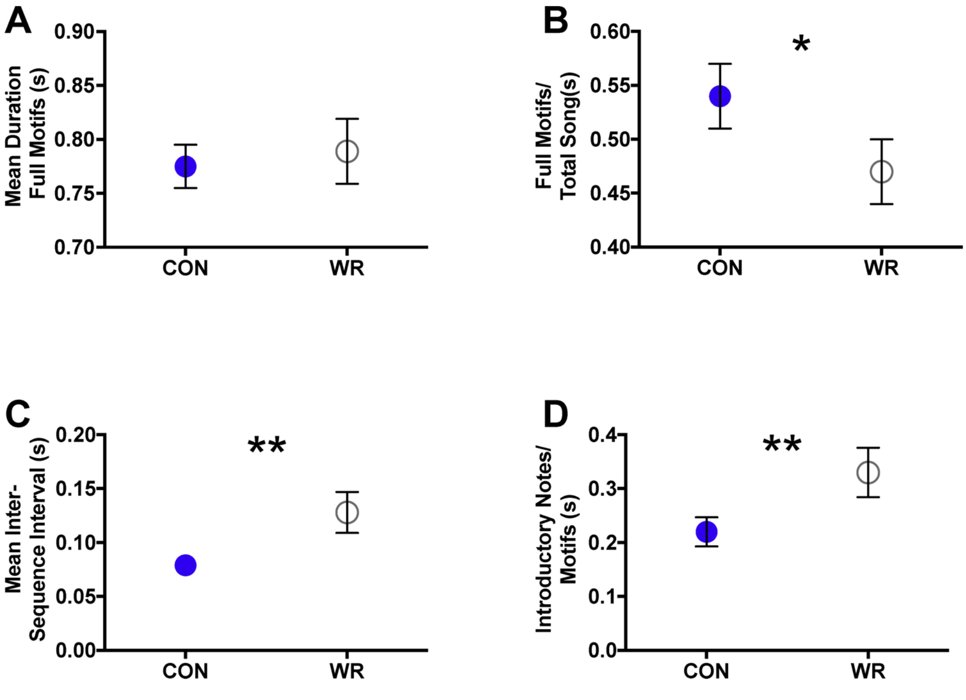

Fig. 4. Effect of water restriction on song composition: (A) duration of full motifs (s), (B) ratio of full motifs to total duration of song bout, (C) duration of inter-sequence interval (s), and (D) ratio of duration of introductory note sequence to duration of full motifs. Mean ± SEM. If error bars are not shown, they are smaller than the circle indicating the mean. * $P < 0.05$, ** $P < 0.01$. CON = control (*blue circles)*, WR = water restricted (*gray circles)*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Condition $\chi^2(1) = 0.65$, $P = 0.420$) (Fig. 3B); however, as with call rate during the entire recording, water restriction caused a decrease in male and female call rate within bursts (Water Condition $\chi^2(1) = 4.53$, $P = 0.033$; Sex $\chi^2(1) = 0.01$, $P = 0.940$; Water Condition × Sex $\chi^2(1) = 0.02$, $P = 0.881$) (Fig. 3C). Throughout the course of the experiment, the burst rate increased from an average of 4.14 ± 0.31 bursts/h in recording 1 to 6.01 ± 0.47 bursts/h in recording 6 (mean ± SEM) (Recording nb $\chi^2(1) = 19.29$, $P < 0.001$); however, call rate within bursts did not change over the course of the experiment (Recording Nb $\chi^2(1) = 0.04$, $P = 0.850$).

3.3. *WR influences song composition*

Water restriction did not change the duration of male full motifs (Water Condition, $\chi^2(1) = 2.88$, $P = 0.090$) (Fig. 4A), but significantly affected other global song elements. More specifically, when water restricted, males produced songs with a decreased proportion of full motifs (duration of full motifs/total song bout (s)) (Water Condition, $\chi^2(1) = 4.46$, $P = 0.037$) (Fig. 4B), an increased duration of inter-element intervals (Water Condition, $\chi^2(1) = 5.81$, $P = 0.016$) (Fig. 4C), and an increased proportion of introductory notes (duration of introductory notes/full motifs (s)) (Water Condition, $\chi^2(1) = 7.18$, $P = 0.007$) (Fig. 4D).

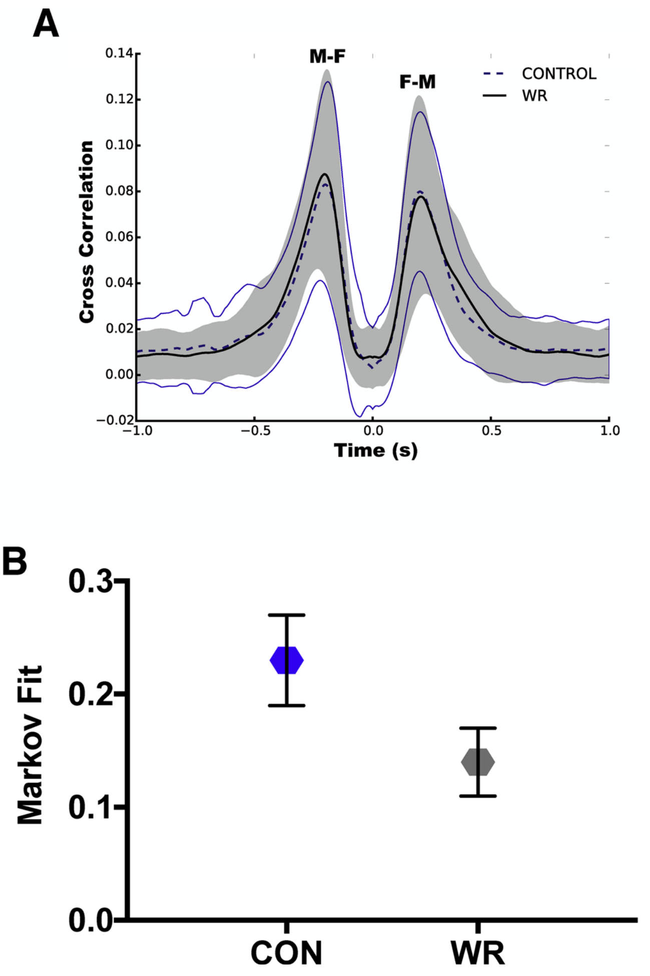

Fig. 5. Effect of water restriction on coordination of calling exchanges. (A) Coordination estimated by the cross-correlation of F-M calls showed no difference between exchanges under WR and CON conditions. Mean ± SEM. M-F labels the female's delay to answer her male partner. F-M labels the male's delay to answer his female partner. (B) Effect of water restriction estimation of turn taking, Markov fit; Mean ± SEM. CON = control (*blue hexagon*), WR = water restricted (*gray hexagon*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. *WR does not affect F-M calling dynamics*

In contrast to male song, there was no significant effect of water restriction on the patterns of intra-pair calling (temporal coordination or turn taking). First, there was no effect of water restriction on our measure of temporal coordination (cross correlation of F-M and M-F calling delay) (Fig. 5A). The cross-correlation demonstrates that there was consistent temporal delay in M-F calling which was unaffected by Water Condition. Calls were answered in ˜200 ms (regardless of whether the male or female was answering). Additionally, there was no effect of water restriction on our estimate of turn-taking within a pair (% Markov Fit) (Water Condition: $\chi^2(1) = 3.03$, P = 0.081; Recording Nb: $\chi^2(1) = 0.07$, P = 0.789, Fig. 5B).

3.5. *WR has sex- and vocalisation-specific effects on acoustic structure*

3.5.1. *WR affects the acoustic parameters of song elements*

In order to describe the effect of Water Condition on the acoustic structure of songs, we used two complementary analyses. Using the full spectrum analysis, we found no effect of Water Condition on song elements, but some effects on individual notes and song syllables (Table 1). More specifically, for the last introductory note PC1 and PC3

Table 1
Effect of water restriction on the first three components of the full spectrum analysis and pre-defined acoustic parameters.

		Full Spectrum						Pre-defined acoustic parameters							
		Axis 1		Axis 2		Axis 3		RMS		Med (kHz)		SD (kHz)		IQR (kHZ)	
		ChiSq	P	ChiSq	P	ChiSq	P	ChiSq	P	ChiSq	P	ChiSq	P	ChiSq	P
Global Song Elements	Full Motif	0.02	0.891	0.25	0.615	0.72	0.397	2.90	0.088	3.03	0.082	0.15	0.696	0.33	0.565
	Partial Motif	0.07	0.791	0.10	0.757	0.05	0.827	**3.85**	**0.049**	0.16	0.689	0.07	0.798	**4.31**	**0.038**
		Q1: Is there evidence of any difference? **NO**						Q2: Are there acoustic differences in traditionally defined parameters? **Yon RMS and IQR in partial motifs**							
Individual Notes	First IN	0.07	0.798	1.26	0.261	0.12	0.726	0.48	0.487	0.26	0.609	0.22	0.641	3.47	0.063
	Last IN	**11.50**	**< 0.001**	2.46	0.117	**6.67**	**0.010**	**5.68**	**0.017**	0.51	0.477	1.71	0.191	0.36	0.546
	Early Song Syllable	2.36	0.125	1.71	0.191	**4.87**	**0.027**	3.08	0.080	1.11	0.293	2.14	0.143	**3.85**	**0.049**
	Late Song Syllable	1.26	0.261	2.17	0.141	0.27	0.605	0.05	0.831	2.50	0.114	2.78	0.096	0.79	0.373
		Q1: Is there evidence of any difference? **YES in the last introductory note and early song syllable**						Q2: Are there acoustic differences in traditionally defined parameters? **YES on RMS in the last introductory note and IQR in the early song syllable**							

Note: To assess the effect of water restriction on the acoustic structure of male song we used mixed linear models (e.g. lmer(*acoustic parameter* ˜ Water Condition + (1|Ind)). Because so few males sang, we only included water condition (not Recording nb) in these models. Bolded values indicate statistical significance ($P < 0.05$). DF = 1 for water condition.

Table 2

Effect of water restriction (Mean ± SEM) on pre-defined acoustic parameters of song.

		RMS		Med (kHz)		SD (kHz)		IQR (kHz)	
		CON	WR	CON	WR	CON	WR	CON	WR
Global Song Elements	Full Motif	6.15 ± 0.08	6.07 ± 0.16	3.76 ± 0.03	3.82 ± 0.04	1.67 ± 0.01	1.64 ± 0.01	2.41 ± 0.03	2.34 ± 0.04
	Partial Motif	**6.32 ± 0.22**	**6.42 ± 0.32**	3.80 ± 0.06	3.80 ± 0.08	1.74 ± 0.03	1.73 ± 0.03	**2.59 ± 0.07**	**2.55 ± 0.09**
Individual Notes	First IN	10.14 ± 0.68	9.22 ± 0.37	2.66 ± 0.09	3.10 ± 0.16	1.89 ± 0.03	1.92 ± 0.05	2.63 ± 0.13	3.09 ± 0.13
	Last IN	**10.41 ± 0.21**	**9.29 ± 0.41**	2.71 ± 0.08	3.06 ± 0.17	1.81 ± 0.04	1.94 ± 0.04	2.59 ± 0.13	2.93 ± 0.13
	Early Song Syllable	10.85 ± 0.29	9.78 ± 0.38	3.25 ± 0.06	3.25 ± 0.06	1.80 ± 0.04	1.87 ± 0.04	**2.6 ± 0.12**	**2.83 ± 0.11**
	Late Song Syllable	10.27 ± 0.24	10.89 ± 0.37	3.65 ± 0.06	3.79 ± 0.06	1.49 ± 0.02	1.49 ± 0.03	2.06 ± 0.07	2.83 ± 0.10

Note: Bolded values indicate statistical significance ($P < 0.05$).

were significantly affected by water restriction. Additionally, for the early song syllable PC3 was affected by Water Condition.

Consistent with the full spectrum analysis, we saw effects of Water Condition on pre-defined acoustic features. Again, there was no effect of Water Condition on full motifs (Table 1, Table 2). There was a significant effect of Water Condition on amplitude and interquartile-range (IQR) for partial motifs (IQR was lower during WR and RMS was higher: Tables 1, 2). Similar to our full spectrum analysis, we saw significant effects of Water Condition on the last introductory note and early song syllable (Table 1,Table 2). More specifically, the last introductory note was at a lower amplitude when produced during water restriction (Table 1, Table 2), and the early song syllable had an increased IQR (Table 1, Table 2).

3.5.2. Sex-specific effects of water restriction on the acoustic parameters of calls

As with song, we used two complementary analyses to examine the effect of Water Condition on the structure of calls (predominately short, stack-like calls). First, we conducted the full spectrum analysis on male and female of the calls together. There was a main effect of Water Condition on PC3 (Table 3). However, there was also a highly significant Water Condition × Sex interaction for PC2 and PC3 (Table 3). Therefore, we also ran the full spectrum analysis on female and male calls separately. From these results, we see a clear effect of Water Condition on both female calls (PC1, Table 3) and male calls (PC1 and PC2, Table 3).

To complement the full spectrum analysis, we also examined the effect of Water Condition on specific pre-defined acoustic features. For each of our acoustic parameters (RMS, median frequency, SD, and IQR), we found highly significant Water Condition × Sex interactions (Table 3 and Table 4). WR had different effects on males and females (Table 3). For female calls, WR decreased amplitude of calls (Tables 3, 4), but increased Median Frequency (Tables 3, 4), StDev (Tables 3, 4), and IQR (Tables 3, 4). In contrast, WR increased the amplitude of male calls (Tables 3, 4), while decreasing the Median Frequency (Tables 3, 4).

4. Discussion

There are widespread changes in both vocal production and auditory perception in seasonally-breeding species, which raise the question of whether auditory-vocal communication in opportunistically-breeding species is also affected by reproductive state and/or environmental condition. Our results suggest that zebra finch vocal production is affected by environmental condition. More specifically, we describe several effects of water restriction on male and female vocal behavior: water restriction (1) decreased the vocal activity of both males and females (calling and male song), (2) shifted the composition of male song so that it more closely resembled undirected song, and (3) influenced the acoustic structure of all vocalizations in sex- and vocalisation- specific ways which we discuss below. Based on previous research, we would anticipate that these changes are discriminable and could be salient to partners and other conspecifics. The fact that these effects are vocalization- and sex- specific raises interesting questions about how WR is impacting the acoustic structure of vocalizations. In addition to neuroendocrine changes associated with decreased breeding readiness, there may be context-specific changes in socio-sexual motivation in response to a poorer environmental conditions. Assuming that these are acoustic indicators of breeding readiness, this raises the question of whether such information is used by the partner and other conspecifics. In order to determine if these effects are specific to pair-directed behavior, it would be useful to identify the effects of water restriction on vocal dynamics for other social relationships and social conditions as well.

4.1. Effects of water restriction on vocal activity

Seasonally breeding bird species experience profound neural and vocal plasticity related to breeding season (Beecher and Brenowitz, 2005). In our current study, the decrease in vocal output is similar to the decrease in song output seen in temperate-breeding songbirds. This is not altogether surprising considering zebra finches have similar shifts in neuroendocrine state associated with breeding as do seasonally-breeding species. For zebra finches, changes in reproductive and/or breeding state are associated with changes in circulating steroid levels (Perfito et al., 2007; Prior et al., 2013; Gill et al., 2015; Prior et al., 2017), brain steroid levels (Prior et al., 2013), and nuclei volume for brain regions associated with song production (HVC and area X) (Perfito et al., 2015). While we did not see changes in circulating testosterone levels in males here, we did not measure other circulating or brain steroids. Furthermore, in zebra finches, as in seasonally-breeding birds, sex steroids can have significant effects on male song (Arnold, 1975; Prior et al., 2016). In temperate, seasonally-breeding species, the decrease in song output during non-breeding periods is generally assumed to be the result of changes in behavioral context and neuroendocrine condition, which together result in the absence of breeding-condition song signals. Similarly, we interpret the effect of water restriction on song output in male zebra finches to reflect the changes in neuroendocrine state induced by water restriction.

The relationship between calling behavior and singing is not well understood, and thus it is particularly interesting that we find evidence that water restriction decreases calling activity in addition to song. This effect could be interpreted as a decrease in (1) general vocal output, (2) attention or focus on the auditory channel, or (3) sociosexual motivation. There is evidence in zebra finches that the same brain nuclei in the song control system that regulate song, also regulate aspects of calling behavior (Ter Maat et al., 2014; Benichov et al., 2016). Therefore, it is possible that the effect of water restriction on specific brain regions could influence call and song output similarly. Another possibility is that the motivation to call and sing are related. The fact that water restriction did not impact the quality of calling exchanges between zebra finch mates suggests that water restriction did not have an impact on the quality of the pair bond and/or motivation to stay bonded. This is consistent with what is known about pair bonding in zebra finches

Table 3
Effect of water restriction, sex, and recording number on the first three components of the full spectrum analysis and pre-defined acoustic parameters.

		Full Spectrum						Pre-defined acoustic parameters							
		Axis 1		Axis 2		Axis 3		RMS		Med (kHz)		SD (kHz)		IQR (kHZ)	
	Factor	ChiSq	P	ChiSq	P	ChiSq	P	ChiSq	P	ChiSq	P	ChiSq	P	ChiSq	P
All Calls	Water Cond	0.31	0.577	0.61	0.435	**11.93**	**< 0.001**	2.13	0.144	**13.21**	**< 0.001**	1.20	0.273	**13.74**	**< 0.001**
	Sex	2.38	0.123	2.80	0.094	0.95	0.331	0.06	0.803	0.04	0.847	0.74	0.390	0.69	0.407
	Record. Nb	0.93	0.334	**9.72**	**0.002**	2.11	0.146	**7.58**	**0.006**	**28.30**	**< 0.001**	1.98	0.160	**0.02**	**0.884**
	Water Cond:Sex	3.36	0.059	**5.58**	**< 0.001**	**13.93**	**< 0.001**	**73.00**	**< 0.001**	**112.10**	**< 0.001**	**11.40**	**< 0.001**	**26.90**	**< 0.001**
		Q1: Is there evidence of any acoustic difference? **YES affecting female and male calls differently**						Q2: Are there acoustic differences in traditionally defined parameters? **YES (for all four parameters there is a Water Condition X Sex interaction)**							
Female Calls	Water Cond	**14.68**	**< 0.001**	0.92	0.338	0.03	0.854	**52.42**	**< 0.001**	**121.90**	**< 0.001**	**12.10**	**< 0.001**	**44.61**	**< 0.001**
	Record. Nb	**55.97**	**< 0.001**	1.67	0.196	0.007	0.935	**21.80**	**< 0.001**	**46.80**	**< 0.001**	**7.73**	**< 0.001**	1.78	0.180
		Q1: Is there evidence of any acoustic difference? **YES**						Q2: Are there acoustic differences in traditionally defined parameters? **YES (all four parameters)**							
Male Calls	Water Cond	**4.91**	**0.027**	**4.98**	**0.026**	1.70	0.195	**30.36**	**< 0.001**	**24.74**	**< 0.001**	3.15	0.080	1.41	0.236
	Record. Nb	**11.16**	**< 0.001**	**7.64**	**0.006**	**7.23**	**0.007**	0.80	0.371	1.07	0.301	0.37	0.542	2.11	0.150
		Q1: Is there evidence of any acoustic difference? **YES**						Q2: Are there acoustic differences in traditionally defined parameters? **YES (RMS and median freq)**							

Note: To assess the effect of water restriction on the acoustic structure of calls we used mixed linear models (e.g. ALL CALLS: lmer(*acoustic parameter* ˜ Water Condition*Sex + scale(Recording nb) + (1|Ind). CALLS BY SEX: lmer(*acoustic parameter* ˜ Water Condition + scale(Recording nb) + (1|Ind)). Bolded values indicate statistical significance ($P < 0.05$). DF = 1 for water condition, sex and recording number.

(Zann, 1996; Prior and Soma, 2015). In this study, we chose to examine behavior under a relatively controlled social context (visual separation) and to focus on pair-bonded birds. Therefore, it is unclear to what extent this effect of water restriction would extend to vocal behavior in other social contexts. In seasonally-breeding song sparrows, for example, there is a decrease in song output in the winter, yet males sing at the same rate during simulated territorial intrusions (Maddison et al., 2012). In zebra finches, which are non-territorial and form life-long pair bonds, it would be particularly interesting to determine whether calling activity is similarly affected by water restriction within other social relationships (e.g. familiar and novel birds) and social contexts (e.g. traveling, foraging, etc).

4.2. Effect of water restriction on acoustic structure

Several lines of more recent research have described plasticity in the acoustic structure of calls depending on ontogeny (Villain et al., 2015), social context (Hile and Striedter, 2000), and internal physiological state (Perez et al., 2012, 2015a; Perez et al., 2016). Based on our current knowledge of zebra finch perception, we have every reason to expect that zebra finches can hear very small differences in the acoustic structure of their harmonic calls. Amongst birds, zebra finches are particularly sensitive to small spectro-temporal changes in harmonic complexes (Lohr and Dooling, 1998; Dooling et al., 2002; Dooling and Lohr, 2006; Lohr et al., 2006; Prior et al., 2018), therefore, while the effects of water restriction that we report here are small (e.g. 100 hz in median frequency), it is reasonable to assume these small differences would be perceptible to zebra finches.

One of the simplest explanations for seasonal plasticity in acoustic structure is that this plasticity is due to changes in syrinx size mediated by circulating testosterone levels. However, the differences we report are unlikely to be related to shifts in syrinx size. First, we did not see changes in circulating testosterone levels. Furthermore, we would expect that changes in syrinx volume would result in a change in fundamental frequency across the entire song (Cynx et al., 2005; Alward et al., 2016). Alternatively, changes in brain sex steroid levels alone within key nuclei of the song control system can impact spectral features of song syllables (Alward et al., 2017a,b). It is likely that zebra finches experience significant changes in brain steroid levels independent of peripheral changes (Prior et al., 2013), and it is possible, although it has not been tested, that there are also effects of WR on other neuromodulatory systems as well as sex steroid receptors which could explain these results. Here we only looked at stack-like calls and male song, thus it is unclear if these changes in acoustic structure extend across call types. Regardless of the mechanism, the changes in acoustic structure could serve as a functional cue of reproductive condition.

4.3. Functional significance of call flexibility

It may seem surprising that the effect of water restriction on calls differed between males and females. The results of our full spectrum analysis suggest that WR has a significant effect on both male and female calls. However, for each of our pre-defined acoustic features, the effect of water restriction was in the opposite direction for males and females. Water-restricted female calls were lower amplitude, higher frequency (median frequency) and more variable (standard deviation and inter-quartile range). In contrast, water-restricted male calls were higher amplitude and had a lower frequency (median frequency). From an ecological perspective, it makes sense that females may be more sensitive to environmental perturbations (Perfito, 2010; Prior et al., 2013), and it is possible that female reproductive condition may be a bottleneck on the timing of breeding bouts. Furthermore, water restriction has a more profound effect in females, including significantly reducing the size of the female ovary and oviduct. In contrast, water restriction has only a small effect on male testis size (Prior et al., 2013;

Table 4
Effect of water restriction (Mean ± SEM) on pre-defined frequency parameters of male and female calls.

	RMS		Med (kHz)		SD (kHz)		IQR (kHZ)	
	CON	WR	CON	WR	CON	WR	CON	WR
Female Calls	**10.31 ± 0.05**	**9.91 ± 0.06**	**3.03 ± 0.01**	**3.15 ± 0.01**	**1.82 ± 0.005**	**1.83 ± 0.005**	**2.56 ± 0.02**	**2.69 ± 0.02**
Male Calls	**10.01 ± 0.05**	**10.44 ± 0.06**	**3.12 ± 0.03**	**3.02 ± 0.01**	1.86 ± 0.005	1.85 ± 0.005	2.73 ± 0.02	2.70 ± 0.02

Note: Bolded values indicate statistical difference ($P < 0.05$) between CON and WR conditions.

Perfito et al., 2006). In the current study, the effects of water restriction on male song suggest that there was a shift in the central neuroendocrine state. Thus, one interpretation of the sex differences in the effect of water restriction on calls is that water restriction had differing effects on the neuroendocrine state of males and females. Further research describing the effect of water restriction and reproductive readiness on vocal dynamics across social conditions and contexts would help clarify what functional relevance this difference may have.

Importantly, the stack-like call that we investigated here is not specific to nesting periods (Gill et al., 2015). Thus, regardless of the mechanisms resulting in changes in acoustic structure, we would expect that environmental and/or reproductive condition-dependent flexibility in stack-like calls would precede other early breeding behaviors such as identifying a nesting site and building a nest. This raises the hypothesis that such vocal flexibility could play a functional role in coordinating partners' breeding attempts.

4.4. Functional significance of the effect of water restriction on male song

This is not the first report suggesting that breeding condition affects male song in zebra finches. Previous paradigms using water restriction have reported similar decreases. In Prior et al., 2013 we did not find a statistically significant effect of water restriction on male song during a partner separation and reunion paradigm; however, qualitatively males did spend less time singing. Additionally, Rashotte et al. (2001) also reported a significant effect of brief (2 day) water deprivation on song output.

Beyond just a decrease in overall song output, we might also expect a change in the type of song and/or performance. Zebra finches produce two types of song, directed and undirected, which are composed of the same stereotyped motif but differ in more subtle aspects such as the number of introductory notes and overall stereotypy of the performance (Sossinka and Böhner, 1980). Performances of directed song, or courtship song, involve the male facing the female and often involve other aspects of courtship dance (Zann, 1996). In contrast, undirected song can be performed anywhere, and the male appears to be singing to himself (Zann, 1996). In our current experiment, these pairs were always visually isolated. Therefore, all song produced under this behavioral paradigm would technically be classified as undirected song. However, taken together, the effects of water restriction on song that we report here are broadly consistent with a shift from directed to undirected song. More specifically, water restriction increased the intersequence interval and the proportion of introductory notes as might be expected if there were a shift from directed to undirected song (Woolley and Doupe, 2008; Rajan and Doupe, 2013). Additionally, our full spectrum analysis revealed that water restriction had the most profound effect on the last introductory note and the early song syllable, again similar to what could be expected from undirected song (Rajan and Doupe, 2013).

A key difference between undirected and directed song is the motivational state of the male. Importantly, we may predict that male zebra finches would experience a similar shift in motivational state (away from courtship/breeding behaviors) following water restriction. Together these results raise the hypothesis that the changes in song are related to shifts in sexual motivation following a reduced state of breeding readiness.

5. Conclusion

Our current results contribute to several lines of evidence suggesting that there are widespread seasonal changes in audio-vocal communication (Catchpole and Slater, 2008; Bass et al., 2016). Our work supports the notion that this vocal plasticity extends to non-seasonally-breeding species as well as to calling behavior. Furthermore, as our data suggests there is vocal plasticity in response to environmental conditions, this raises the question of whether information on breeding state is present within zebra finch vocalisations and how zebra finches may use this information to coordinate breeding attempts.

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Ethical approval

This work was conducted in accordance with the French and European animal care legislation under authorization number 42-218-0901-38 SV 09 (ENES Lab, Direction Départementale des Services Vétérinaires de la Loire).

Informed consent

Not applicable.

Conflict of interest

The authors have no conflict of interest to declare.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2019.02.007.

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