Quantifying parameters of bottlenose dolphin signature whistles

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Bottlenose dolphins (*Tursiops truncatus*) produce individually distinctive vocalizations called signature whistles, first described by Melba and David Caldwell (1965). The Caldwells observed that isolated, captive dolphins produced whistles with individually distinctive frequency contours, or patterns of frequency changes over time, and hypothesized that these whistles were used to transmit identity information (Caldwell and Caldwell 1965; Caldwell *et al.* 1990). Since the Caldwell's work with isolated, captive dolphins, several studies have documented signature whistles in a variety of contexts, including free-swimming captive dolphins (*e.g.*, Janik and Slater 1998; Tyack 1986), briefly restrained wild dolphins (*e.g.*, Sayigh *et al.* 1990, 2007, Watwood *et al.* 2005), and free-ranging wild dolphins (*e.g.*, Watwood 2003; Watwood *et al.* 2004, 2005; Buckstaff 2004; Cook *et al.* 2004). Janik and Slater (1998) demonstrated that signature whistles are used to maintain group cohesion, thus supporting the Caldwells' hypothesis. Janik et al. (2006) verified experimentally that bottlenose dolphins respond to signature whistles produced by familiar conspecifics even after voice featured have been removed, reinforcing the notion that the contour of a signature whistle carries identity information.

Signature whistle parameters vary by age (Caldwell *et al.* 1990; Esch *et al.* in press), sex (Sayigh *et al.* 1995, Esch *et al.* in press), and context (Caldwell *et al.* 1990; Janik *et al.* 1994; Watwood *et al.* 2005; Esch *et al.* in press). Young dolphins (both male and female) have higher signature whistle rates than adults, but whistle rate decreases more quickly with age in males than females (Caldwell *et al.* 1990, Esch *et al.* in press). Adult dolphins produce more loops per whistle (and therefore longer whistles) than infants and sub-adults (Caldwell *et al.* 1990). Caldwell *et al.* (1990) found that certain parameters of signature whistles (*e.g.*, frequency, number of loops and duration of loops) appeared to be closely related to the level of arousal of an individual dolphin; however, these differences were not consistent across individuals. Esch *et al.* (in press) found that whistle rate and the number of loops produced per whistle varied by context, and hypothesized that increases in these whistle parameters may be indicative of stress in bottlenose dolphins. Similarly, Janik *et al.* (1994) found that 9 of 14 signature whistle frequency and time parameters differed significantly between isolation and interaction conditions, supporting the existence of both identity and context related information in signature whistles. However, despite this variability in an individual dolphin's signature whistle parameters, the overall contour usually remains highly stereotyped for at least a decade (Caldwell *et al.* 1990; Sayigh et al. 1990; Janik and Slater 1994; Esch et al. in press).

As described above, signature whistles may consist of a single element (or loop; *e.g.*, FB24, FB35, Figure 1), or variable numbers of repeated loops, which may or may not be connected (*e.g.*, connected, FB20, FB118; disconnected, FB138, FB220, Figure 1). Some multi-looped whistles also contain an introductory and/or terminal loop, which differ in contour from the central loops (*e.g.*, FB48, FB97, Figure 1; Caldwell *et al.* 1973, 1990, Sayigh *et al.* 1990). For whistles with multiple disconnected loops some studies have considered each loop repetition as a separate whistle (*e.g.,* Schevill and Watkins 1962; Tavolga 1968; McCowan and Reiss 2001), while others have distinguished loops from whistles (*e.g.,* Caldwell *et al.* 1973, 1990, Sayigh *et al.* 1990, 2007; Buckstaff 2004;

Watwood 2003; Watwood et al. 2005; Esch et al. in press). In the present study, we hypothesized that loops are separated by highly stereotyped time intervals, and that stereotyped loops and silences between loops both play a part in the production of a unique signal (based on Caldwell *et al.* 1990). The presence of an introductory and/or terminal loop (*e.g.*, Figure 1: FB25, FB48, FB54, FB84, FB97, and FB220) supports the idea that multiple disconnected loops should be considered part of the same unit if separated by stereotyped silences (Caldwell *et al.* 1973, 1990). It is important that studies of dolphin communication are consistent in how multi-looped whistles are treated; otherwise studies that include this type of signal are difficult to compare. Thus, a goal of this study was to quantify inter-loop intervals in stereotyped sequences of disconnected loops, in order to test the hypothesis that these intervals are shorter and more consistent (less variable) than are the intervals between successive whistles.

A second goal of this study was to quantify the acoustic parameters of signature whistles (especially maximum frequency, but measurements were also made of minimum frequency, and overall duration) to update the documented ranges of these values. Many studies of dolphin signature whistles utilized recording equipment with upper frequency cut-offs at or below 24 kHz, and were thus unable to measure higher frequencies (*e.g.*, Azevedo and Oliveira 2007, Dreher 1961, Evans and Prescott 1962, Sayigh *et al.* 1990, Steiner 1981, Tyack 1986, Wang *et al.* 1995). Currently, the value of 24 kHz reported by Caldwell et al. (1990) is the highest maximum frequency for signature whistles in the literature. We report values for the fundamental frequency of signature whistles and do not include harmonics or other types of vocalizations (*e.g*., echolocation).

Recordings of long-term resident bottlenose dolphins from brief capture-release events in Sarasota Bay, Florida (Scott *et al.* 1990; Wells 1991, 2003; Wells *et al.* 2004), have been collected over a period of 34 years (1975-2008), and many dolphins have been recorded multiple times (maximum = 15, mean = 3.3). Custom-built suction cup hydrophones were placed directly on the head of each individual, allowing researchers to unequivocally identify the vocalizing dolphin. The hydrophones were developed and built at the Woods Hole Oceanographic Institution (WHOI; circuitry described in Tyack 1985), and were equipped with 1-2 kHz high-pass filters, above which their frequency response was flat to 25 kHz. The hydrophones were not calibrated because amplitude values were not being measured. Whistles were recorded onto either Marantz PMD-430 or Sony TC-D5M stereo-cassette recorders (frequency response »30-20000 Hz, digitization sampling rate 96 kHz, 24bit), Panasonic AG-6400 or AG-7400 video-cassette recorders (frequency response »20-32000 Hz, digitization sampling rate 96 kHz, 24bit), or a Sound Devices 744-T digital recorder (frequency response 10-48000 Hz, sampling rate 96 kHz, 24 bit). The predominant whistle produced by an animal during a brief capture-release event is defined as its signature whistle. Other whistles produced during these recording sessions are called non-signature whistles. The Sarasota Dolphin Community Signature Whistle Catalogue (Sayigh, unpublished data) currently contains signature whistles from 205 dolphins. Since most dolphins in Sarasota Bay have been captured and released more than once, signature whistle identifications for all dolphins included in this study have been confirmed by reviewing multiple recordings for an individual animal.

Twenty whistles produced by each of 28 different dolphins (12 male, 16 female) were randomly selected from all whistles produced by an individual dolphin in a single recording session during brief capture-release events between 1988 and 2001 in Sarasota Bay, FL. These randomly selected whistles were primarily signatures, but in some cases non-signatures were selected. Dolphins were chosen so a variety of different types of signature whistle were represented, including:

1. Loops sometimes connected, sometimes not; may vary in number and/or contour (4 of 28 dolphins; *e.g.*, FB146, FB151, FB166, FB186, Figure 1);
2. Loops always disconnected, may vary in number and/or contour (14 of 28 dolphins; *e.g.*, FB7, FB9, FB11, FB25, FB38, FB48, FB54, FB55, FB84, FB90, FB97, FB101, FB138, FB220. Figure 1);
3. Loops always connected, may vary in number and/or contour (8 of 28 dolphins; *e.g.*, FB3, FB20, FB67, FB105, FB118, FB122, FB140, FB163, Figure 1);
4. No repetitive loop structure (2 of 28 dolphins; *e.g.*, FB24, FB35, Figure 1). In the recording library of 205 dolphins used as a resource in this study, the four whistle types listed above were represented as follows: type 1, 4.3%, type 2, 39.9%, type 3, 33.7%, and type 4, 22.1%.

A continuous whistle was classified as multi-looped (*i.e.*, consisting of multiple connected repeated elements) based on previous visual classification of a large dataset of whistles by human judges (Sayigh *et al.* 2007). To develop a criterion for classifying whistle elements as disconnected loops or as separate whistles, inter-element intervals were measured during 30 min of a recording for each of 5 dolphins (FB2, FB15, FB33, FB38, FB101). None of these recordings were included in the data set used for later analyses. The mean number of whistle elements in these recordings was 461 ± 315. Individual elements were assigned to a single whistle *(i.e.*, a whistle with multiple disconnected loops) using the criterion defined by Janik and Slater (1998): elements separated by 0.5 seconds or less were considered loops in a single whistle. Whistle classification using this criterion agreed with visual classification in all cases (Table 1); therefore, this criterion (*i.e.*, elements that occurred within 0.5 sec of each other) was used to classify whistle elements as loops *vs*. separate whistles in the current study.

When possible, a single recording session for each dolphin was analyzed utilizing Signal/RTSD (Version 3.0, Engineering Design, Belmont, MA) or Avisoft-SASLab Pro 3.2 (Raimund Specht, Berlin, Germany), which are software packages that display real-time spectrograms. Every whistle produced during the chosen recording session was noted and numbered, with a minimum sample size of 200 whistles for each dolphin. In six cases, 200 whistles did not occur in the recording session chosen. In these cases, an additional session was also analyzed in order to reach a minimum of 200 whistles. Sample sizes ranged from 201 to 2,144 whistles per dolphin (mean = 308 ± 416). A table of 20 random numbers was generated (in Microsoft Excel) for each dolphin, based on its total quantity of whistles. These 20 randomly selected whistles were then subjected to further analyses. For six dolphins in this study, non-signature whistles were present in the random sample; however, parameter measurements for signature and non-signature whistles are presented separately. Only signature whistles were included in inter-loop and inter-whistle interval comparisons.

Inter-loop intervals can be distinguished from inter-whistle intervals on the basis of significant differences in duration and variability. Inter-loop intervals in stereotyped sequences of disconnected loops were significantly shorter (Table 2, mean inter-loop interval = 0.10 s, mean inter-whistle interval = 17.1 s; paired t-test, df = 15, $P = 0.01$) and less variable (F-test, Table 2) than intervals between successive whistles. Standard deviations ranged from 0.01 to 0.06 sec for inter-loop intervals versus 1.74 to 163.17 s for inter-whistle intervals. Coefficients of variation (CV, calculated as the ratio of standard deviation to the mean) ranged from 0.09 to 0.77 for inter-loop intervals versus 0.63 to 2.34 for inter-whistle intervals. Inter-loop interval values were more normally distributed while inter-whistle interval values were logarithmically distributed (Figure 2 a, b). This difference should be even more pronounced in contexts other than capture-release, when whistle rates are much lower (*i.e.*, inter-whistle intervals are longer; Esch *et al.* in press). These different distributions and resulting difference in variances between the two groups support the conclusion that inter-loop intervals are significantly less variable than inter-whistle intervals, and may be an important component of signature whistle stereotypy.

Means, standard deviations, and CV values for frequency maxima and minima, and duration of each dolphin's signature whistle are presented in Table 3. Values for the 12 non-signature whistles included in the random sample are also shown. Mean maximum frequencies for signature whistles ranged from 9.3 to 27.3 kHz, with the latter exceeding the published upper range for bottlenose dolphin signature whistles (24 kHz, Caldwell *et al.* 1990; 17.8 kHz, Janik et al. 1994; 23.48 kHz, Buckstaff 2004). Mean minimum frequencies for signature whistles ranged from 3 to 13.3 kHz, and durations ranged from 0.5 – 2.3 s, similar to values reported in other studies.

These results indicate that signature whistles have a greater range of frequencies than was previously reported, due to the increased maximum frequency value presented here. Variability in maximum or minimum frequencies may be caused by an introductory or terminal loop, such as a final upsweep or downsweep that tails off at a different frequency from one whistle to another (*e.g.*, FB48, FB54, FB97, FB105, Figure 1). Coefficients of variation were often higher for dolphins that produced signature whistles with a variable introductory or terminal loop (Figure 1, Table 3, FB48, FB54, FB97, FB105). While several dolphins showed higher CV values for maximum than minimum frequency (Table 3, FB25, FB105), others showed the reverse pattern (Table 3, FB55, FB90, FB122). Thus, perhaps one frequency parameter (maximum or minimum) plays a more consistent role in signature whistle stereotypy in a given individual.

Bottlenose dolphin whistle parameters have been reported in multiple studies, although few studies distinguish between signature and non-signature whistles. With the exception of maximum frequency, our findings fall within previously published ranges. Caldwell et al. (1990) reported maximum frequencies for bottlenose dolphin signature whistles ranging from 8 – 24 kHz, with minimum frequencies ranging from 1 – 9 kHz. Signature whistle duration ranged from 0.2 – 2.1 s (Caldwell et al. 1990). Janik et al. (1994) documented signature whistle parameters for a single captive bottlenose dolphin in multiple contexts (minimum frequency: 4 kHz, maximum frequency: 17.8 kHz, duration range: 0.13 - 0.18 s). Buckstaff (2004) reported signature whistle parameters for dolphins in Sarasota Bay, Florida, as part of a study on the effects of watercraft activity on acoustic behavior (frequency range: 2.91 – 23.48 kHz, duration range: 0.10 – 4.11 s). Wang et al. (1995) determined whistle (combined signature and non-signature) parameters for bottlenose dolphins in Argentina, reporting frequencies ranging from 1.17 – 21.6 kHz, and a mean duration of 1.14 s. Azevedo and Oliviero (2007) documented characteristics of whistles from a resident population of bottlenose dolphins in southern Brazil (minimum frequency range: 1.2 – 17.2 kHz, maximum frequency range: 3.6 – 22.3 kHz, duration range: 0.048 – 2.458 s). Finally, in a recent study of geographic variation in bottlenose dolphin whistles (combined signature and non-signature), May-Collado and Wartzok (2008) provide an extensive review of whistle parameters for bottlenose dolphins in the Atlantic (minimum frequency range: 1.6 kHz – 18.92 kHz, maximum frequency range: 1.7 kHz – 28.48 kHz, duration range: 0.005 – 1.3 s). May-Collado and Wartzok (2008) report a higher maximum frequency than our study; however, our study focuses only on signature whistles while May-Collado and Wartzok (2008) do not distinguish among whistle types. Therefore, our study is the first to extend the frequency range of signature whistles above 24 kHz.

Caldwell et al. (1990) were the first to suggest that “rather than repeating a constant section of whistle, dolphins[s] [may] repeat both a section of whistle and an interval of silence”, and that those intervals may be highly consistent (although inter-loop interval values were not presented in their study). Our results indicate that inter-loop intervals can be quantitatively distinguished from inter-whistle intervals, and that inter-loop durations are much more consistent than inter-whistle durations for dolphins that produced multiple disconnected loops. While variations in frequency contour provide one mechanism for creating an individually distinctive whistle, the possible conformations are finite. For whistles with multiple disconnected loops, the stereotyped silence between loops may serve as another characteristic by which individual dolphins can distinguish themselves uniquely. In addition, the presence of a characteristic introductory or terminal loop in some signature whistles implies that the series of elements is produced as a punctuated unit. The results of this study indicate that it is appropriate to consider these loops as components of a single whistle, rather than as separate whistles.

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Figure and Table legends

Figure 1. Spectrograms of the signature whistle for each of 28 dolphins. Frequency (kHz) is on the y-axis and time (s) is on the x-axis. Identical time and frequency scaling was used among all signature whistle exemplars.

Figure 2 (a, b). Inter-loop (n = 521) and inter-whistle (n = 290) interval distributions. Intervals are shown in seconds (note different scales).

Table 1. Results of transition matrix (TM) and visual classifications (VC) of disconnected element whistle membership.

Table 2. Mean ± SD (CV) inter-loop and inter-whistle durations(s) for each dolphin. CV values were calculated as the ratio of the SD to the mean. F-tests comparing inter-loop and inter-whistle variance values were all significant at $P < 0.001$.

Table 3. Means, standard deviations (SD), and coefficients of variation (CV) for 20 whistles from each of the 28 dolphins. Non-signature whistle values are shown for six dolphins for which the 20 randomly selected whistles included non-signature whistles (*).

Animal	# of elements	# of whistles: TM	# of whistles: VC
FB2	862	442	442
FB15	641	319	319
FB33	396	137	137
FB38	64	28	28
FB101	340	147	147

Table 1

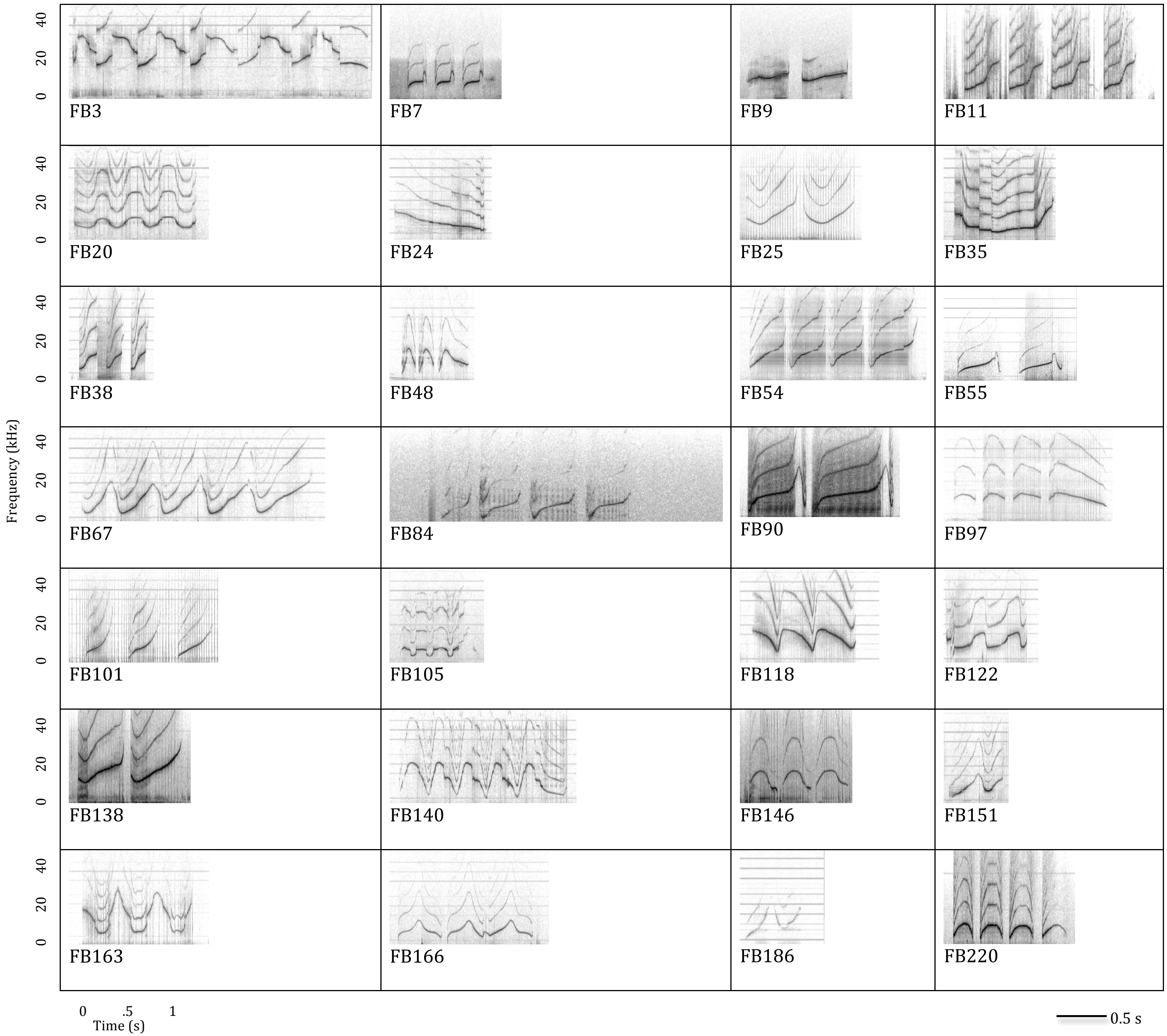
Animal	Inter-loop duration ± SD (CV)	Inter-whistle duration ± SD (CV)	F
FB7	0.12 ± 0.01 (0.09)	15.40 ± 12.21 (0.79)	$1.4x10^{6}$
FB9	0.13 ± 0.04 (0.31)	8.09 ± 10.96 (1.35)	$7.5x10^{4}$
FB11	0.07 ± 0.02 (0.31)	8.14 ± 11.02 (1.35)	$3.0x10^{4}$
FB25	0.07 ± 0.02 (0.30)	6.28 ± 14.91 (2.26)	$5.2x10^{4}$
FB38	0.09 ± 0.01 (0.11)	10.76 ± 10.97 (0.98)	$1.2x10^{6}$
FB48	0.05 ± 0.01 (0.19)	29.33 ± 26.15 (0.89)	$6.8x10^{6}$
FB54	0.09 ± 0.04 (0.46)	35.08 ± 60.49 (1.72)	2.3x106
FB55	0.19 ± 0.03 (0.14)	13.63 ± 14.31 (1.05)	$2.3x10^{5}$
FB84	0.11 ± 0.01 (0.12)	107.24 ± 163.17 (1.52)	$2.7x10^{8}$
FB90	0.10 ± 0.03 (0.27)	6.34 ± 6.99 (1.10)	$5.4x10^{4}$
FB97	0.07 ± 0.01 (0.13)	6.79 ± 15.88 (2.34)	$2.5x10^{6}$
FB101	0.23 ± 0.06 (0.24)	11.92 ± 18.59 (1.56)	$5.9x10^{4}$
FB138	0.11 ± 0.01 (0.09)	2.75 ± 1.74 (0.63)	$3.7x10^{2}$
FB146	0.06 ± 0.02 (0.35)	3.41 ± 2.66 (0.78)	$5.8x10^{1}$
FB166	0.07 ± 0.01 (0.14)	5.25 ± 3.86 (0.74)	$7.6x10^{2}$
FB220	0.09 ± 0.01 (0.13)	2.95 ± 2.59 (0.88)	$3.9x10^{2}$

Table 2

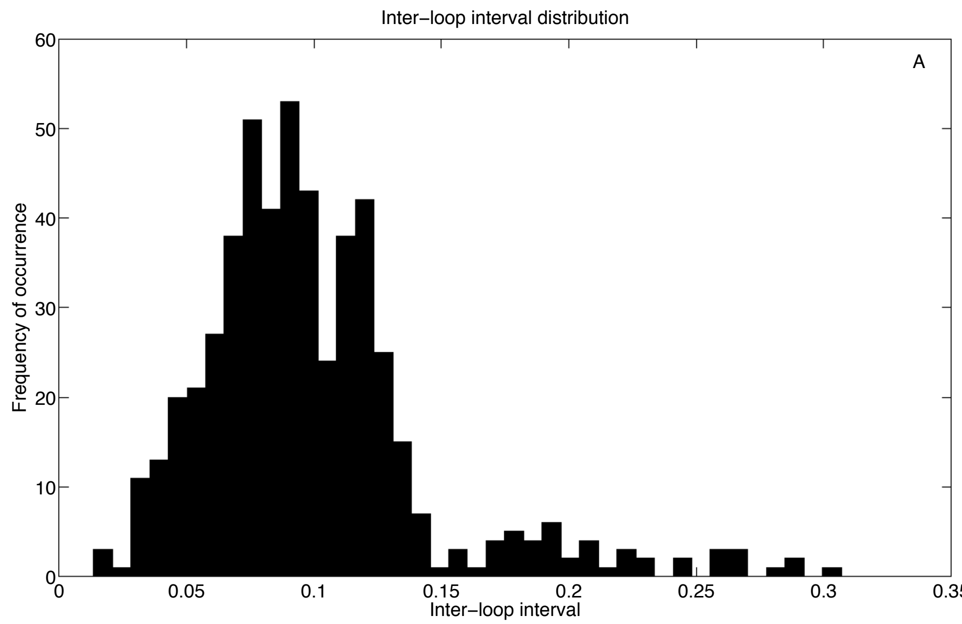
Animal	Sex	Mean freq. max. ± SD (CV) kHz	Mean freq. min. ± SD (CV) kHz	Mean duration ± SD (CV) sec
FB3	F	27.30 ± 1.87 (0.07)	13.33 ± 0.53 (0.04)	2.3 ± 0.69 (0.3)
FB7	F	12.86 ± 0.48 (0.04)	4.21 ± 0.30 (0.07)	1.3 ± 0.23 (0.18)
FB9	F	11.21 ± 0.53 (0.05)	6.24 ± 0.41 (0.06)	0.8 ± 0.15 (0.19)
FB11	F	23.50 ± 0.78 (0.03)	5.86 ± 0.20 (0.03)	1.3 ± 0.47 (0.37)
FB20	M	11.60 ± 1.40 (0.12)	5.90 ± 0.49 (0.08)	1.2 ± 0.55 (0.45)
FB24	M	13.43 ± 1.55 (0.12)	5.22 ± 0.88 (0.17)	0.9 ± 0.16 (0.18)
FB25	F	22.17 ± 3.55 (0.16)	7.18 ± 0.18 (0.03)	1 ± 0.3 (0.31)
FB35	F	15.07 ± 1.98 (0.13)	5.43 ± 0.51 (0.09)	0.9 ± 0.22 (0.24)
FB38	M	14.95 ± 1.01 (0.07)	5.31 ± 0.28 (0.05)	0.7 ± 0.19 (0.28)
*		14.81	5.15	0.1
*		14.68	5.65	0.2
FB48	M	14.42 ± 0.30 (0.02)	4.14 ± 0.91 (0.22)	0.9 ± 0.34 (0.39)
*		9.29	5.27	0.8
*		8.53	6.40	0.2
*		7.03	6.02	0.1
*		9.54	5.15	0.9
*		10.67	7.28	0.8
FB54	F	21.46 ± 3.65 (0.17)	6.20 ± 0.57 (0.09)	1.2 ± 0.37 (0.31)
*		15.06	5.40	0.1
FB55	F	14.97 ± 0.77 (0.05)	4.35 ± 1.08 (0.25)	0.9 ± 0.26 (0.29)

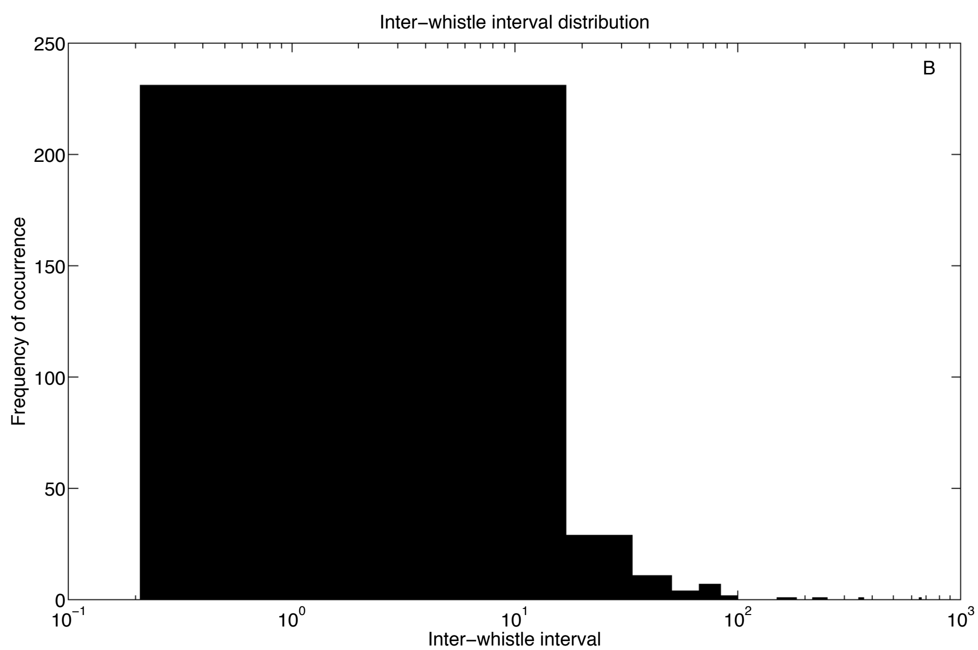
*		14.85	6.40	0.1
FB67	F	23.02 ± 2.04 (0.09)	4.99 ± 0.19 (0.04)	2 ± 0.38 (0.19)
FB84	F	19.47 ± 1.76 (0.09)	6.58 ± 0.31 (0.05)	1.2 ± 0.33 (0.27)
FB90	F	24.68 ± 2.00 (0.08)	3.31 ± 0.70 (0.21)	1.2 ± 0.1 (0.08)
FB97	F	12.50 ± 0.28 (0.02)	7.00 ± 0.45 (0.06)	1.2 ± 0.35 (0.3)
FB101	F	15.68 ± 4.51 (0.29)	4.09 ± 0.88 (0.21)	0.8 ± 0.45 (0.53)
FB105	F	11.56 ± 2.40 (0.21)	4.76 ± 0.42 (0.09)	0.5 ± 0.19 (0.35)
FB118	M	17.55 ± 1.31 (0.07)	6.73 ± 0.66 (0.10)	1 ± 0.42 (0.41)
FB122	M	14.21 ± 0.26 (0.02)	5.28 ± 1.66 (0.31)	0.8 ± 0.16 (0.2)
FB138	M	20.74 ± 1.54 (0.07)	10.09 ± 0.28 (0.03)	1.7 ± 0.36 (0.21)
FB140	M	18.62 ± 0.71 (0.04)	4.09 ± 0.55 (0.13)	1.8 ± 0.67 (0.37)
FB146	M	15.40 ± 1.42 (0.09)	6.11 ± 1.21 (0.20)	1.1 ± 0.36 (0.32)
FB151	F	15.34 ± 2.10 (0.14)	5.23 ± 0.66 (0.13)	0.7 ± 0.14 (0.2)
*		9.41	6.15	0.3
FB163	F	25.36 ± 1.72 (0.07)	3.62 ± 0.68 (0.19)	1.3 ± 0.44 (0.33)
*		9.54	3.39	0.5
*		15.18	2.13	0.9
FB166	M	12.34 ± 2.01 (0.16)	3.65 ± 0.91 (0.25)	1.1 ± 0.36 (0.34)
FB186	M	22.65 ± 1.86 (0.08)	4.26 ± 0.16 (0.04)	0.7 ± 0.25 (0.35)
FB220	M	9.34 ± 0.35 (0.04)	3.01 ± 0.32 (0.11)	1 ± 0.21 (0.21)

Table 3



Frequency (kHz)
0
20
40
FB3
FB7
FB9
FB11
FB20
FB24
FB25
FB35
FB38
FB48
FB54
FB55
FB67
FB84
FB90
FB97
FB101
FB105
FB118
FB122
FB138
FB140
FB146
FB151
FB163
FB166
FB186
FB220
0
.5
1
Time (s)
0.5 s


Inter−loop interval distribution
A
Frequency of occurrence
Inter−loop interval
0
10
20
30
40
50
60
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35


Inter−whistle interval distribution
B
Frequency of occurrence
Inter−whistle interval
0
50
100
150
200
250
10^{-1}
10^{0}
10^{1}
10^{2}
10^{3}