



**ICA 2013 Montreal
Montreal, Canada
2 - 7 June 2013**

**Animal Bioacoustics
Session 3pAB: Perceiving Objects II**

3pAB1. Categories, concepts, and calls: Auditory perceptual mechanisms and cognitive abilities across different types of birds

Allison H. Hahn, Lauren M. Guillette, Marisa Hoeschele, Robert G. Cook and Christopher Sturdy*

***Corresponding author's address: csturdy@ualberta.ca**

Although involving different animals, preparations, and objectives, our laboratories (Sturdy's and Cook's) are mutually interested in category perception and concept formation. The Sturdy laboratory has a history of studying perceptual categories in songbirds, while Cook laboratory has a history of studying abstract concept formation in pigeons. Recently, we undertook a suite of collaborative projects to combine our investigations to examine abstract concept formation in songbirds, and perception of songbird vocalizations in pigeons. This talk will include our recent findings of songbird category perception, songbird abstract concept formation (same/different task), and early results from pigeons' processing of songbird vocalizations in a same/different task. Our findings indicate that (1) categorization in birds seems to be most heavily influenced by acoustic, rather than genetic or experiential factors (2) songbirds treat their vocalizations as perceptual categories, both at the level of the note and species/whole call, (3) chickadees, like pigeons, can perceive abstract, same-different relations, and (4) pigeons are not as good at discriminating chickadee vocalizations as songbirds (chickadees and finches). Our findings suggest that although there are commonalities in complex auditory processing among birds, there are potentially important comparative differences between songbirds and non-songbirds in their treatment of certain types of auditory objects.

Published by the Acoustical Society of America through the American Institute of Physics

INTRODUCTION

Category perception is the idea that discriminable stimuli can be sorted into groups based on perceptual similarity, thus forming larger *categories*. Categorization by nonhuman animals has been demonstrated in both the visual (for review see Herrnstein, 1990; Wasserman, 1995) and auditory (for review see Sturdy *et al.*, 2007) domains. Herrnstein (1990) outlined five levels of categorization: (1) discrimination, (2) categorization by rote, (3) open-ended categories, (4) concepts, and (5) abstract relations. Here, we discuss perceptual categorization by songbirds. We provide evidence that birds treat their vocalizations as open-ended categories and are also able to learn abstract-concept relationships. For songbirds in the wild, the ability to classify natural vocalizations has adaptive significance. Songbirds can use vocalizations to discriminate between territory neighbors and strangers (Stoddard *et al.*, 1990), discriminate flocks (Nowicki, 1983), and identify a mate (Miller, 1979; Lind *et al.*, 1996). Using operant conditioning paradigms, several research groups have demonstrated that a variety of songbird species classify vocalizations into perceptual categories (e.g., Gentner and Hulse, 1998; Sturdy *et al.*, 1999; Braaten, 2000). In the following we discuss a range of classification abilities from perceptual categorization to abstract concept formation across a range of bird species, including auditory categorization of conspecific and heterospecific vocalizations by songbirds, abstract-concept discriminations by songbirds and a non-songbird (pigeons), and the auditory discrimination of songbird vocalizations by pigeons. We end with an outline of future directions to be taken by us and the field at large, and speculate about the extent of these abilities and what we can learn from such investigations.

SONGBIRD VOCALIZATIONS AS PERCEPTUAL CATEGORIES

The namesake *chick-a-dee* call of the black-capped chickadee (*Poecile atricapillus*) is an extremely well-studied vocalization. The *chick-a-dee* call is comprised of four note types, termed A, B, C, and D notes by bioacousticians (Ficken *et al.*, 1978; see Figure 1, (a,b) for calls produced by black-capped chickadees). The call follows a strict syntax (Hailman *et al.*, 1985), with the four note types produced in a fixed order ($A \rightarrow B \rightarrow C \rightarrow D$). Within this framework, however, note types can be repeated (e.g., AABBBBCD) or omitted (e.g., ABD).

In addition to note-type categorization by bioacousticians, statistical classifications and artificial neural networks have been employed successfully to classify *chick-a-dee* call notes into these four note-type categories (Nowicki and Nelson, 1990; Dawson *et al.*, 2006b). In other species of songbirds, individuals can discriminate large numbers of conspecific vocalizations (e.g., Stoddard *et al.*, 1992). Evidence from the statistical classifications of *chick-a-dee* call notes suggest that sufficient acoustic differences exist that birds could be able to discriminate among the separate notes within conspecific calls.

Assuming birds can discriminate among call notes, there are two strategies for categorization that birds could be using: rote categorization or open-ended categorization. If an animal were to use rote memorization, that individual must have experience with and memorize all exemplars. On the other hand, open-ended categorization does not require memorization of each individual stimulus, but rather perceptual similarities or a general ‘category’ rule can be learned and used for successful discrimination (Herrnstein, 1990). One method to demonstrate that an animal is employing open-ended categorization as a strategy to solve a discrimination problem is by assessing the results of simultaneous within-category and between-category discrimination tasks (e.g., Astley and Wasserman, 1992). For the within-category task, exemplars from one perceptual category are both reinforced and nonreinforced; to successfully solve this task, individuals need to rely on rote memorization of the individual stimuli. For the between-category task, exemplars from one perceptual category are reinforced, while exemplars from another perceptual category are nonreinforced; to learn this task, individuals could use open-ended categorization, by responding to all perceptually-similar stimuli within a category. Individuals should be able to learn both discriminations, but they should learn the between-category discrimination faster. Using a go/no-go operant procedure with both a within-category and between-category discrimination task, Sturdy *et al.* (2000) demonstrated that black-capped chickadees perceive their call notes as open-ended categories that map onto those used by human and statistical classifications.

While the results of Sturdy *et al.* (2000) demonstrated that chickadees perceive their own call notes as open-ended categories, in a series of experiments, members of our group examined whether chickadees perceive different species’ *chick-a-dee* calls as species-based categories (Bloomfield *et al.*, 2003; 2008a; 2008b; Bloomfield and Sturdy, 2008). These studies demonstrated that black-capped chickadees similarly perceive conspecific and closely-related heterospecific (i.e., Carolina chickadee, *Poecile carolinensis*, Bloomfield *et al.*, 2003; mountain chickadee, *P. gambeli*, Bloomfield and Sturdy, 2008) *chick-a-dee* calls as species-based open-ended categories. These

perceptual categorization abilities did not require prior experience with both species' calls. Allopatric black-capped chickadees (birds with no prior experience with mountain chickadees), sympatric black-capped chickadees (birds with prior experience with mountain chickadees), and mountain chickadees showed no significant differences in their discrimination and classification abilities with either black-capped or mountain *chick-a-dee* calls (Sturdy and Bloomfield, 2008; see Figure 1 for calls produced by black-capped and mountain chickadees). Moreover, hand-reared black-capped chickadees did not perform significantly differently from wild-caught birds on this species-based categorization task (Bloomfield *et al.*, 2008b). Taken together, these studies suggest black-capped and mountain chickadees are able to perform a species-based classification of their calls and prior experience is not necessary in order to accurately categorize the calls.

To further examine the perceptual mechanisms controlling species-based discrimination, we completed an additional series of experiments. By presenting the birds with manipulated stimuli that contained notes from both species' calls we aimed to better understand how birds performed the discrimination. The results of these mechanistic experiments suggest that the perceptual categorization of *chick-a-dee* calls appears to be controlled by the terminal *dee* portion of the call (i.e., D notes in both species' call and D_{hybrid} notes in the mountain chickadee call) to a greater degree than the introductory *chick-a* portion of the call (i.e., A, B, and C notes in both species' call and AB notes in the mountain chickadee call; Bloomfield *et al.*, 2008a). Results from statistical classifications, however, suggest that acoustic features within all note types contain sufficient differences to allow black-capped and mountain chickadees to discriminate between these two species' calls (Dawson *et al.*, 2006a). Using discriminant function analyses, Dawson *et al.* found that the D notes were correctly classified based on species of the signaler with 94% accuracy, while the notes found in the *chick-a* portion of the call (i.e., A, B, C) resulted in perfect classification.

In order to clarify the previous behavioral (Bloomfield *et al.*, 2008a) and statistical (Dawson *et al.*, 2006a) results, we conducted additional go/no-go operant conditioning experiments to further examine chickadees' perceptual categorization abilities on two species-based *chick-a-dee* call discriminations (Guillette *et al.*, 2010). In Experiment 1, chickadees were trained to discriminate entire *chick-a-dee* calls and then transferred to individual note-types from the calls. D notes are longer compared to A, B, or C notes; however, in Experiment 1 we controlled for this temporal difference by repeating a single note type. The results suggested that extending the temporal window does not facilitate birds' discrimination abilities compared to presentation of a single note, with two exceptions: black-capped chickadee C notes and mountain chickadee AB notes. In Experiment 2, chickadees were trained to discriminate individual note-types in order to determine which note-types are the easiest to discriminate. Results from Experiment 2 demonstrated that chickadees learned the D-note discrimination in significantly fewer trials (i.e., faster) than the B- or C-note discriminations, suggesting that D notes contain the most species-specific information, followed by A notes. In sum, the results from these experiments suggest that the D notes contain more species-specific information that birds can use to solve the discrimination compared to the other note types, and the longer duration of the D notes alone does not explain birds' abilities to discriminate the D notes most easily. These perceptual studies demonstrate that the D note of black-capped and mountain chickadee calls is important for chickadees' species-based discrimination abilities.

Although experience in the wild with both species does not aid performance on a species-based classification task (Bloomfield and Sturdy, 2008), in all of the discrimination studies mentioned above, chickadees had prior experience with at least one of the species' calls, namely their own species *chick-a-dee* calls (i.e., conspecific calls). What remained to be tested was the extent to which experience controlled the birds' perception and discrimination, versus the importance of acoustic complexity to these abilities.

In order to compare the roles of experience versus acoustic complexity, we trained zebra finches (*Taeniopygia guttata*) on a black-capped and mountain chickadee species-based discrimination using the same methods and stimuli in Experiment 2 of Guillette *et al.* (2010). Zebra finches served as an ideal species to clarify whether experience or acoustics was the main factor underlying birds' ability to solve species-based discriminations, because zebra finches are vocal-learning songbirds, just like chickadees, but are distantly-related to the chickadee species tested previously, and have no prior experience with chickadee vocalizations. Results from these newer experiments revealed that zebra finches performed similarly to chickadees, solving the D-note discrimination in significantly fewer trials compared to the other note-types (Guillette *et al.*, 2012). These results suggest that there are sufficient acoustical differences within all note-types for songbirds to learn the species-based discrimination; however, acoustic features within the D notes aid in the discrimination of this note-type compared to other *chick-a-dee* call notes (i.e., A, B, C notes). While zebra finches learned the D-note discrimination faster compared to all other note-types, chickadees did not learn the D-note discrimination in significantly fewer trials compared to the A-note discrimination (Guillette *et al.*, 2010). This difference in the discrimination performance of the songbird species tested suggests that the A notes may contain species-specific cues that are learned.

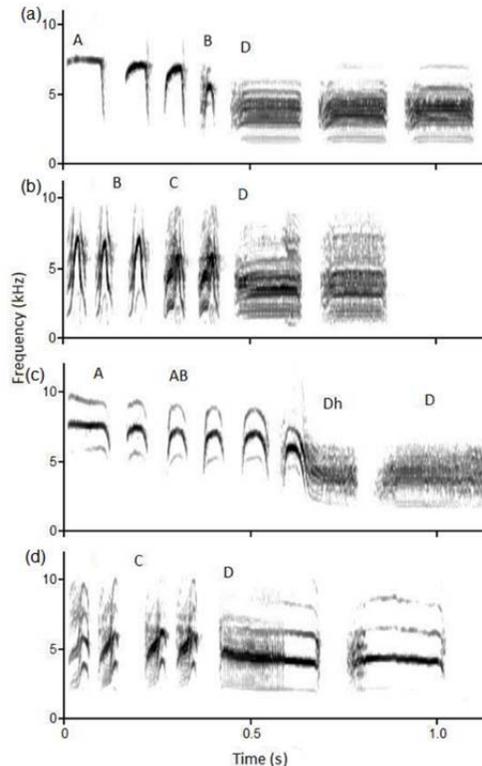


FIGURE 1. Sound spectrograms showing representative notes from *chick-a-dee* calls. Calls produced by black-capped chickadees (a,b) and calls produced by mountain chickadees (c,d). Note names appear above the call. This figure originally appeared in Guillette *et al.*, 2010.

PERCEPTION OF ABSTRACT RELATIONS

The studies described in the previous section all examined songbird classification abilities while classifying conspecific or heterospecific calls or call notes. These studies established that black-capped chickadees form open-ended perceptual categories of natural stimuli, specifically *chick-a-dee* calls. Birds form open-ended categories of individual notes within conspecific calls, and birds form species-based open-ended categories of whole calls or call notes.

While black-capped chickadees produce an acoustically complex *chick-a-dee* call (i.e., multiple note types that may be repeated within one call), male black-capped chickadees sing a two-note song that is relatively simple compared to the complex songs of many songbirds. This *fee-bee* song is sung over a continuum of frequencies (Horn *et al.*, 1992) and as a signal of aggression, a male will pitch shift their song to match the singing of rival males (Mennill and Ratcliffe, 2004). The first note within the *fee-bee* song (i.e., *fee* note) is sung at a higher frequency than the second note (i.e., *bee* note). As males shift the absolute frequency of their songs, the relative pitch interval between the two notes remains consistent (Weisman *et al.*, 1990) and dominant males are better able to maintain this consistency as they frequency shift their songs (Christie *et al.*, 2004).

In general, pitch can be categorized according to absolute or relative relations. Absolute pitch is the ability to classify a note's frequency without external reference. While relative pitch discriminations require the ability to perceive the frequency relationship among notes. Studies have found that songbird species will rely on absolute pitch relations, even on tasks designed to use relative pitch rules, and the birds learned the absolute relations by rote memorization (e.g., Hulse and Cynx, 1985; Cynx *et al.*, 1986). However, it has been demonstrated that black-capped chickadees can learn discrimination tasks using both absolute (Lee *et al.*, 2006) and relative (Hoeschele, Cook, Guillette, Brooks *et al.*, 2012; Hoeschele, Guillette *et al.*, 2012) pitch relations. Chickadees' abilities to learn tasks utilizing absolute and relative pitch relationships may be the result of the pitch relations that they attend to within their songs.

That black-capped chickadees attend to pitch relations in their songs and other auditory stimuli has been well established, but their abilities to perceive abstract-concept relations needed further assessment. Same/different relations are one type of abstract-concept relationship that has been well studied in other avian and non-avian

species (e.g., Pepperberg, 1987; Cook *et al.*, 1997; Wright and Katz, 2007). In same/different discriminations, subjects are presented with multiple items and must determine if the stimuli are all the *same* or *different*. Often, these tasks use visual stimuli; however, evidence that chickadees can attend to both the absolute and relative frequency relations contained within black-capped chickadee songs suggest that chickadees may attend to auditory same/different relationships in the wild while engaging in acoustic communication (e.g., countersinging contests) with conspecifics. As previously mentioned, all species of chickadee produce the *chick-a-dee* call, and black-capped and mountain chickadees are able to discriminate whole calls and call notes. In areas where more than one species of chickadee live, chickadees may use a same/different concept to discriminate whether a call is produced by a conspecific or heterospecific. In addition, birds may use a same/different concept when attending to the note type composition of the call, with the information encoded within the call varying depending on the call's composition. For example, it has been demonstrated that the number of D notes within the *chick-a-dee* call varies with the degree of perceived threat (Templeton *et al.*, 2005).

Based on the methodology of an auditory same/different task done with pigeons (*Columba livia*, Cook and Brooks, 2009; Murphy and Cook; 2010), we examined black-capped chickadees' abilities in an abstract same/different task using synthesized sound sequences (Hoeschele, Cook, Guillette, Hahn *et al.*, 2012). During training, *different* sequences contained 12 stimuli each with a different pitch and timbre, while *same* sequences consisted of the same stimulus repeated 12 times. Birds were reinforced for responding following *different*, but not *same*, sequences. The chickadees were then presented with novel sequences and novel stimuli. Response patterns during the novel sequence test indicated that birds were using a same/different concept to solve the task and not simply memorizing *different* sequences. In addition, the final six stimuli within the sequence were more influential in determining the chickadees' responses compared to the first six stimuli. The novel stimulus test revealed that chickadees' responding generalized when pitch or timbre was held constant, and when novel pitches and timbres from within the range of training stimuli were tested. When transfer tested with novel pitches from outside the range of frequencies used during training, however, the chickadees did not show transfer. In addition, chickadees only showed transfer to novel complex stimuli (i.e., sounds with more complex harmonic structure) after being trained with other complex sounds, but prior to this training, they did not demonstrate transfer. These results demonstrate that black-capped chickadees can form abstract concepts of *same* versus *different* at least when tested with stimuli having partial similarity to that experienced during training.

Numerous studies have examined pigeons' abilities on visual same/different tasks (Cook *et al.*, 1997; Young and Wasserman, 2001; Cook *et al.*, 2003; Katz and Wright, 2006), but few have examined pigeons' abilities on same/different concept formation in the auditory domain (Cook and Brooks, 2009; Cook and Murphy, 2010). Because of the procedural similarities incorporated in these studies, comparisons can be made between the chickadee and pigeon results. Both species were able to solve the auditory same/different task; however, chickadees were able to learn the task faster. One potential reason for this difference is that as songbirds, chickadees are vocal learners, and auditory stimuli may be especially relevant to them. In comparison, pigeons do not learn their vocalizations. While they communicate with these vocalizations for a variety of functions (e.g., courtship behavior, Partan *et al.*, 2005) they may rely more on visual information in many settings. Nonetheless, they can solve abstract-concept tasks using auditory stimuli suggesting that this capacity is widespread in this class.

DISCRIMINATION OF SONGBIRD VOCALIZATIONS BY PIGEONS

As reviewed above, chickadees can readily learn a species-based discrimination of conspecific versus heterospecific calls (Bloomfield *et al.*, 2003; 2008a; 2008b; Bloomfield and Sturdy, 2008; Guillette *et al.*, 2010), and zebra finches can also discriminate between two chickadee species' call notes (Guillette *et al.*, 2012). Both chickadees and zebra finches, however, are vocal-learning songbirds. This raises the possibility that songbirds are generally just more adept at discriminating songbird vocalizations, rather than being tied to any species-specific perceptual capabilities. To evaluate this latter possibility, it would be valuable to determine whether a non-songbird species also similarly perceives *chick-a-dee* calls as open-ended categories. Pigeons are a good species to test this idea as they are a readily available non-vocal learning avian species that has been demonstrated to be capable of discriminating a wide variety of auditory stimuli in different settings (e.g., Porter and Neuringer, 1984; Cook and Brooks, 2009).

Recently, we began testing pigeons to examine if and how this non-songbird processes the vocalizations of other birds. While we ultimately want to test this species in the same types of species-based categorization tasks using the stimuli and procedures tested above with songbirds, we had a ready-made opportunity with already-trained pigeons in one of our labs to examine if they could even discriminate among the calls of different chickadee species. This seemed like a good first step in at least revealing whether they could possibly do such a categorization task at all.

We tested five pigeons already performing a complex auditory go/no-go same/different task (Cook and Brooks, 2009; Murphy and Cook, 2010). In this task, the pigeons were presented sequences of 12 1.5 s sounds in a touchscreen operant chamber from speakers located in the right and left walls. After a peck to a ready signal, if the same sound was repeated 12 times within a trial, this was considered an S- trial and pecks to an illuminated area on the monitor were not reinforced. If 12 different sounds or two alternating different sounds were presented, this was considered an S+ trial and pecks to the display were reinforced on a variable-interval schedule. Prior to the test described here, these pigeons had considerable experience discriminating among a wide variety of simple and complex sounds in this procedure. Testing with these numerous stimuli revealed that pigeons' discrimination abilities included the capacity to discriminate the timbre of 12 different instruments, the difference in pitch over three octaves with these instruments, sine waves, seven types of chords, complex man-made and natural sounds and birdsongs of various types.

Figure 2 shows the established same/different discrimination by pigeons for all of these sounds within a trial during testing. Beginning around the fourth sound, all the pigeons show declining peck rates on same trials, while correctly maintaining higher peck rates of either type of different trial (different trial performance was judged from probe trials in which no reinforcement is provided). Thus, the relative height of their peck rate over time reveals the relative similarity and difference among different sounds, with high peck rates indicative of greater perceived difference among the sequence of sounds and lower peck rates indicative of more perceived similarity.

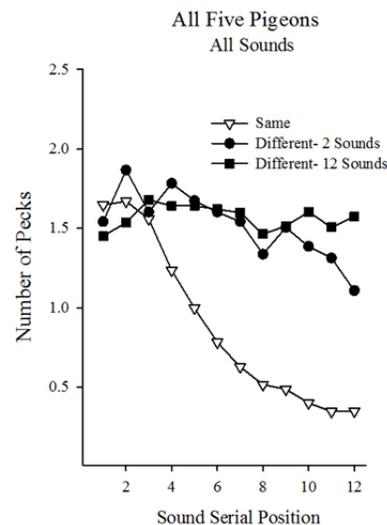


FIGURE 2. Same/Different results from five pigeons tested with all sounds.

Because these pigeons were already quite good at discriminating different sounds, we then introduced and tested them for eight 90-trial sessions with combinations of eight black-capped and mountain chickadee calls to see how they would respond. All six chickadee test trials within an otherwise typical session of mixed stimuli were conducted as non-reinforced probes. Different trials were conducted in which two calls were alternated across the sequence between examples from the two chickadee species (different-between species) or examples of different individuals calling within a species (different-within species). Same trials were repetitions of a single exemplar of any of these 12 calls. We were interested in whether the pigeons could discriminate among the different calls and if so whether it depended on whether the calls were from within the same species or between the species.

Preliminary results reveal that all five pigeons generally perceived these chickadee calls as being similar within a sequence. Some pigeons responded to all *chick-a-dee* calls as “same”. While other birds showed evidence of being able to discriminate among the *chick-a-dee* calls, and some pigeons were better at discriminating when the different trials were composed from calls between the two species compared to trials when the calls were from within the same species.

These results suggest that both species of chickadee calls have features that are discriminable to a non-songbird species. The data also suggest that these calls were perceived as highly similar by the pigeons and perhaps more challenging for this species to discriminate than would be the case for chickadees. However, it is difficult to draw a direct comparison with the songbird data, because the tasks involved were so different. We plan to continue testing this non-songbird species in a manner that would be more comparable to that done with chickadees and zebra

finches. It will be important to learn the relative difficulty of such tasks for each of these species and whether the same acoustic features or categorical mechanisms are used by each species to accomplish their discrimination.

CONCLUSIONS

In sum, these studies have revealed that: (1) chickadees treat both their entire *chick-a-dee* call and *chick-a-dee* call notes as open-ended perceptual categories (2) zebra finches appear also to treat *chick-a-dee* call notes as open-ended categories (3) this perceptual categorization by songbirds (chickadees and finches) appears to be driven by acoustic, rather than genetic or experiential factors, (4) chickadees and pigeons can perceive abstract auditory same/different relations, and (5) some pigeons can discriminate acoustic features between the vocalizations of two chickadee species.

Based on the results of these studies, we have a better understanding of auditory categorization of chickadee vocalizations by black-capped and mountain chickadees, and chickadees' perceptual abilities of abstract-concept discriminations. In the future, we plan to conduct additional studies in which we can further examine how these songbirds perceive auditory same/different relations by testing this abstract-concept relationship using biologically-relevant stimuli (e.g., different species' *chick-a-dee* calls, or varying pitch relationships in *fee-bee* songs). These types of studies can provide insight into how the general ability to perceive more abstract concepts can be used when perceiving vocalizations in the wild.

In addition, while we have only begun examining pigeons' abilities to discriminate chickadee and pigeon calls, it appears that this non-songbird is able to detect acoustic differences between black-capped and mountain chickadee calls. We plan to further examine pigeons' abilities for categorizing *chick-a-dee* calls using species-based tasks, to evaluate if a non-songbird species will perceive these vocalizations as open-ended categories. By testing pigeons with methodologies similar to that used when testing songbirds, we can directly compare the categorization abilities of these avian species. In addition, by examining if pigeons will treat *chick-a-dee* calls as open-ended categories we can further evaluate the role of experience in this task. While our results with zebra finches suggest that prior experience with the vocalizations is not necessary to perceive chickadee call notes as open-ended categories, as a vocal-learning songbird, zebra finches may possess either the necessary neural systems, experience, or both, required for learning their own vocalizations and this may affect their ability to perceive and accurately classify these stimuli. Testing the categorization abilities of a non-vocal learning avian species using these stimuli, begins to provide insights into how general these auditory perceptual categorization abilities are across species and how they may be same or different within this class of animal.

ACKNOWLEDGMENTS

This research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant and Discovery Accelerator Supplement, an Alberta Ingenuity Fund (AIF) New Faculty Grant, a Canada Foundation for Innovation (CFI) New Opportunities Fund (NOF) and Infrastructure Operating Fund (IOF) grants along with start-up funding and CFI partner funding from the University of Alberta (UofA) to CBS and a grant from the National Science Foundation (NSF) to RGC. LMG was supported by an Izaak Walton Killam Memorial Scholarship (IWKMS) at UofA. MH was supported by an NSERC Post Graduate Scholarship-Doctoral, an Alberta Ingenuity Graduate Student Scholarship and an IWKMS at UofA. All studies were conducted in accordance with approved protocols for the species tested.

REFERENCES

- Astley, S.L., and Wasserman, E.D. (1992). "Categorical discrimination and generalization in pigeons: All negative stimuli are not created equal," *J. Exp Psychol: Anim. Behav. Processes*, **18**, 193-207.
- Bloomfield, L.L., Farrell, T.M., and Sturdy, C.B. (2008a). "All "chick-a-dee" calls are not created equally Part II. Mechanisms for discrimination by sympatric and allopatric chickadees," *Behav. Processes*, **77**, 87-99.
- Bloomfield, L.L., Farrell, T.M., and Sturdy, C.B. (2008b). "Categorization and discrimination of "chick-a-dee" calls by wild-caught and hand-reared chickadees," *Behav. Processes*, **77**, 166-176.
- Bloomfield, L.L. and Sturdy, C.B. (2008). "All "chick-a-dee" calls are not created equally. Part I. Open-ended categorization of chick-a-dee calls by sympatric and allopatric chickadees," *Behav. Processes*, **77**, 73-86.
- Bloomfield, L.L., Sturdy, C.B., Phillmore, L.S., and Weisman, R.G. (2003). "Open-ended categorization of chick-a-dee calls by black-capped chickadees (*Poecile atricapilla*)," *J. Comp. Psychol.*, **117**, 290-301.

- Braaten, R.F. (2000). "Multiple levels of representation of song by European starling (*Sturnus vulgaris*): Open-ended categorization of starling song types and differential forgetting of song categories and exemplars," *J.Comp. Psychol.*, **114**, 61-72.
- Christie, P.J., Mennill, D.J., and Ratcliffe, L.M. (2004). "Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees," *Behav. Ecol. Sociobiol.*, **55**, 341-348.
- Cook, R.G., and Brooks, D.I. (2009). "Generalized auditory same-different discrimination by pigeons," *J. Exp. Psychol. Anim. B.*, **35**, 108-115.
- Cook, R.G., Katz, J.S., and Cavoto, B.R. (1997). "Pigeon same-different concept learning with multiple stimulus classes," *J. Exp Psychol: Anim. Behav. Processes*, **23**, 417-433.
- Cook, R.G., Kelly, D.M., and Katz, J.S. (2003). "Successive two-item same-different discrimination and concept learning by pigeons," *Behav. Processes*, **62**, 125-144.
- Cynx, J., Hulse, S.H., and Polyzois, S. (1986). "A psychophysical measure of pitch discrimination loss resulting from a frequency range constraint in European starlings (*Sturnus vulgaris*)," *J. Exp Psychol: Anim. Behav. Processes*, **12**, 394-402.
- Dawson, M.R., Bloomfield, L.L., Charrier, I., and Sturdy, C.B. (2006a). "Statistical classification of black-capped (*Poecile atricapillus*) and mountain chickadee (*Poecile gambeli*) call notes," *J. Comp. Psychol.*, **120**, 147-153.
- Dawson, M.R., Charrier, I., and Sturdy, C.B. (2006b). "Using an artificial neural network to classify black-capped chickadee (*Poecile atricapillus*) call note types," *J. Acoust. Soc. Am.* **119**, 3161-3172.
- Ficken, M.S., Ficken, R.W., and Witkin, S.R. (1978). "Vocal repertoire of the black-capped chickadee," *Auk*, **95**, 34-48.
- Gentner, T.Q., and Hulse, S.H. (1998). "Perceptual mechanisms for individual vocal recognition in European starlings," *Sturnus vulgaris*," *Anim. Behav.* **56**, 579-594.
- Guillette, L.M., Farrell, T.M., Hoeschele, M., and Sturdy, C.B. (2010). "Acoustic mechanisms of a species-based discrimination of the chick-a-dee call in sympatric black-capped (*Poecile atricapillus*) and mountain chickadees (*P. gambeli*)," *Frontiers in Psychology*, **1**, 229. doi:10.3389/fpsyg.2010.00229
- Guillette, L.M., Hoeschele, M., Hahn, A.H., and Sturdy, C.B. (2012). "Heterospecific discrimination of *Poecile* vocalizations by zebra finches (*Taeniopygia guttata*)," *J. Comp. Psychol.*, doi: 10.1037/a0029992
- Hailman, J.P., Ficken, M.S., and Ficken, R.W. (1985). "The 'chick-a-dee' calls of *Parus atricapillus*: A recombinant system of animal communication compared with written English," *Semiotica*, **56**, 191-224.
- Herrnstein, R.J. (1990). "Levels of stimulus control: A functional approach," *Cognition*, **37**, 133-166.
- Hoeschele, M., Cook, R.G., Guillette, L.M., Brooks, D.I., and Sturdy, C.B. (2012). "Black-capped chickadee (*Poecile atricapillus*) and human (*Homo sapiens*) chord discrimination," *J. Comp. Psychol.*, **126**, 57-67.
- Hoeschele, M., Cook, R.G., Guillette, L.M., Hahn, A.H., and Sturdy, C.B. (2012). "Auditory same/different concept learning and generalization in black-capped chickadee (*Poecile atricapillus*)," *PLoS ONE*, **7**, e47691. doi:10.1371/journal.pone.0047691.
- Hoeschele, M., Guillette, L.M., and Sturdy, C.B. (2012). "Biological relevance of acoustic signal affects discrimination performance in a songbird," *Anim. Cogn.*, **15**, 677-688.
- Horn, A.G., Leonard, M.L., Ratcliffe, L., Shackleton, S.A., and Weisman, R.G. (1992). "Frequency variation in songs of black-capped chickadees (*Parus atricapillus*)," *Auk*, **109**, 847-852.
- Hulse, S.H., and Cynx, J. (1985). "Relative pitch perception is constrained by absolute pitch in songbirds (*Mimus*, *Molothrus*, and *Sturnus*)," *J. Comp. Psychol.*, **99**, 176-196.
- Katz, J.S., and Wright, A.A. (2006). "Same/different abstract-concept learning by pigeons," *J. Exp Psychol: Anim. Behav. Processes*, **32**, 80-86.
- Lee, T.T.Y., Charrier, T., Bloomfield, L.L., Weisman, R.G., and Sturdy, C.B. (2006). "Frequency-range discriminations and absolute pitch in black-capped chickadees (*Poecile atricapillus*), mountain chickadees (*Poecile gambeli*), and zebra finches (*Taeniopygia guttata*)," *J. Comp. Psychol.*, **120**, 217-228.
- Lind, H., Dabelsteen, T., and McGregor, P.K. (1996). "Female great tits can identify mates by song," *Anim. Behav.*, **52**, 667-671.
- Mennill, D.J., and Ratcliffe, L.M. (2004). "Overlapping and matching in the song contests of black-capped chickadees," *Anim. Behav.*, **67**, 441-450.
- Miller, D.B. (1979). "The acoustic basis of mate recognition by female zebra finches (*Taeniopygia guttata*)," *Anim. Behav.*, **27**, 376-380.
- Murphy, M.S., and Cook, R.G. (2008). "Absolute and relational control of a sequential auditory discrimination by pigeons (*Columba livia*)," *Behav. Processes* **77**, 210-222.
- Nowicki, S. (1983). "Flock-specific recognition of chickadee calls," *Behav. Ecol. Sociobiol.*, **12**, 317-320.
- Nowicki, S., and Nelson, D.A. (1990). "Defining natural categories in acoustic signals: comparison of three methods applied to 'chick-a-dee' call notes," *Ethology*, **86**, 89-101.
- Partan, S., Yelda, S., Price, V., and Shimizu, T. (2005). "Female pigeons, *Columba livia*, respond to multisensory audio/visual playbacks of male courtship behaviour," *Anim. Behav.*, **70**, 957-966.
- Pepperberg, I.M. (1987). "Acquisition of the same/different concept by an African Grey parrot (*Psittacus erithacus*): Learning with respect to categories of color, shape and material," *Anim. Learn. Behav.*, **15**, 423-432.
- Porter, D., and Neuringer, A. (1984). "Music discriminations by pigeons," *J. Exp Psychol: Anim. Behav. Processes*, **10**, 138-148.
- Stoddard, P.K., Beecher, M.D., Horning, C.L. and Willis, M.S. (1990). "Strong neighbor-stranger discrimination in song sparrows," *Condor*, **92**, 1051-1056.
- Stoddard, P.K., Beecher, M.D., Loesche, P., and Campbell, S.E. (1992). "Memory does not constrain individual recognition in a bird with song repertoires," *Behaviour*, **122**, 274-287.

- Sturdy, C.B., Bloomfield, L.L., Farrell, T.M., Avey, M.T., and Weisman, R.G. (2007). "Auditory category perception as a natural cognitive activity in songbirds," *Comp. Cogn. Behav. Rev.*, **2**, 93-110.
- Sturdy, C.B., Phillmore, L.S., Price, J.L., and Weisman, R.G. (1999). "Song-note discriminations in zebra finches (*Taeniopygia guttata*): Categories and pseudocategories," *J. Comp. Psychol.*, **113**, 204-212.
- Sturdy, C.B., Phillmore, L.S., and Weisman, R.G. (2000). "Call-note discrimination in black-capped chickadees (*Poecile atricapillus*)," *J. Comp. Psychol.*, **114**, 357-364
- Templeton, C.N., Greene, E., and Davis, K. (2005). "Allometry of alarm calls: Black-capped chickadees encode information about predator size," *Science*, **308**, 1934-1937.
- Wasserman, E.A. (1995). "The conceptual abilities of pigeons," *Am. Sci.* **83**, 246-255.
- Weisman, R., Ratcliffe, L., Johnsrude, I., and Hurly, T.A. (1990). "Absolute and relative pitch production in the song of the black-capped chickadee," *Condor*, **92**, 118-124.
- Wright, A.A., and Katz, J.S. (2007). "Generalization hypothesis of abstract-concept learning: Learning strategies and related issues in *Macaca mulatta*, *Cebus paella*, and *Columba livia*," *J. Comp. Psychol.*, **121**, 387-397.
- Young, M.E., and Wasserman, E.A. (2001). "Evidence for a conceptual account of same-different discrimination learning in the pigeon," *Psychon. Bull. Rev.*, **8**, 677-684.