Quantifying Variation in Bat Echolocation Calls

Charles Frankhouser

Candidate for the degree

Bachelor of Science

Submitted in partial fulfilment of the requirements for

College Honors

Departmental Distinction in Biology

Karen A. Campbell, Ph.D.

Gerald L. Kreider, Ph.D.

Jerry A. Tartaglia, M.A.

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Signature of Author: Charles Frankhouser Date: 5/9/06

Printed Name of Author: Charles Frankhouser

Current Home Address: P.O. Box 152

City, State, Zip Code: Centerport, PA 19516

Quantifying Variation in Bat Echolocation Calls

By Charles Frankhouser

INTRODUCTION

The ability of bats to navigate and maneuver in total darkness has long been a topic of interest in mammalian research. During the late 1700's, Lazarro Spallanzani conducted a series of experiments on Pipistrelle bats which led him to conclude that bats "see" with their ears (Fenton 2004). This conclusion was not widely accepted until the late 1930's when Donald R. Griffin used a wide range microphone to prove that Little Brown Bats (*Myotis lucifugus*) emit sounds in the range of frequencies beyond the range of the human ear – ultrasonic sounds. Griffin also discovered that these sounds were emitted as pulsations that seemed to be used by the bats for navigation. He later published these foundational findings in Listening in the Dark (Griffin 1958) and coined the term echolocation for this behavior. Over the past 50 years, our understanding about bat echolocation has flourished as the technology necessary to study these ultrasonic signals become more refined.

Echolocation is not restricted to only bats but they certainly do take it to a more sophisticated level than do other animals that echolocate. Some birds and cetaceans (whales and dolphins) are able to emit simple series of clicks. Microchiroptera, the suborder of which all North American bats belong are able to make use of structured tonal signals with varied use which reflects different strategies to catch a variety of airborne insect prey in various environments. It is believed that bats can detect the echoes from small targets around 5 meters away while it is estimated that their range for navigating is about 15 meters. (Denny 2004)

Certain echolocation call characteristics have traditionally been identified to be specific to the species of bat: call frequency, duration, and patterns of frequency change over time (Fenton and Bell 1981). Researchers working with echolocation calls as characteristics for identifying bats have recently experienced a paradigm shift. Models previously guiding research in this field presumed that bat calls were stereotypic enough that call-based identifications ultimately would be routine in most cases, such as is usually found in similar research based upon bird song. Most field guides that provide anatomical measurements as taxonomic features for bat identification also routinely include a table of echolocation features intended to serve the same purpose (e.g. van Zyll de Jong 1985) As recording techniques and methods used for the analysis of bat echolocation signals have improved over the past few years, particularly in natural settings rather than in controlled laboratory experiments, a wider appreciation of intraspecific variation in echolocation calls has emerged. This, in turn, generates questions concerning both the causes and implications of such variation.

Bat research facilities generally are very controlled environments which are sound proofed and acoustically favorable. Bats in such experiments are usually captured and kept for the length of the experiments. Juveniles are typically born in captivity and have never experienced the challenges of echolocating in the wild, let alone having to adapt their calls due to the presence of conspecific species (Kazial *et al*. 2001). This highly controlled environment can be very dissimilar to that seen in the bat's natural environment so it is important to try and do field research as much as possible even though there are then issues of quality and problems with logistics of moving equipment through the woods.

Previous research had indicated that intraspecific variation in echolocation calls can be a result of compensation for the environment, geography, function of a call, and the presence of other bats (Burnett *et al*. 2004). Bats change their call structure to maximize their reception and perception of pertinent information during the different stages of hunting. Three general stages and associated call phases have been identified during hunting by insectivorous bats: search, approach and termination (simmon et al. 1979). Individuals may alter call characteristics to "fine tune" their reception in different microhabitats (Simmon and O'Farrell 1977). For example, a bat may shorten the duration and decrease the intensity of its calls to reduce extraneous echoes, background noise, when flying through rocky ravines. Bat biologists have adopted the term "clutter" (echoes from other than the target of interest) from radar terminology and often refer to the differences between calls obtained from animals flying in the open as opposed to flying in forest. Indeed, this distinction can be important, providing useful information about the situation in which a bat is operating and permitting other researchers to compare their findings from similar or different situations. The problem is that it's not really clear what "clutter" means. While the term is used widely, its physical manifestations are not well elucidated in the literature. In addition to its practical implications for those trying to understand call variation, there are at least two components to clutter. One is the bat's ability to maneuver, and the other is the bat's perceptual field. There is a great need for an index of "clutter" that is scaled to bat size and flight speed (to model the mechanical situation facing the bat) and to the duration and interpulse intervals of calls (to model the bat's perceptual field).

Many individual bats leave their own signature within their call, a slight variation on their call to help identify their own echoes from those of conspecifics (Masters et al. 1995). When several conspecific individuals are flying together, social calls often are intermixed with what appear to be echolocation calls. Although this suggests separation of function between social and echolocation calls, echolocation calls may also serve a social (communication) function.

The actual physics of bat echolocation is quite complicated with different species of bats using combinations of constant frequency (CF) and frequency modulated (FM) acoustic signals. Many bats can often use both types of signal and may adjust the signal depending on which phase of prey detection the bat is utilizing. The detection phase is typically long CF pulses at low pulse repetition frequency. The approach phase is typically shorter CF pulses and are transmitted at higher pulse repetition frequency. The terminal phase is characterized by descending FM pulses of short duration and high bandwidth with high pulse repetition frequency. The terminal phase is typically called the "feeding buzz" due the quick and intense call. Regardless of call type the call needs to be able to detect and identify the airborne prey, determine the direction and speed of the prey and determine the range from the bat to the prey.

The acoustic power of the bat's output can range by five orders of magnitude, mainly depending on the species. Notably for this study, big brown bats (*Eptesicus fuscus*) have intense calls while northern long eared bats (*Myotis septentrionalis*) have much less intense calls which would seem to be quieter in an effort not to startle the prey.

The power of the call also depends on the proximity of the bat to the prey. The bat must be able to make softer calls when it is closer to the prey so that the reflected signal is not deafening to the bat. Additionally due to the high sensitivity of the bat's ears they must be able to mute their own transmitted signal so that they are not deafened and are able to hear the reflected echo. To overcome this problem bats who are able to transmit constant frequency acoustic signals have developed a physiological adaptation between their ear and brain which allows the bat to ignore the frequencies that they emit while listening to the narrow band of frequencies that are reflected from the target, which are Doppler shifted from those emitted. (Denny 2004)

The usefulness of being able to identify a flying bat based on its echolocation signature has profound implications in surveys of bat communities, particularly when there is the potential involvement of endangered bat species. In the northeastern United States, this type of survey work is generally focused on habitat use of the Indiana Bat, *Myotis sodalis*, a small, insectivorous species that lives only in the eastern United States (Thomson 1982). This species was declared endangered in the United States in 1967, under the Endangered Species Preservation Act of 1966, because of large decreases in population size and an apparent lack of critical habitat in winter (Clawson 1987; United States Fish and Wildlife Service 1983, 1999). The original recovery plan for this species stressed prevention of disturbance during hibernation, but despite current protection of all major hibernacula, the species continues to decline in number. The ongoing decline, despite protection in winter, suggests that this species has significant problems on its summer range (United States Fish and Wildlife Service 1999). In spring, these species disperse from hibernacula and migrate to summer quarters, where the bats form maternity colonies and typically seek shelter underneath the loose bark of dead trees (Callahan et al. 1997). Consequently, development of properties in close proximity to known hibernacula, particularly where trees will be removed, is closely regulated by the United States Fish and Wildlife Service.

In Pennsylvania and New Jersey, which are the two states where bats have been collected for this survey, there are a several species of bat which we could have encountered during our project. The most common bat in this region is the little brown bat (*Myotis lucifugus*) which roosts in large maternity colonies, often in manmade structures which may have been abandoned or are seldom used. The northern long-eared bat (*Myotis septentrionalis*) and the endangered Indiana bat (*Myotis sodalis*) are both very similar to the little brown bat in size and foraging habits. Their roosting habits differ though with the northern long-eared typically preferring dead trees as roosts and typically roosting in small groups compared to the potentially thousands that can live together in a little brown maternity colony. During the summer months Indiana bats roost in trees much like the northern long eared bat. The Indiana bats hibernate in large colonies, often in caves, and are so similar looking to the little brown bat that DNA testing is required to properly identify an Indiana bat. While some physical characteristics exist between the two species none are so striking as the long extended ears of the northern long-eared which defines that species from the little brown. The related size and foraging habits of these three species makes it important to be able to identify these three species as non-invasively as possible. Typically these bats would be need to be caught in a mist net and then identified by sight, which is often very stressful on the bats, particularly on pregnant females. By being able to identify the bats while they are still flying, by their echolocation signals, we make great improvements in monitoring, but not interfering with nature.

Several other species of bats make their homes within Pennsylvania and New Jersey woodland. The second most common bat in the region is the big brown bat (*Eptesicus fuscus*) which is about twice the size of the little brown and has considerably larger teeth. The smallest bat in the region is the eastern pipistrelle (*Pipistrellus subflavus*) which is about half the size of the little brown and is also identified by its tricolored fur. The hoary bat is the largest bat in the region and is known to eat both insects and even pipistrelles. Another bat about the same size as the big brown is the red bat (*Lasiurus borealis*) which has red fur and often lives solitarily in trees. Two additional species, the silver haired bat (*Lasionycteris noctivagans*) and the small-footed bat (*Myotis leibii*) have been seen in Pennsylvania but are considered rare.

MATERIALS AND METHODS

The equipment that was used to gather data was acquired from Avisoft Bioacoustics. The model we acquired was the UltraSoundGate 416-200 along with four UltraSoundGate CM16 microphones, which allowed for simultaneous recording from four microphones. The equipment was then connected to a laptop computer which ran the appropriate software, Avisoft recorder and SASlab pro. The microphones were each mounted on musical microphone stands, which allowed the microphones to be raised up to five feet from the ground.

Two large maternity colonies of little brown bats are located near Blue Marsh Lake in Reading, Pennsylvania. The one is in a covered bridge located on the Tulpehocken river near the Gruber wagon works. Approximately 1,000 little brown bats roost at this site and typically exit from one of the two entrances to the bridge. The other maternity colony is a barn dating back to the 1700's, which the Army Corp of Engineers uses as a storage facility at Blue Marsh Lake spillway. This maternity colony holds between two to four thousand little brown bats, which exit from a series of air holes built into the side of the barn as well as spaces along the large barn doors. These two maternity colonies are located within five miles of each other and were a source of a single species echolocation signals.

The project extended during the summer months from the end of May until the first few weeks in August when the bats were in summer residence and most active. Additional recordings were made during a survey at Great Swamp National Refuge from August 1 -3 with most of the recording being done on the third due to some technical difficulties on August 1st and 2nd. Bats were captured from dusk (~9pm) until about midnight, when the bats typically seek a secondary roost site and don't resume feeding until later.

Initially we focused on acquiring signals from the bats as they exited the structures, regardless of sex or reproductive state. This was done by setting up the equipment at the openings of the roosts where the bats were likely to exit. Once dusk settled the bats exited the structures and began echolocating as they flew over the equipment. We placed the microphones right at the opening of the bridge while we moved the microphones approximately 30 feet from the side of the barn as there was no one clear area where the bats would exit from.

A variety of arrangements were used for the microphone setup to determine the best type of pattern to place the microphones so that we would get representative recordings. Initially we placed the microphones in a parallel line to the opening of the bridge, but then a perpendicular line was used, so the bats flew past each microphone in the series. Finally we settled on a diamond shape with all four of the microphones pointed at the opening. This was rationalized so that the bat would fly over the front point of the diamond (microphone 1) and towards the opposite point (microphone 4). If the bat changed directions while over the microphones one of the two side microphones should pick up the signal (microphones 2 and 3). In this arrangement the sides of the diamond were of a length which seemed beneficial to the area we were surveying, typically four to ten feet, depending on the space available.

Later in the season we wished to check the echolocation calls of individual little brown bats depending on their age and sexual status (juvenile male and female, pregnant female, non-reporoductive female, male). This was done by capturing bats using a harp trap at the barn and by hand selecting them at the bridge. Bats were then held by hand and released over the microphones, which were kept farther away from the bridge and barn than normal so as not to record other bats in the vicinity.

A mixed species environment exists at Great Swamp National Wildlife Refuge in Morris County, New Jersey. This is a 7,600 acre wetland which was filled with bat and insect activity once dusk fell. Over the course of three nights, mist nets were placed along pathways and trails at potential points of capture in the park. The mist nets are large (30ft.

by 30ft.) thin nets which are strung high into the air by a set of poles which are supported on the ground much like an A-frame tent. When a bat hits the nets they become entangled and then the nets can be lowered and the bat can be removed. The nets were checked every five to ten minutes by either Dr. Campbell, a park ranger or myself and the capture results were radioed back to the group once the bat had been removed and placed in a holding cage.

Captured bats were brought back to a central location where the banding and recording equipment was kept. The bats were then identified, their forearm, tragis and hindfoot were measured, and they were weighed. Indiana bats had hairs plucked from them so that the follicle remained for DNA testing. These hair strands were then sealed in an envelope. Following this all of the bats were then banded with a unique numbered aluminum band around their wrist so that they could be identified at a later time. This band number along with the bat's information was stored in a notebook detailing where and when the bat was caught. These are then kept on record in case the bat is recaptured so that any migration can be noted and a history of the bat can be established.

Following banding, most of the bats were then held near the recording equipment so that any echolocation they emitted would be recorded. Typically we would hold their back feet and hope that they would echolocate their surroundings. The bat would then be released to hopefully fly away from us and go over the recording equipment. While in the woods, we kept the microphones in a four foot diamond due to space issues with a point nearest to the person releasing the bat.

Results

Data were recorded using the Avisoft recorder software and analyzed using the SASlab pro software which was purchased from Avisoft Bioaccoustics along with the hardware. Calls were recorded in 60 second clips so as to create files of manageable size. We had been advised that longer files, in addition to consuming computer memory space, were very difficult to work with and analyze (B. Fenton, personal communication). Data were analyzed by creating a spectrogram of the recordings and then using the automatic parameter measurement option in the SASlab pro software. The data were then exported to Excel.

The automatic parameter measurement option allowed for quantification of multiple parameters in the calls by selecting the regions of highest intensity (in decibels) and assuming those are the bat's echolocation signals. The parameters we chose for this project were call duration, inter-pulse-interval, start frequency, end frequency and maximum frequency. Some of the features are commonly used to define species specific calls, (Table 1) although we expected to recorde some variation which would help differentiate species. The duration of the call is the length of each individual pulse from start until end in seconds. The inter-pulse-interval is the time from the end of one pulse until the beginning of the next in seconds. The start frequency is the frequency that the bat's call begins at and then the end frequency is where the call ends at. The maximum frequency should then be the most intense frequency which occurs in the call. All frequencies are given in kilohertz.

The duration of each call is very short with most of the calls ranging between 0.001 seconds and 0.03 seconds for each pulse. There are some of longer duration but those are most likely not actually bat calls but some other sound picked up by the recorder. The interval is also typically very quick ranging from 0.05 seconds to 0.2 seconds although there are significantly greater intervals. Since a bat's call is multiple pulses each with its own interval, once that call ends there will be a much greater interval until the bat begins a new call. Also due to changing proximity of a flying bat to the microphone and the directionality of the microphones, the call of the bat may die out due to sensitivity only to be picked up later as the bat circles back in front of the microphone.

The start frequencies for the calls range from 4 kilohertz to over 100 kilohertz with most in the 40 to 60 kilohertz range (Table 2). The end frequencies dipped as low as 400 hertz to around 80 KHz with most falling around 30 to 40 KHz. Maximum frequencies again had a wide range from about 10 KHz to about 80 KHz with most often the maximum frequency being the start frequency. The range was then calculated taking the start frequency and subtracting the end frequency, this was done in excel and is not listed as a parameter which was used in the SASlab software.

While these parameters are useful it is important to note that we did not use the highest or lowest frequencies as parameters. Due to the shape of most FM calls the start frequency should be the highest and the end frequency should be the lowest but it may not be the case (see figure 1). In some examples in the data the maximum frequency is greater than either the start or end frequencies. This additionally is not surprising because some bat calls can have an initial rise in frequency and then drop down in frequency. Most of the problems with the data are that some instances show the end frequencies being higher than the start frequencies so that there is a negative range. Some of these abnormal calls could be social calls as opposed to echolocation calls which would explain why they fell in the range of human hearing (20 Hz to 20KHz). They would most likely be displeasure over being held by myself or perhaps calls for help. Another possible reason for these abnormal signals is that they are merely background noise which was close enough to the microphones to create an intense signal which was mistaken as a call by the software.

DISCUSSION

The results of this research lend themselves more to revisions in experimental design than to arriving at conclusions involving variations in bat echolocation signals. We do have a better understanding of why most bat research is done in controlled laboratories in complete silence as most of our data has crippling amounts of background noise. The sounds of the forest at night are more than enough to cover up any useable data that could be obtained under the conditions in which we were working (see figure 3). While there is some ability to remove background noise from the data using the software, it is still limited in scope. Some experimentation was needed to arrive at any appropriate configuration for the microphone array. The original microphone array that we set up at the bridge did not take into account the echoes which bounced off of the wooden floors and walls and created havoc on our data. In many ways we have learned our limitations with the microphones and have become more comfortable in working with them in various conditions.

The software itself presented us with the greatest challenge. As we had just purchased the hardware and software we were still quite unfamiliar with either and the manual was filled with technical jargon which confused more than helped. It took me about a week to learn how to save the recordings and discover which settings the software needed to be at before it would record. Most of our issues were resolved by consulting with Dr. Brock Fenton, a world renown bat expert, who uses this software during his work in Canada.

The data itself seems acceptable in some regions but most of what was taken in the field needs to be more expertly reduced in noise. The ranges for the data seem greater than those previously reported for the species. The frequencies in the lower extreme (below 20KHz) are obviously social noises emitted by the bat, most likely displeasure at being held. Frequencies in the higher extremes (above 75 KHz) are most likely insects in the region. (see table 1 for typical bat call frequencies per species and table 2 for the extremes of the data sets) The Indiana bat recordings are the first of this kind obtained from this endangered species, and so they are of interest to other researchers. Some of the recordings from the bridge and barn are fairly clear but most of those taken at Great Swamp National Wildlife Refuge are filled with so many insect and frog noises that they require additional filtering for more detailed analysis. .

As the project went as a whole, I believe this was a good pilot project to get used to the recording setup but I do not believe that very many inferences can be drawn from the data. Perhaps with time and a better grasp of the analysis program the data can be cleaned up and useful parameters can be quantified. I believe that the recordings, particularly from the Indiana Bats are better off in the hands of Dr. Fenton, who will most likely be able to get use out of them as he expressed some delight that we were able to get Indiana Bat recordings.

Table 1

Species	Highest Frequency (kHz)	Lowest Frequency (kHz)	Maximum Duration (ms)
M. lucifugus	78	38	5
M. septentrionalis	110	38	3
P. subflavus	73	45	3
L. borealis	97	40	3
E. fuscus	48	27	10

(Zyll de Jong *et al*. 1985)

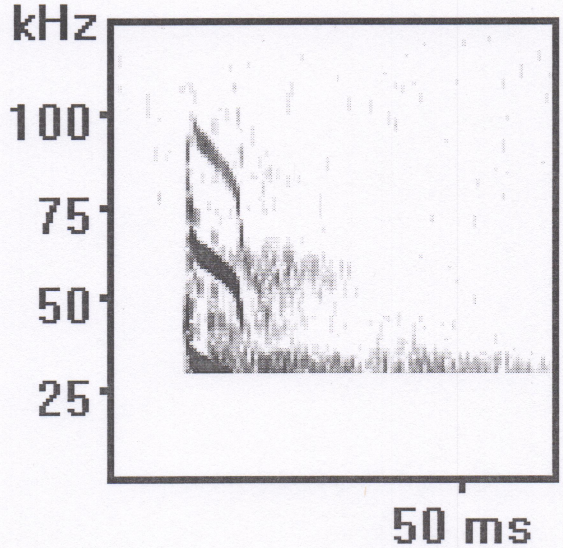
This table details the expected call frequencies and call duration of native bats that were common to the area of the study.

Table 2

Parameter	High	Low	Range
Start Frequency	102.5	4.8	97.7
End Frequency	92.7	.4	92.3
Max Frequency	91.7	4.8	86.9
Call Duration	.2437	.0005	.2432
Call Interval	9.6184	.025	9.5934
Range	57.7	0	57.7

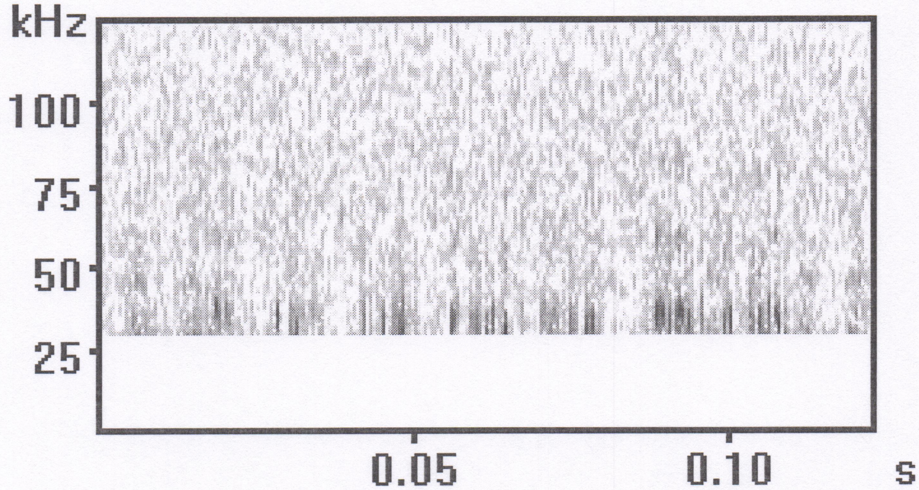
This table is the extremes taken from the entirety of the data sets. The high frequencies are clearly not within the range of most of the bat species recorded and the lows are well within the range of human hearing.

Figure 1



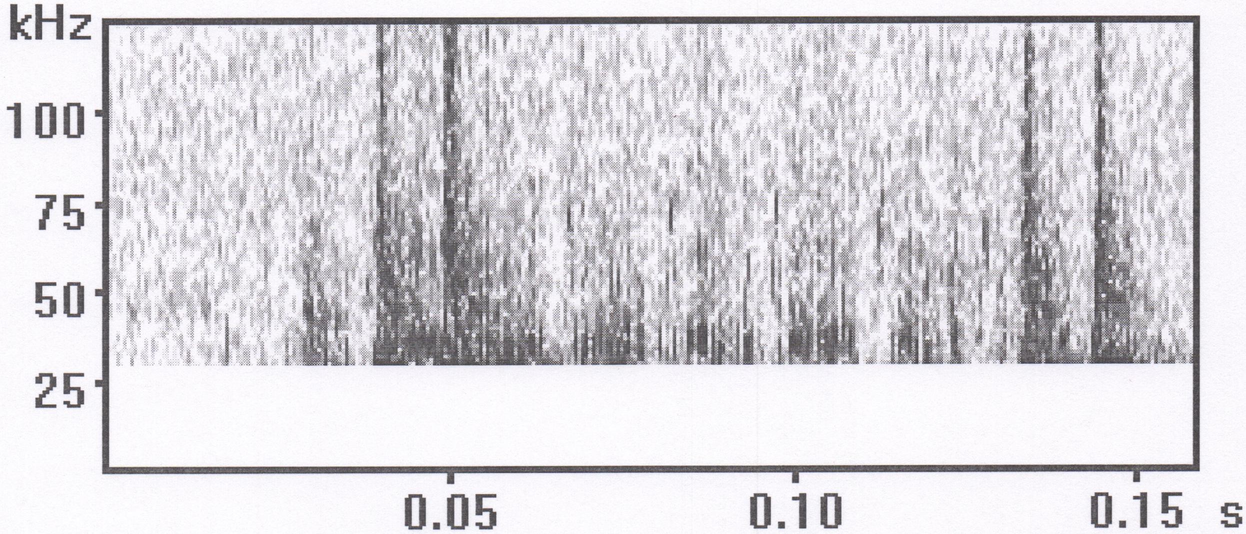
In this image we see the shape of a typical bat call with a single harmonic. Data below28 KHz had to be cutoff to reduce the large amount of noise below that region. Noise reduction was also used which helped to clear up the background of the picture. The echolocation pulse typically begins high in frequency with a quick downward drop in frequency.

Figure 2



This picture shows a larger section of a spectrogram of the background noise that exists in most of the data. The lower limit cutoff is still in effect for all data below 28 KHz.

Figure 3



This picture shows a bat pulse train located in a significant amount of noise. Several pulses can be seen here particularly from about 0.07 seconds until about 0.13 seconds. The 28 KHz cutoff is seen here as well.

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