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## Stress-induced flexibility and individuality in female and male zebra finch distance calls

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### ABSTRACT

Vocal recognition is central to the coordination and organization of behavior in pair-bonding species such as zebra finches. Zebra finches' vocalizations are individualized and support acoustic discrimination processes. Physiological states - such as the ones involved in emotional stress - can modify vocal production and consequently the structure of vocalizations. These modifications might signal the state of the caller but also impair individual recognition processes. This may represent a signaling trade-off, especially in contexts where both pieces of information can be critically important, for example when mates use calls to reunite after social isolation. Here we study the impact of a stress on the individual vocal signature in both female and male zebra finch distance calls.

We built a manually curated database of distance calls of several individuals (both females and males) recorded in control and stress conditions. The stress was induced either by social isolation of the bird or using exogenous corticosterone. We developed a machine learning approach to assess the impact of stress on the individual characterization of calls.

We show that while calls' spectral structure is significantly modified by stress, it still allows for the correct classification of calls to the caller. Moreover, we also show that the stress-induced modification of calls' structure is not a 'general feature signal' that can be detected as a 'stress' signal regardless of identity. Thus, female and male zebra finch calls' structure show stress-induced flexibility that stays within the range of individual vocal signatures.

### 1. Introduction

Vocal recognition or discrimination is central to the coordination and organization of behavior in many social species. The acoustic structure of vocalizations may inform conspecifics on a caller's species, sex, group membership, relatedness or individual identity (Bradbury and Vehrencamp, 2011; Marler and Slabbekoorn, 2004). To allow efficient discrimination, vocalizations must bear stable acoustic signatures (Beecher, 1989). For instance, individualized features of vocalizations make individual vocal recognition possible (e.g. Aubin and Jouventin, 1998, Bee and Gerhardt, 2002; Charrier et al., 2001; Janik et al., 2006; Jouventin and Aubin, 2002; Mathevon et al., 2008).

Beside stable information on the caller, vocalizations may also bear labile and transient pieces of information, like context, motivation or emotion (Morton, 1977, Manser, 2001; Briefer, 2012). Such temporary information can be detected in modifications of the temporal pattern of

calling behavior: as e.g. in birds (Kilner and Johnstone, 1997) and frogs (Tobias et al., 2004). Instantaneous information can also be expressed in changes in the vocalization units using for instance call type variations like in the great gerbil (Randall and Rogovin, 2002) or acoustic structure variations as in white-browed scrubwren (Leavesley and Magrath, 2005).

Both types of information, stable and transient, may be encoded in different categories of vocalizations: besides their species-specific and individualized songs, many small passerine species share the 'seet hawk alarm call' in response to a bird of prey in flight, a high-pitched and narrow band pure tone (Marler, 2004). But the two categories of information, stable and transient, can also be encoded in the same vocalizations see for examples African elephants (Soltis et al., 2005), domestic dogs (Yin and McCowan, 2004) or meerkats (Schibler and Manser, 2007). If one vocalization transmits information pertaining to multiple pieces of information, those can still be encoded in different

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parameters (segregation hypothesis, Marler). For example, in mongoose the segregation is temporal and within the syllable (Jansen et al., 2012) whereas in baboons it is both in tempo and spectral structure (Rendall, 2003).

Stable and transient pieces of information can also be coded in the same sets of parameters of the vocalization, and in that case there might be a trade-off in the signal's reliability, with one component more accurately communicated than the other (trade-off hypothesis, Briefer et al., 2010). In fallow deer (*Dama dama*), some acoustic features of the groans code for both individual identity and phenotypic quality (age and dominance status), so vocal cues coding for individuality change over years and information about quality is more reliable than identity (Briefer et al., 2010).

This signaling trade-off might be particularly stringent when both pieces of information can be critically important to the receiver. In zebra finches (*Taeniopygia guttata*), birds from life-long pair-bonds and mated partners have highly synchronized activities (Zann, 1996; Mariette and Griffith, 2012). When mates lose visual contact or reunite after a separation, they exchange distance calls, which are highly individualized harmonic stacks (Elie and Theunissen, 2016; Forstmeier et al., 2009; Mouterde et al., 2015) and allow mate discrimination (Vignal et al., 2004, 2008; Hernandez et al., 2016). These calls can also convey information on the physiological stress of the caller: calls produced in social isolation (a stressful situation of negative valence in this species (Remage-Healey et al., 2003; Banerjee and Adkins-Regan, 2011)) or after experimental corticosterone elevation show specific structural changes (Perez et al., 2012). Moreover, these stress-induced calls promote emotional contagion in mates, as females show increased corticosterone levels after hearing the stressed calls of their mate, and not after hearing the stressed calls of another male (Perez et al., 2015). In an operant discrimination task, females grouped the stressed calls and the control calls of the same male in the same category (Perez et al., 2015).

Zebra finch distance calls seem to reliably convey both individual identity and stress, defined here as an emotion of high arousal and negative valence (Briefer, 2012). But how do these two pieces of information impact each other? Does stress modify all individuals' calls the same way, making it a universal superimposed feature allowing any listener to detect stress in the calls of any caller (universality hypothesis)? Or do stress modifications of call structure stay within the caller's acoustic features space, so it is possible only for a familiar listener to detect stress in the vocalizations of a caller (familiarity hypothesis)?

To test these hypotheses, we built a manually curated database of distance calls of female and male zebra finches recorded in control and stress conditions. The stress was induced either by social isolation or by experimental increase of corticosterone (oral ingestion). We developed a machine learning approach using random forests to assess the impact of a stress on the individual vocal signature in both female and male calls.

## 2. Material and methods

### 2.1. Dataset

We used recordings of zebra finch distance calls from 4 different experiments (described in Table 1). For the purpose of this article all

vocalizations have been pooled and no distinction of the origin of the data has been made. However, all recordings were made using bird from the same aviary - similar housing conditions, daylight cycles and food type and quantities - in addition to similar recording rooms and apparatus. The total number of calls was 1780 control calls (53%) 1548 stress calls (44%) spanning 57 different individuals (see Table 1 for summary).

Most control calls were elicited using a playback of opposite sex calls (female calls for male subjects, male calls for female subjects) and in the presence of an audience of 2 other birds (dataset 1, 2 & 4, see Perez et al. (2012) for details on protocol) with exception for dataset 3 where the stimulus was a physical and visual separation but within hearing distance from partner (see Perez et al. (2015) for details on protocol). The stress condition was either obtained via social isolation (dataset 1, 2 & 4) or after exogenous corticosterone (CORT) ingestion (dataset 3) (see Perez et al. (2012) for details on protocol).

### 2.2. Data pre-processing - duration extraction

Calls were separated wave files (16bit 44.1 kHz sampling mono-channel) that were processed automatically using custom software written in Python. The first step of pre-processing was to compute the amplitude using the spectrograms, which were obtained using an FFT with frequency band of 125 Hz using a Gaussian Filtering. The temporal sampling frequency was set at 1 kHz. Within each wave file, the maximum amplitude time was extracted and a call was defined as the interval around the maximum amplitude time such that the amplitude within this interval remained 10% of the maximum amplitude. This processing allows us to extract a call reliably within a recording by obtaining the same amplitude variation. This also yields a reproducible call length independent of the recording levels defining the duration of the calls.

### 2.3. Spectrogram matrix

For this analysis, the spectrogram of a call will be viewed as a matrix of acoustic parameters. In order to compare those matrices between calls, we needed to standardize their sizes across the entire dataset. To do so, we first find the longest call of the dataset, which then sets the duration reference. We compute the spectrogram of each call for the same duration as this reference duration by padding with zeros (both in time and frequency) to obtain matrices with identical dimension for every calls (shorted calls were centered). Finally, we selected a frequency band - between 200 Hz and 8 kHz as it contained most of the spectral information for calls and ignored spectral information beyond that interval. In this dataset, the longest call was 888 ms long and the frequency band had 59 points. So each call of the dataset has been described as a series of 59\*888 values (parameters) corresponding to its full spectrogram. The so-called spectrogram matrix data which will contain the spectrogram values of all the calls of the dataset is a matrix of 3328 lines (the number of calls) and 52392 columns (59 \* 888 the spec). We reduced the dimensionality of this matrix data by using a principal component analysis (PCA). We kept the 20 first components to obtain a SPEC matrix data of 3328 lines and 20 columns (similar to the technique used in Mouterde et al., 2015).

**Table 1**

Dataset summary.

Set	Sex	# Ind	Stimulus	Control	# Control calls	Stress	# Stress calls
1	F	25	Playback	Audience	528	Isolation	490
2	M	15	Playback	Audience	423	Isolation or Audience + Exogenous CORT	456
3	M	11	Separation	Acoustic contact with partner	677	Acoustic contact with partner + Exogenous CORT	410
4	M	6	Playback	Audience	152	Isolation	192
Total		57			1780		1548

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