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Characteristics, contexts, and possible functions of the vocalizations of Blue Jays

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Characteristics, contexts, and possible functions of the vocalizations of Blue Jays

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Abstract

Many species in the family Corvidae, including Blue Jays (*Cyanocitta cristata*), are known to have large vocal repertoires. However, perhaps due to its perceived complexity, few investigators have attempted to describe the vocal repertoire of Blue Jays. Therefore, my objectives were to describe the vocal repertoire of Blue Jays, determine the characteristics of their calls, and suggest possible functions. During 2015 and 2016, I studied free-living Blue Jays in and near Richmond, Madison County, Kentucky. I observed Blue Jays at 17 different locations, recorded their vocalizations, and noted the behavioral contexts during which calls were uttered. I also conducted playback experiments with four different Blue Jay calls and with the calls of several species of raptors to provide additional contexts that might provide insight into call function. I recorded 7213 calls uttered during 488 vocal bouts during 103 observation sessions, and identified 40 distinct call types distinguished by their characteristics (peak frequency, high frequency, low frequency, frequency range, and duration). Three call types were only uttered by nestling and fledgling Blue Jays, and two call types were only uttered by adult Blue Jays during playback experiments. Some call types were used more often during either the breeding or non-breeding season and in certain behavioral contexts, suggesting that they served particular functions. However, most call types of adult Blue Jays were used throughout the year and in a variety of behavioral contexts, making it difficult to determine possible functions. Differences in call types used and use of the same calls in different contexts by Blue Jays at different locations suggest that they learn some call types in their vocal repertoires. Further, Blue Jays at different locations or in different flocks may have distinct vocal repertoires and particular calls may serve

different functions. A possible explanation for the large vocal repertoire of Blue Jays and other species of birds is the social complexity hypothesis. Species, like Blue Jays, that regularly interact with large numbers of conspecifics in a variety of behavioral contexts are more likely to benefit from having larger vocal repertoires than solitary or less social species. Additional detailed study of species of songbirds with large vocal repertoires, including Blue Jays, will improve our understanding of how such repertoires are used as well as the selective pressures that have favored their evolution.

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Chapter I

Introduction

Passerine song has been well-studied and shown to function in attracting mates (Mountjoy and Lemon 1990), defending territory boundaries (Nowicki et al. 1998), and facilitating mating (Eriksson and Wallin 1986, Reid et al. 2004). Calls are typically structurally simpler than, and have been the focus of fewer studies than, passerine song. As noted by Marler (2004), calls are mostly innate vocalizations that are versatile modes of communication because of the many ways that their characteristics can vary.

Boogert et al. (2008) demonstrated that the complexity of avian vocalizations, in at least one species, was positively correlated with problem-solving ability. Species in the family Corvidae are known for their intelligence (Emery and Clayton 2004, Heinrich and Bugnyar 2005), a characteristic likely correlated with advanced and complex systems of communication. As an example of corvid intelligence, Blue Jays (*Cyanocitta cristata*) have been observed using tools (Jones and Kamil 1973), vocally imitating raptors with possible kleptoparasitic intent (Clench 1991, Loftin 1991), and displaying a moderate level of sociality (Racine and Thompson 1983).

Blue Jays and other corvids, although in the songbird order Passeriformes, rely primarily on calls for vocal communication. Although known to have a complex vocal repertoire (Conant 1972, Cohen 1977), questions remain about the size of the vocal

repertoire of Blue Jays, how they might vary their use of calls in different contexts to convey different information to conspecifics, and the possible function(s) of their many calls. Perhaps because of the size of their vocal repertoire, as well as both individual and context-specific variation in the characteristics of some of their calls, few investigators have attempted to either describe the vocal repertoire Blue Jays or determine the possible functions of their many call types (Conant 1972, Cohen 1977).

The vocal behavior of other corvids, such as Common Ravens (*Corvus corax*) and American Crows (*Corvus brachyrhynchos*), has been studied more extensively. For example, Thompson (1982) observed hierarchical organization of the 'caw' calls of American Crows and Carrion Crows (*Corvus corone*), suggesting an advanced system of communication. For Common Ravens, Conner (1985) categorized 18 call types, with some used in specific contexts. Mexican Jays (*Aphelocoma wollweberi*) are able to discriminate between group members and non-group members based on vocal cues (Hopp et al. 2001) and, using vocal cues, Pinon Jays (*Gymnorhinus cyanocephalus*) are likely able to distinguish between individuals within social groups (Berger 1977). Hope (1980) described 15 call types in the repertoire of Steller's Jays (*Cyanocitta stellerii*), but did not definitively link specific call types with particular contexts.

Conant (1972) studied captive, hand-raised Blue Jays and described 20 distinct calls. Cohen (1977) studied free-living Blue Jays, but described only 15 distinct calls. An accepted naming system of Blue Jay calls would allow investigators to better collaborate and concert efforts. However, nomenclature is inconsistent in regard to Blue Jay calls. For example, what Conant (1972) called the 'pump handle' and 'soft keu' calls, Cohen (1977) called the 'squeaky gate' and 'yurp' calls, respectively.

These authors and others have discussed possible functions of some Blue Jay call types. For example, the 'bell call' may allow identification of individuals (Kramer and Thompson 1979). Hailman (1990, 2009) noted that Blue Jays sometimes imitated other species, especially raptors, and hypothesized that such calls might be used either to deceive and steal food from other birds or to warn conspecifics of danger. Possible functions of other call types in their vocal repertoire remain to be determined. Clearly, more detailed observations of free-living Blue Jays, in combination with experiments designed to gain insight into the possible functions of different calls, are needed to better understand their apparently complex vocal behavior. Thus, the objectives of my study were to 1) describe the vocal repertoire of free-living Blue Jays, 2) examine possible relationships between call use and context, and 3) suggest a universal nomenclature for their calls.

Chapter II

Methods

Study Area

During the non-breeding season, my study took place primarily at and near the Blue Grass Army Depot (BGAD), located 11 km southeast of Richmond, Madison County, Kentucky. The 6070-ha BGAD consists largely of pasture and grassland, with several woodlots of various sizes constituting nearly half of the property (46%). Some experiments and observations took place on private property in or near Richmond and on the campus of Eastern Kentucky University (EKU) in Richmond. During the breeding season, most experiments and observations were made on or near the campus of EKU.

Eight feeding stations stocked with cracked corn and sunflower seeds were established at the BGAD during late October 2014. Once Blue Jays began visiting hanging feeders (60 cm x 60 cm wooden platforms with a plastic container attached to hold sunflower seeds, peanuts, and cracked corn), I attempted to capture as many individuals as possible using mist-nets or walk-in traps placed near the feeders. However, too few Blue Jays were captured (n = 5) to be able to reliably identify different individuals during observation sessions. As a result, I could only discriminate between Blue Jays at different locations, and considered all jays at a location (mean range size = 21.5 ± 3.2 ha, range = 0.09 - 21.51 ha, N = 17) to be isolated from those at other locations

if separated by at least 600 m, a distance that precluded intermingling of banded jays at separate feeding stations in a previous study (Racine and Thompson 1983). In addition, during the breeding season, locations less than 600 m apart were considered distinct if mated pairs had nests at those locations.

Observations/Experiments

Blue Jays at each location (n = 21) were studied from 1 August to 17 March (non-breeding season) and from 18 March to 31 July (breeding season) (Hardy 1961, pers. obs.). I followed, observed, and recorded Blue Jays during December 2014, from January to July 2015, and during January and February 2016. Twelve locations were visited during the non-breeding season, and the mean number of visits per location was 4.5 ± 1.11 S.E. (range = 1 – 12). Eleven locations were visited during the breeding season, and the mean number of visits per location was 4 ± 1.07 (range = 1 – 14). Overall, Blue Jays at 17 locations were observed and recorded during non-experimental observation periods. At eight nest sites, I both observed and recorded Blue Jays and, during other visits, conducted playback experiments. At four nest sites, I only conducted playback experiments (Table 1)[1].

Observations

Blue Jays were observed at different times during the day, and observation periods varied in duration from 1 min (when an individual or group flew away after 1 min of observation and recording) to 91 min, with an average duration of 17.8 min (n = 103

[1] See Appendix for all tables and figures

observations). I spent 917 min observing Blue Jays during the breeding season, and 932 min during the non-breeding season. During all observation periods, I attempted to maintain visual and vocal contact, but also remained sufficiently distant (≥10 m) in an attempt to minimize the effect of my presence on Blue Jay behavior. Vocalizations uttered by Blue Jays during observations were recorded using one of two digital solid state recorders (Marantz Professional, Model PMD620MK II or Tascam Linear PCM Recorder DR-05) with a unidirectional shotgun microphone (Audio-technica Telemike, Model ATR55).

During each observation period, I noted the time, date, and, during the breeding season, the breeding stage. The breeding season was divided into five stages, including rowdy grouping (8 April to 3 June, when groups of four or more Blue Jays flew together, apparently chasing each other), courtship (mid-April when I observed males feeding females or pairs building nests), incubation/brooding (11 May - 6 July when jays were incubating eggs or brooding nestlings < 5 days old), nestling provisioning (10 May - 13 July when jays were feeding nestlings), and post-fledging (31 May - 20 July when adult jays were feeding fledged young). During observation periods, I continuously recorded Blue Jays and verbally described behavioral contexts. Behavioral contexts, determined by the behavior of vocalizing birds, conspecifics, and heterospecifics (e.g., predators), were categorized into both specific contexts and more general context-families so that different levels of contextual resolution could be used during analysis (Table 2). Context-families included contexts that were related in some way. For example, the predator-related context and human-related context were both in the threat context-family. When recording the calls of Blue Jays, the single most appropriate context was assigned

whenever possible. I also noted when call types were paired (successive calls with inter-call intervals ≤ 0.5 sec).

Raven software (Cornell Lab of Ornithology, Ithaca, NY) was used to analyze, characterize, and categorize Blue Jay vocalizations based on their duration, peak frequency (frequency with the maximum amplitude or volume), high frequency, low frequency, frequency range (difference between high and low frequency), and number of notes (with 'note' defined as a continuous line on a spectrogram). For each call type recorded, I chose 30 individual calls of the best sound quality to measure these characteristics, or as many that I recorded, with representation from as many locations as possible. Based on call morphology and the measurements listed above, with the exception of imitated predator calls that were placed in the same call-family regardless of structure, I placed these call types in 15 different 'call-families' to aid in assigning possible functions of calls at different resolutions (call type = finer resolution; and call-family = coarser resolution). For example, all call types in the descending jay call-family had a peak frequency of approximately 3200 hertz (3.2 kHz), a frequency range of approximately 1000 hertz, and consisted of a single, down-slurred note (Figure 1). I have also provided spectrograms for all of the other call types, grouped by call-family (Figures 2 to 15). I analyzed the use of different call types and call-families based on both total number of calls uttered and total number of bouts (bout = all calls of a call type uttered in a specific context during a specific observation session) uttered in different contexts and context-families to better understand possible functions. All analyses were conducted using the Statistical Analysis System (SAS Institute 2014). Values are presented as means ± SE.

Experiments

In addition to observing and recording Blue Jays and noting contexts during which calls were uttered, I also conducted experiments in an attempt to better understand the functions of specific calls types. During these experiments, I (1) broadcast calls of Blue Jays over a speaker and noted the responses of focal individuals or groups, and (2) broadcast calls of aerial predators in combination with the presentation of study skins of these predators, and noted the responses of Blue Jays. All experiments were recorded with a camcorder (Sony HDR-XR100 High Definition).

Experiment one: Four Blue Jay call types, including jay calls (flat and descending), squeaky gate calls (squeaky gate and partial squeaky gate), bell calls, and rattle calls (continuous rattle only), were broadcast to either individual Blue Jays or groups of Blue Jays during both the breeding and non-breeding seasons. Conant (1972) described jay calls as being used in situations of conflict, squeaky gate calls in situations of suspicion, rattle calls in situations of distress, and bell calls in territorial situations. By playing back call types and then quantifying the reactions of jays, I hoped to gain insight concerning the possible functions of the calls. The 'kwirr' call of Red-bellied Woodpeckers (*Melanerpes carolinus*) was used as a control, i.e., a vocalization that would likely elicit no or minimal responses from Blue Jays. To avoid pseudoreplication, I used different recordings of each Blue Jay call type during playback experiments, including four squeaky gate calls, four rattle calls, three jay calls, and three bell calls. All Blue Jay call types and the control recording were downloaded from the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology, Ithaca, NY). All of the recordings were from Blue Jays in either Florida or Maryland because no recordings of

Blue Jays in Kentucky were available. Playback recordings were broadcast with an iPod attached to a speaker (iHome, model iD48) at a volume comparable to calls uttered by live Blue Jays. Experiments were only conducted if I was able to approach within 50 m of jays without having them respond to me vocally or by making flights. During the breeding season, these experiments were always conducted approximately 20 m from a nest. I never approached to closer than ~10 m of focal jays and, after the playback recording began, I did not move until the post-playback period had concluded. If possible, although doing so was not always possible, I tried to conceal myself so that the jays could not see me during experiments.

During both the breeding (incubation and nestling stages) and non-breeding seasons, recordings of each call type and the control were broadcast at different locations (non-breeding season: n = 6; breeding season: n = 3). Playback experiments at each location were at least two days apart. During playback and for an additional 3-min post-playback period, I recorded the vocal responses of Blue Jays and also noted their behavior. Specifically, I noted the number of flights (any movement that required flapping) made by individuals as a possible measure of the degree of agitation or stimulation elicited by the playback recording (Radford and Blakey 2000). I noted responses as calls or flights per 'jay minute' to account for variation in the number of jays present during playback experiments and the amount of time that jays were present (e.g., two jays present for the same minute equaled two jay minutes and 10 calls uttered during that time would equal 5 calls/jay minute). I also estimated the distance of all Blue Jays that were within 100 of the playback speaker every 30 sec during playback and post-playback periods.

Raven software (Cornell Lab of Ornithology, Ithaca, NY) was used to identify call types, by measurements of structural characteristics and visual appearance of spectrograms, uttered by Blue Jays during both the playback and post-playback period. I used repeated measures analysis of variance to compare the behavioral responses of Blue Jays during playback of different calls, with location as a blocking factor. When differences were significant, a post-hoc Tukey's test was used to compare means. All analyses were conducted using the Statistical Analysis System (SAS Institute 2014). Summary values are presented as means ± SE.

Experiment two: Predator recordings were downloaded from the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology, Ithaca, NY), with recordings of three different individuals of each species used in the experiments to avoid pseudoreplication. Eastern Screech-Owls (*Megascops asio*) (whinny call), Cooper's Hawks (*Accipter cooperii*) (kek-kek call), and Great-Horned Owls (*Bubo virginianus*) (hoo-hoo call), aerial predators that likely pose different levels of threat to Blue Jays, were broadcast to Blue Jays at five locations (n = 5) during the breeding season (incubation and nestling provisioning stages) and six locations (n = 6) during the non-breeding season. As a control, the 'kwirr' call of Red-bellied Woodpeckers was used. During the breeding season, Sharp-shinned Hawk (*Accipiter striatus*) calls (squeal call) were also broadcast, although playback experiments were not conducted at all locations either due to nest predation or fledging of young for nests located late in the nestling stage (Table 3). Playback sessions consisted of 3-min recordings of the calls of each predator. During playback and for an additional 3-min post-playback period, I recorded the vocal responses of Blue Jays and noted the behavior of focal Blue Jays. Specifically, I

noted the number of flights made by individuals as a possible measure of the degree of agitation or stimulation (Radford and Blakey, 2000). Again, I analyzed data based on calls and flights per jay minute. I also estimated the distance of all Blue Jays that were within 100 m of the playback speaker every 30 sec during playback and post-playback periods.

Raven software (Cornell Lab of Ornithology, Ithaca, NY) was used to identify call types, by measurements of structural characteristics and visual appearance of spectrograms, uttered by Blue Jays during both the playback and post-playback period. I used repeated measures analysis of variance to compare the behavioral responses of Blue Jays during playback of different calls, with location as a blocking factor. All analyses were conducted using the Statistical Analysis System (SAS Institute 2014). Summary values are presented as means ± SE.

Chapter 3

Results

I observed Blue Jays at 17 different locations representing 17 different groups, and the mean number of jays at these locations was 2.8 ± 0.3 birds (range = 1.4 – 5 birds). The mean number of observation periods per location was 6.0 ± 1.2 (range = 1 – 16), and the mean time spent observing Blue Jays at each location was 113.7 min (range = 10 min – 327.1 min). The mean duration of observation periods was 19.6 ± 2.9 min (range = 30 sec – 85 min). The mean number of different call types recorded for each location was 11.6 ± 1.7 (range = 2 – 24), with a significant positive correlation between the number of different call types recorded and the total amount of times locations were visited ($r_s = 0.84$, $P < 0.0001$). The relationship between number of different call types recorded and mean birds at a location was not significant ($r_s = 0.32$, $P = 0.21$). However, I found a significant positive correlation between the size of the largest number of Blue Jays observed at a location (mean = 5.6 ± 0.6, range = 3 – 9) and the number of different call types recorded ($r_s = 0.64$, $P = 0.025$).

Overall, I recorded 488 context and observation-specific bouts (single call type associated with a single context during a single observation period) and a total of 7213 individual calls. I recorded 301 bouts of calling during the breeding season and 187 during the non-breeding season, with Blue Jays uttering 4137 and 3076 calls, respectively, during those two seasons. Overall, I identified 42 different Blue Jay

vocalizations, including 40 recorded during observations of Blue Jays and two recorded only during playback experiments. Of the 42 different call types, three were uttered only by nestlings or fledglings (nestling twitter, juvenile extended whine jay, and juvenile whine jay).

None of the 40 call types recorded during observation periods were recorded at all 17 locations. Three call types were recorded at 12 of 17 locations (70.6%), one call type at 10 locations (58.8%), and two call types at 9 locations (52.9%), but the remaining call types (34, or 85%) were recorded at seven or fewer locations (Figure 16). Call types uttered at ≥ 9 locations constituted over 50% of all of the calls that I recorded (3642/7213 [50.5%]) and 42% of the bouts that I recorded (205/488). In addition, whereas I recorded from 31 to 46 bouts of six call types, including burry descending jays (46 bouts), harsh descending jays (40 bouts), flat jays (39 bouts), short descending jays (38 bouts), yurping bouts (32 bouts), and squeaky gate calls (31 bouts), four or fewer bouts were recorded for 16 call types (Table 4).

Contexts

The calls of nestling and fledgling Blue Jays were only recorded during the breeding season, but several other call types were also recorded more often during either the breeding or non-breeding season. For example, I recorded 25 bouts of the yurping bout during the breeding season and only seven bouts during the non-breeding season. Call types in the imitation call-family were uttered during 24 bouts during the breeding season and only 10 bouts during the non-breeding season. I have summarized all call

types that were uttered at least twice as much in one part of the year (breeding or non-breeding) compared to the other, as well as the use of all call-families by season (Table 5). Blue Jays were more vocal during the breeding season (4.5 calls/min of observation) than the non-breeding season (3.3 calls/min). Specifically, jays were the most vocal early in the breeding season during what I termed the 'rowdy grouping' stage when Blue Jays chased other Blue Jays (on some occasions I could tell that females were being chased because they were uttering the rattle call, which has been reported to be a female-specific call [Conant 1971]). Of all calls recorded during the breeding season, more than half were uttered during the rowdy grouping stage (109/204 bouts [53.4%]; 1917/3123 calls [61.4%]). Specifically, flat jay calls (17/109 bouts [15.6%]; 578/1917 calls [30.2%]) and harsh descending jay calls (9/109 bouts [8.3%]; 251/1917 calls [13.1%]) were used most often of all calls uttered during the rowdy grouping stage. The short crow (4/109 bouts [3.7%]; 182/1917 calls [9.5%]) and partial squeaky gate (5/109 bouts [4.6%]; 144/1917 calls [7.5%]) were also used relatively frequently. The remaining 74 bouts and 762 calls uttered during the rowdy grouping stage were represented by 22 different call types.

Some call types appeared to be associated with certain behavioral contexts. For example, yurping bouts were associated with adults provisioning young (3/6 bouts [50%]; 10/16 calls [66.7%]) more than other call types, and most grunt calls were uttered in situations of distress such as when a jay was in the hand or a mist net (4/6 bouts [66.6%]; 17/24 calls [70.8%]). The flat jay was most used as a flight call, based on bouts and number of calls, (13/63 bouts [40.6%]; 211/511 calls [40.6%]), though the short descending jay (10/63 bouts [15.9%]; 77/511 calls [14.8%]) was also used often as a flight call. Some call types were used in multiple contexts and context-families, such as

the harsh descending jay, which was the most commonly used call type based on bouts and total number of calls in the threat context-family, social context-family, and foraging context-family. The flat jay was the second most commonly used call, based on total number of calls, in the spontaneous, social, and foraging context-families (Table 6).

Within context-families, use of some call types varied based on specific context. In the social context-family, for example, short descending jays (based on total number of bouts uttered) were most often uttered in the social context (17/144 bouts in this context were the short descending jay), with the yurping bout, squeaky gate, and burry descending jay calls occurring in 14 bouts. The chasing context, also included in the social context-family, had even less specific call context association than the social context. More yurping bouts (4/27 bouts) and flat jay calls (3/27 bouts) than any other call type were used in this context, with 12 other call types being uttered in two or less bouts. Call use the threat context-family varied with the type of threat. For example, based on total number of bouts, harsh descending jays (6/44 bouts), squeaky gate calls (4 bouts), and burry descending jays (4 bouts) were used most in the predator-related context whereas the Red-tailed Hawk call was often used in the human-related context (4/10 bouts). Six other call types (including the individual yurp, perfect crow, squeaky gate, whistle, and yurping bout) were also uttered, during one bout, in the human-related context.

Use of at least five call types (burry descending jay, burry flat jay, juvenile extended whine jay, short descending jay, and yurping bout) seemed more or less likely to be uttered depending on the presence or absence of conspecifics and, if present, the proximity of the apparent recipient. For example, burry descending jays were used when

there was no obvious recipient more than when there was one (no recipient = 14/21 bouts [66.7%]; 570/632 calls [90.2%]). Burry flat jays were uttered exclusively when there was no obvious recipient (6 bouts; 59 calls). The yurping bout was used more when Blue Jays were ≤ 3 m from conspecifics than when conspecifics were either distant or absent (17/22 bouts [77.3%]; 86/93 calls [92.5%]) (Table 7).

Experiments

Playback of conspecific call types: I found no difference in the average number of calls/jay minute ($F_{3,12} = 0.1$, $P = 0.96$) or average number of call types uttered ($F_{3,12} = 0.6$, $P = 0.66$) in response to the different treatments (bell, jay, rattle, squeaky gate, and Red-bellied Woodpecker calls) when treatments from the breeding and non-breeding experiments were combined. Playing back conspecific vocalizations did not generally result in individuals responding with the same call type (e.g., playback of bell, rattle, or squeaky gate calls elicited no bell, rattle, or squeaky gate calls, respectively). Some jay calls were uttered in response to the playback of jay calls, though not more than in response to other playback experiments. In response to playbacks of the bell call, six different call types were uttered (burry descending jay, burry flat jay, hoarse jay, partial squeaky gate, whisper song, and whistle). In response to playbacks of jay calls, seven different call types were uttered (burry descending jay, burry flat jay, continuous rattle, flat jay, murmur bout, short descending jay, and squeaky gate). In response to the playbacks of rattle calls, eight different call types were uttered (burry descending jay, extended descending jay, flat jay, harsh descending jay, murmur bout, short crow, short

descending jay, and squeaky gate). In response to the playbacks of squeaky gate calls, eight different call types were uttered (burry descending jay, bell, extended descending jay, flat jay, harsh descending jay, individual yurp, short descending jay, and segmented rattle).

There was also no difference in the average distance of jays from the playback speaker (28.9 ± 3.0 m, n = 36) ($F_{3,20}$ = 1.5, P = 0.24) during playback of the four types of calls. The bell call treatment elicited less flights/jay minute than other treatments ($F_{3,20}$ = 5.0, P = 0.0039) during the playback period, although a Tukey's test failed to detect any differences among the means (P > 0.05; Figure 6).

Playback of the calls of potential predators: I found no difference in mean number of calls/jay minute ($F_{4,20}$ = 1.1, P = 0.39) or the mean number of call types uttered ($F_{4,22}$ = 0.4, P = 0.82) in response to the different treatments (Cooper's Hawk, Eastern Screech-Owl, Great-Horned Owl, Sharp-shinned Hawk, and Red-bellied Woodpecker). Predator playback experiments yielded some imitated predator calls. Two distinct Bald Eagle call types (similar to the 'wail' call) were uttered in response to playback of the calls of Eastern Screech-Owls. A Cooper's Hawk call (kek-kek) was uttered in response to the playback of the calls of Great-Horned Owls. A Red-tailed Hawk call was uttered in response to playback of the calls of Red-bellied Woodpeckers. In response to playbacks of Cooper's Hawk calls, 10 call types were uttered (burry descending jay, burry flat jay, bell jay, extended descending jay, flat jay, harsh descending jay, hiccup, short descending jay, squeaky gate, and whistle). In response to the playbacks of Eastern Screech-Owl calls, 11 call types were uttered (burry descending jay, Bald Eagle bout, bell jay, flat jay, harsh descending jay, hiccup, individual Bald

Eagle note, short crow, short descending jay, squeaky gate, and yurping bout). In response to playbacks of the Great-Horned Owl, 16 call types were uttered (burry descending jay, burry bell, bell, bell jay, Cooper's Hawk, flat jay, harsh descending jay, hiccup, o-we, partial squeaky gate, short crow, short descending jay, squeaky gate, segmented rattle, whistle, and yurping bout). No jays vocally responded to playback of Sharp-shinned Hawk calls.

I found no difference in either the mean distance of jays from the playback speaker ($F_{4,26} = 1.0$, $P = 0.41$) or the mean number of flights per jay per minute ($F_{4,20} = 0.9$, $P = 0.47$) during playback of the five different raptor calls.

Characteristics and Use of Different Call Types

Descending jay family (Figure 1): All six call types in this family typically consisted of a single down-slurred note with a peak frequency between 3000 and 3500 hertz (Table 8). The **short descending jay** (Figure 1A) (so-named because it was shortest in duration of the calls in this family) averaged 0.24 ± 0.01 sec in duration, and had a higher mean peak frequency than other call types in this family (3503 ± 51 hertz). Short descending jay calls were often used in the social context (17/38 bouts [44.7%]; 230/446 calls [52.6%]) and the flight context-family (10/38 bouts [23.3%]; 76/446 calls [17.0%]). This call type was uttered in the conflicted-related context more than any other call type (2/5 bouts [40%]; 17/36 calls [40.5%]) (Table 6), and was often uttered when there were no conspecifics nearby (10/12 bouts [83.3%]; 95/113 calls [84.1%]) (Table 7). These calls were sometimes uttered in quick succession (i.e., pairs; 79 occasions [158 calls of

446 recorded, 35.4%]), often in the social context (7/19 bouts [36.8%]; 33/79 paired calls [41.8%]) and the flight context (4/19 bouts [21.1%]; 9/79 paired calls [11.4%]).

Although similar to the harsh descending jay in duration (mean = 0.36 ± 0.01 sec), the **extended descending jay** (Figure 1C) exhibited a narrower range of frequencies (904 ± 27 hertz) (Table 8). This call was used in eight different contexts, including the social context (4/14 bouts [28.6%]; 106/212 calls [50.0%]), spontaneous context (2/14 bouts [4.3%]; 18/212 calls [8.5%]), and group foraging context (2/14 bouts [4.3%]; 6/212 calls [2.8%]). With the exception of the burry harsh descending jay, the **harsh descending jay** (Figure 1E) had the broadest frequency range of any call in this family (1120 ± 26 hertz) (Table 8) and was recorded more often than any other call type in my study (based on total number of calls, not bouts). This call was often used in the social context (13/40 bouts [32.5%]; 719/1257 calls [57.0%]), the predator-related context (6/40 bouts [15.0%]; 269/1257 calls [20.0%]), and the foraging context-family (8/40 bouts [20.0%]; 172/1257, [13.7%]). The **burry harsh descending jay** (Figure 1D) was similar in duration to the harsh descending jay (means = 0.39 ± 0.02 sec and 0.36 ± 0.01 sec, respectively), had a slightly lower mean frequency (2455 ± 55 hertz for burry harsh descending jay; 2627 ± 30 hertz for harsh descending jay) (Table 8), and the second half of the call exhibited a series of frequency modulations. The burry harsh descending jay call was often used by Blue Jays in the predator-related context (2/9 bouts [22.2%]; 132/233 calls [57%]) and the social context (2/9 bouts [22.2%]; 51/233 calls [21.9%]). The **growl** call (Figure 1B) exhibited a series of frequency modulations, was longer in duration than other calls in this call-family (mean = 0.46 ± 0.07 sec) (Table 8), and was only used in the predator-related context (3/3 bouts; 4/4 calls). The **juvenile descending**

jay (Figure 1F) was relatively short in duration (0.32 ± 0.11 sec), harsh-sounding, and was most often uttered by fledglings waiting to be fed by parents (2/4 bouts [50.0%]; 169/172 calls [98.3%]).

Flat jay family (Figure 2): Both calls in this family consisted of one note, did not exhibit declining frequencies (i.e., not down-slurred, hence the name 'flat' jay), and had a peak frequency of about 3200 hertz (Table 8). **Flat jay** calls (Figure 2A) were short in duration (0.36 ± 0.01 sec) (Table 8), and were often used in the flight context-family (13/39 bouts [33.3%]; 212/986 calls [21.5%]) and the social context (11/39 bouts [28.2%]; 490/986 calls [49.7%]). Flat jays were also uttered more than other call types, in regard to total number of calls uttered, during the chasing context (3 flat jay bouts/31 total chasing bouts [9.7%]; 204/540 calls [38%]), and the only call type that equaled or exceeded this call in total bouts was the yurping bout (n = 4). Two flat jay calls were sometimes uttered in quick succession (110 calls were part of a pair [55 pairs]; 986 total calls were recorded [11.2% of flat jays were part of a pair]). These paired calls were, based on number of bouts, used most in the group flight context (3/8 bouts of paired flat jays were in this context [37.5%]; 8/55 pairs uttered were in this context [14.5%]) and also in the chasing, solo foraging, social, spontaneous, and unknown contexts (one bout each). Based on number of calls, most pairs of flat jay calls (58.2% or 32/55) were uttered in the spontaneous context. Most characteristics of **short growl** calls (Figure 2B) were similar to those of flat jays, but, in contrast to flat jays, short growl calls exhibited a rapid series of frequency modulations (Figure 2B). Based on total number of calls, most short growl calls were uttered in the predator-related context (1/2 bouts [50%]; 5/6 calls [83.3%]), with just a single bout and call uttered in the social context.

Burry jay family (Figure 3): All three call types in this family were frequency-modulated and had a peak frequency of about 2900 hertz (Table 8). Calls in this call-family were used more in the spontaneous context (12/71 bouts [16.9%]; 637/1638 calls [39%]) than those in all other call-families except the descending jay call-family (14 bouts). I recorded more bouts of **burry descending jay calls** (36 bouts; Figure 3A) than any other call in my study. These calls had the highest mean high frequency of the calls in this family (3433 ± 55 hertz), and were often used in the spontaneous context (6/46 bouts [13.0%]; 526/925 calls [57%]) and social context (14/46 bouts [30.4%]; 205/925 calls [22.1%]). Of the calls in this call-family, the **burry flat jay** (Figure 3B) had the narrowest frequency range (689.1 ± 17.6 hertz) and the highest low frequency (2606 ± 33 hertz) (Table 8). These calls were often used in the spontaneous context (4/15 bouts [26.7%]; 54/124 [43.5%]) and the social context (4/15 bouts [26.7%]; 36/124 calls [29.0%]). Burry flat jay calls were recorded more often during the breeding season than the non-breeding season (10/15 bouts [66%]; 106/124 calls [85.5%] during the non-breeding season; Table 5). The **hoarse jay** (Figure 3C), with a frequency-modulated mid-section, was distinct from other calls in this call-family. Hoarse jay calls were used in the spontaneous context (2/6 bouts [33.3%]; 57/125 calls [46%]), long-distance communication context (1/6 bouts [16.7%]; 44/125 calls [35%]), chasing context (2/6 bouts [33.3%]; 9/125 calls [7.2%]) and social context (1/6 bouts [16.7%]; 15/125 calls [12.0%]).

Bell family (Figure 4): The **Bell** call (Figure 4A), the only call in this family, had a resonating quality similar to the chime of a bell. These calls usually consisted of a single note, with few or no harmonics, had a lower peak frequency than most other call types

(1640 ± 20 hertz) in my study, and had the narrowest frequency range of any call type (570 ± 11 hertz) (Table 8). Bell calls were used primarily during the non-breeding season (9/11 bouts [81.8%]; 96/98 calls [98%]; Table 7), specifically during March, and many were uttered in the social context (3/11 bouts [27.3%]; 45/98 calls [45.9%]) and the spontaneous context (4/11 bouts [36.6%]; 40/98 calls [40.8%]). This call was also uttered in the predator-related context (3/11 bouts [27.3%]; 4/98 calls [4.1%]) and the solo foraging context (3/11 bouts [27.3%]; 9/98 calls [9.2%]).

Song family (Figure 5): The **whisper song** (Figure 5A), the only call in this family, was longer in duration (mean = 7.72 ± 2.16 sec) than all other vocalizations of Blue Jays in my study, and was uttered at low volume (hence the name 'whisper' song), and included whistles and occasionally murmur (Figure 8) notes. I recorded few whisper songs (4 bouts; 7 songs), all during February and March and always in the spontaneous context.

Imitation family (Figure 6): All imitated call types were included in this category, regardless of their characteristics. Most imitated calls were recorded during the breeding season (24/34 bouts [70.6%]; 430/532 calls [80.8%]; Table 5). Based on total number of bouts, calls in the imitation family were uttered in the threat context-family (10/59 bouts recorded in this context-family were imitated calls) more than those in any other call-family except the descending jay family (15/59 bouts). I only recorded jays imitating the calls of potential predators of either nests (American Crow) or fledglings and adults (raptors). The **perfect crow** call (Figure 6A) (so-named because unlike the short crow call, I could not tell the difference between this call and one given by a crow unless I saw the vocalizing bird) was short in duration (0.36 ± 0.10 sec), had a low peak frequency

(1608 ± 57 hertz; Table 8), and was only recorded once as I was approaching recently fledged young. **Short crow** calls (Figure 6B) were even shorter in duration (hence the name) (0.20 ± 0.01 sec), and had a higher peak frequency than the perfect crow call (2199 ± 96 hertz) (Table 8). Short crow calls were often used in the social context-family (9/16 bouts [56.3%]; 238/467 calls [51.0%]), the spontaneous context (3/16 bouts [18.8%]; 181/467 calls [38.8%]), and were one of only three call types, including the hoarse jay and burry descending jay, used in the long-distance communication context (2/16 bouts in this context were the short crow [12.5%]; 34/89 calls [38.2%]). Short crow calls were recorded more often during the breeding season than the non-breeding season (10/16 bouts [62.3%] and 368/467 calls [78.8%] in the breeding season; Table 5). Short crow calls were often paired (155 pairs, 310 calls of 467 total calls recorded [66.4%]; see Figure 6B for an example of paired short crow calls), often in the spontaneous context (2/10 bouts of pairs [20%] and 79/155 pairs [51.0%]) and the social context-family (5/10 bouts of pairs [50%]; 64/155 pairs [41.2%]).

The only time I recorded the **Bald Eagle bout** (Figure 6C) (n = 8) and an **Individual Bald Eagle note** (Figure 6D) (n = 3) (both were most similar to the 'wail call' of Bald Eagles) was during one experiment where I played back the calls of an Eastern Screech-Owl. Bald Eagle bouts averaged 5.3 ± 0.8 notes per bout, and the individual Bald Eagle note, in addition to only having one note, had a narrower range of frequencies (996 ± 128 hertz; Table 8). Imitations of the calls of a **Cooper's Hawk** (Figure 6E), **Red-tailed Hawk** (Figure 6F), and **Red-shouldered Hawk** (Figure 6G) all had peak frequencies of about 3000 hertz (Table 8). The Cooper's Hawk call consisted of a series of kek-kek notes (mean = 4.8 ± 1.1 notes), the Red-tailed Hawk call was

generally a single note (kee-ee-arr), and the Red-shouldered Hawk call (recorded only once) consisted of two whistled notes (keer, keer) (Table 8). The Cooper's Hawk call was uttered most often in the social context (2/3 bouts [66.6%]; 3/4 calls [75.0%]), the Red-tailed Hawk call most often in the threat context-family (7/11 bouts [63.6%]; 36/69 calls [52.2%]), and the Red-shouldered Hawk call most often in the predator-related (1/2 bouts [50%]; 3/7 calls [42.9%]) and social (1/2 bouts [50.0%]; 4/7 calls [57.1%]) contexts. The Broad-winged Hawk call was not recorded, and was heard on just one occasion in an unknown context.

Bell/jay family (Figure 7): All three call types in this family had a peak frequency of about 2600 hertz. Like other calls in this family, **Bell jay** calls **(**so-named because the two notes of this call were at the frequencies similar to bell and jay calls**)** had a relatively low lowest frequency (1578 ± 69 hertz; Table 8, Figure 7A). This call was used in five different contexts, including the social context (2/11 bouts [18.2%]; 27/73 calls [37.0%]), solo flight context (3/9 bouts [17.8%]; 22/72 calls [30.6%]), and the spontaneous, solo foraging, and predator-related contexts (one bout in each context). On two occasions, I recorded the call, but did not see the vocalizing bird.

The **burry bell** call (Figure 7B) (so-named because it had a resonating quality similar to the bell call, but was frequency-modulated) had a narrower frequency range than other calls in this family (719 ± 76 hertz; Table 8) and was often used in the predator-related context (3/10 bouts [30.0%]; 40/96 calls [41.7%]). This call was also used in the social context (4/10 bouts [40.0%]; 23/96 [24.0%], and in the conflict-related, chasing, and provisioning contexts (one bout in each context). The **o-we** call (Figure 7C), named after how the call sounded, was similar to the bell jay call, but had a broader

frequency range (1842 ± 28) (Table 8). The call was only recorded in the spontaneous context (1 bout; 7 calls).

Yurp/murmur family (Figure 8): All four calls in this family had a peak frequency between 2000 and 2800 hertz (yurps had lower peak frequencies, murmurs higher; Table 8) and consisted of short, simple notes uttered either singly or in bouts. The **yurping bout** (Figure 8A) and **individual yurp** call (Figure 8B) (the term 'yurp' from Cohen 1977) had peak frequencies of about 2300 hertz; yurping bouts consisted of an average of 8.8 ± 1.0 yurp calls uttered in quick succession (Figure 8A). Both yurping bouts (25/32 bouts [78.1%]; 98/124 calls [79.0%]) and individual yurp calls (13/18 bouts [72.2%]; 92/134 calls [68.7%]) (Table 5) were uttered primarily during the breeding season. Individual yurps were associated less with being close (≤ 3 m) to another jay (9/15 bouts [60%]); 27/113 [24%]) than yurping bouts (17/22 bouts [77.3%]; 86/93 [92%]). Yurping bouts were the call recorded most often in the courtship context (3/7 calls in this context were yurping bouts [42.9%]; 5/18 calls [27.8%]) (Table 6). This call was also used recorded more often than any other call type in the provisioning context (3/6 bouts [50.0%]; 10/15 calls [66.7%]), and the individual yurp (2/6 bouts [33.3%]; 5/16 calls [31.3%]) was the second most commonly used call in provisioning context (Table 6). **Murmur bouts** (Figure 8C) (so-named because of the low volume and rapidly repeated notes) were superficially similar to yurping bouts, but differed in both peak frequency (2704 ± 102 hertz for murmur bouts; 2251 ± 138 hertz for yurping bouts) and the mean interval between notes was longer (0.34 ± 0.18 sec for murmur bouts; 0.16 ± 0.1 sec for yurping bouts) (Table 8). Murmur bouts included an average of 5.5 ± 0.6 notes, and the characteristics of the notes were similar to those of **individual murmur** calls (Figure

BD) (Table 8). Murmur bouts were sometimes uttered during close interactions with conspecifics (4/6 bouts [66.7%]; 13/45 calls **[**28.9%]) whereas individual murmur calls were always uttered during close interactions (3 bouts; 30 calls). Most murmur bouts (10/11 bouts [90.9%]; 58/59 calls [98.3%]) and all individual murmur calls (3/3 bouts; 30/30 calls) (Table 5) were uttered during the breeding season. Murmur bouts were used primarily in the social context-family (7/11 bouts [63.6%]; 54/59 calls [91.5%]) and individual murmur calls were used exclusively the social context-family (3 bouts; 30 calls).

Squeaky family (Figure 9): Both calls in this family typically consisted of a series of notes that sound similar to a 'squeaky gate' being opened or closed. **Squeaky gate** calls (Figure 9A) consisted of an average of 9.9 ± 0.3 notes compared to an average of 2.8 ± 0.2 notes for **partial squeaky gate** calls (Figure 9B) (so-named because these calls had fewer notes than squeaky gate calls) (Table 8). Squeaky gate calls also had a higher peak frequency (3411 ± 150 hertz) than partial squeaky gate calls (2362 ± 74 hertz) (Table 8). Squeaky gate calls were often used in the spontaneous context (8/31 bouts [25.8%]; 198/483 calls[41.0%]) and the predator-related context (4/31 bouts [12.9%]; 155/483 calls [32.1%]), were uttered more often during the non-breeding season than the breeding season (17/31 bouts in the non-breeding season [54.8%]; 322/483 calls [66.7%]) (Table 5), and were often paired (210 calls, or 105 pairs; 483 total calls were recorded so 42.4% of calls were part of a pair). Paired squeaky gate calls were used in the spontaneous context (4/11 bouts of pairs [36.4%]; 50/105 pairs [47.6%]), the social context-family (5/11 bouts of pairs [45.5%]; 11/105 pairs [10.5%]), and the predator-related context (2/11 bouts of pairs [18.2%]; 44/105 pairs [41.9%]). Unpaired partial

squeaky gate calls were often recorded in the social context-family (7/14 bouts [50%]; 234/273 calls [85.7%]) and the spontaneous context (3/14 bouts [21.4%]; 29/273 calls [10.6%]). After flat jay calls, unpaired partial squeaky gate calls were the second most frequently used call, based on total number of calls uttered, in the chasing context (2/31 bouts [4.5%]; 69/540 calls [12.8%]). More partial squeaky gate calls were recorded during the breeding season (9/14 bouts [64.3%]; 228/273 calls [83.5%]; Table 5) and, during the breeding season, were only recorded during the rowdy grouping stage (5/5 bouts; 145 calls).

Whine jay family (Figure 10): Calls in this family were uttered by young Blue Jays (calls with juvenile in the name), but adults sometimes uttered similar calls at lower frequencies (calls without juvenile in the name). All calls in this family were frequency-modulated. **Juvenile whine jay** calls (Figure 10C) and **juvenile extended whine jay** calls (Figure 10D) had similar peak **frequencies** (about 5700 hertz), but juvenile whine jays were shorter in duration (0.27 ± 0.01 sec for whine jays; 0.58 ± 0.03 sec for juvenile extended whine jays; Table 8). Both juvenile whine jays (7/10 bouts [70.0%]; 120/251 calls [47.8%]) and juvenile extended whine jays (7/9 bouts [77.8%]; 58/84 calls [69.0%]) were recorded most often when young Blue Jays were being fed by adults; in all other cases, these calls were uttered when juveniles were waiting to receive food when parents were not present. Unlike the other calls in this family, **whine jay** calls (Figure 10A) and **extended whine jay** calls (Figure 10B) were occasionally used by adults. Both of these adult calls had similar peak frequencies (~2900 hertz), but the adult whine jay was shorter in duration (0.35 ± 0.01 sec) than the adult extended whine jay (0.50 ± 0.02 sec; Table 8). I recorded the adult whine jay in the social context (1/2 bouts [50.0%]; 9/17

calls [52.9%]) and when an adult Blue Jay was foraging alone (1/2 bouts [50.0%]; 8/17 calls [47.1%]). I recorded the adult extended whine jay only once in the solo foraging context (1 bout; 7 calls). **Inverted whine jay** calls (Figure 10E) were also uttered by adult Blue Jays and only recorded in the chasing context (2 bouts; 18 calls).

Nestling twitter family (Figure 11): The **nestling twitter** (Figure 11A), the only call in this family, had a mean peak frequency of 5245 ± 168 hertz (Table 8), was only uttered by young nestlings (3 to 10 days old), and was always used when nestlings were either receiving (2/3 bouts [66.6%]; 22/29 calls [76%]) or awaiting (1/3 bouts [33.3%]; 7/29 [24%]) food from parents.

*Hiccup/whistle family (*Figure 12): **Whistle** and **hiccup** calls were similar structurally, but the hiccup call (Figure 12B) began with an up-slurred note (which made it sound similar to a hiccup) and the whistle call (Figure 12A) (which sounded like a brief whistle) did not. These two calls were sometimes uttered together (of the 14 bouts that a call in this family was uttered, the whistle and hiccup occurred together during three bouts). Hiccup calls had a higher peak frequency than whistle calls (2992 ± 122 hertz for hiccup calls; 2364 ± 85 hertz for whistle calls) (Table 8) and were often uttered in pairs (38 calls, or 19 pairs, 124 total calls recorded total, so 30.6% of calls were part of a pair), usually in the spontaneous context (2/4 bouts of paired calls [50.0%]; 17/19 pairs were in this context [89.5%]). Whistle calls were always uttered as single notes and were often recorded in the predator-related context (3/9 bouts [33.3%]; 50/73 calls [68.5%]); these calls were also recorded in the distress, human-related, solo flight, solo foraging, social, and spontaneous contexts (one bout in each context). Unpaired hiccup calls were uttered in the spontaneous context (3/11 bouts [27.3%]; 71/124 calls [57.3%]), predator-related

context (2/11 bouts [18.2%]; 4/124 calls [3.2%]), and the solo flight, social, spontaneous, and group flight contexts (one bout in each context).

Grunt family (Figure 13): **Grunt** (Figure 13A) calls were uttered by all four jays that I held. Only one call was recorded and analyzed. It covered a wide range of frequencies (9870 hertz).

*Rattle family (*Figure 14): Both call types in this family had a mean peak frequency of about 2000 hertz, a duration of about 0.7 sec, and consisted of short-duration click notes. **Continuous rattle** calls (Figure 14B) were uninterrupted trills whereas **segmented rattle** calls (Figure 14A) consisted of two or three repeated notes. Continuous rattles were most often recorded in the chasing context during the breeding season (2/3 bouts [66.7%]; 41/44 calls [93.2%]) and in the spontaneous context during the non-breeding season (2/5 bouts [40.0%]; 28/35 calls [80.0%]). Segmented rattles were also primarily associated with the chasing context during the breeding season (2/4 bouts [50.0%]; 17/19 calls [89.5%]) and exclusively with the social context during the non-breeding season (2/2 bouts; 16/16 calls).

Cry family (Figure 15): The **cry** call (Figure 15A), the only call in this family, had the highest peak frequency of any adult call (5719 ± 1838 hertz) (Table 8) and was uttered only in situations with a perceived threat of predation, such as when I was attempting to remove individuals from mist-nets or traps. I only recorded this call on one occasion.

Chapter IV

Discussion

The call repertories of songbirds typically include about five to 14 distinct vocalizations (Gill 2007), but some species, including the Blue Jays in my study, have far more complex vocal repertoires. Other species in the family Corvidae also have relatively large call repertoires. For example, Conner (1985) identified 18 distinct call types used by Common Ravens. Colonial-nesting Pinon Jays were reported to have at least 15 distinct call types (Berger 1977). Hope (1980) documented at least 15 distinct call types in the repertoire of Steller's Jays, and suggested that, because of their ability to imitate and innovate, jays in some flocks may have additional, unique call types. Cooperatively breeding Florida Scrub Jays (Barbour 1977) have at least 14 distinct call types and White-throated Magpie-jays (*Calocitta formosa*), also cooperative-breeders, have at least 150 structurally distinct vocalizations (Ellis 2008).

One possible explanation for the evolution of large call repertoires among some species of birds is the social complexity hypothesis (Freeberg et al. 2012). According to this hypothesis, species that regularly interact with large numbers of conspecifics in a variety of contexts are likely to benefit from having a larger vocal repertoire than solitary or less social species. For example, species in the family Paridae, including Carolina Chickadees (*Poecile carolinensis*), use calls with greater complexity when flock size increases (Freeberg 2006, Krams et al. 2012). Smooth-billed Anis (*Crotophaga ani,*

Cuculiformes) have a relatively large vocal repertoire for a non-passerine (11 call types), which may be a result of the many social interactions needed in a cooperatively breeding species (Grieves et al. 2015). Blue Jays do not breed cooperatively, but are gregarious and, during the non-breeding season, are typically found in flocks (Smith et al. 2013). These flocks typically include fewer than 10 Blue Jays, but different flocks sometimes forage together so individuals may interact with many conspecifics both in and outside of their flocks (Smith et al. 2013). In addition, prior to breeding, multiple Blue Jays may engage in what have been termed 'elaborate social displays' (what I refer to as the rowdy grouping stage) where individuals, sometimes as many as 20 or more, display and call (Bent 1946, Smith et al. 2013). These displays may play a role in the acquisition of nesting territories (Smith et al. 2013). Thus, although not cooperative breeders, Blue Jays are a social species and, therefore, need to communicate with many conspecifics in a wide variety of behavioral contexts. This may have contributed to the relative complexity of their vocal repertoire, as suggested by the social complexity hypothesis.

Although calls are usually described as innate vocalizations (Marler 1990), in contrast to the songs of songbirds that must be learned (Marler 2004), Blue Jays in my study appeared to learn some of their calls. Such learning may also occur in other species of songbirds. For example, both cardueline finches and Brown-headed Cowbirds (*Molothrus ater*) have been found to learn flight calls (Mundinger 1979, Dufty 1988). In another apparent case of call learning, adult Budgerigars (*Melospittacus undulatus*) that had individually distinctive contact calls prior to experimentation learned to use the same primary contact call as a conspecific that was experimentally confined nearby (Farabaugh et al. 1994). Other corvids have also been found to learn calls. For example, in addition to

mimicking human sounds such as speech, New Caledonian Crows (*Corvus moneduloides*) uttered the same call type with different peak frequencies at different locations, suggesting social learning and cultural (i.e., learned) variation among different groups (Bluff et al. 2010). In addition, a Western Scrub-Jay (*Aphelocoma californica*) raised in captivity near several Florida Scrub-Jays learned to use two call types only known to be uttered by Florida Scrub-Jays (Webber and Stefanil 1990). In a possible demonstration of the importance of learning calls in Blue Jays, Cohen (1977) found that individuals isolated as juveniles, which did not hear other jays vocalize, never uttered squeaky gate calls. In addition, the characteristics of other calls uttered by these isolated jays (including jay, bell, and rattle calls), although recognizable, differed substantially from normal calls (Cohen 1977). Kramer and Thompson (1979) found that the characteristics of bell calls of Blue Jays varied geographically, suggesting that these calls may be learned. Further, I found that Blue Jays in my study only imitated the calls of species of predators (American Crows and raptors) that were present in the same area, suggesting that the calls were learned. The ability to learn calls may be advantageous because it allows greater vocal complexity (such as using predator calls to indicate danger, and possibly the extent of that danger) than likely possible for species where calls are innate. For example, the ability to learn calls could aid in recognizing different individuals or attracting mates (Nottebohm 1972).

Blue Jays are not unique in their ability to imitate the vocalizations of other species, with 15-20% of passerine species reportedly able to do so (Garamszegi 2007). The function of vocal mimicry in most species of birds is poorly understood, and many functions have been proposed, such as predator avoidance or deterrence, mate attraction,

and deception of competitors (Hailman 2009, Dalziell et al. 2015). However, there is little experimental evidence that songbirds mimic in functionally important ways. In some species, mimicked call types are used in inappropriate contexts (Kelley et al. 2008). In a few species, mimicked calls are used in apparently appropriate contexts (such as when they appear to serve a warning, or other, function). For example, Racket-tailed Drongos (*Dicrurus paradiseus*) imitate the mobbing calls of other species when mobbing predators, apparently learning the calls and associated contexts while interacting with these species in mixed-species flocks, and imitate predator calls in alarm contexts (Goodale and Kotagama 2006). Blue Jays may also imitate non-randomly. At least two groups of Blue Jays apparently learned to imitate the calls of predators to scare other species from bird feeders (Clench 1991, Loftin 1991). Further, Blue Jays in my study sometimes responded to the presence of a predator by imitating the call of that predator and, at other times, used imitations of predator calls in apparent response to the presence of a different species of predator. Although I could not determine if such calls were directed at predators or conspecifics, such calls, if directed at the predator, might represent an attempt to deceive, e.g., the predator's attention will focus on a conspecific trespassing in its territory rather than potential prey. If directed at conspecifics, imitated predator calls could function as alarm calls, alerting those nearby to the presence of a predator.

For most call types in the vocal repertoires of Blue Jays in my study, assigning specific functions was either difficult or not possible. For example, one pair of Blue Jays in my study uttered a Red-tailed Hawk call when I approached their nest on three separate occasions, but another pair usually uttered whistle calls when I approached their

nest. At least one corvid species, the White-throated Magpie-jay, also uses different call types in the same context (of >150 call types identified in a study, only 14 were functionally distinct) (Ellis 2008). Because Blue Jays appear to learn calls, it is also possible that, among different flocks or groups, they learn to associate certain call types with different contexts. If so, this would help explain why most calls of Blue Jays in my study were used in a variety of behavioral contexts.

In previous studies, Conant (1971) described 20 call types of Blue Jays and Cohen described 15 call types. I tended towards being a 'splitter' rather than a 'lumper' which, in addition to observing new calls, resulted in me describing 42 call types (Table 9). Future investigators who use my system will be able to make inferences about less specific call-families and/or more specific call types.

My results suggest that the call repertoires of Blue Jays likely vary among different individuals/flocks and also that the amount of time investigators spend observing Blue Jays can impact the reported size of call repertoires. This is supported by examination of the relationship between the number of observations and the number of different call types recorded at different locations in my study. For example, at two locations, new call types were still being recorded after 12 and 16 observations (locations A and C, respectively), but no new call types were recorded after 10 observations at a third location (B; Figure 18). In addition, although 10 call types were used at all three locations, the other 20 call types were used at only one or two locations, suggesting that many call types may be used by certain groups of jays and not others (Table 10). Similarly, Hope (1980) suggested that Steller's Jays use different calls geographically, sometimes entirely novel call types, due to their ability to innovate and imitate.

Possible Functions of Blue Jay Calls

Descending jay family (Figure 1): The **short descending jay** appeared to be one of the primary flight calls used by Blue Jays, and may function to provide information about a bird's location to distant conspecifics because these calls were uttered when conspecifics were either distant (≥ 3 m) or absent (Table 7). These calls were used in the conflict-related context and, therefore, may indicate aggression toward conspecifics or non-predator heterospecifics. The **extended descending jay** appears to be a contact call used mainly in social contexts, possibly to provide information about a bird's location to nearby conspecifics. The **harsh descending jay** appeared to have multiple functions. For example, these calls were used more than any other call type in the threat context-family, suggesting they may function to harass threatening heterospecifics or to recruit conspecifics to help mob a predator. Harsh descending jays were also used more than any other call type in the social and foraging context, suggesting that they may also function as contact calls. The **burry harsh descending jay** was used in aggressive contexts, such as when approaching a Sharp-shinned Hawk. These calls may function to harass predators or attract conspecifics to help mob a predator and may be functionally similar to **growl** calls that generally preceded burry harsh descending jays in apparently aggressive contexts. The **juvenile descending jay** was sometimes uttered by nestlings, but more often by fledglings, and likely functions as a begging call to solicit food from parents.

Flat jay family (Figure 2): The **flat jay** was the primary flight call of Blue Jays, and may both inform conspecifics that the calling individual has taken flight and of its location. These calls were also used in social contexts when jays were not flying, so they

may also serve as contact calls. Flat jays were often uttered in pairs, mostly when multiple Blue Jays were flying (group flight context), possibly allowing certain flock members to stay in contact when others Blue Jays in the area (such as during the rowdy grouping stage) were uttering unpaired flat jay calls. The **short growl** was most often used in aggressive contexts, like the growl, and may function to recruit conspecifics to help mob predators. During one of the two occasions when I recorded this call, it was being uttered by Blue Jays mobbing a Barred Owl.

Burry jay family (Figure 3): Calls in this family were used spontaneously more than those in other call-families, making it difficult to determine possible functions. However, **hoarse jay** calls and **burry descending jay** calls were recorded in the long-distance communication context, when I sometimes heard distant Blue Jays apparently responding with these same calls. Given this association with long-distance communication, these calls may provide conspecifics with information about the location of Blue Jays at longer distances (≥ 50 m). **Burry flat jay** calls were often used as flight calls, and were often uttered in spontaneous contexts when it appeared to me that no conspecifics were nearby (Table 7). As with other calls in this call-family, burry flat jay calls may function in long-distance communicate with distant conspecifics.

Bell family (Figure 4): **Bell** calls were usually uttered just prior to the start of the breeding season, suggesting a possible role in defending areas around potential nest sites or in attracting mates. Conant (1972) also suggested that this call may serve a territorial function. On other occasions, however, bell calls appeared to indicate alarm, e.g., when I approached nests with nestlings or when a predator was nearby.

Song family (Figure 5): All **whisper songs** were recorded prior to the breeding season in February and March, suggesting a possible function in mate attraction. However, these songs were uttered at such low volumes that it seems unlikely they would be heard by conspecifics. These songs could only function in mate attraction if a potential mate was very close to a vocalizing bird.

Imitation family (Figure 6): I found that Blue Jays imitated the calls of other species more often during the breeding season, and such calls could serve to warn conspecifics about the presence of predators. Calls in the imitation family were used in the threat context-family more often during the breeding season (8/24 bouts; 33.3%) than the non-breeding season (2/10 bouts; 20%). Further, all imitated calls of Blue Jays in my study were those of either American Crows or raptors, species that could potentially prey on eggs, nestlings, or adult Blue Jays. Conant (1972) described only one imitated call type uttered by Blue Jays, an imitated call of a domestic cat (*Felis catus*), a species which could also prey on Blue Jays. I did not observe jays using any imitated calls kleptoparasitically, as reported by other investigators (Clench 1991, Loftin 1991, Hailman 2009).

The **perfect crow** call was only uttered during my study when I approached fledglings, so it may function as a warning call. Unlike the other imitated calls, the **short crow** call did not appear to be associated with the threat context-family. This call was paired more than any other call type, and sometimes appeared to be used for long-distance communication. The short crow call was only uttered during the rowdy grouping stage of the breeding season (all 182 calls). Because of its association with the early breeding season (before eggs had been laid), this call could play a role in mate attraction

and may be used to maintain contact between Blue Jays that are part of 'rowdy groups' if they become separated (long-distance communication).

Bald Eagle bouts and **individual Bald Eagle notes** were uttered in apparent response to playback of the calls of an Eastern Screech-Owl, only in a location near a reservoir where Bald Eagles were present, suggesting a possible function as a warning call. The **Cooper's Hawk** call did not appear to be used as a warning call because, when uttered, there did not appear to be a predator nearby. This call was used infrequently and only in the social context, but its possible function is unknown. The **Red-tailed Hawk** and **Red-shouldered Hawk** calls were used primarily in response to a possible threat of predation, such as when I approached a nest or a hawk was nearby, and may serve to warn conspecifics about the presence of a predator.

Bell/jay family (Figure 7): **Bell jay** calls, like flat jay calls, were uttered in the flight context and may provide conspecifics with information about a Blue Jay's location. **Burry bell** calls were sometimes (n=3 bouts) uttered in the predator-related context so may function as a warning call. However, these calls were also uttered in the social context family when no predator appeared to be present. Therefore, burry bell calls may also serve as a contact call, helping Blue Jays maintain contact with nearby conspecifics. The **o-we** call was uttered by Blue Jays at only one location and its function is unknown.

Yurp/murmur family (Figure 8): The **yurping bout** was the primary close-contact call of Blue Jays, and was almost always uttered during courtship feeding by the feeder (pers. obs.), as well as when adults fed young. Other investigators have also reported that yurps were uttered by Blue Jays during courtship feeding, when adults fed young birds, and in other situations when they were near conspecifics (Conant 1972, Cohen 1977).

Individual yurp calls were also often uttered when Blue Jays were near conspecifics, but, unlike the yurping bout, were uttered when jays were alone. Calls in this family were often uttered at different volumes and, when uttered with greater volume, appeared to function as an alarm call, e.g., when I approached fledglings.

Murmur bouts appeared to serve a function similar to that of the songs of other songbirds, i.e., attracting mates. Blue Jays uttering murmur bouts sometimes perched near or at the top of trees, suggesting they may have been advertising their presence to conspecifics. This call was almost always uttered during the breeding season, supporting the hypothesis that it plays a role in attracting mates. The **individual murmur** was also uttered almost exclusively in the breeding season and was only used during close-contact situations, suggesting a possible role in the formation and maintenance of pair-bonds.

Squeaky family (Figure 9): The **squeaky gate** call was often used in the predator-related context, but was also uttered in spontaneously, possibly when Blue Jays perceived threats that I did not detect. This call was often paired, but the function of paired squeaky gate calls is unclear. Conant (1972) described this call as being used in 'suspicious' contexts, perhaps referring to a predator-related context. The **partial squeaky gate** call was often used in the social context, particularly during the rowdy grouping stage of the breeding season. Assuming that males were chasing females during the rowdy grouping stage, this use of partial squeaky gate calls suggests a possible role in mate attraction. However, these calls might also convey a threat of aggression to nearby conspecifics, specifically between males in 'rowdy groups.' Blue Jays may include more notes in their squeaky gate calls to indicate a greater threat of predation because the longer-duration

squeaky gate calls appeared to serve as warning calls whereas the shorter-duration partial squeaky gate calls did not.

Whine jay family (Figure 10): The **juvenile whine jay** was uttered by nestling and fledgling Blue Jays when awaiting or receiving food from adults. Most **juvenile extended whine jay** calls were uttered when juveniles were receiving food from parents. Both of these calls, therefore, probably function to advertise hunger levels and solicit food from adults. The **whine jay** and **extended whine jay** calls of adult Blue Jays were used infrequently in the social context and their function is unknown. I only recorded the **inverted whine jay** calls during chases, possibly males chasing females, and the function of this call is also unknown.

Nestling twitter family (Figure 11): The **nestling twitter** was used by young nestlings (3 to 10 days old) when being fed by adults so likely functions as a begging call, i.e., to advertise hunger level and solicit food from adults.

Hiccup/whistle family (Figure 12): **Hiccup** calls were most often uttered in the human-related context, i.e., when I approached a nest, suggesting that this call may serve to warn mates or nestlings. **Whistle** calls were most often uttered in the predator-related context, so this call may also serve to warn conspecifics. Blue Jays uttered hiccup calls during experiments when I played back the calls of raptors, suggesting that this call could be used to recruit conspecifics for mobbing a predator or to warn conspecifics.

Grunt family (Figure 13): The **grunt** call was uttered by all four jays that I held, but was uttered at a very low volume so would likely not be heard by conspecifics. As such, the possible function of this call is unclear.

Rattle family (Figure 14): Conant (1972) suggested that rattle calls were only uttered by female Blue Jays, but I was not able to verify this. Blue Jays in my study used two distinct types of rattle calls, the **continuous rattle** and **segmented rattle**. Both of these calls were used primarily in the chasing context (uttered by the individual being chased) during the breeding season. If only uttered by females (Conant 1973), these calls apparently convey information to the Blue Jays (possibly males) chasing a female, perhaps concerning the female's status (paired or unpaired) and to convey aggression, i.e., an increased likelihood of an aggressive response to those chasing the female. During the non-breeding season, these calls were used in the social context, but their function is unknown.

Cry family (Figure 15): The **cry** call was uttered only in situations of a perceived predation threat, such as when I was removing Blue Jays from mist-nets or traps. Therefore, this call may function to attract conspecifics to mob potential predators. The characteristics of this call, e.g., high volume and abrupt beginning and ending, may make it easier for conspecifics to locate the calling individual. This call could also serve to surprise a predator, perhaps causing it to loosen its grip so that the vocalizing bird can escape.

Conclusion and Opportunities for Further Study

In summary, I found that Blue Jays in east-central Kentucky have a relatively large vocal repertoire and that most call types in their repertoire were used in more than one behavioral context, making it difficult to determine their possible functions. I also

found that Blue Jays learn some call types in their vocal repertoires, including calls that are imitations of the calls of predators. One possible explanation for the large vocal repertoire of Blue Jays is the social complexity hypothesis, i.e., species that regularly interact with many conspecifics in a variety of behavioral contexts may benefit from having complex vocal repertoires that improve their ability to interact and communicate with those conspecifics. Additional studies of Blue Jays are needed to better understand the extent to which the size of their vocal repertoires, and the functions of specific calls, might vary geographically.

Studies of Blue Jays and other species with complex vocal repertoires could also improve our understanding of the selective factors that favor the evolution of such repertoires. Further, comparison of Blue Jays at different locations, or of Blue Jays with other species in the family Corvidae, could help identify life history traits that, in addition to social complexity, may be associated with the development of large vocal repertoires. Considering that cognitive ability has been found to be correlated with vocal complexity (Boogert 2008), the study of intelligent species of birds with large vocal repertoires such as Blue Jays and other corvids may also provide insight concerning the evolution of advanced cognitive capabilities.

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Appendix

Table 1. Locations of observations and experiments during both the breeding and non-breeding season. Numbers in the 'Obs. Non-br.' and 'Obs. Br.' columns are the number of visits during observational periods in the non-breeding season and breeding seasons, respectively. Letters in the 'Ex. Br.?' and 'Ex. Non-br.?' columns indicate whether experiments took place (Y) or did not take place (N) during the breeding and non-breeding season, respectively.

Location	Latitude, Longitude	Obs. Non-br.	Obs. Br.	Ex. Br.?	Ex. Non-br.?	Notes
BGAD 1	37.68304, -84.23470	11	4	N	Y	11 km southeast of Richmond
BGAD 2	37.72256, -84.22423	12	-	N	Y	11 km southeast of Richmond
BGAD 3	37.66741, -84.23419	3	2	N	Y	11 km southeast of Richmond
Private Res. 1	37.74601, -84.29710	4	1	N	N	In Richmond, adjacent to EKU campus
Private Res. 2	37.78223, -84.24170	4	-	N	Y	6 km northeast of Richmond
Private Res. 3	37.74404, -84.29148	8	-	N	N	In Richmond, adjacent to EKU campus
Elmwood	37.74447, -84.30392	5	3	N	N	In Richmond, adjacent to EKU campus
Campus 1	37.74208, -84.29977	1	4	N	N	In Richmond, On EKU campus
Campus 2	37.74242, -84.30082	-	2	Y	N	In Richmond, On EKU campus
Campus 3	37.74303, -84.29370	-	2	Y	N	In Richmond, On EKU campus
Campus 4	37.74080, -84.29665	-	2	Y	N	In Richmond, On EKU campus
Campus 5	37.74113, -84.29731	-	3	Y	N	In Richmond, On EKU campus
Campus 6	37.74311, -84.29920	-	-	Y	N	In Richmond, On EKU campus
Campus 7	37.74334, -84.30091	-	-	Y	N	In Richmond, On EKU campus
TF Nest 1	37.71653, -84.29557	-	-	Y	N	In Richmond, adjacent to EKU campus
TF Nest 2	37.71593, -84.29386	-	-	Y	N	In Richmond, adjacent to EKU campus
Taylor Fork	37.71584, -84.29562	2	14	N	N	Near Richmond, adjacent to EKU campus
Cemetery	37.74127, -84.29345	1	-	N	Y	In Richmond, adjacent to EKU campus
Hidden Valley	37.89046, -83.98691	-	7	N	N	60 km northeast of Richmond
Louisville	38.13934, -85.74472	1	-	N	N	160 km west of Richmond
Michigan	41.81902, -86.49232	2	-	N	N	640 km northwest of Richmond

Table 2. Contexts and context-families used to determine possible functions of vocalizations.

Context-family	Context	Context Notes
Conflict-related	Conflict-related	Agonistic display towards non-predator
Courtship	Courtship	In close proximity (≤ 3 m) to mate
	Courtship feeding	When male fed female
Distress	Distress	Perceived threat of predation (e.g., in trap)
Foraging	Solo foraging	When jay was foraging alone
	Group foraging	When jay was foraging with other jays
Flight	Group flight	When a jay flew away alone
	Solo flight	When a jay flew away with flock
Social	Social	Near non-mate, for a non-obvious reason
	Long-distance communication	Jays far away (50 + m) uttering same call
	Chasing	Jays being chased by other jays
Threat	Human-related	Directed at me
	Predator-related	Directed at a predator
Provisioning	Parent feeding young	Parent feeding young
Spontaneous	Spontaneous	No apparent recipient, and no apparent reason
Food-related	Young awaiting food	Young jays waiting for adults to bring food
	Young receiving food	Young jays receiving food from an adult

Table 3. Overview of playback experiments conducted with Blue Jays during the breeding season. Bolded and italicized print indicates a playback that was not able to be done due to either a predation event or a fledging event. Nest 8 was found just before the nestlings fledged. RBWO = Red-bellied Woodpecker, COHA = Cooper's Hawk, GHOW = Great-Horned Owl, EASO = Eastern Screech-Owl, and SSHA = Sharp-shinned Hawk. The non-breeding season followed a similar schedule, though all locations received the same treatments.

Nest	11 May	14 May	17 May	21 May	24 May	
1	Rattle	Squeaky gate	Jay	Bell	RBWO	
2	Squeaky gate	Bell	Rattle	***RBWO***	***Jay***	
3	Rattle	Bell	Jay	RBWO	***Squeaky gate***	
	25 May	28 May	31 May	3 June	6 June	9 June
4	RBWO	COHA	EASO	SSHA	GHOW	-
5	-	COHA	GHOW	EASO	RBWO	***SSHA***
	6 July	9 July	12 July	15 July	18 July	
6	RBWO	***SSHA***	***EASO***	***COHA***	***GHOW***	
	28 June	1 July	5 July	8 July	11 July	
7	GHOW	RBWO	COHA	EASO	***SSHA***	
8	-	-	-	-	SSHA	

Table 4. Number of bouts during which each call type of Blue Jays was uttered.

Call type	No. of bouts	Call type	No. of bouts
Burry descending jay	46	Continuous rattle	8
Harsh descending jay	40	Hoarse jay	6
Flat jay	39	Segmented rattle	6
Short descending day	38	Juvenile descending jay	4
Yurping bout	32	Whisper song	4
Squeaky gate	31	Grunt	3
Individual yurp	18	Growl	3
Short crow	16	Cooper's Hawk	3
Burry flat jay	15	Individual murmur	3
Extended descending jay	14	Nestling twitter	3
Partial squeaky gate	14	Whine jay	2
Red-tailed Hawk	11	Short growl	2
Murmur bout	11	Red-shouldered Hawk	2
Hiccup	11	Cry	2
Bell jay	11	Inverted whine jay	2
Bell	11	O-we	1
Burry bell	10	Perfect crow	1
Juvenile whine jay	10	Broad-winged Hawk	1
Whistle	9	Extended whine jay	1
Juvenile extended whine jay	9	Bald Eagle bout[a]	1
Burry harsh descending jay	9	Individ. Bald Eagle note[a]	1

[a] Call that was recorded only during an experiment

Table 5. Comparisons of call type use by Blue Jays during the breeding and non-breeding seasons. I have included every call type uttered more than 10 times total, during at least five bouts, which was uttered at least twice as often in one season (breeding or non-breeding) compared to the other (for total calls and/or total bouts). I have also included all of the call-families uttered more than 10 times total, during at least five bouts, and what percentage they constituted in regard to total call types and total bouts, whether or not there was a difference in use between the breeding and non-breeding seasons. I have bolded call types and call-families that had a percentage of use in one season that at least doubled the same call type/call-family in the other season in regard to what percentage (for total calls and total bouts) that it constituted.

Call Type	Breeding		Non-breeding		Call-family	Breeding		Non-breeding	
	Calls	Bouts	Calls	Bouts		Calls	Bouts	Calls	Bouts
Burry descending jay	203 (21.9%)	21 (45.7%)	722 (78.1%)	25 (54.3%)	***Bell***	**2 (2.0%)**	**2 (18.2%)**	**96 (98%)**	**9 (81.8%)**
Bell	**2 (2.0%)**	**2 (18.2%)**	**96 (98.0%)**	**9 (81.8%)**	*Belljay*	92 (52.3%)	14 (63.6%)	84 (47.7%)	8 (36.4%)
Burry harsh descending jay	182 (78.1%)	5 (55.6%)	51 (21.9%)	4 (44.4%)	*Burry jay*	366 (31.2%)	35 (52.2%)	808 (38.8%)	32 (47.8%)
Burry flat jay	**106 (85.5%)**	**10 (66.6%)**	**18 (14.5%)**	**5 (33.3%)**	*Descending jay*	1290 (55.3%)	56 (50.5%)	1043 (44.7%)	55 (49.5%)
Extended descending jay	125 (59.0%)	10 (71.4%)	87 (41.0%)	4 (28.6%)	*Flat kay*	643 (64.7%)	28 (66.6%)	351 (35.3%)	14 (33.3%)
Flat jay	636 (64.5%)	26 (66.6%)	350 (35.5%)	13 (33.3%)	***Imitation***	**430 (79.3%)**	**24 (70.6%)**	**112 (20.7%)**	**10 (29.4%)**
Hiccup	65 (52.4%)	8 (72.7%)	59 (47.6%)	3 (27.3%)	*Rattle*	84 (59.6%)	9 (47.3%)	57 (40.4%)	10 (53.6%)
Murmur bout	**58 (98.3%)**	**10 (90.9%)**	**1 (1.7%)**	**1 (9.1%)**	*Squeaky*	389 (51.5%)	23 (51.1%)	367 (48.5%)	22 (48.9%)
Partial squeaky gate	228 (83.5%)	9 (64.3%)	45 (16.5%)	5 (35.7%)	***Whine Jay***	**362 (96.0%)**	**22 (91.7%)**	**15 (4.0)**	**2 (8.3%)**
Red-tailed Hawk	**50 (84.7%)**	**9 (91.8%)**	**9 (15.3%)**	**2 (8.2%)**	*Whistle/hiccup*	128 (65.0%)	14 (70%)	69 (35.0%)	6 (30%)
Short creak	368 (78.8%)	10 (62.5)	99 (21.2%)	6 (37.5%)	***Yurp/murmur***	**302 (80.7%)**	**67 (83.7%)**	**72 (19.3%)**	**14 (17.3%)**
Squeaky gate	161 (33.3%)	14 (45.2%)	322 (66.6%)	17 (54.8%)					
Whistle	**63 (86.3%)**	**6 (66.6%)**	**10 (13.7%)**	**3 (33.3%)**					
Yurping bout	**98 (79.0%)**	25 (78.1%)	**26 (21.0%)**	7 (21.9%)					

Table 6. The most common calls (based primarily on number of calls and secondarily on number of bouts) of Blue Jays uttered in each context-family. In parenthesis is the percentage of calls and bouts of a given call type that were uttered in a specific context-family. SDJ = short descending jay, BBE = burry bell, BHDJ = burry harsh descending jay, JDJ = juvenile descending jay, YBO = yurping bout, BDJ = burry descending jay, EDJ = extended descending jay, MBO = murmur bout, GRU = grunt, WHI = whine, CRY = cry, FJA = flat jay, HDJ = harsh descending jay, JWJ = juvenile whine jay, JEWJ = juvenile extended whine jay, NTW = nestling twitter, IYU = individual yurp, SCR = short crow, and SGA = squeaky gate.

Context-family	1st Calls	1st Bouts	2nd Calls	2nd Bouts	3rd Calls	3rd Bouts	4th Calls	4th Bouts	All Others Calls	All Others Bouts	Total Calls	Total Bouts
	SDJ		BBE		BHDJ and JDJ		-					
Conflict-related	17 (40.5%)	2 (40.0%)	13 (30.0%)	1 (20.0%)	3 (7.1%)	1 (20%) each	-	-	-	-	36	5
	YBO		BDJ		EDJ and MBO		-					
Courtship	5 (27.8%)	3 (42.9%)	3 (16.7%)	1 (14.3%)	2 (11.1%)	1 (14.3%) each	-	-	6 (33.0%)	1 (14.3%)	18	7
	GRU		WHI		CRY		-					
Distress	17 (70.8%)	4 (66.7%)	5 (20.8%)	1 (16.7%)	2 (8.3%)	1 (16.7%)	-	-	-	-	24	6
	FJA		SDJ		BDJ		HDJ					
Flight	211 (40.6%)	13 (20.6%)	77 (14.8%)	10 (15.9%)	74 (14.2%)	12 (19.0%)	40 (7.7%)	6 (9.5%)	115 (22.2%)	22 (34.9%)	517	63
	HDJ		FJA		BHDJ		BDJ					
Foraging	172 (52.9%)	8 (27.6%)	28 (8.6%)	1 (3.5%)	26 (8%)	1 (3.5%)	22 (6.8%)	1 (3.5%)	77 (23.7%)	18 (62.1%)	325	29
	JWJ		JDJ		JEWJ		NTW					
Food-related	211 (48.6%)	9 (36.0%)	89 (20.5%)	2 (8.0%)	84 (19.3%)	9 (36.0%)	29 (6.7%)	3 (12.0%)	21 (4.8%)	6 (20.7%)	434	29
	YBO		IYU		BBE		-					
Provisioning	10 (66.7%)	3 (50%)	5 (33.3%)	2 (33.3%)	1 (6.3%)	1 (16.7%)	-	-	-	-	16	6

Table 6 (continued)

Context-family	1° Calls	1° Bouts	2nd Calls	2nd Bouts	3rd Calls	3rd Bouts	4th Calls	4th Bouts	All Others Calls	All Others Bouts	Total Calls	Total Bouts
	HDJ		FJA		SCR		BDJ					
Social	722 (22.9%)	14 (8.0%)	490 (15.5%)	9 (5.1%)	251 (8.0%)	9 (5.1%)	238 (7.5%)	2 (1.1%)	1458 (46.2%)	141 (80.6%)	3159	175
	BDJ		FJA		SGA		SCR					
Spontaneous	526 (32.1%)	6 (8.8%)	203 (12.4%)	4 (5.9%)	198 (12.1%)	8 (11.8%)	181 (11.1%)	3 (4.4%)	530 (32.4%)	47 (69.1%)	1638	68
	HDJ		BHDJ		SGA		WHI					
Threat	276 (30.5%)	7 (12.5%)	132 (14.6%)	2 (3.6%)	157 (17.4%)	5 (8.9%)	58 (6.4%)	4 (7.1%)	282 (31.2%)	38 (67.9%)	905	56

Table 7. Use of call types by Blue Jays related to distance from the nearest conspecific, based on the occasions that I noted this information. Data are provided for all call types with ≥ 10 call types and ≥ 5 bouts. Close = conspecific ≤ 3 m away, distant = conspecific ≥ 3 m away, none = no conspecific apparently present. I have bolded the names of call type and bout percentage values with ≥ 60% in a category.

	Close		Distant		None	
Call Type	Calls	Bouts	Calls	Bouts	Calls	Bouts
Burry descending jay	1 (0.1%)	1 (4.5%)	61 (9.7%)	6 (28.6%)	**570 (90.2%)**	**14 (66.7%)**
Bell	21 (27.6%)	2 (25.0%)	6 (7.9%)	1 (12.5%)	**49 (64.5%)**	**5 (62.5%)**
Burry flat jay	0	0	0	0	**59 (100%)**	**6 (100%)**
Burry harsh descending jay	14 (15.4%)	1 (16.7%)	56 (61.5%)	2 (33.3%)	21 (23.1%)	3 (50%)
Continuous rattle	39 (54.2%)	1 (20.0%)	0	0	33 (45.8%)	4 (80.0%)
Flat jay	101 (25.7%)	3 (23.1%)	52 (13.2%)	3 (23.1%)	240 (61.1%)	7 (53.8%)
Harsh descending jay	266 (63.3%)	4 (19.0%)	66 (15.7%)	9 (42.9%)	88 (30.0%)	8 (38.1%)
Hoarse jay	1 (0.9%)	1 (20%)	59 (50.4%)	2 (40%)	57 (48.7%)	2 (40%)
Juvenile extended whine jay	**63 (75%)**	**8 (88.9%)**	21 (25%)	1 (11.1%)	0	0
Juvenile whine jay	120 (58%)	7 (87.5%)	87 (42%)	1 (12.5%)	0	0
Murmur bout	13 (28.9%)	4 (66.7%)	31 (68.9%)	1 (16.7%)	1 (2.2%)	1 (16.7%)
Short crow	0	0	44 (18.6%)	3 (42.9%)	192 (81.4%)	4 (51.1%)
Short descending jay	0	0	18 (15.9%)	2 (16.7%)	**95 (84.1%)**	**10 (83.3%)**
Squeaky gate	60 (20.3%)	3 (23.1%)	48 (16.3%)	3 (23.1%)	187 (63.4%)	7 (53.8%)
Segmented rattle	16 (48.5%)	2 (40.0%)	17 (51.5%)	3 (60.0%)	0	0
Yurping bout	**86 (92.5%)**	**17 (77.3%)**	3 (3.2%)	2 (9.2%)	4 (4.3%)	3 (13.6%)

Table 8. Mean characteristics (± SE) of calls uttered by Blue Jays.

Call-family/Name*	Number of notes	Low frequency (hertz)	High frequency (hertz)	Delta frequency range. (hertz)	Peak frequency (hertz)	Duration (sec)
Descending jay						
Short descending jay (30, 9)	1 ± 0	2909 ± 40	3840 ± 43	931 ± 29	3503 ± 51	0.24 ± 0.01
Extended descending jay (30, 7)	1 ± 0	2607 ± 47	3511 ± 55	904 ± 27	3147 ± 51	0.36 ± 0.01
Harsh descending jay (30, 11)	1.1 ± 0.04	2627 ± 30	3747 ± 27	1120 ± 26	3367 ± 31	0.36 ± 0.01
Burry harsh descending jay (30, 5)	1 ± 0	2455 ± 55	3672 ± 49	1218 ± 40	3250 ± 53	0.39 ± 0.02
Growl (4, 2)	1 ± 0	2503 ± 150	3398 ± 124	896 ± 75	3058 ± 83	0.46 ± 0.07
Juvenile Descending Jay (30, 2)	1 ± 0	2625 ± 36	3649 ± 43	1023 ± 36	3267 ± 37	0.32 ± 0.11
Flat jay						
Flat jay (30, 7)	1 ± 0	2786 ± 19	3405 ± 18	619 ± 13	3118 ± 21	0.27 ± 0.01
Short Growl (3, 2)	1 ± 0	2530 ± 100	375 ± 218	845 ± 134	2930 ± 100	0.25 ± 0.04
Burry jay						
Burry descending jay (30, 11)	1 ± 0	2518 ± 37	3433 ± 55	915 ± 31	2992 ± 48	0.28 ± 0.004
Burry flat jay (30, 6)	1 ± 0	2606 ± 33	3295 ± 30	689 ± 18	2957 ± 39	0.27 ± 0.01
Hoarse jay (30, 2)	1 ± 0	2420 ± 14	3377 ± 15	957 ± 19	2934 ± 27	0.34 ± 0.003
Bell						
Bell (30, 5)	1.1 ± 0.1	1358 ± 16	1928 ± 14	570 ± 11	1640 ± 20	0.35 ± 0.02
Song						
Whisper song (6, 3)	22.8 ± 7.1	2066 ± 291	6309 ± 348	4242 ± 489	4271 ± 392	7.72 ± 2.16
Mimicry						
Perfect crow (3, 1)	1 ± 0	979 ± 16	2534 ± 66	1554 ± 78	1608 ± 57	0.36 ± 0.10
Short crow (30, 4)	1 ± 0	1887 ± 86	2504 ± 97	617 ± 18	2199 ± 96	0.20 ± 0.01
Bald Eagle bout (6, 1)	5.3 ± 0.8	1636 ± 49	3159 ± 260	1523 ± 275	2067 ± 0	1.23 ± 0.31
Individual Bald Eagle note (3, 1)	1 ± 0	1719 ± 52	2715 ± 103	996 ± 128.	1952 ± 57	0.07 ± 0.01
Cooper's Hawk (4, 4)	4.8 ± 1.1	2149 ± 159	3700 ± 357	1552 ± 241	2842 ± 228	0.84 ± 0.12
Red-tailed Hawk (22, 4)	1.5 ± 0.2	1969 ± 39	3542 ± 95	1573 ± 104	3023 ± 106	0.69 ± 0.04
Red-shouldered Hawk (1, 1)	2	2392	3492	1100	3101	0.92
Broad-winged Hawk (0, 1)	-	-	-	-	-	-
Bell/jay						
Bell jay (30, 3)	2.6 ± 0.1	1578 ± 69	3201 ± 67	1623 ± 76	2739 ± 118	0.30 ± 0.01
Burry bell (30, 4)	1.3 ± 0.1	2388 ± 47	3107 ± 37	719 ± 76	2601 ± 50	0.41 ± 0.01
O-we (10, 1)	3 ± 0	1240 ± 23	3093 ± 29	1842 ± 28	2618 ± 140	0.29 ± 0.01
Yurp/murmur						
Murmur bout (30, 5)	5.5 ± 0.6	1916 ± 69	3409 ± 75	1493 ± 102	2705 ± 103	2.25 ± 0.26
Individual murmur (30, 2)	1 ± 0	2465 ± 52	106 ± 52	641 ± 19	2768 ± 52	0.12 ± 0.004
Yurping bout (29, 9)	8.8 ± 1.0	1689 ± 88	2691 ± 134	1002 ± 115	2251 ± 138	1.63 ± 0.26
Individual yurp (30, 10)	1 ± 0	2008 ± 115	2695 ± 128	687 ± 36	2366 ± 127	0.06 ± 0.004
Squeaky						
Squeaky gate (30, 12)	9.9 ± 0.3	1824 ± 80	5115 ± 170	3291 ± 206	3411 ± 149	0.38 ± 0.01

* After each call name, in parenthesis, I first indicate the number of calls measured and, second, the number of locations where that call type was recorded.

Table 8 (continued)

Call-family/Name[a]	Number of notes	Low frequency (hertz)	High frequency (hertz)	Delta frequency range. (hertz)	Peak frequency (hertz)	Duration (sec)
Squeaky ctd.						
Partial squeaky gate (30, 8)	2.8 ± 0.2	1966 ± 57	3353 ± 179	1386 ± 145	2362 ± 74	0.28 ± 0.01
Whine jay						
Juvenile whine jay (30, 5)	1 ± 0	5272 ± 161	6013 ± 154	741 ± 23	5639 ± 158	0.27 ± 0.01
Juvenile extended whine Jay (30, 5)	1 ± 0	5284 ± 146	6258 ± 163	973 ± 65	5779 ± 151	0.58 ± 0.03
Whine jay (13, 1)	1 ± 0	2362 ± 77	3178 ± 119	816 ± 77	2828 ± 97	0.35 ± 0.01
Extended whine jay (7, 1)	1 ± 0	2368 ± 52	3371 ± 51	1103 ± 92	2978 ± 32	0.50 ± 0.02
Inverted whine jay (10, 2)	1 ± 0	3356 ± 271	4921 ± 362	1565 ± 147	3773 ± 294	0.40 ± 0.04
Hiccup/whistle						
Whistle (30, 5)	1.1 ± 0.1	1812 ± 61	2795 ± 83	983 ± 267	2364 ± 85	0.10 ± 0.01
Hiccup (30, 5)	2.2 ± 0.1	2154 ± 96	5623 ± 93	3469 ± 131	2992 ± 122	0.36 ± 0.01
Rattle						
Segmented rattle (27, 4)	7.7 ± 0.9	1533 ± 26	3138 ± 50	1605 ± 44	2067 ± 64	0.69 ± 0.08
Continuous rattle (30, 6)	28.8 ± 1.6	1292 ± 44	4297 ± 312	3006 ± 291	1981 ± 150	0.75 ± 0.04
Cry						
Cry (2, 1)	2.5 ± 0.5	4594 ± 189	6432 ± 108	1838 ± 81	5719 ± 1838	0.26 ± 0.08
Grunt						
Grunt (1, 3)	2	1642	11512	9870	5168	0.44
Nestling twitter						
Nestling Twitter (18, 2)	2.1 ± 0.2	4793 ± 176	6010 ± 118	1217 ± 124	5245 ± 168	0.27 ± 0.03

[a] After each call name, in parenthesis, I first indicate the number of calls measured and, second, the number of locations where that call type was recorded.

Table 9. The names of call types of Blue Jays provided in previous studies and in this study.

My Call-family	My Classification	Cohen (1977)	Conant (1972)
Descending jay	Short descending jay	Ditonal jay	Alarm
	Extended descending jay	"	"
	Growl	"	"
	Burry harsh descending jay	"	"
	Harsh descending jay	"	"
	Juvenile descending jay	"	"
Burry jay	Burry descending jay	"	"
	Burry flat jay	"	"
	Hoarse jay	"	"
Flat jay	Flat jay	Monotonal jay	Flock contact
	Short growl	"	"
Bell/jay	Bell jay	"	Wheedle-bell song?
	Burry bell	"	"
	O-we	"	"
Imitation	Short crow	-	Crow
	Perfect crow	-	-
	Bald Eagle bout	-	-
	Individual Bald Eagle note	-	-
	Cooper's Hawk	-	-
	Red-tailed Hawk	-	-
	Broad-winged Hawk	-	-
	Red-shouldered Hawk	-	-
	-	-	Meow
Yurp/murmur	Murmur bout	-	Begging keu?
	Individual murmur	-	"
	Yurping bout	Yurp	Soft keu
	Individual yurp	"	-
	-	-	Loud keu
Bell	Bell	Bell	Bell song
Squeaky	Squeaky gate	Squeaky gate	Pumphandle
	Partial squeaky gate	"	"
Whine jay	Juvenile whine jay	Begging	Young food begging 2
	Juvenile extended whine jay	"	Young food begging 3
	-	-	Young food begging 4
	Extended whine jay	-	-
	Whine jay	-	-
	Inverted whine jay	-	-
Nestling twitter	Nestling twitter	Peeping?	Young food begging 3
Whistle/hiccup	Whistle	-	Descending whistle?
	Hiccup	-	"?
	-	-	Triple descending whistle?
Rattle	Segmented rattle	Rattle	Rolling click
	Continuous rattle	"	"
Grunt	Grunt	-	-
Cry	Cry	Squacking?	Distress?
Song	Whisper song	Chortling	Song
?	-	Churring	-
?	-	Swallowing	-
?	-	Chucking	-
?	-	Chirping	-
?	-	Mewing	-
?	-	-	Growl

Table 10. Call types uttered at the three locations where I observed and recorded Blue Jays most often. Ten call types were uttered at all three locations, eight call types at two locations, and 11 call types at just one location.

	A (12 visits)	B (16 visits)	C (15 visits)
All locations	Burry bell	Burry bell	Burry bell
"	Burry descending jay	Burry descending jay	Burry descending jay
"	Extended descending jay	Extended descending jay	Extended descending jay
"	Flat jay	Flat jay	Flat jay
"	Harsh descending jay	Harsh descending jay	Harsh descending jay
"	Partial squeaky gate	Partial squeaky gate	Partial squeaky gate
"	Red-tailed Hawk	Red-tailed Hawk	Red-tailed Hawk
"	Short descending jay	Short descending jay	Short descending jay
"	Squeaky gate	Squeaky gate	Squeaky gate
"	Yurping bout	Yurping bout	Yurping bout
Two locations	Burry harsh descending jay	Burry harsh descending jay	-
"	Continuous rattle	Continuous rattle	-
"	-	Hiccup	Hiccup
"	-	Hoarse Jay	Hoarse jay
"	-	Murmur bout	Murmur bout
"	-	Segmented rattle	Segmented rattle
"	-	Whistle	Whistle
"	Short crow	-	Short crow
"	-	Individual yurp	Individual yurp
One location	-	-	Burry flat jay
"	-	Bell jay	-
"	-	Broad-winged Hawk	-
"	Cooper's Hawk	-	-
"	-	-	Extended whine jay
"	-	Cry	-
"	-	Individual murmur	-
"	-	-	Inverted whine jay
"	-	-	O-we
"	Whisper song	-	-
"	-	-	Whine jay
Total call types	15	22	22

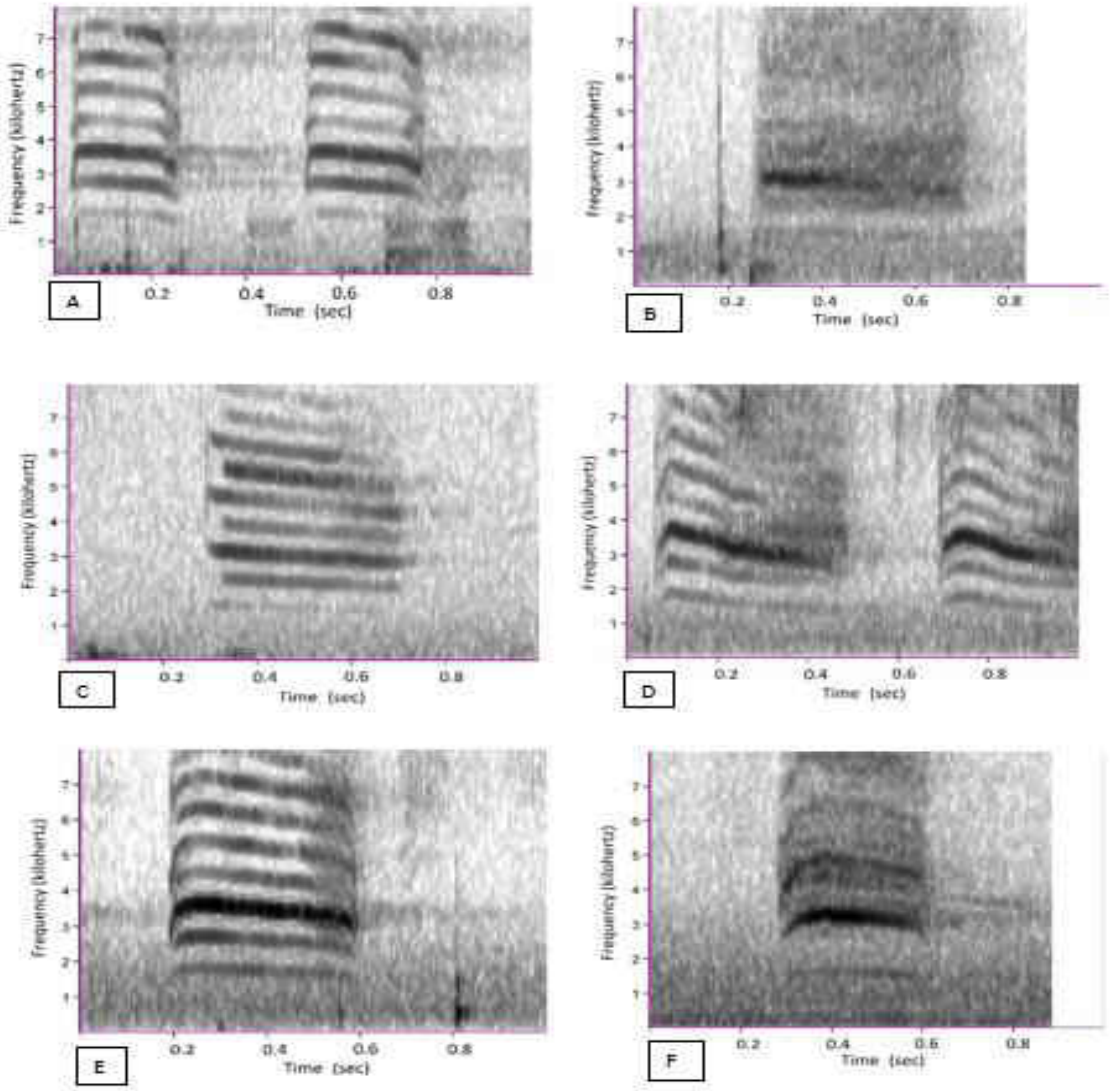

Figure 1. The descending jay call-family included the (A) short descending jay, (B) growl, (C) extended descending jay, (D) burry harsh descending jay, (E) harsh descending jay, and (F) juvenile descending jay.

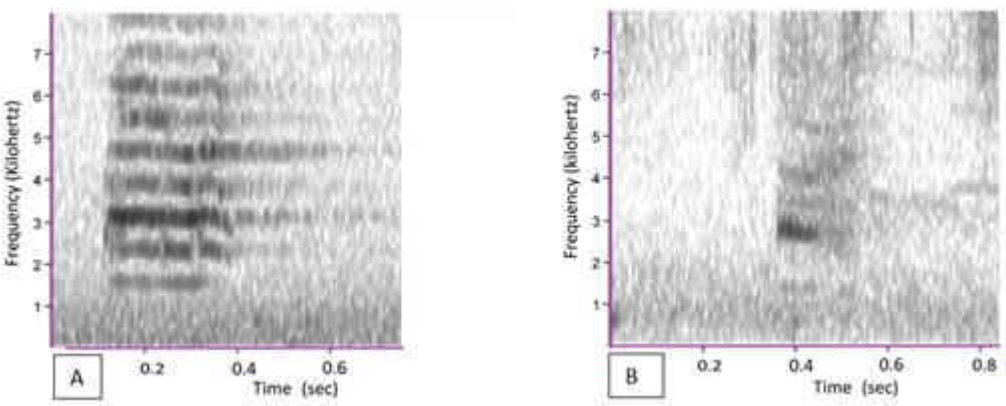

Figure 2. The flat jay call-family included the (A) flat jay and (B) short growl.

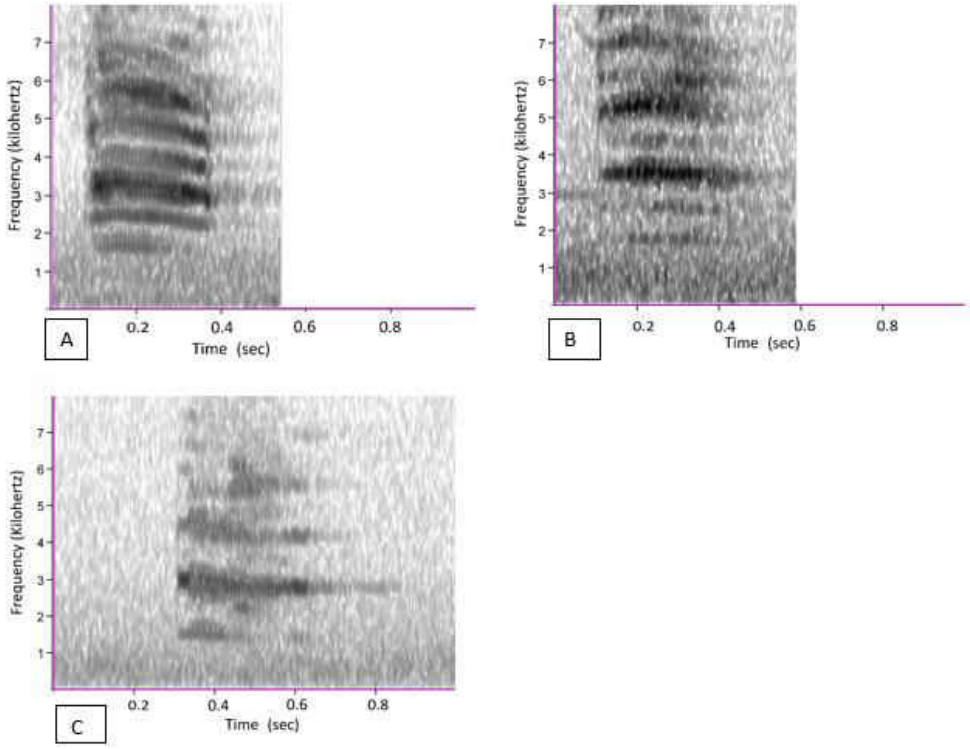

Figure 3. The burry call-family included the (A) burry descending jay, (B) burry flat jay, and (C) hoarse jay.

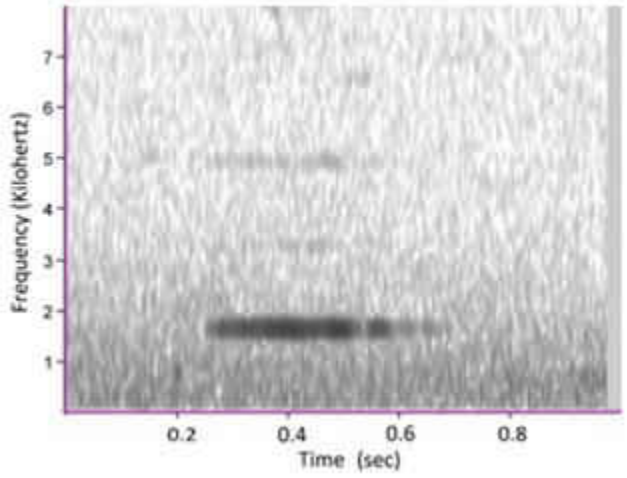

Figure 4. The bell call of a Blue Jay.

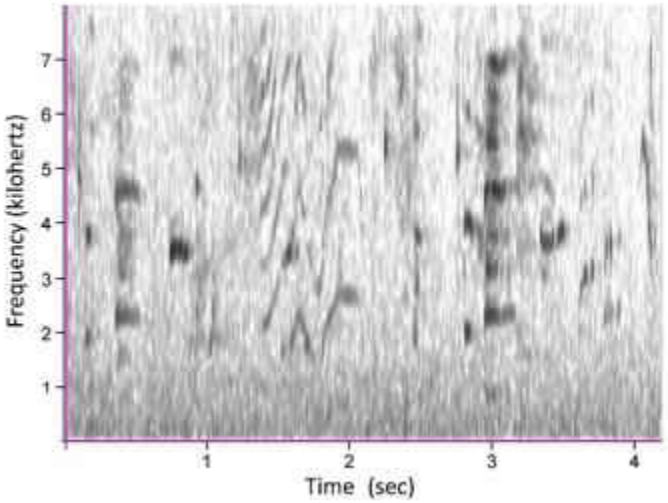

Figure 5. The whisper song of a Blue Jay (the time scale is different compared to other spectrograms).

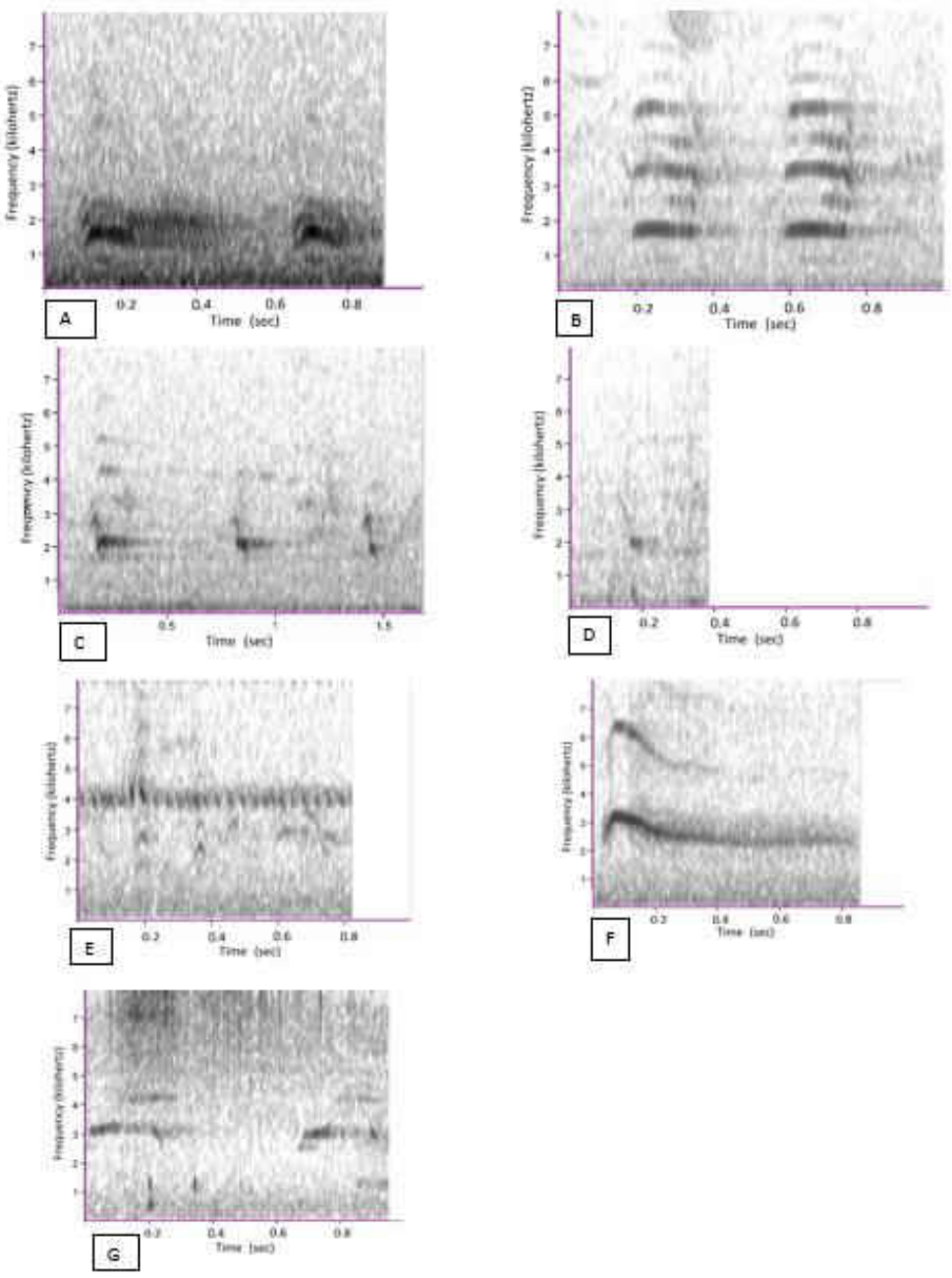

Figure 6. The imitation call-family included the (A) perfect crow, (B) short crow, (C) Bald Eagle bout (the time scale is different compared to other spectrograms), (D) individual Bald Eagle note, (E) Cooper's Hawk call (the trill in back ground is another bird), (F) Red-tailed Hawk call, and (G) Red-shouldered Hawk call.

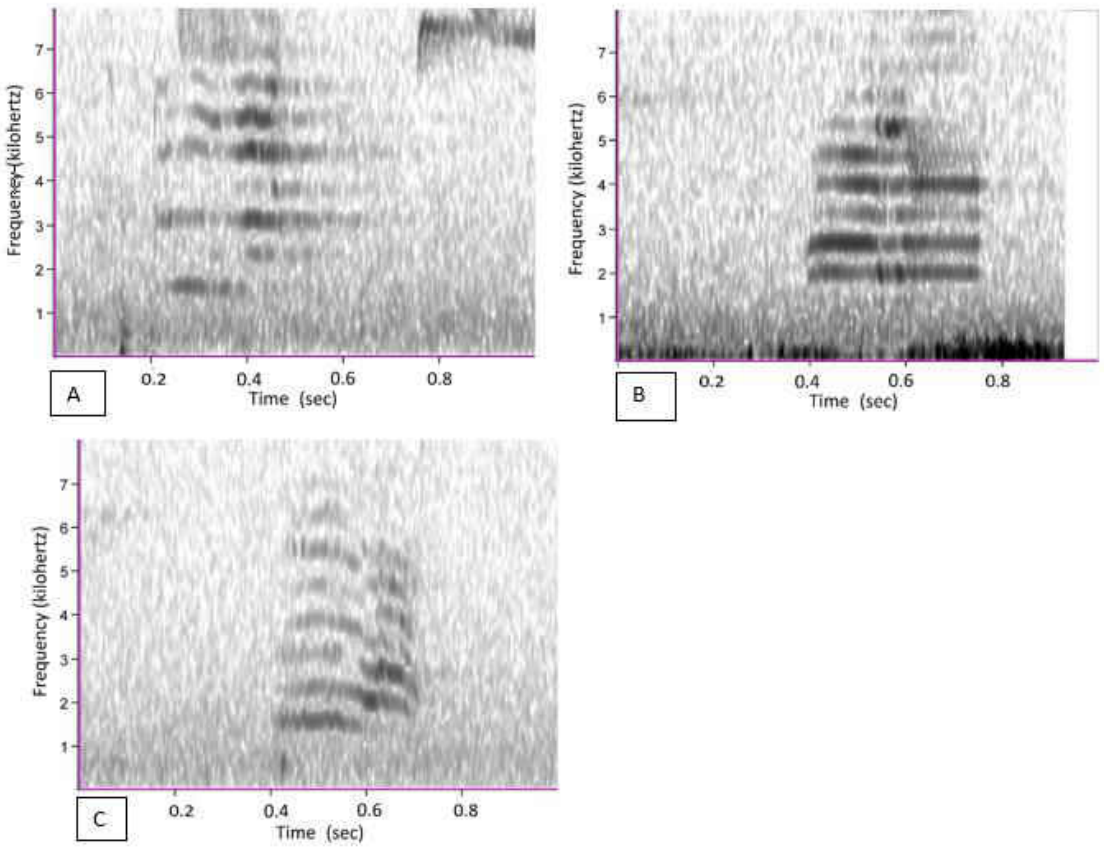

Figure 7. The bell/jay call-family included the (A) bell jay call, (B) burry bell call, and (C) o-we call.

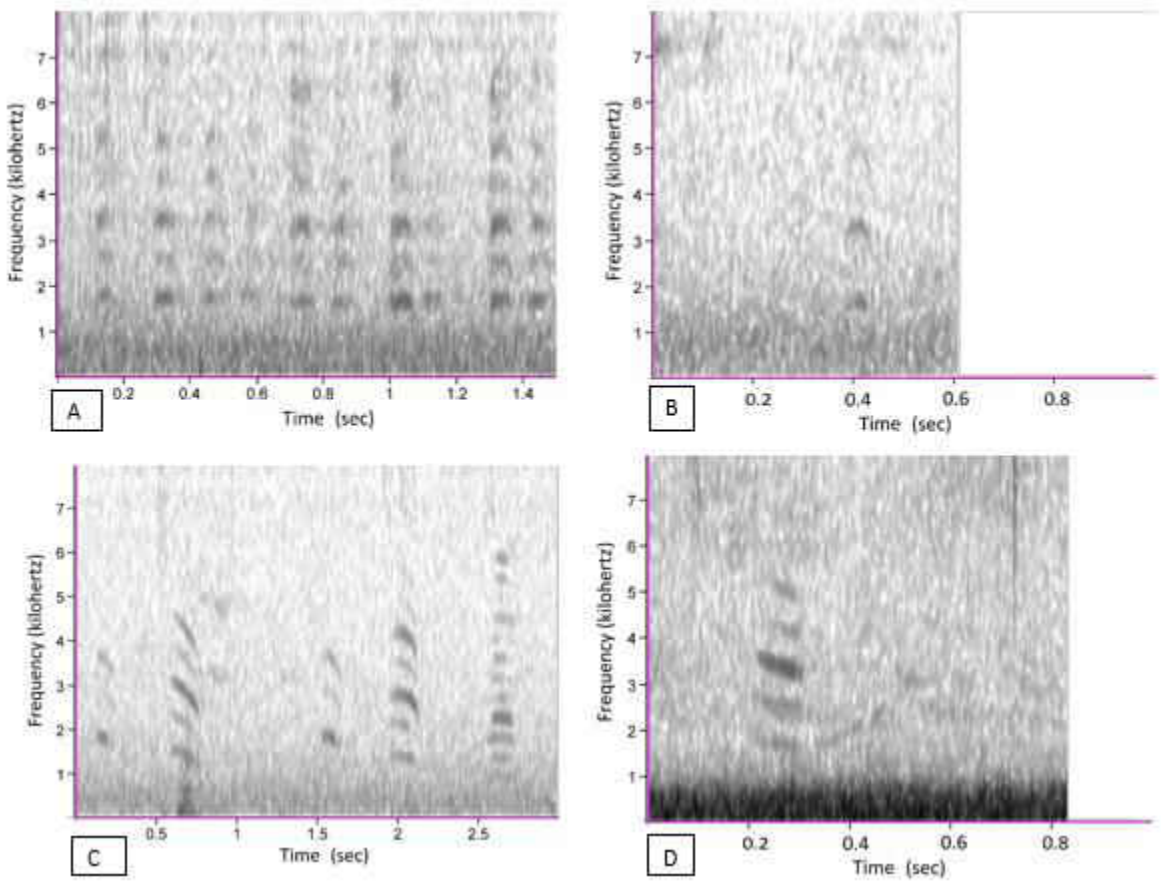

Figure 8. The yurp/murmur call-family included the (A) yurping bout, (B) individual yurp, (C) murmur bout, and (D) individual murmur. Note the different time scales for A and C.

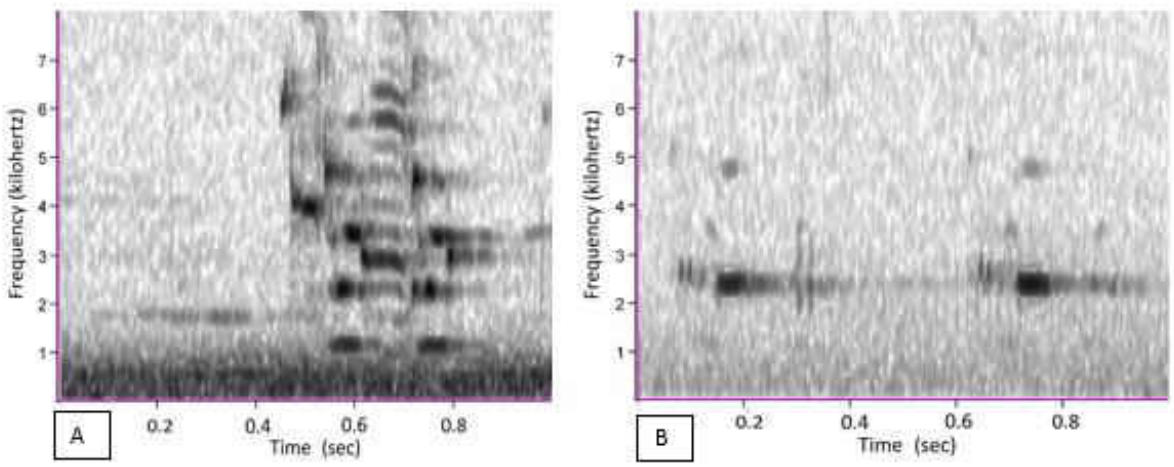

Figure 9. The squeaky call-family included the (A) squeaky gate call and (B) partial squeaky gate call.

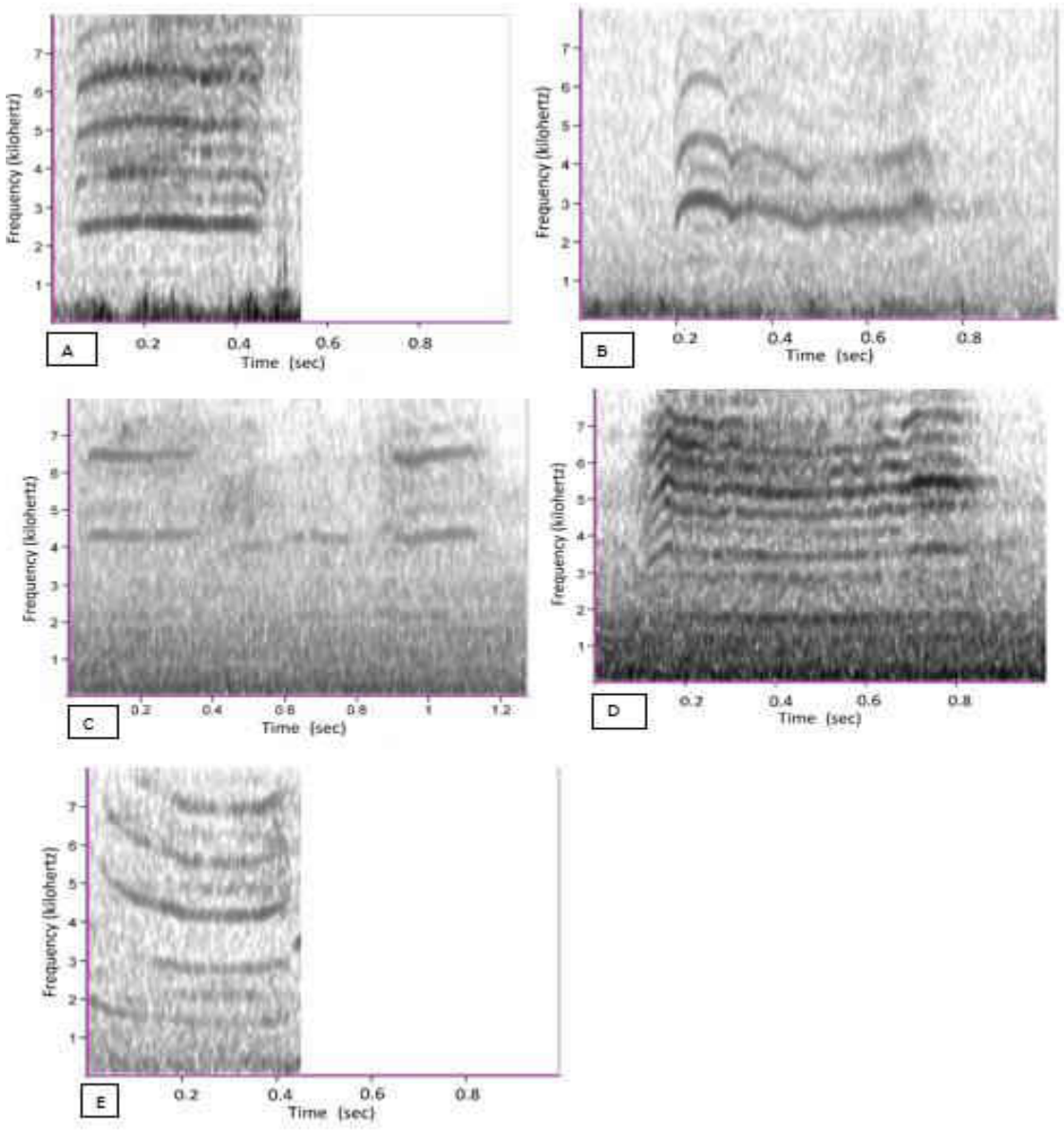

Figure 10. The whine jay call-family included the (A) whine jay, (B) extended whine jay, (C) juvenile whine jay, (D) juvenile extended whine jay (the time scale is different compared to other spectrograms) and (E) inverted whine jay.

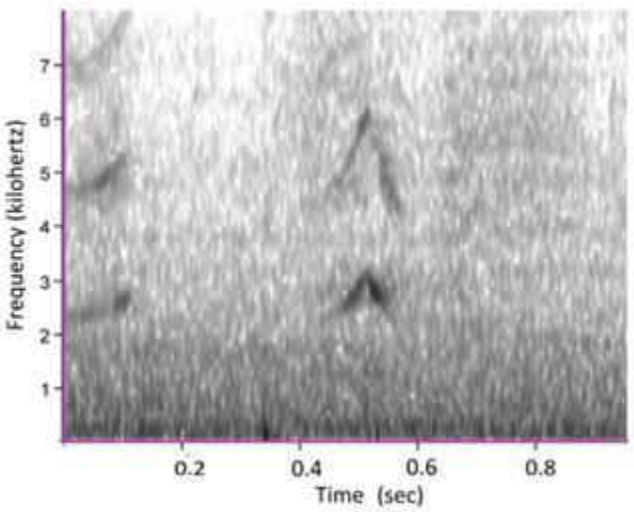

Figure 11. The nestling twitter call of a nestling Blue Jay.

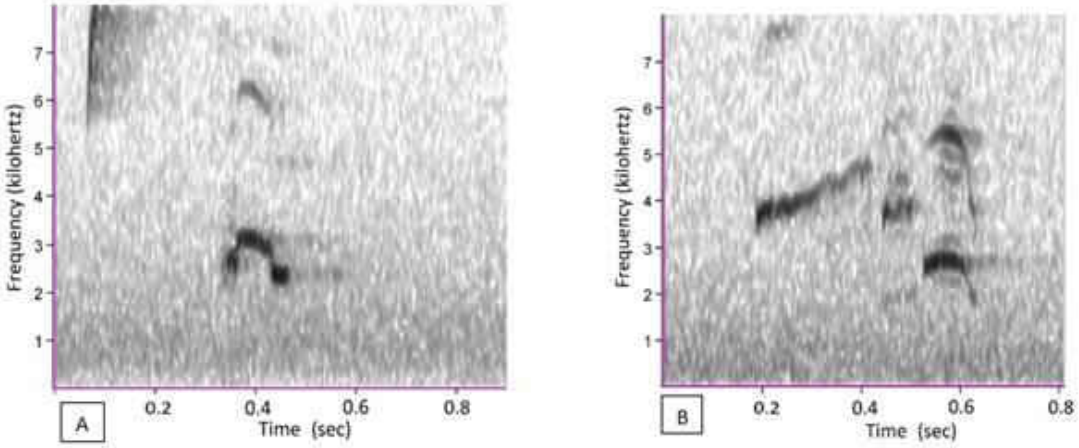

Figure 12. The hiccup/whistle call-family included the (A) whistle and (B) hiccup.

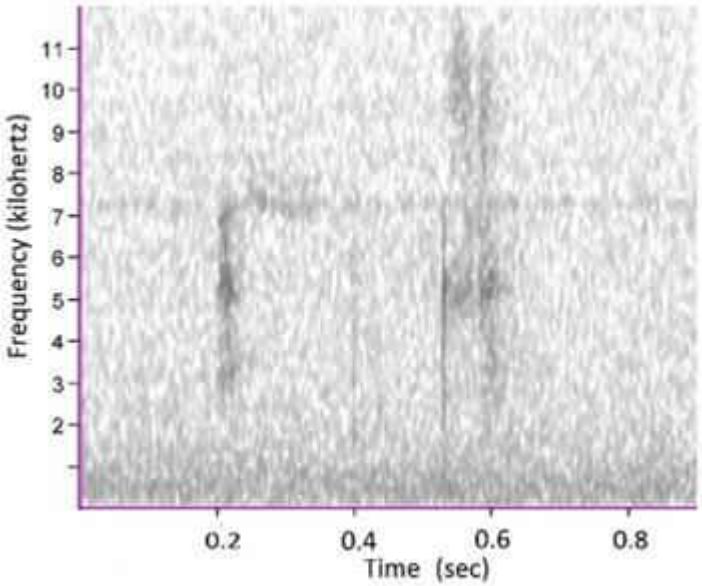

Figure 13. The grunt call of a Blue Jay.

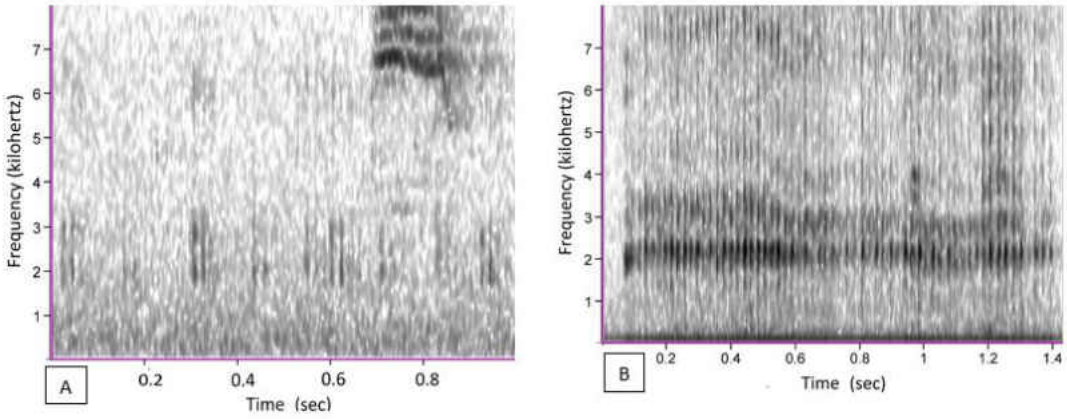

Figure 14. The rattle call-family included the (A) segmented rattle and (B) continuous rattle (the time scale is different compared to other spectrograms).

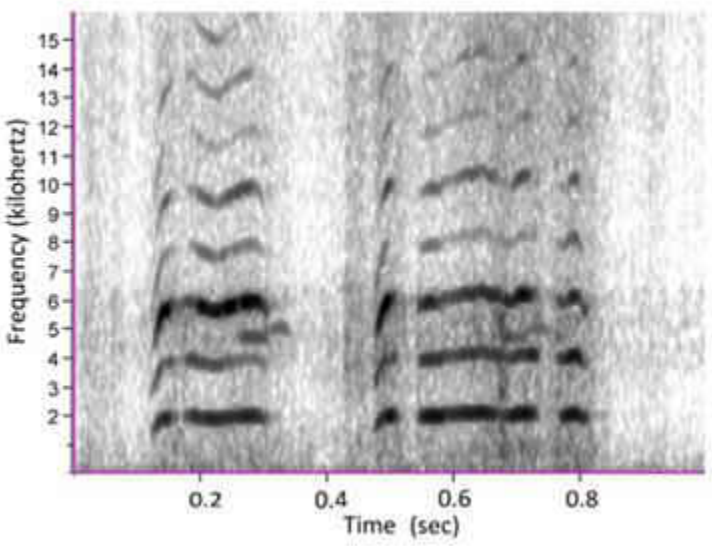

Figure 15. The cry call of a Blue Jay.

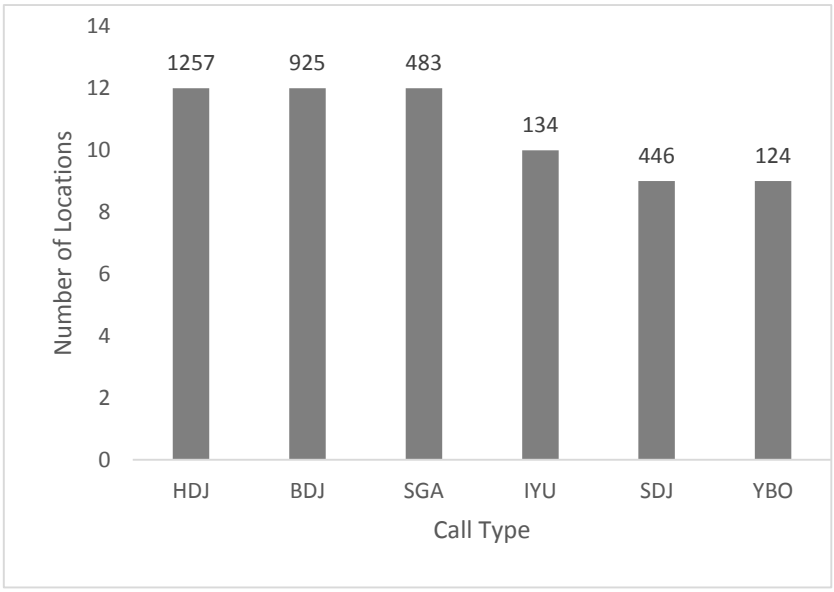

Figure 16. Call types of Blue Jays recorded at the most locations (out of 17 locations), with total number of times that I recorded each call at these locations above the bars. HDJ = harsh descending jay, BDJ = burry descending jay, SGA = squeaky gate, IYU = individual yurp, SDJ = short descending jay, and YBO = yurping bout.

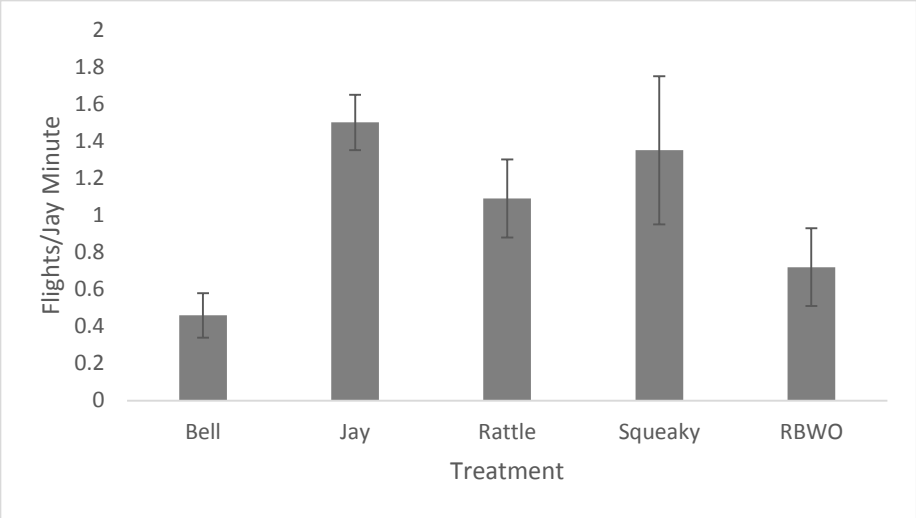

Figure 17. Average number of flights/jay minute (± S.E.) in response to playback of different calls in the vocal repertoire of Blue Jays plus a control (RBWO = call of a Red-bellied Woodpecker).

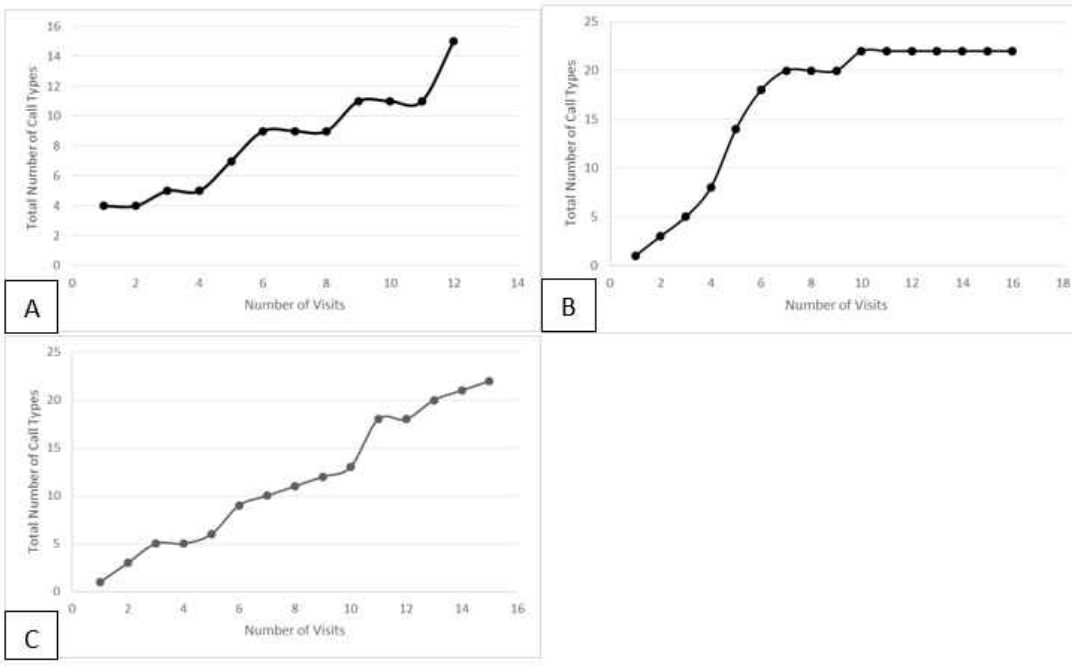

Figure 18. Relationship between number of observation periods and number of different call types recorded at three different locations. Location A averaged 1.45 ± 0.32 new calls per visit and did not reach an asymptote after 12 visits. Location B averaged 1.38 ± 0.34 new calls per visit and reached an asymptote of 22 call types after 10 visits. Location C averaged 1.25 ± 0.36 new call types per visit and did not reach an asymptote after 16 visits.