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Slave to the Rhythm: Variation in the Acoustic Signaling of Picoides Woodpeckers

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Slave to the Rhythm: Variation in the Acoustic Signaling of *Picoides* Woodpeckers

by

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Abstract

We explored rhythmic variation in acoustic signals by geography across four species of *Picoides* woodpeckers. We hypothesized that there would be an effect of geographic location on the cadence of drums and rattle-type calls. No significant effect was observed. However, drum cadence was observed to significantly impact conspecific recognition in playbacks.

Keywords: *Picoides*, cadence, geographic variation

Geographic Variation in Acoustic Signaling of *Picoides* Woodpeckers

Using sound to communicate information from one organism to another is a ubiquitous characteristic in the animal kingdom as it is invaluable to engaging in social behavior (Hauser, 1996). Many groups of animals have evolved fascinating and unique communication systems, though few are as robust or as well-known as those of birds. Chief among these systems is that of acoustic communication: nearly all birds use some form of acoustic signals, and several taxa have developed complex acoustic sequences (Bradbury & Vehrencamp, 2011). As such, using birds as model organisms in the field of bioacoustics and the study of acoustic communication in animals has become widespread as sound recording technology has advanced (Merchant et al., 2015). Most birds communicate primarily through vocalizations, which are produced through the syrinx, a derived vocal organ that evolved in birds as early as the Late Cretaceous (Trevisan & Mindlin, 2009; Clarke *et al.*, 2016). The most complex of these vocalizations are signals collectively referred to as ‘songs’, which are series of vocal sequences that are produced for a variety of social functions (Searcy & Andersson, 1986).

Among birds, the most complex songs are produced by passerines, hence known as songbirds, a group that includes such vocally complex species as wrens, finches, and titmice (Beecher & Brenowitz, 2005). Songs are used to achieve two major functions: territory maintenance and mate attraction (Baker, 2001). Territory maintenance is largely achieved through male-male communication: song playback experiments have found that male songbirds are much slower to occupy territorial space in which many complex song types can be heard (Krebs, Ashcroft, & Webber, 1978). Research into how complex vocalizations such as song facilitates mate attraction is well-documented. Lehrman (1959) was the first to document this in birds: he showed that vocalizations from male ring doves (*Streptopelia capicola*) stimulate the

release of the follicle-stimulating hormone (FSH) in female ring doves. Further studies found that female canaries (*Serinus canarius*) laid more eggs and built their nests faster when exposed to more complex song types (Kroodsma, 1976). Recent research suggests that in over half of all passerine species, female songbirds will readily produce song vocalizations as much as males (Odom *et al.*, 2014). Additionally, it is well known that there are often geographical differences in song types in songbirds, which are sometimes referred to as ‘dialects’ (Marler & Tamura, 1962). In addition to inherently conveying the group identity of the singer or signaller, there is also evidence that dialects influence sexual selection. In a study of yellowhammers (*Emberiza citrinella*), a Eurasian songbird, females from Norway responded with more solicitation displays when exposed to their natal dialect than when they were exposed to dialects from nearby Denmark (Baker *et al.*, 1987).

However, some groups of birds can produce sounds mechanically, or independent of the syrinx, and may do so using their feathers or bills (Koch, Krakauer, & Patricelli, 2015). Soma and Mori (2015) discovered that bill-clicking behavior in the Javan Sparrow (*Lonchura oryzivora*) followed similar syntactic rules as their song. Among non-passerine birds which produce mechanical signals, woodpeckers are arguably the most well known. In addition to vocalizing, woodpecker individuals communicate by drumming on hard surfaces, e.g. tree trunks or limbs; this is done independently of the tapping associated with feeding or boring into tree bark (Gibson, 2006). Stark *et al.* (1998) outlined four principal variables of drums: the number of drums in a series, the length of the drum series, the cadence or rhythm (defined as the number of drums divided by the total time), and the interdrum interval. These variables provide a robust quantifiable framework for bioacoustic analyses of woodpecker drumming.

Compared to their songbird cousins, the vocalizations of woodpeckers are relatively simple (Lucas *et al.*, 2002). Of concern is whether such drumming is analogous to the songs of passerines. As noted above, birdsong achieves two major functions: territory maintenance through male-male communication, and mate attraction through male-female communication. As several early ornithologists and ethologists noted, woodpecker drumming is most often heard during the breeding season; for many North American species, this occurs in the spring months, e.g. March through May (de Kiriline Lawrence, 1967). In a study of drumming patterns in male and female Red-Bellied Woodpeckers (*Melanerpes carolinus*), male and female individuals drummed the most just prior to pairing up (Wilkins & Ritchison, 1999). Similar to songbirds, both male and female woodpeckers drum equally readily, though early researchers focused on communication from male individuals (de Kiriline Lawrence, 1967). In his exhaustive review of acoustic communication in *Picoides* woodpeckers, de Kiriline Lawrence (1967) also notes that because both sexes of Downy (*Picoides pubescens*) and Hairy Woodpeckers (*Picoides villosus*) may establish territories, female individuals may drum just as frequently as males.

Just as vocal signals can convey species or individual identity, research suggests that the drum sequences of woodpeckers may also convey species-specific information. In a study of 11 syntopic and allotopic woodpecker species, Stark *et al.* (1998) found that drum cadence, or rhythm, was the principal acoustic variable that separated syntopic species. Similarly, playback experiments with four species of *Picoides* woodpeckers found that individuals were more likely to respond to drum sequences if they shared similar drum cadence (Dodenhoff *et al.*, 2001). Winkler and Short (1978) noted that while the pitch of a drum sequence may vary considerably due to drumming substrate, ambient temperature, or barometric pressure, Hairy and Downy

Woodpecker individuals responded to drums regardless of pitch. Our knowledge, however, about just how mechanical drum sequences code for species identity is rather limited.

Though dialects can have significant effects on the evolution of species, e.g. by driving sexual selection of mates, no research has been devoted to woodpeckers on this topic.

Furthermore, studies on avian dialects have been restricted to their vocal signals and it is not known if sounds produced by another mechanism, in this case drumming, could also be affected by the geographic isolation of populations. Prior research has discovered some evidence for geographic variation in the Hairy Woodpecker (Winkler & Short, 1978), and the Black-Backed Woodpecker (*Picoides arcticus*) (Stark, 2002).

Though the genus *Picoides* has seen some comparatively recent taxonomic adjustments to account for paraphyly, the phylogenetic relationships of *Picoides* themselves are quite well known, and are supported by genetic assays (Benz *et al.*, 2006; Moore *et al.*, 2006) and acoustic analyses (Mathevon, personal communication, 2015). *Picoides* have wide geographic ranges, with each species being found across much of North America in similar environments throughout temperate and boreal forests with the Downy Woodpecker also having adapted to rural, suburban as well as urban areas such as Manhattan with relative ease (personal observation). Despite such widespread ranges, most *Picoides* species are quite sedentary. Over the some 25-year span of his study, de Kiriline Lawrence (1967) observed the transition from migrant Downy and Hairy Woodpeckers to residents after the establishment of a bird feeder apparatus near his home in Pimisi Bay, Ontario. All four species of *Picoides* studied in the current experiment have been observed to be non-migratory, and express much lower dispersal than other ecologically similar species. C. Bock & J.H. Bock (1974), in a comparative study of the then recently split species of American Three-Toed Woodpecker (*Picoides tridactylus*) and

the Black-Backed Woodpecker, noted that members of both species resided in boreal forest environments across Canada and the northwestern United States year-round. As Browning (1995) calls attention to, earlier studies of migration in Downy Woodpeckers erroneously assumed that non-recovery of banded birds proved that the birds had migrated; after reviewing state and regional data, he concluded that there is no evidence for migration in the Downy. Curiously enough, Ball Jr and Avise (1992), in an early study of mitochondrial DNA across woodpeckers and songbirds, found that despite exhibiting low dispersal and no migration, Downy Woodpeckers had significantly lower genetic variation than migratory species. Conversely, Klicka et al. (2011) found evidence for three significantly divergent clades of Hairy Woodpeckers, despite their lack of migration.

Considering their static ranges, it would seem probable that acoustic differentiation between populations would occur over time. This makes *Picooides* an ideal model for a study of potential geographic variation in acoustic signaling in woodpeckers. Three hypotheses will be tested: (1) there is an effect of latitude or longitude on the cadence of *Picooides* drumming signals, (2) there is an effect of latitude or longitude on the cadence of *Picooides* rattle calls, stronger than the observed effect of drums, (3) there exists a relationship between the cadence of the species' drum signal and recognition by conspecifics.

Method

Subjects and Materials

Experiment 1: Signal acquisition and analysis.

In the first part of the study, we collected digital recordings of drum and call signals from four species of *Picooides*: the Black-Backed Woodpecker, the American Three-Toed Woodpecker (*Picooides dorsalis*), the Downy Woodpecker, and the Hairy Woodpecker. Recordings of drum

and call sequences were downloaded from publicly available sound libraries: Xeno-Canto, Macaulay Library, and the Borror Laboratory of Bioacoustics. Recordings from adult individuals of each *Picoides* species were downloaded and catalogued into a separate Microsoft Excel sheet. In addition to recording the reference ID of each recording, we also noted: the species identification number (Downy = 1, Black-Backed = 2, Three-Toed = 3, Hairy = 4); the number of the recording by species; full genus and species; the average size and weight of the species; the quality of the recording, with 'A' referring to the highest quality available; the elevation at which the recording was taken; the date and time the recording was made; the listed recorder(s); the country, geographic region, as well as the latitude and longitude of the site where the recording was made. When the latitude and longitude were not listed by the database, the geolocation information of the nearest landmark referenced in the recorder notes was used. The final count of drum recordings included 47 for the Downy, 35 for the Black-Backed, 39 for the Three-Toed, and 28 for the Hairy ($n_{\text{total}} = 149$). The final count of call recordings included 25 for the Downy, 17 for the Black-Backed, 9 for the Three-Toed, and 36 for the Hairy ($n_{\text{total}} = 87$).

Experiment two: Playback of experimental signals.

We used a Behringer Europort MPA40BT PA as the speaker, and a Motorola Moto X was used to queue and play each experimental sequence via Bluetooth. Google Play Music was used as the audio playback software. During each playback, the speaker was placed on the ground roughly 5 meters from the subject, and was placed away and out of the line of sight of the subject. The speaker volume was limited to 50 percent of auxiliary input capacity, while the input volume via the Moto X was placed at 90 percent. The intensity of the recordings was measured at a sound pressure level of 86 decibels (dB) immediately adjacent to the speaker, with the signal decaying by 2 dB for each meter away from the signal source. Thus, at 5 meters, the subjects were

exposed to roughly 76 dB of signal intensity. Anecdotal reports of robust playback responses despite much greater distances, up to 100 meters, were made (personal observations). Accurate measurement of signal quality in acoustically fragmented environments (e.g. forests) is difficult, and thus could not be obtained.

Experiment three: Analysis of interdrum interval.

In the final stage of the study, we returned to the original drum recordings to analyze the interdrum interval of select drum series, and selected the highest quality recordings. Each recording was loaded into g-Prime (Lott, 2007) to calculate the interval duration between the peak of each drum hit. From there, this information, as well as the latitude and longitude where each recording was made was transferred into a Microsoft Excel spreadsheet.

Procedure

Experiment one.

Using Praat v.6.0.0.7, each recording was checked for fidelity, sampled down to 44.1 kHz, reduced to monophonic sound. One acoustic sequence (i.e. one discrete drum or call series) was selected from each recording. In order to control for motivational confound, sequences were selected from the middle of series, rather than the beginning or end. Following this, the call and drum sequences were analyzed using Seewave, a package of R (a statistical software language) dedicated to bioacoustic analysis. The R script in use during the analysis was designed in a previous research project by Renard and Mathevon (2015). The script identified each drum and call note as it passed a non-arbitrary threshold of the total amplitude of the recording. The amplitude threshold of background noise was identified for each signal in order to limit measurement error. For example, if a drum recording was nearly without noise, the threshold could be set as low as 10% of the total recording. For other lower quality recordings, the

threshold was often set much higher, over 50%. The script took each hit gathered when a drum or call note passed this threshold, and counted the number of hits per recording. The sequences were analyzed for the number of drums or calls, rate of drums or calls (which was measured by dividing the number of drums or calls by the recording length), interdrum or intercall interval, duration of drum or call series, and mean frequency of the drum or rattle call, which provided descriptive statistics.

Experiment two.

Using the results from the first part of the experiment, experimental Downy Woodpecker drum and call sequences were created for playback experiments in the field. The experimental drum sequences were synthesized from a single drum from one series in a sequence gathered from a digital recording used in the first part of the experiment. The drums were copied and repeated for a set number of times for each experimental sequence. As the number of drums in a drumming sequence has been shown to be correlated with territorial aggression (Schuppe *et al.*, 2016), the number of drums in each experimental sequence was limited to 17. Three separate signal types were created to demonstrate the measured range of drum cadence: a control drum series set at 16.5 drums per second, the median drum cadence measured in the first phase of our study, with slow-type and fast-type drum series created at \pm one standard deviation, set at 14 and 19 drums per second, respectively. The same procedure was used in creating the experimental call sequences. Because of the Downy Woodpecker's expressed range of drum and call cadences discovered in the first part of the experimental study, we created three types of experimental sequences that illustrate this range: slow, medium, and fast-type. For calls, slow-type signals were set at 6.5 notes per second, control calls at 11 notes per second, and fast-type calls at 18

notes per second. As Downy Woodpeckers are known to respond to drums irrespective of pitch or tone, we did not modify the pitch of the experimental drum sequences.

Playback experiments were conducted at three separate sites in Upstate New York: (1) SUNY Oswego at Rice Creek Field Station, (2) the woods surrounding a small cabin in East Branch, New York, and (3) a swamp forest in the town of Oswego, New York. Playbacks were carried out over two weekends and one full week between April 1 and May 1, 2016, as this was the height of the breeding season for the Downy Woodpecker (Schuppe et al., 2016).

Playbacks were largely done during the morning, from 0700 to 1100, though some playback sessions occurred in the afternoon. Single individuals were targeted for playback and recording. Simultaneous responses by nearby Downy Woodpeckers were noted but not recorded (personal observation). The subject's response to the experimental signal was measured by its latency to respond to the first drum sequence in an experimental drum series, hence known as 'first latency to respond'. First latency to respond for both drum and call responses was calculated by taking the elapsed time between the two initial signal peaks, as in between the experimental signal and the individual's response. Mean latency was calculated by averaging the time to respond to each experimental signal. This was the case irrespective of the number of times that the woodpecker drummed. Drum cadence was calculated by taking the number of drums and dividing by time between the first and last peak.

Drums were identified through audio review, as well as looking at the spectrogram in Praat. Mean Cadence was calculated by averaging drum cadence across all series. Mean Call Cadence was calculated by taking the number of calls and dividing by the time between the first and last peaks. In cases where the subject's drum overlapped with an experimental signal, the series was filtered using bandpass. In a few instances, playbacks at the East Branch site elicited

responses from Pileated Woodpeckers (*Dryocopus pileatus*). These recordings were not used in the analysis.

Experiment three: Analysis of interdrum intervals.

In order to measure the interdrum interval for each species, the highest quality drum recordings were first selected. Ten recordings were selected for the Downy and Black-Backed Woodpeckers, respectively, whereas only five high quality recordings were selected for the Three-Toed and Hairy Woodpeckers. Recordings were loaded into g-Prime (Lott, 2007), an open-source program built off of MATLAB as a dedicated oscilloscope/event detection and recorder. Similar to the procedure used in the first phase of the study, a threshold for detection was set that was tailored to filter out noise from each recording. As the amplitude of the recording crossed the threshold, it was registered as a peak, here a discrete drum hit. The data were imported into a Microsoft Excel spreadsheet, and the elapsed time between each drum was calculated (interdrum interval). Scatter plots of the interdrum intervals for each recording together with best fit functions were generated to describe each series of interdrum intervals.

Results

Experiment One

The average duration of drum sequences varied across species, with the Hairy and Downy species expressing shorter durations than those of the Three-Toed and Black-Backed (Figure 1). Accordingly, the Hairy and Downy also expressed higher average drum cadences. The Hairy had the fastest average drum cadence, at around 25 drums per second. The drum cadence of the Downy, Three-Toed, and Black-Backed overlapped quite a bit, with the Downy and Three-Toed sharing the most similar cadences (Figure 1). There was much greater variation seen in the cadence of the rattle calls (Figure 2). The Downy had the slowest mean call cadence,

while the Black-Backed had the fastest call cadence (Figure 2). This difference was not found to be significant. Both the Three-Toed and the Black-Backed had the greatest variation in call cadence, $\sigma^2_{\text{Three-Toed}} = 7.178$, $\sigma^2_{\text{Black-Backed}} = 7.256$, $\sigma^2_{\text{Downy}} = 2.776$, $\sigma^2_{\text{Hairy}} = 6.09$. After calculating the acoustic variables of the recordings, descriptives of each variable were selected. Pearson's correlations were performed in R between the acoustic variables and the descriptive variables of the recordings. We first examined the relationships between geographic location and duration and cadence of the drums and rattle calls as a function of species. No significant relationship was observed between longitude and cadence, $p = 0.7533$, latitude and cadence, $p = 0.227$, or for duration in drums by longitude, $p = 0.2338$, or latitude, $p = 0.2673$. These trends continued when examining each species' cadence individually. The Downy, Black-Backed, and Hairy Woodpeckers expressed almost entirely flat relationships between cadence and longitude (Figures 4, 8, 9). Only the Three-Toed was found to have a significant relationship between drum cadence and longitude, $p=0.35$, with a caveat that there were several geographic outliers which may have confounded the correlation (Figure 7). All four species expressed little variation in cadence or duration as a function of longitude or latitude (Figures 9, 10).

These findings generally held true for the call cadences as well, as no significant effects were observed between longitude and cadence, $p = 0.5164$, latitude and cadence, $p = 0.7274$, or for longitude and duration, $p = 0.1373$, or latitude and duration, $p = 0.8033$.

Experiment Two

We performed Pearson's correlation tests on the playback data using R. No significant effects were discovered between the variables of the experimental signals (mean cadence, number of series in signal, series duration, and total signal duration) and the playback response variables (behavioral response, drum/call response, first latency to response [in seconds and

proportion of experimental signal], mean latency to respond [in seconds and signal proportion], number of drum series in response, drum cadence on first series, mean cadence on all series, loudspeaker approach, proximity to speaker). Individuals responded to control-type drum and rattle call signals more quickly than they did to slow and fast-type signals (Figures 5, 6). As the playback response data did not meet normalcy, we performed nonparametric tests using IBM SPSS 20. After performing an independent samples Kruskal-Wallis test, we found significant effects for signal type on (1) an individual's latency to first drum, sig = .004, or call, sig = .000, after hearing the signal, (2) their latency to continue drumming, sig = .016, or call, sig = .000, (3) and the number of drums they responded with, sig = .014 (Table 1). This relationship did not extend to calling behavior, sig = 0.814.

Experiment Three

In the final phase of the study, Pearson's correlations were performed on the interdrum interval data. We then performed correlations between the latitude and longitude of each recording. After determining that power functions best fit the trend lines generated to describe the interdrum interval, we then performed correlations between geographic information and the R^2 value of each power function trend. There was no significant correlation for longitude and interdrum interval (Table 2), or for latitude and interdrum interval (Table 3). There were trends in the power functions for interdrum interval across species. The relationship between interdrum interval and duration of the Downy and Hairy Woodpeckers were observed to have weakly positive power functions, indicating an increase in the interdrum interval as the drum series continued (Figures 11, 14). In several series between the two species, the interdrum intervals remained constant or nearly constant as the drums continued, indicating that there was no change in the rate of drumming as the drum continued. Conversely, this relationship was observed to

have negative power functions in the Black-Backed and Three-Toed Woodpeckers. This means that these species accelerate their drumming as the drum series continues, as shown in a decrease in the interdrum interval (Figures 12, 13).

Discussion

The Downy, Three-Toed, and Black-Backed Woodpeckers expressed considerable overlap in the cadence of their drumming signals, with the Hairy expressing the highest mean drum cadence. Much greater variability was observed in the call cadences. The variation in both the drum and call cadence cannot be attributed to geographic variation across all species. The discovery of such considerable overlap between the species' drum cadences is a puzzling finding. Consider the principal drum variables outlined by Stark *et al.* (1998): cadence, the number of drum hits per series, interdrum interval, and the duration of the drum series. There are far more woodpecker species than there are functional permutations of these four variables, so it would follow that sympatric species would adopt more dissimilar drum patterning than allopatric species. All four species are known to be sympatric with at least one other species across their ranges. In some regions, especially in Canada and the northern United States, all four species may be sympatric (eBird, 2012). As such, the discovery of considerable overlap in the cadence and duration of drumming signals between the Downy and the Black-Backed (and to a lesser extent, the Three-Toed as well) is an interesting finding. It should be noted that the Downy and Hairy Woodpeckers express the greatest overlap in their ranges from northern Canada through to the southeastern United States (eBird, 2012), and displayed little overlap in drum cadence in the first experiment. Sympatric species must have uniquely identifiable mating signals, or they risk attracting unsuitable partners. This is compounded by the similarities in plumage seen between the Downy and the Hairy: males of both species display similar black and white patterning

across their breast and wings, with a red 'cap' behind their head. This may also explain the convergent cadence seen between the Downy, Three-Toed, and Black-Backed, which may be sympatric across northern boreal forests. Males of these three species share black-and-white patterned plumage, though the Downy is the only to express red head feathers, while the Three-Toed has a similarly-placed patch of yellow plumage.

There was no clear evidence indicating a relationship between geographic location and variations in drum and rattle call signals across *Picoides*: drum and call cadences were found to be incredibly stable despite their extensive ranges. Though our hypotheses could not be supported, these results are nonetheless thought-provoking. One of the widely agreed upon and documented requisite criteria for speciation is geographic isolation. All four studied species are known to be sedentary throughout the calendar year. This penchant for *Picoides* woodpeckers to reside in the same territory throughout the year is itself a geographic isolation barrier. Some variation should be expected, all things being equal. However, this is not the case: the duration and cadence of drumming signals are incredibly stable across the ranges of *Picoides*. This is especially surprising in the case of the Downy, who is arguably the most successful, widely-distributed picid woodpecker, as its range extends from Central America through all continental United States, Canada, and Alaska. Research by Pulgarin-Restrepo (2011) may present one potential hypothesis. As the author identifies, most Downy Woodpeckers radiated out from a single population, likely from glacial refugia during the last significant glacial period. It may be the case that these populations have not developed their own regional differences simply because not enough time has elapsed. However, passerines have been observed to develop such differences in a geologically short time. In a longitudinal study of a Neotropical songbird, Garcia *et al.* (2015) found significant variation in the number of notes and frequency of song over the

nearly 30 year period of data. Thus, it seems unlikely that the drums are subject to the same selection pressures as bird song, despite serving analogous functions.

With respect to the playbacks, statistically significant relationships were observed between the acoustic variables of the playback signals and the individual response signals. We observed a weak trend that individuals responded to control type signals more quickly than to slow and fast-type signals (Figure 9). This relationship held true for both drum as well as call responses to drum and call playbacks (Figure 10). This is complicated by the small number of individuals per experimental signal group ($n=2$). The simultaneous responses to playbacks by multiple Downy individuals adds to their usefulness as model organisms, especially when considered with their prevalence in North American deciduous forests.

The analysis of interdrum intervals across species provided further insight into drumming behavior in *Picoides*. The Downy Woodpecker showed considerable stability in interdrum intervals, as most fell between 60 and 80 milliseconds (Figure 11). The Black-Backed Woodpecker showed somewhat greater variation, between roughly 60 and 90 milliseconds (Figure 12). Three-Toed Woodpeckers showed remarkably greater variation in interdrum intervals, as they fell between 50 and 100 milliseconds (Figure 13). Low variation was also found in the interdrum intervals of Hairy Woodpecker drums, as they largely fell between 25 and 40 milliseconds (Figure 14). The discovery of similar accelerating trends in the interdrum intervals of Black-Backed and Three-Toed drums (Figures 12, 13), as well as trends toward deceleration between the Downy and Hairy could indicate a greater level of phylogenetic relatedness (Figures 11, 14). Previous research has noted their relatedness in simple habitat use and plumage (Goggans *et al.*, 1989). Phylogenetic studies of *Picoides* have traditionally excluded these species in favor of the Downy and Hairy, likely in favor of ease of data collection

in the latter species. Future phylogenetic assays of *Picooides* should include the Three-Toed and Black-Backed, in order to gain a much better picture of this potentially paraphyletic group.

The possibility of confounds cannot be ignored. Chief among these in this study was the range of recordings gathered in the first part of the study. The recordings covered almost all regions of the United States with comparatively fewer from southwestern states as *Picooides* is less common in the southwestern United States (eBird, 2012). The majority of recordings were gathered from the northern and eastern U.S., perhaps reflecting the location of the Macaulay and Borer libraries (upstate New York and Ohio, respectively). However, it should be noted that the drum and call signals were found to be stable across the ranges of the Downy, Hairy, Black-Backed, and Three-Toed Woodpecker. The drums of a Downy from the Pacific Northwest is functionally indistinguishable from those of a Downy in the Sapsucker Woods of Cornell. Therefore, future studies of *Picooides* drum and rattle calls should be able to use recordings from across their ranges irrespective of location and context. Additionally, though male and female Downy Woodpeckers are known to both drum quite readily, it is not known if there are any sort of consistent acoustic variation between the two sexes' drum signals. Many of the drum recordings we acquired did not list a recording time, let alone the potential sex of the signaling individual. Thus, we were not able to completely control for confound from sex of the signaler.

Further comparative studies of *Picooides* drumming signals may yet answer these questions. First and foremost should be conducting further playback experiments in order to see whether the trends of the Downy Woodpeckers to respond more quickly to cadences of 16.5 drums per second than slower or faster cadences remain significant (see Results). Future playback experiments could also examine the extent to which cadence facilitates recognition across *Picooides*. One way to measure this could be to perform playbacks of syntopic drums of

dissimilar cadence and allotopic drums of similar cadence with Downy Woodpeckers. For example, though the Black-Backed and Downy have very similar drum cadences, they do not co-occur across their entire ranges. Conversely, the Hairy and Downy are syntopic across the majority of their ranges, but express very different drum cadences. Potential playbacks could expose such Downy Woodpecker populations to these drum signals, and compare whether sympatry or cadence best facilitates recognition in heterospecifics.

Future studies of potential geographic variation may also be conducted on other acoustic parameters of woodpecker drums. In this study, we measured three of the four variables outlined by Stark *et al.* (1998), save for the number of drum hits per series. As Schuppe *et al.* (2016) observed, this variable correlates significantly with the level of aggression in territorial and mating contexts. Perhaps certain populations have lower thresholds for drum-based aggressive displays.

One particularly interesting avenue for research stemming from this study may investigate the considerable stability in cadence seen in the drumming signals of the Downy, Black-Backed, and Three-Toed Woodpeckers. As woodpeckers have evolved a considerable suite of morphological characteristics in order to handle the physical taxation of drumming (Yoon & Park, 2011), it may be the case that these traits act as a physical constraint on the cadence and duration of drums, whereas passerine song is only constrained by the limitations of the syrinx and individual fatigue (e.g. a bird can't sing indefinitely). In a recent playback study of Downy Woodpeckers, Schuppe and Fuxjager (2017) found that Downy individuals modulated the speed of their drumming in an attempt to match experimental signals, even if they did not always reach the extreme 53 millisecond interdrum interval. This finding indicates that while

there is some physical constraints on the drumming display, that there remains considerable flexibility.

These hypothetical constraints may also be behavioral in nature. As Soma and Mori (2015) noted, the bill-clicking behavior of young sparrows was similar to that of older males they were socialized with, indicating that bill-clicking is sensitive to learning. No such data exists for *Picoides*; it is not known whether these woodpeckers learn drumming displays from their parents, or if they are an innate behavior.

Conclusion

Though there appears to be no significant effect of geography on the variation in the cadence of drums or rattle calls in *Picoides* woodpeckers, despite the ecological similarity of drums to bird song, this finding is as puzzling as it is intriguing. The drums of these species are incredibly stable across their ranges, indicating there is some constraint on these signals. Playbacks with Downy Woodpeckers were useful in identifying how cadence facilitates recognition, though future studies are necessitated to expand on these findings. Despite the ecological and evolutionary importance of woodpecker drums, there remains a paucity of data on the variation and recognition of these signals. There are numerous avenues of research that future bioacousticians and ornithologists alike may examine.

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Table 1. Independent Samples Kruskal-Wallis Test.

| Hypothesis Test Summary | | | | |
|--------------------------------|--|---|-------------|-----------------------------|
| | Null Hypothesis | Test | Sig. | Decision |
| 1 | The distribution of Lat_Drum is the same across categories of Exp_Signal. | Independent-Samples Kruskal-Wallis Test | .004 | Reject the null hypothesis. |
| 2 | The distribution of MeanDrumLat is the same across categories of Exp_Signal. | Independent-Samples Kruskal-Wallis Test | .016 | Reject the null hypothesis. |
| 3 | The distribution of NumDrumSeries is the same across categories of Exp_Signal. | Independent-Samples Kruskal-Wallis Test | .014 | Reject the null hypothesis. |
| 4 | The distribution of Lat_Call is the same across categories of Exp_Signal. | Independent-Samples Kruskal-Wallis Test | .000 | Reject the null hypothesis. |
| 5 | The distribution of MeanCallLat is the same across categories of Exp_Signal. | Independent-Samples Kruskal-Wallis Test | .000 | Reject the null hypothesis. |
| 6 | The distribution of Num_Calls is the same across categories of Exp_Signal. | Independent-Samples Kruskal-Wallis Test | .814 | Retain the null hypothesis. |

Asymptotic significances are displayed. The significance level is .05.

Table 2. Interdrum Interval by Longitude in *Picoides*

| | | Longitude | R ² |
|----------------|---------------------|-----------|----------------|
| Longitude | Pearson Correlation | 1 | -0.47 |
| | <i>p</i> value | | .812 |
| | N | 28 | 28 |
| R ² | Pearson Correlation | -0.47 | 1 |
| | <i>p</i> value | .812 | |
| | N | 28 | 28 |

Table 3. Interdrum Interval by Latitude in *Picoides*

| | | Latitude | R ² |
|----------------|---------------------|----------|----------------|
| Latitude | Pearson Correlation | 1 | .232 |
| | <i>p</i> value | | .236 |
| | N | 28 | 28 |
| R ² | Pearson Correlation | .232 | 1 |
| | <i>p</i> value | .236 | |
| | N | 28 | 28 |

Figure 1. Drum Cadence in *Picoides*. Ranges of drum cadence in four *Picoides* species are shown using a color-coded bar (shown on left side of figure). The black bars illustrate the variation in drum cadence seen in each species. This provides a descriptive overview of drum rhythms in the 4 *Picoides* species, and was not tested for significance.

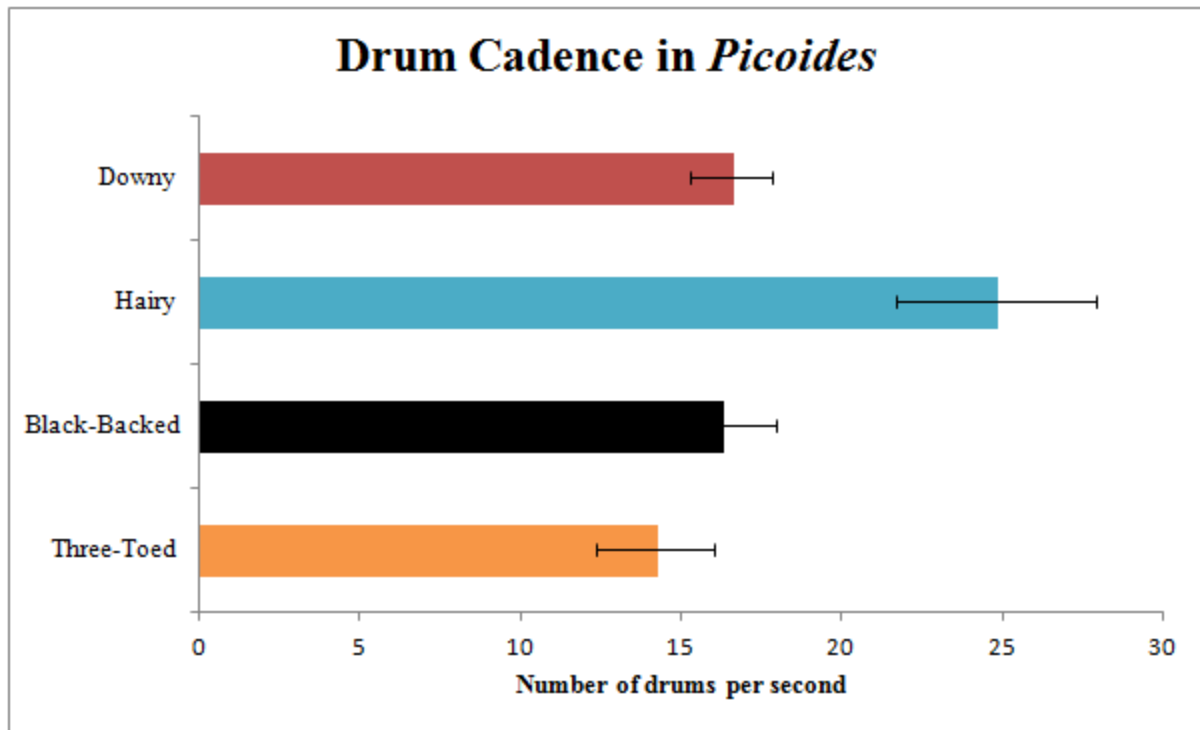


Figure 2. Call Cadence in *Picoides*. The call cadences of four *Picoides* species is shown using a color-coded bar. The black bars illustrate the variation in drum cadence seen in each species.

This provides a descriptive overview of call rhythm in the 4 *Picoides* species.

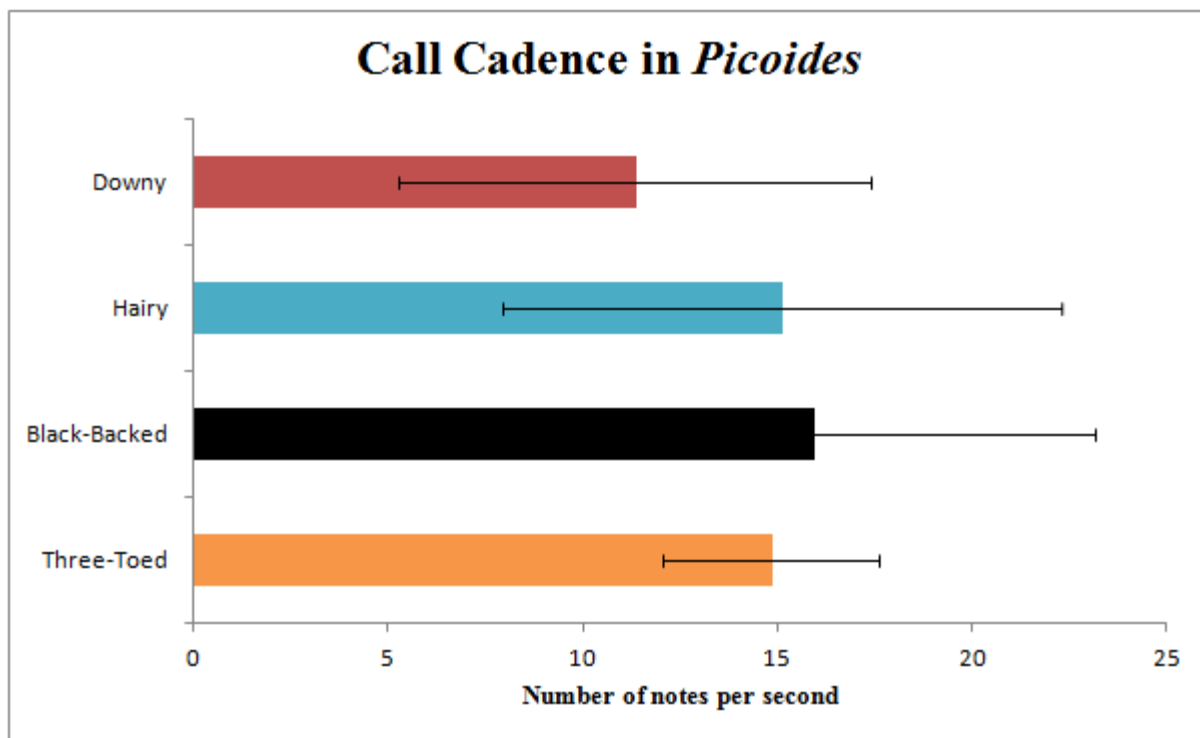


Figure 3. Drum cadence in *Picoides* as a function of longitude. This figure plots the *Picoides* drum cadence from all individuals as a function of the longitude of the recording location. The black line illustrates the line of best fit for the data, $r = 0.154$, $p = 0.616$. This did not pass the level of significance. Each dot corresponds to a recorded drum sequences from a *Picoides* individual.

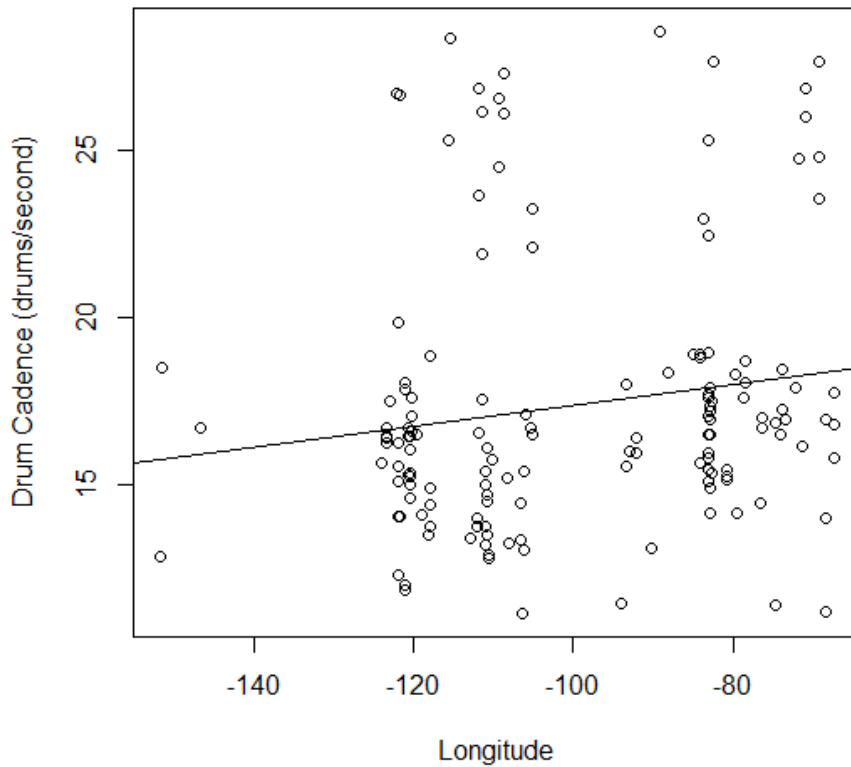


Figure 4. Drum duration in *Picoides* as a function of longitude. This figure plots the *Picoides* drum series duration from all individuals as a function of the longitude of the recording location. The black line illustrates the line of best fit for the data, $r = -0.1707$, $p = 0.3799$. This did not pass the level of significance. Each dot corresponds to a recorded drum sequences from a *Picoides* individual.

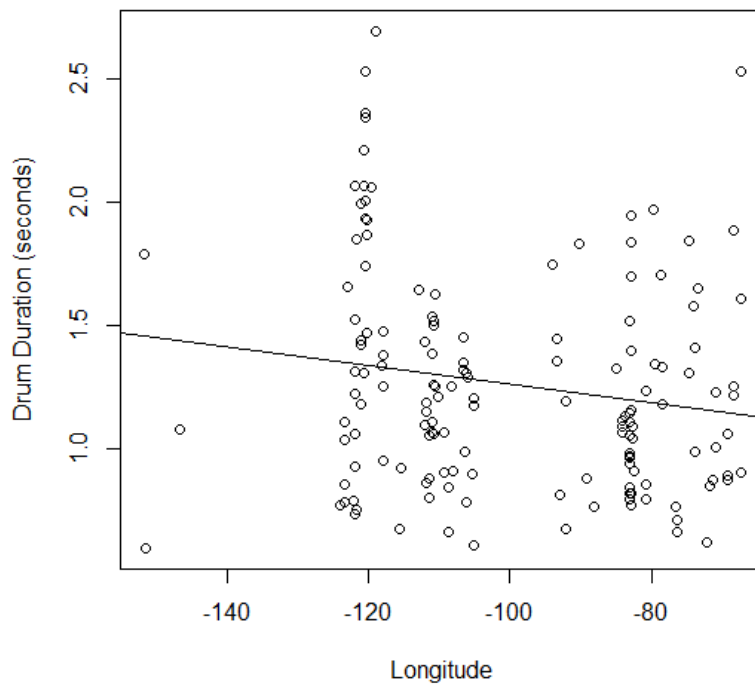


Figure 5. Drum cadence in Downy as a function of longitude. This figure plots the drum cadence from all Downy Woodpeckers as a function of the longitude of the recording location. The black line illustrates the line of best fit for the data, $r = 0.143$, $p = .4342$. This did not pass the level of significance. Each dot corresponds to a recorded drum sequences from a Downy individual.

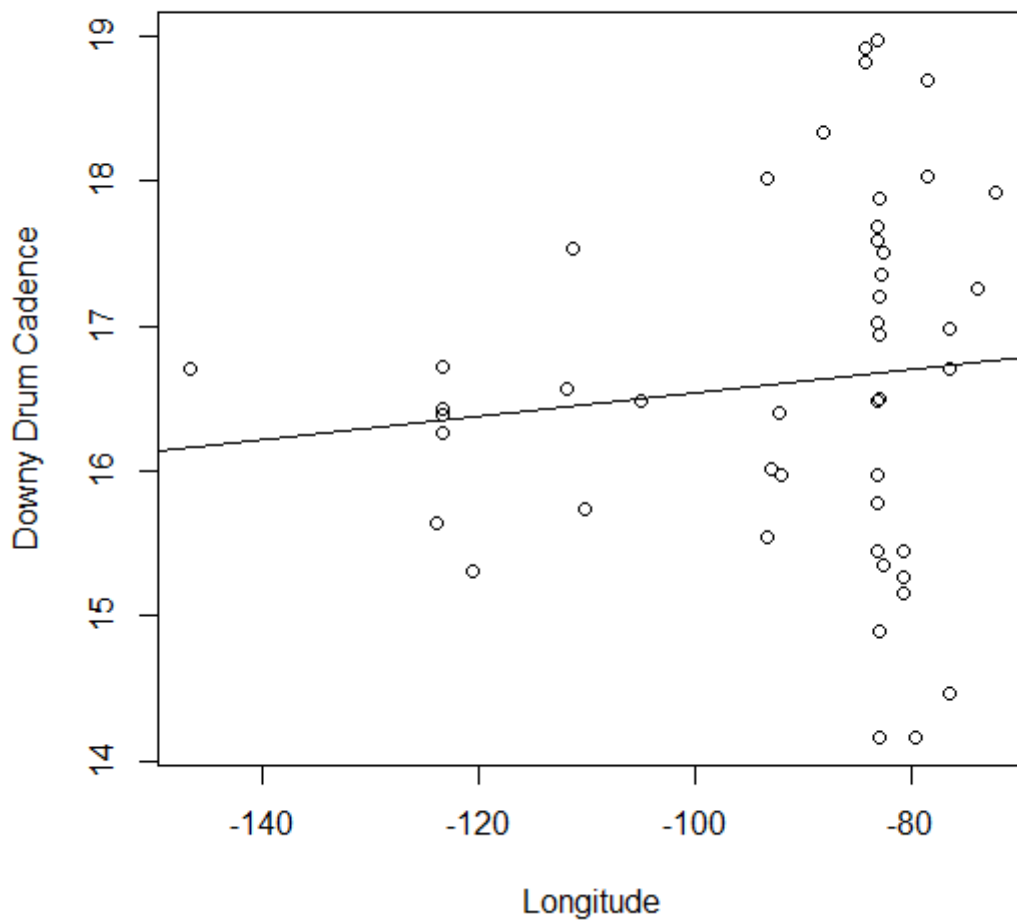


Figure 6. Drum cadence in Black-Backed Woodpeckers as a function of longitude. This figure plots the drum cadence from all Black-Backed Woodpeckers as a function of the longitude of the recording location. The black line illustrates the line of best fit for the data, $r = 0.091$, $p=0.4375$. This did not pass the level of significance. Each dot corresponds to a recorded drum sequences from a Black-Backed individual.

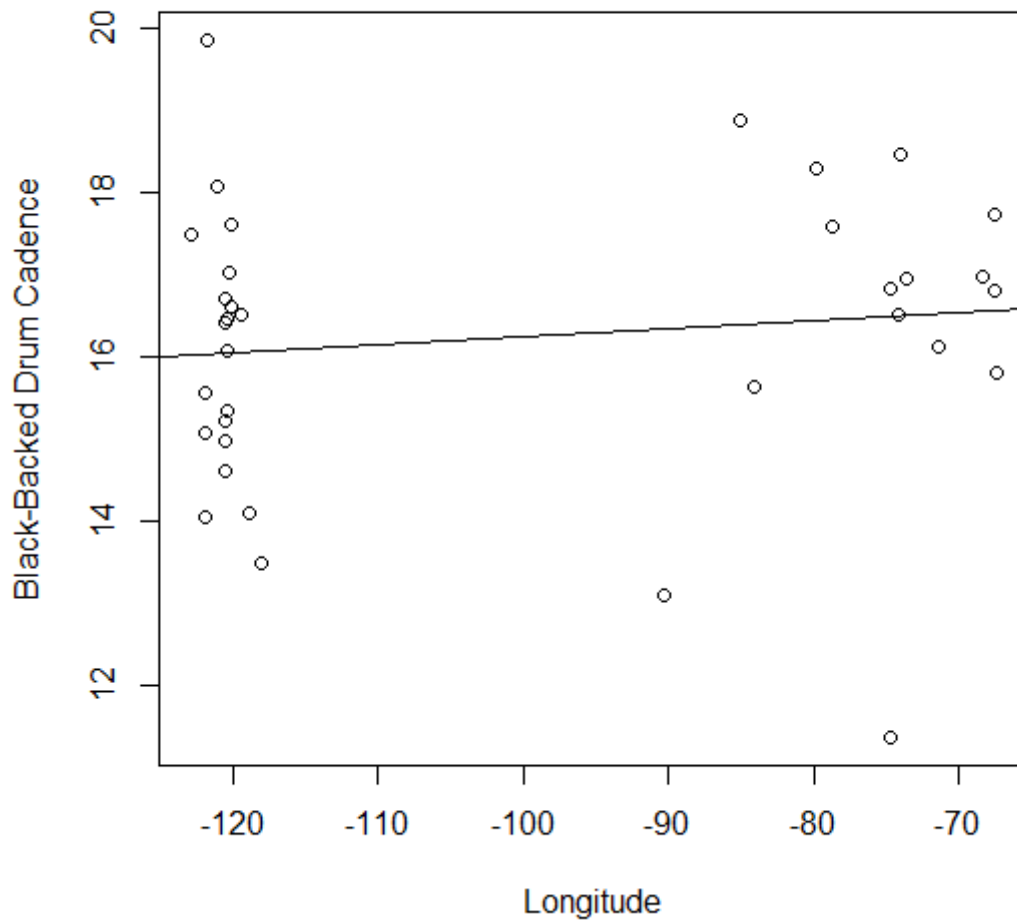


Figure 7. Drum cadence in Three-Toed Woodpeckers as a function of longitude. This figure plots the drum cadence from all Three-Toed Woodpeckers as a function of the longitude of the recording location. The black line illustrates the line of best fit for the data, $r = -0.71$, $p = 0.3499$. This did not pass the level of significance, with a caveat that it may be skewed by geographic outliers. Each dot corresponds to a recorded drum sequence from a Three-Toed individual.

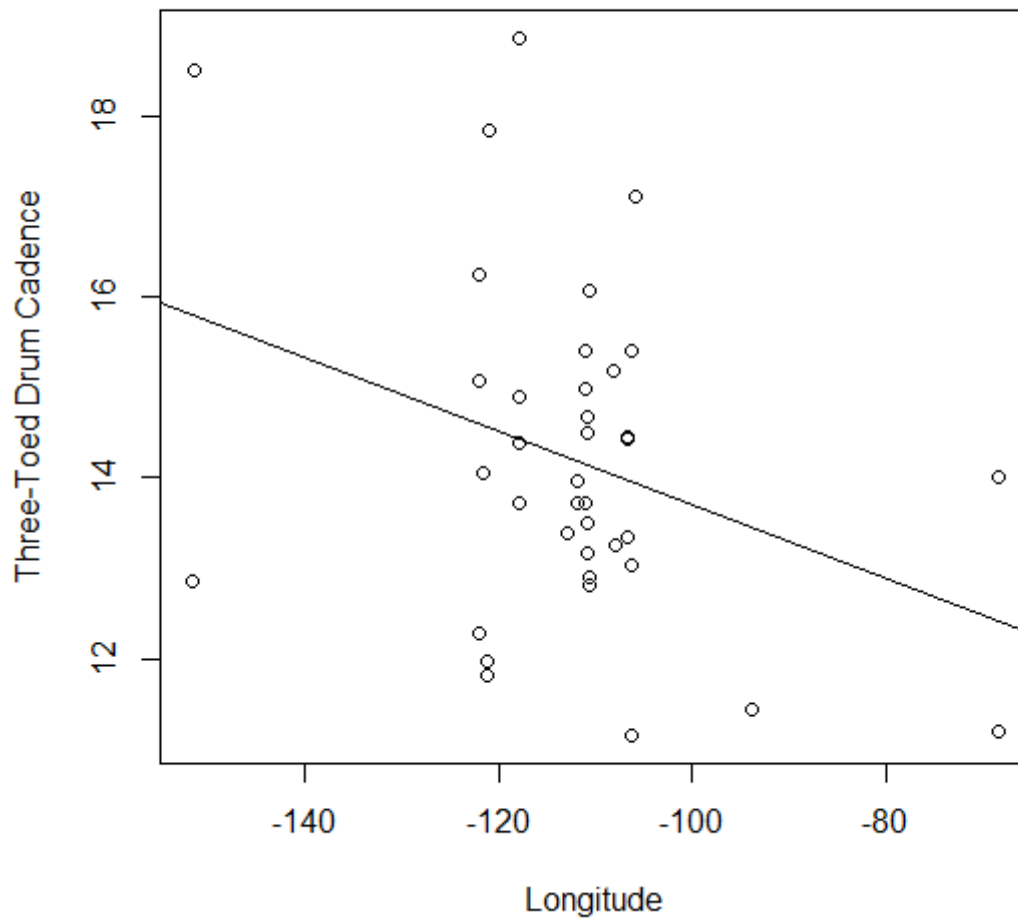


Figure 8. Drum cadence in Hairy Woodpeckers as a function of longitude. This figure plots the drum cadence from all Hairy Woodpeckers as a function of the longitude of the recording location. The black line illustrates the line of best fit for the data, $r=-0.84$, $p=0.7221$. This did not pass the level of significance, with a caveat that it may be skewed by geographic outliers. Each dot corresponds to a recorded drum sequences from a Hairy individual.

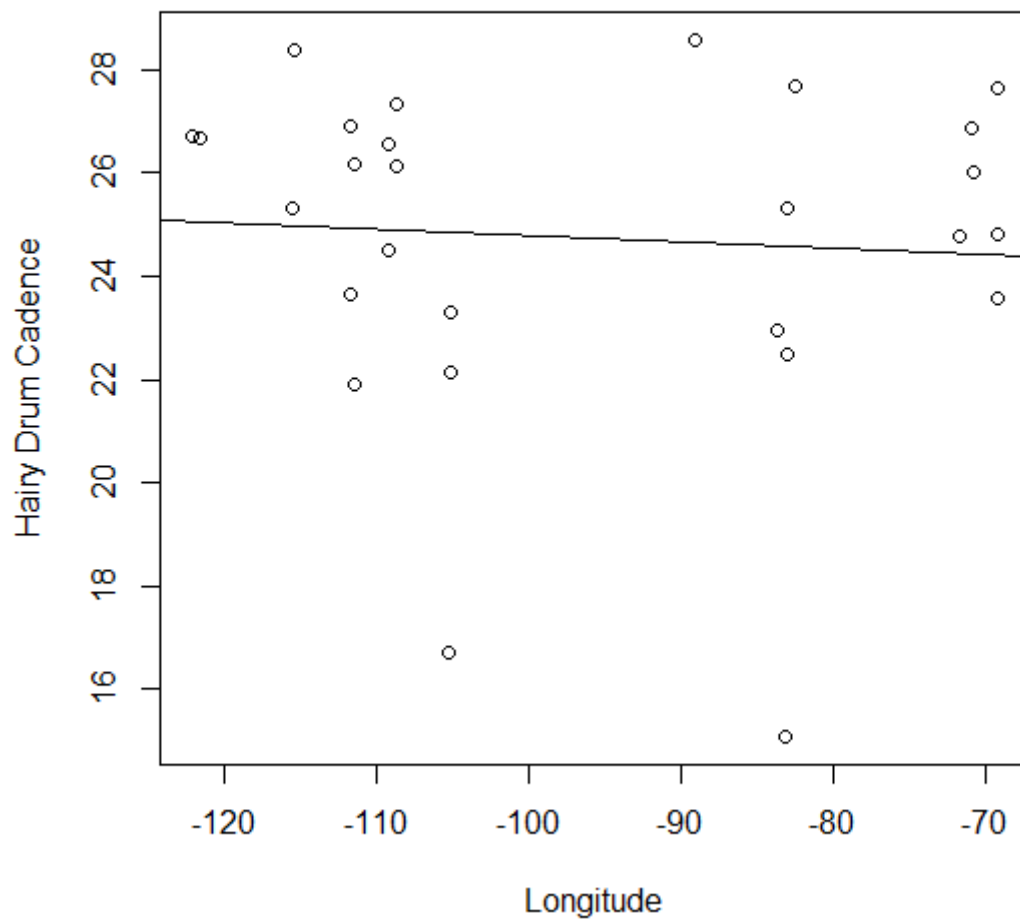


Figure 9. Reaction times to experimental drum signals. This figure illustrates the Downy individual's latency to react to the playback drum signal. The black bars illustrate the median reaction time per signal type. The boxes extending on either side of the median illustrate the interquartile ranges of the response rate. The ID names used below each boxplot refers to the type of experimental signal used (e.g. control = 16.5 drums per second). Each individual bird is represented by a line linking three points, with one point for each playback. These trends were significant with a caveat that there were only two individuals per group, asym sig = 0.004.

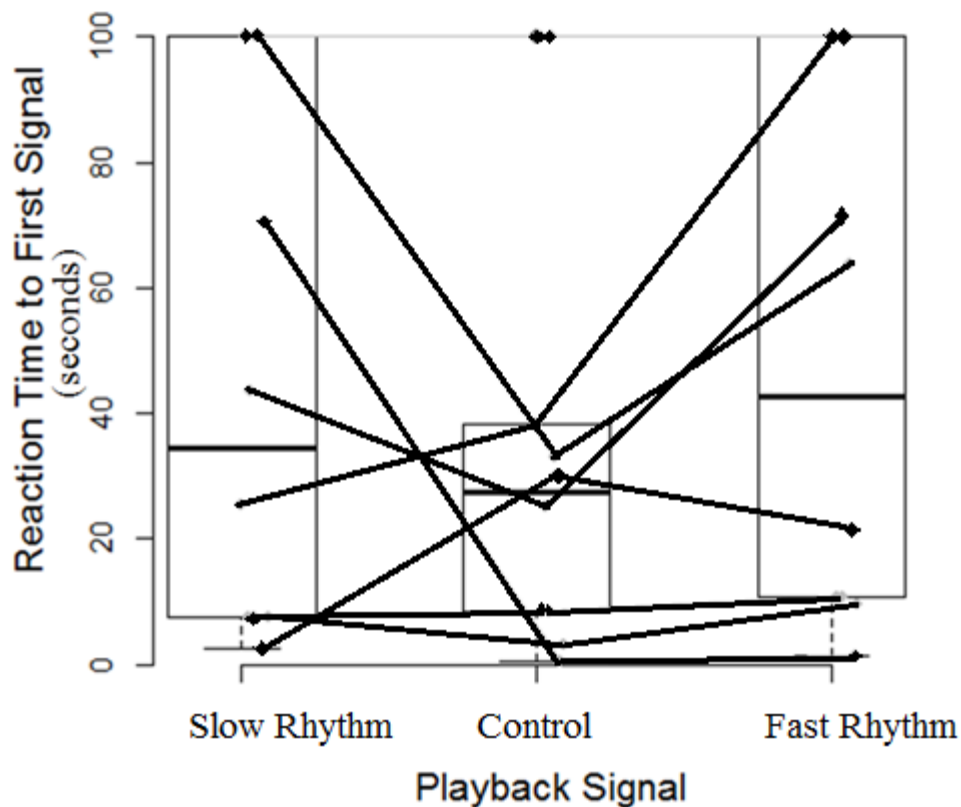


Figure 10. Reaction time to experimental call signals. This figure illustrates individual Downy reaction times to respond to the playback call signal. The black bars illustrate the median reaction time per call type. The boxes extending on either side of the median illustrate the interquartile ranges of the response rate. The ID names used below each boxplot refers to the type of experimental signal used (e.g. 11 notes per second). The trends were significant, with a caveat that there were only two individuals, asym. sig = 0.000. Symbol lines same as in Figure 9.

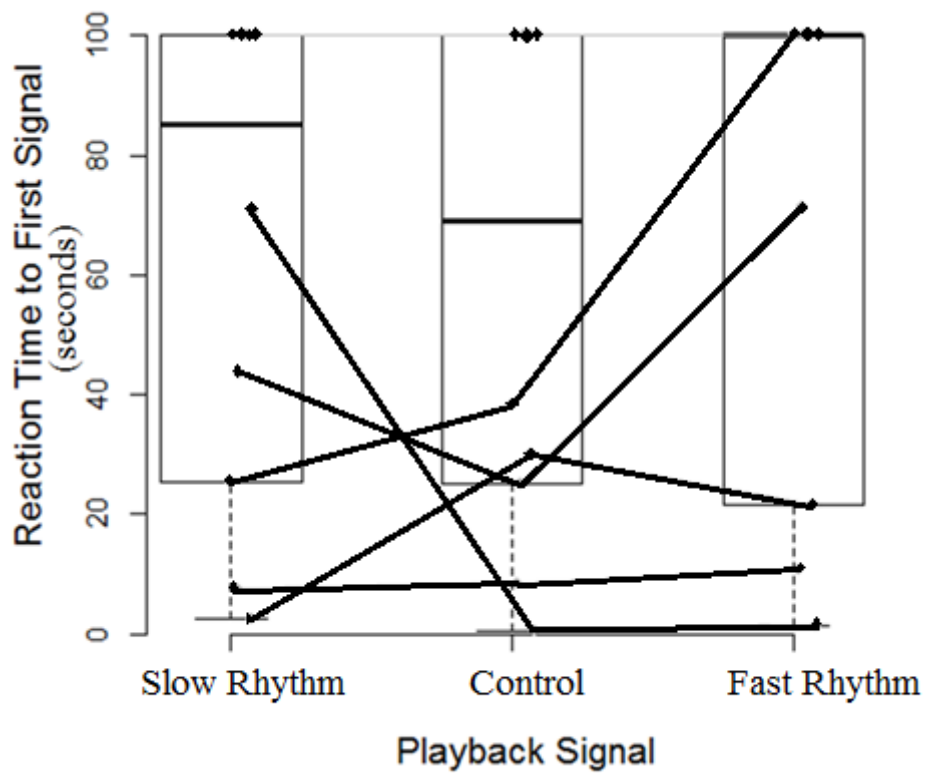


Figure 11. Interdrum interval recorded from five unique Downy Woodpecker drums. This graph illustrates the interdrum interval of five Downy Woodpecker drum as a function of time elapsed. The squares indicate a single drum hit, with square color denoting a unique individual, while the black line illustrates the line of best fit for each function.

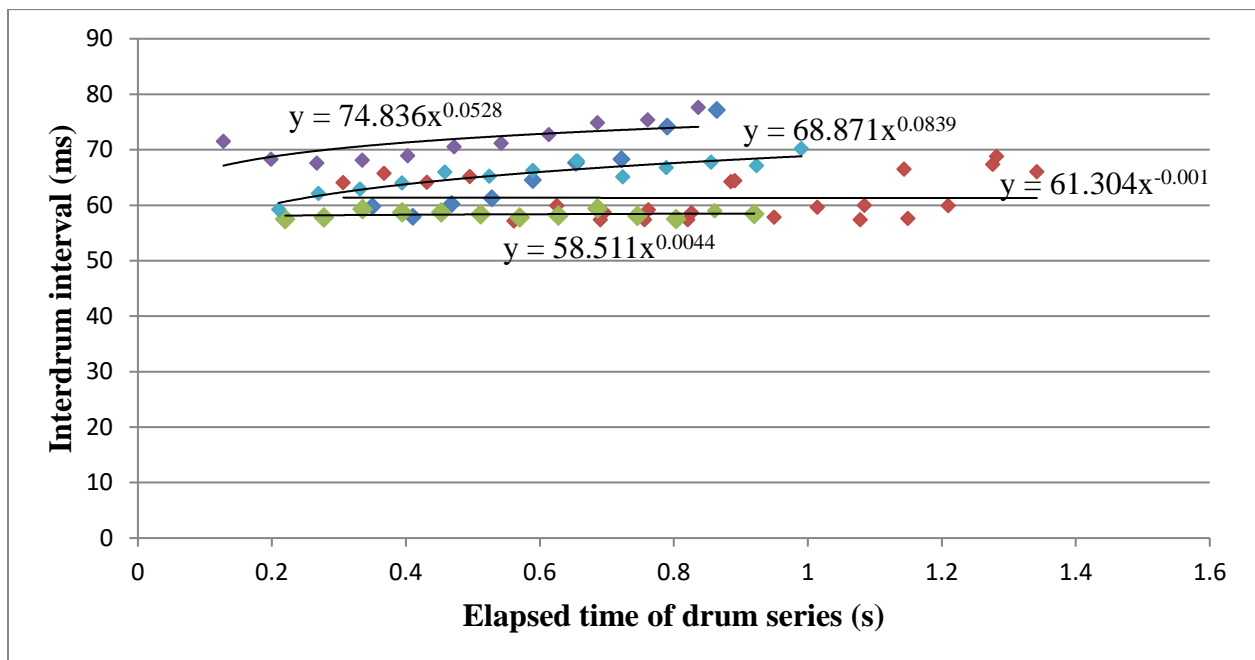


Figure 12. Sample interdrum interval graph for Black-Backed Woodpeckers. This graph illustrates the interdrum interval of five Black-Backed Woodpecker drums as a function of time elapsed. The squares indicate a single drum hit, with unique colors denoting unique individuals, while the black line illustrates the line of best fit for each function.

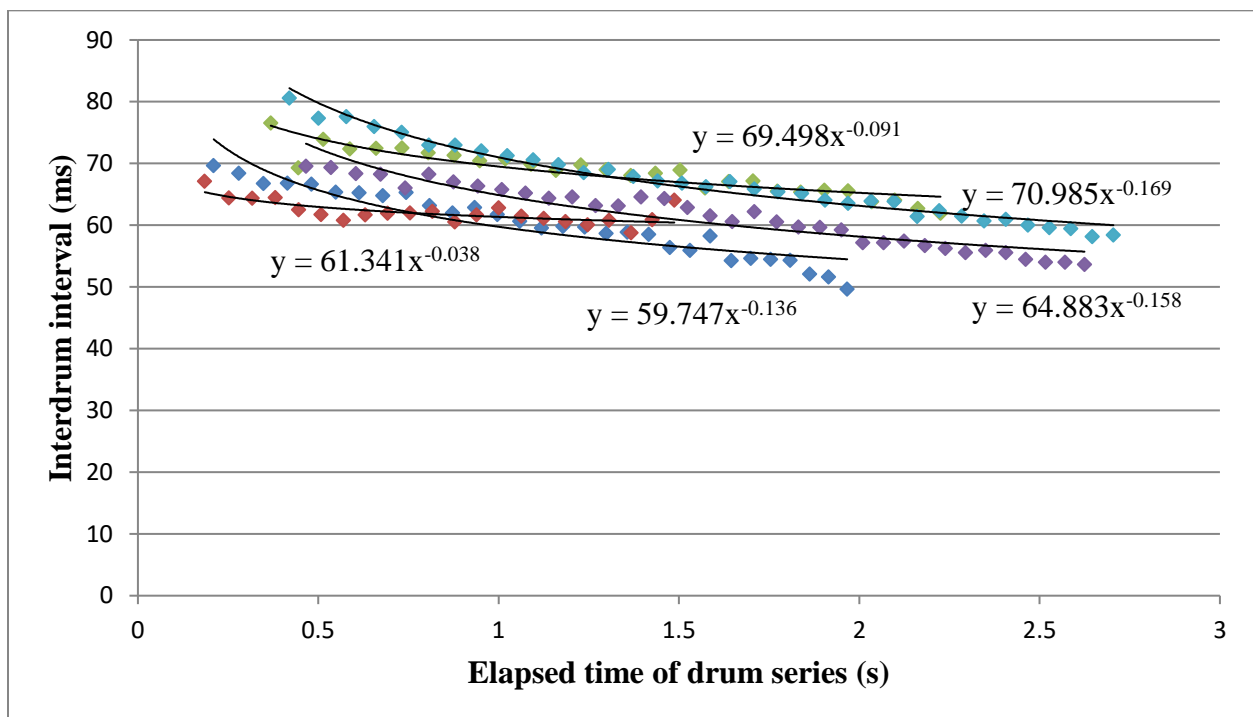


Figure 13. Sample interdrum interval graph for Three-Toed Woodpeckers. This graph illustrates the interdrum interval of three Three-Toed Woodpecker drums as a function of time elapsed. The squares indicate a single drum hit, with unique colors denoting unique individuals, while the black line illustrates the line of best fit for each function.

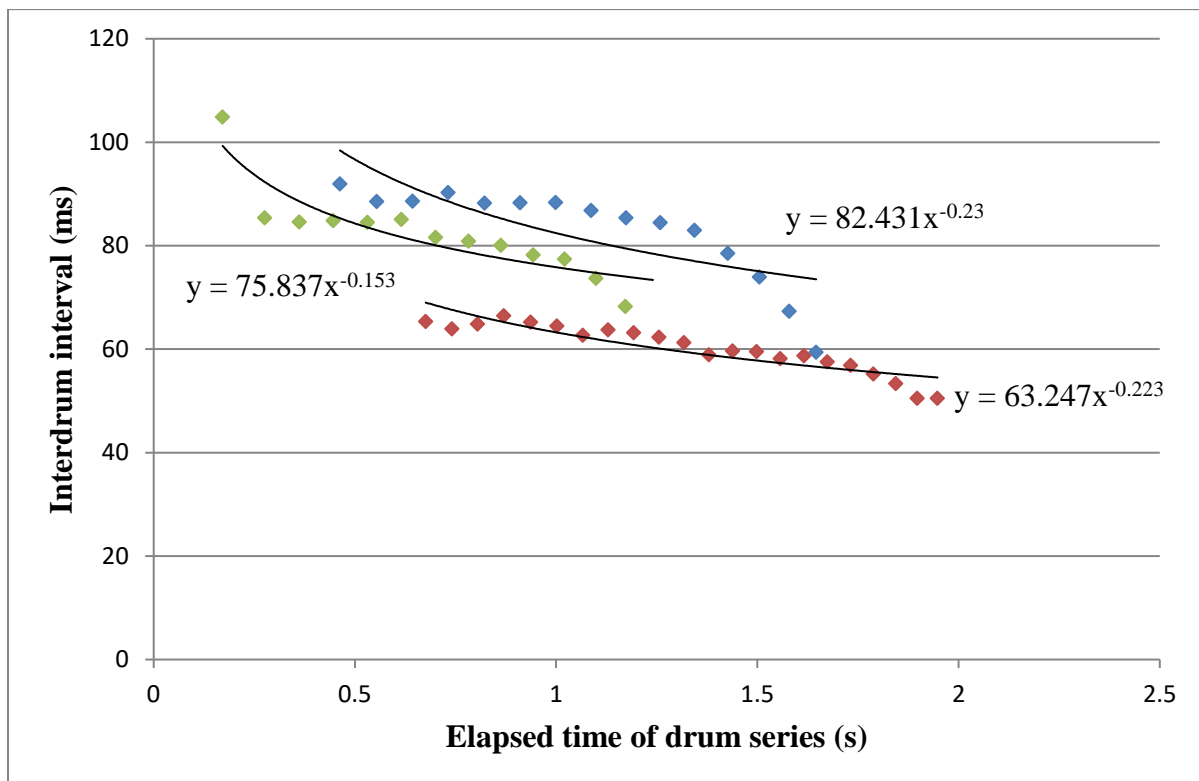
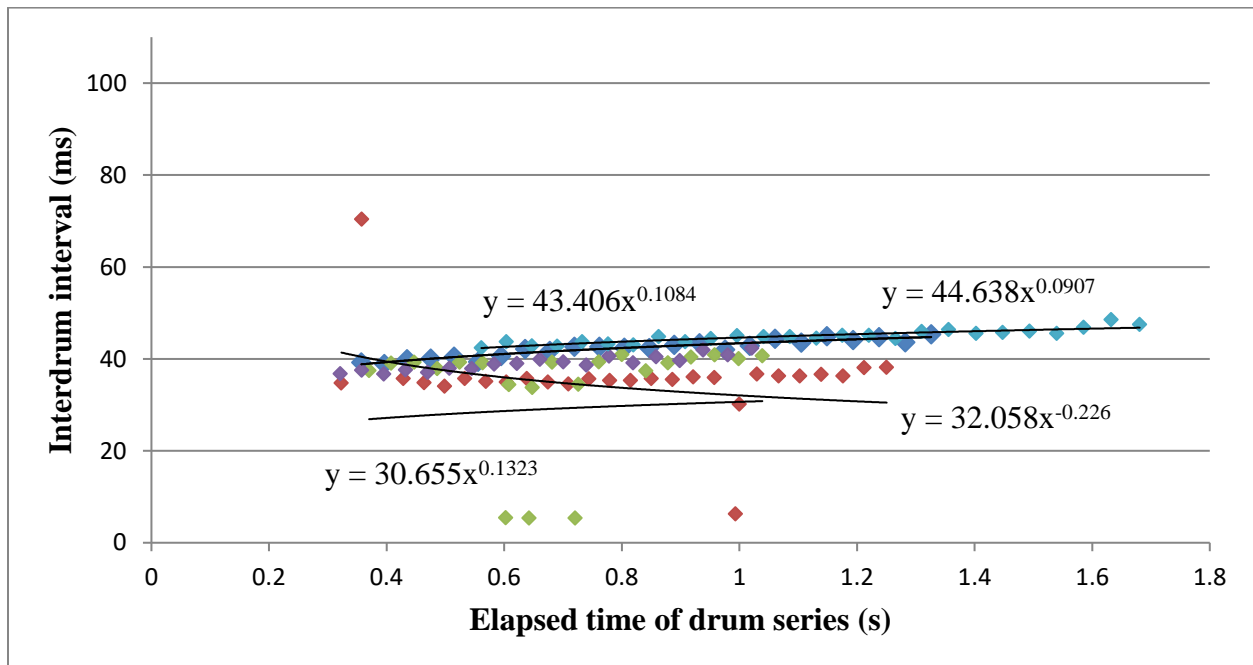


Figure 14. Sample interdrum interval graph for Hairy Woodpeckers. This graph illustrates the interdrum interval of five Hairy Woodpecker drums as a function of time elapsed. The squares indicate a single drum hit, with unique colors denoting unique individuals, while the black line illustrates the line of best fit for each function.



Abbreviations & Key Terms

Cadence - a measure of mechanical rate, operationally defined by Stark *et al.* (1998) as the number of drums divided by the length of time of an acoustic sequence, or drums \bullet cadence⁻¹.

Cadence on First Series - measure of drum or call rate for the individual's first response to the playback.

Dialect - a system of communication characteristic of a unique group developing in isolation from other related groups.

Geographic variation - the variation in a behavior or trait attributed to isolation from other related groups due to geographic isolating barriers.

Latency to Drum - an operational measure of the time elapsed between the playback of the experimental drum sequence and the individual's drum response.

p - significance value, or the probability that a result is significant.

Picoides - a genus of North American and Eurasian woodpeckers which contains the species in this study.

Picid - referring to woodpeckers in the genus *Picoides*.

Rattle call - a short burst of vocalizations made by *Picoides* woodpeckers, elsewhere referred to as a 'whinny'.