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Moving from Perceptual to Functional Categories in Songbirds

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Category perception, as Herrnstein (1990) defined it, is a powerful and pervasive cognitive ability possessed by every species in which it has been adequately tested. In fact, Herrnstein was even more direct, stating that categorization had "turned up at every level of the animal kingdom where it has been competently sought" (p. 138). We have studied category perception of vocal communication signals in songbirds for over 20 years. Our first studies provided us with an understanding of songbird vocal category production and perception, clarifying perceptual categorization and the underlying mechanisms. More recent work has moved towards understanding functional vocal categories such as sex, dominance, species, and geography. Some of our most recent work has moved into the realm of conceptual knowledge, with studies aimed at understanding birds' ability to deal with concepts of sameness and danger (i.e., threat level). Here we provide key examples that effectively show the wide range of abilities possessed and used by songbirds.

Category perception is a widespread cognitive phenomenon that has been investigated, and shown to be possessed, by many animals (e.g., Katz, Wright, & Bachevalier, 2002; Lea, 1984; Wasserman, Kiedinger, & Bhatt, 1988). In general, category perception allows animals to simultaneously group items based on similarity while also being able to discriminate among similar group members and between members of different groups. This ability increases processing speed when attending to environmental stimuli, allowing animals to take appropriate and timely action. Although once erroneously believed to be a faculty only possessed by humans, and inextricably linked to human speech, the ubiquity of category perception has been increasingly well known for over four decades (e.g., see Herrnstein & Loveland, 1964). The advantages of category perception can be easily understood when considering the environmental, ecological, and perceptual demands faced by Oscine songbirds, and in particular one group of songbirds, North American chickadees, which will be the focus of this review.

Chickadees are small songbirds whose range extends across the bulk of North America. Chickadees have an interesting social structure in which they form flocks in late autumn and early winter. Winter flocks defend a territory until spring when they disband and defend smaller territories as mated pairs. As Smith (1991) points out, breeding pairs are often composed of members from the same winter flock. Likewise, flocks may be formed by a hierarchy of breeding pairs from the previous spring. During the fall and winter a dominance hierarchy is established that has implications not only for access to resources in winter (e.g., feeders) but also in spring when more dominant birds have advantages over subordinate birds (for review see Ratcliffe, Mennill, & Schubert, 2007). In addition to a complex and seasonally-varied social structure, chickadees possess a complex suite of vocalizations. The importance of producing and perceiving these vocalizations for chickadees has afforded us a model species that is useful for studying perceptual categorization.

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Evolution of a Program

For over 20 years we (students, postdocs, mentors, collaborators) have been studying songbird vocal production, perception, and cognition. One focus that has been a touchstone during this time has been that of category perception. In this review we will outline our progress in this area. The approach will be semi-chronological in nature but with departures from the timeline as is appropriate to maintain continuity in our narrative. We plan to first discuss perceptual categories, including the building blocks of song and call notes, followed by a discussion of vocal categories, and finishing the section with a discussion of species-level categories. In each case we will largely confine ourselves to one or two descriptive cases that best make our point, rather than an exhaustive discussion.

Main Vocalizations

For this review, we will confine our discussion to two of the main types of vocalizations produced by black-capped chickadees (*Poecile atricapillus*; see Figure 1): *fee-bee* songs and *chick-a-dee* calls; however, chickadees produce several types of vocalizations used in a wide variety of contexts (Smith, 1991). The fee-bee song is a tonal vocalization produced at high rates during the spring breeding season. In the past, this vocalization was thought to only be produced by males, and used for mate attraction and territorial defence. More recent work (Hahn, Krysler, & Sturdy, 2013) has shown that females also produce fee-bee songs, although the genesis and function of the vocalization in females is unknown at this stage, and in fact, has gone largely under or unreported until recently (except see Hahn et al., 2013; Hill & Lein, 1987).

Chick-a-dee calls are produced by both sexes year-round and are used to coordinate flock movement and raise alarm. All members of the genus *Poecile* produce these calls, but here we focus on the calls of black-capped chickadees. In black-capped chickadees, *chick-a-dee* calls comprise five note types, A, B, C, D, and D-hybrid (Dh) notes, although typically only the first four (i.e., A, B, C, D) are reported. Notes are produced A through D/Dh with rare exception, however notes can be repeated or omitted. A and B notes are highly tonal, whereas C and D notes are more broadband, possessing overtones. Dh notes are, as the name suggests, a hybrid note composed of an A note that transitions into a D note.

Perceptual Categories (Notes, Vocalizations)

Early research in songbird communication attempted to understand the vast complexity of vocalizations that birds produced. To reduce the complexity of these vocalizations (i.e., songs and calls), they were often first categorized into smaller, acoustically similar groups or categories (e.g., different note types) and once this process was complete, the acoustic properties of the resulting groups of vocalizations were measured. This then allowed researchers to calculate descriptive statistics for key acoustic features and observe these features organized by the constituent groups. By doing this, we and others could reduce the sometimes bewildering array of vocalizations (observed as squiggly lines on sound spectrographs) to general descriptions and statistics that could characterize the main groups of vocal units within birds' vocalizations. We had success reducing complexity and increasing our human understanding of bird vocalizations, but as Nowicki and Nelson (1990) pointed out, this effort was not complete until we determined the extent to which the birds who produced these vocalizations agreed with the humans who had conducted the sorting and measuring. To address this very valid point, we needed to determine whether the birds agreed with our classification system.

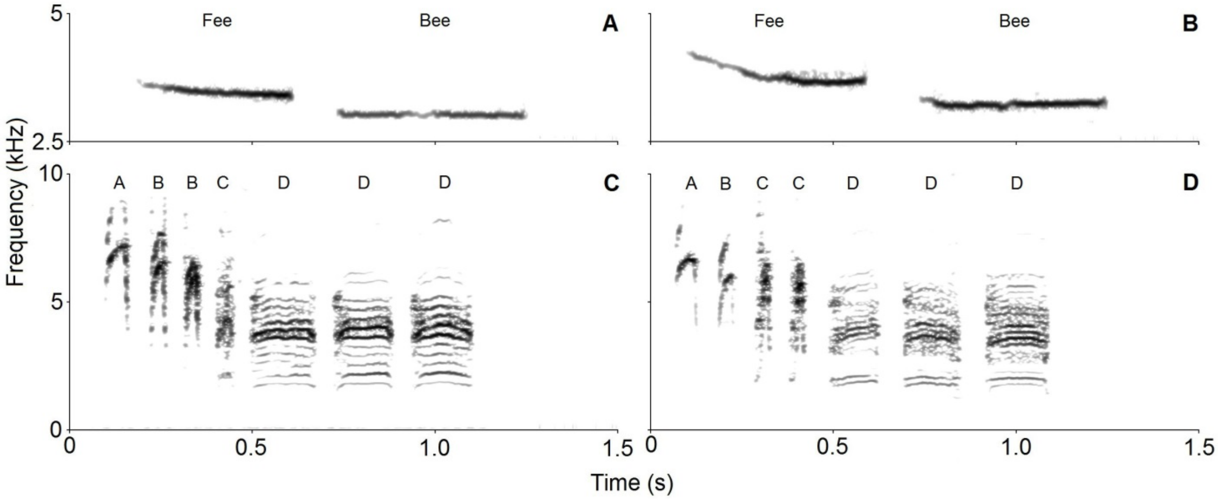

Figure 1. **Sound spectrograms (transform length = 1024 points, frequency precision = 43.1 Hz, amplitude cut-offs = 0 to -35 dB) of black-capped chickadee *fee-bee* songs (A, B) and *chick-a-dee* calls (C, D) showing vocalizations produced by males (A, C) and females (B, D).** Labels indicating note type are included above each note.

Concomitant with research focused on vocalizations, researchers devised experimental methods and designs that were capable of determining whether or not animals perceive stimuli as groups (i.e., category perception). Herrnstein and Loveland (1964) were the first to show that nonhuman animals could discriminate pictures based on group membership, and importantly, definitively showed that they did so not through memorization but rather by categorization. In their work, Herrnstein and Loveland trained pigeons to respond to pictures of one category (e.g., people) and withhold responding to pictures that did not contain people. They showed that it did not matter which particular image containing a person was used, and after birds acquired the rule, they would continue to respond appropriately when novel images were presented. This groundbreaking research set the stage for our work studying acoustic categories in songbird vocalizations.

Other research groups developed modified Skinner boxes that allowed the training and testing of small birds with auditory stimuli as discriminative stimuli (for examples see Hulse & Cynx, 1985; Park, Okanoya, & Dooling, 1985; Weisman, Njegovan, & Stephen, 1994). Although the details of the experimental setups in these laboratories were different from one another, they all shared the common ability to use acoustic signals as discriminative stimuli and training techniques that would bring small birds under stimulus control of these acoustic stimuli. For our lab group in particular, we have used variations of Weisman's original conditioning setup for small birds (Njegovan, Hilhorst, Ferguson, & Weisman, 1994; Sturdy & Weisman, 2006). In brief, we train birds to use a perch and feeder so that we may test their perceptual abilities. We first teach birds that food is available in the feeder, and then progressively train them to associate auditory stimuli with food. After this training period, we can test birds by associating some stimulus classes with food reward and other classes with no reward. Following training we can test birds with a wide variety of stimuli to assess the perceptual and cognitive mechanisms at play (Sturdy, Bloomfield, Charrier, & Lee 2007; Sturdy, Bloomfield, Farrell, Avey, & Weisman 2007) These specific methodological and design innovations combined with the pioneering work investigating category perception in nonhuman animals allowed us to make great strides in our research, some of which we describe below.

Call Notes: Mechanisms of Perception

Early on, scientists described the note types of the *chick-a-dee* call, and the song and call notes produced by other species, but did not test whether birds themselves agreed with the note type categories created by the scientists studying these vocalizations. It was also unclear whether birds would learn groups of items as open-ended categories, that is, whether they perceive similarities among category members in spite of perceptible differences. Open-ended categorization allows animals to learn general rules that apply to category members, and by extension, allows animals to generalize these rules to newly encountered exemplars. Herrnstein and Loveland (1964), Wasserman et al. (1988), Lea (1984), and others had shown category perception of visual categories in birds, but few examples existed for vocal categories (but see Gray's PhD dissertation; Gray, 1995). Sturdy, Phillmore, Price, and Weisman (1999) showed that zebra finches agreed with the human classification of song notes and treated these notes as open-ended categories (Sturdy, Phillmore, & Weisman 1999). Black-capped chickadees also treated conspecific call notes (as classified by Ficken, Ficken, & Witken, 1978) as open-ended categories, as demonstrated by Sturdy, Phillmore, and Weisman (2000) using operant discrimination techniques in which call notes were discriminative stimuli. That is to say that birds considered notes of one type to be more similar as a group than notes of different categories, and, importantly, when novel exemplars of notes were presented, birds responded similarly to the way in which they responded to trained notes.

Following up on the research that showed black-capped chickadees perceive their call notes as open-ended categories (Sturdy et al., 2000), Charrier, Lee, Bloomfield, and Sturdy (2005) sought to uncover which specific acoustic features birds were attending to in order to discriminate one note type from the next. This latter work was informed by detailed bioacoustic analyses (Charrier, Bloomfield, & Sturdy, 2004) that pointed to the starting frequency of notes as a possible feature that would drive note type discrimination. Charrier and colleagues (2005) clearly demonstrated that birds attended to the frequency of note types and modified their responding when note frequency changed. In particular, when the frequency of A notes, which generally have a higher start frequency than B notes, were progressively lowered in frequency, birds responded increasingly as if they were B notes. This work, along with artificial neural network (ANN) studies, was key in moving past simply verifying the categories used by birds, pointing instead to the particular acoustic features that differentiated one note type from the next. The ANNs we used (see Nickerson, Bloomfield, Dawson, & Sturdy, 2006) were computer-based simulations that could be trained and tested on tasks that were analogous to the tasks performed by the birds. Artificial Neural Networks were shown to produce patterns of responding highly similar to the patterns of responding produced by the birds. Artificial Neural Networks provide a convenient method to expand our investigations and are not influenced by the forces of evolution and experience in the same way as wild-caught birds (i.e., Artificial Neural Networks learn only what we train them as opposed to birds that have a rich history from their lives in nature). Taken as a whole, these studies were key in describing the building blocks of vocalizations, a fundamental step in building a comprehensive understanding of songbird communication and cognition. These efforts need to continue across species and vocalizations to test for generality. Beyond these replications and extensions, there are higher-level vocal categories that needed to be explored. It is these higher-level categories to which we now turn our attention.

Neural Activation by Vocalizations

In all species tested, including chickadees, song and call notes are perceived as open-ended categories. These notes form the building blocks of complete vocalizations, either songs or calls. There is behavioral evidence that birds respond differently to classes of vocalizations. In general, when played back at the seasonally-appropriate time (i.e., song played in spring/breeding season and calls played in fall/flock formation), song playback elicits territorial defense (Wilson, Ratcliffe, & Mennill, 2016) while call playback elicits recruitment behaviors (Smith, 1991). These behavioral responses are not fixed; response to playback is also under seasonal/contextual control, such that call playbacks in the breeding season are also effective at eliciting a territorial response. Given that these (and all) overt behaviors are controlled by the brain, it is plausible that brain areas would react differentially to several classes of vocalizations; thus, this brain activation would reflect a higher level category at the neurobiological level.

Ribeiro, Cecchi, Magnasco, and Mello (1998) elegantly showed that different notes from canary (*Serinus canaria*, Waterslager breed) song led to different patterns of immediate early gene (IEG) ZENK expression in canary brains. IEGs, such as ZENK, are transcription factors that are upregulated in the brain following sensory stimulation and are believed to lead to long-term memory formation (e.g., Goelet, Castelucci, Schacher, & Kandel, 1986; Mello, Vicario, & Clayton, 1992; Roberts, Higgins, O'Shaughnessy, Stone, & Morris, 1996). This is possibly the first work to show the neural representation of vocal categories. Similar work by Phillmore, Bloomfield, and Weisman (2003), using complete vocalizations and black-capped chickadees as subjects, showed that songs and calls produced different levels of IEG expression that varied depending on whether the bird listening was a male or a female, with males having more IEG expression than females and both sexes having more gene expression following song rather than call playback. However, this study contrasted IEG expression following vocal playback using vocalizations where the sex of the singer was unknown. Presumably songs were male song since they were recorded in the field from a well-studied population; however, it is possible that some of the songs were in fact produced by females. We have recently shown that females also produce loud whistled fee-bee songs very similar, but not identical in structure, to male song (Hahn et al., 2013). Therefore, an open question was whether or not the sex of the producer also affected the results in a manner similar to how the type of vocalization affects IEG response. To test this directly, we presented male and female black-capped chickadees with male or female songs or calls (Avey, Kanyo, Irwin, & Sturdy, 2008) and measured IEG response. Interestingly, and in contrast to the results of Phillmore et al. (2003), we obtained higher IEG expression in response to call playback, but we also found that males had more expression overall than females; also, male vocalizations, both songs and calls, elicited higher levels of IEG expression in both sexes (Avey et al., 2008). Therefore, not only do the different notes and vocalizations behave in a manner consistent with categories, or at least, in a manner that one might expect categories to operate, but these results also yielded another important insight; namely that the sex of the producer might also serve as a category, and a very functional and useful category at that. The categories next described are most often considered functional categories, however, they can also be thought of as perceptual categories, as these two types of categories are not necessarily mutually exclusive. For example, birds can perceive and respond differentially to vocalizations from individuals of different sexes. Birds can also treat vocalizations from male and female birds as perceptual categories. We have divided the paper and consideration of categories the way that we have out of considerations of clarity and convenience, not because of a dogmatic belief that these are the only ways these cases can be considered.

Functional Categories (Sex, Dominance, Geography, Species)

Sex: Birds and Networks

Initial IEG work that showed marked effects of sex of producer and receiver led to a more detailed examination of fee-bee song produced by female black-capped chickadees. Hahn et al. (2013) recorded songs from a large sample of male and female black-capped chickadees in the laboratory. Overall, songs from both sexes were very similar in acoustic structure. Importantly, both males and females produced their fee-bee songs at a similar, high amplitude. A detailed acoustic analysis, however, revealed some important structural differences. The main difference that we observed was a difference in the frequency drop, sometimes termed the glissando, of the first fee note, with female fees being more frequency modulated than male *fees*. Although suggestive as a possible acoustic mechanism for sex discrimination, we needed to test the birds to see whether they agreed with our supposition.

We (Hahn et al., 2015) designed an operant discrimination in which birds learned to respond to songs from one sex and withhold responding to songs from the other sex. Chickadees were separated into two groups; birds in the true category group were trained to respond to songs produced by one sex and withhold responding to the other sex, while birds in the pseudo category group were trained to respond to an equal number of songs from each sex and to withhold responding to another set of songs produced by each sex (i.e., could not identify vocalizations by category and were forced to memorize each individual stimulus and its response-outcome relationship). The intent of this design is to observe a difference in acquisition between the two discrimination groups if the stimuli are perceived as categories, in which case we expected that the true category group would learn faster than the group that could only memorize by rote (termed the *pseudo category group*). In this particular experiment, birds in the true and pseudo category groups did not differ in their speed of acquisition, not providing evidence that birds perceived the category of *sex*. In most true/pseudo category experiments, birds in the true category group are trained to discriminate between categories of exemplars. For instance, birds might be trained to respond to one note type and not to another. In this experiment, however, birds in the true category group were trained to discriminate between categories (i.e., the sex of the signaler) using signals that belonged to one larger category (i.e., fee-bee song), making the task a within-category discrimination in which sex, a functional category, is nested within the larger category of "*song*. Many studies, including our own, show that within-category discriminations are more difficult, and hence learned slower, than between-category discriminations (e.g., Astley & Wasserman, 1992; Bloomfield & Sturdy, 2008; Sturdy et al., 2000). Therefore, the type of discrimination that we were requiring birds to perform could be contributing to our failure to observe the typical difference between experimental groups.

However, the experiment did not end after acquisition training. Following acquisition, there was a generalization phase, in which birds were presented with untrained stimuli from both groups (i.e., male and female songs). In contrast to acquisition data that provided no evidence of category perception, generalization tests provided evidence of transfer of training to untrained stimuli, whereas birds in the pseudo category group responded at chance levels to new stimuli, subjects in the true category group responded with above-chance discrimination between novel stimuli belonging to male versus female categories. This supports the hypothesis that birds did perceive the category of sex. Further probe tests conducted with manipulated stimuli provided some evidence that birds were attending to the difference in frequency modulation of the *fee* note to discriminate between male and female songs.

We also used ANNs to conduct simulations of discrimination tasks that were analogous to those performed by the birds. The results of the ANNs were unambiguous and completely in line with our predictions. Networks trained on the true category discrimination learned the task significantly faster than those trained on the pseudo-category task. This difference was striking in that pseudo category-trained ANNs never completed training, while true category trained ANNs completed training quicky. Artificial Neural Networks in the true category group also showed excellent generalization to untrained stimuli, and showed clear evidence of using the difference in *fee* note phonology to discriminate males from females on the basis of their song structure. The results of the ANNs are helpful for understanding perception in a manner that is not impacted by biological salience and experience, contrary to how birds experience and react to these stimuli. Because songs have no inherent biological salience to ANNs and ANNs do not have experience with songs, this corresponds to our suggestion of how biological salience affected acquisition training speeds, and simultaneously suggests that the *fee* note carries informative properties outside of their biological salience. Our studies on fee-bee song not only identified that female black-capped chickadees do produce song, but our perceptual follow-up studies showed that they perceived these songs in open-ended sex-based categories, as well as identifying at least one possible perceptual mechanism for performing this discrimination (*fee* glissando). Therefore, in spite of the seemingly simple acoustic structure of the song, much information was encoded in its two notes. Next, we will discuss what other information can be transmitted by song. In this case, we will describe our studies on song mediated dominance perception.

Dominance: Who's the Boss?

One interesting aspect of chickadee behavior is that chickadees vary their social behavior across seasons. In spring and summer, birds form mating pairs and defend a territory. In autumn, birds form flocks and defend a larger, more loosely defined territory. Flocks have the additional feature of stable linear dominance hierarchies. Dominant birds have many clear advantages, including obtaining larger mating territories (Mennill, Ramsay, Boag, & Ratcliffe, 2004) and females will preferentially choose dominant males as mates (Otter & Ratcliffe, 1996) and for extra-pair copulations (Mennill et al., 2004; Otter, Ratcliffe, Michaud, & Boag, 1998). How dominance is conveyed through physical interactions is straightforward: Dominant birds supplant subordinate birds from feeders and there is no mistaking who is dominant in such behavioral interactions. How this status is communicated, which might work to avoid such potentially costly aggressive interactions, was less well known.

Christie, Mennill, and Ratcliffe (2004) examined the song structure of dominant and subordinate males from a well-studied banded population of black-capped chickadees. Members of this particular population had been followed for many years, and interactions at feeder platforms has informed researchers of the dominance status of every bird in all of the focal flocks. Careful bioacoustic analyses revealed an interesting pattern: All black-capped chickadees produce their two-note songs with a common, relatively invariant pitch interval between the first and second notes. Since their song changes in absolute frequency, the interval is best expressed as a frequency ratio that is calculated by dividing the frequency of the end of the *fee* note by the start frequency of the *bee* note. On average, this ratio falls in the neighbourhood of 1.13, such that the frequency of the end of the *fee* note is about 1.13 times higher than the *bee* note. Dominant birds produced the notes in their songs with a more consistent relationship between their notes such that the frequency ratio between the notes was significantly less variable than in subordinate males. The researchers posited that females could listen to song bouts, and based in part on the fidelity of this ratio across song renditions, could make informed mate choices.

Christie et al.'s (2004) supposition was that female birds in the field must respond differentially to songs based on the dominance status of the singer, otherwise all of the advantages observed for dominant males would not be so pronounced. We sought to examine whether female chickadees could or would differentiate between non-local males of different status. We tested Alberta females in the laboratory, where they could be closely monitored, with songs from Northern British Columbia (Hoeschele et al., 2010). Our results were clear: Even though birds tested in Alberta had no experience with the stimuli used during playback experiments, females acted differentially depending on the status of the playback bird; females vocalized more and were generally more active following dominant song than following subordinate song playback. Follow up acoustic analyses on British Columbia song stimuli and later on songs from Ontario chickadees (with similar dominance assessments conducted) showed that, while dominance seemed to be reflected in the consistency of frequency ratio for Ontario birds, dominance was encoded in the relative amplitude of the songs from British Columbia birds, with dominant males producing more consistent amplitudes between the *fee* and the *bee* notes, while subordinate birds produced more variable amplitudes.

Clearly, assessing the dominance status of an individual is a biologically relevant and important task for an individual to perform. The combination of excellent behavioral ecologically driven field research with careful laboratory experimentation and bioacoustic analyses yielded important findings. Not only did it confirm that *dominance* or *status* is a natural category in the truest sense, but it also showed that experience with the stimulus animals used in the experiment was not necessary for birds to determine and demonstrate that they perceived this category. Moreover, these results from this series of studies and analyses clearly shows that even though the status category might be universal within a particular study species, the particular acoustic stimulus features that convey this information can and do vary from one population to another.

An argument can be made that dominance status is a continuum, with most individuals being dominant over others while being simultaneously subordinate to other individuals. However, when birds are tested either behaviorally or perceptually, as we have done in our work, we see that birds differentially response to vocalizations from the different dominance categories (i.e., the vocalizations are either from birds that are the most dominant or most subordinate in a winter flock). This differential responding can either be untrained in a playback experiment (Hoeschele et al., 2010) or trained in an operant conditioning test (Hahn et al., 2016). While there is a continuum of dominance or rank, when grouped and presented the way we and others do in our tasks, chickadees treat them as belonging to a category. It is important to realize that birds can treat stimuli as being members of categories without treating stimuli categorically, the latter being something common in speech perception and not synonymous with category perception (Sturdy et al., 1999); this is also consistent with other grouped continua, such as geographical origin to which we next turn our attention.

Geography: Where are You From?

Our work on dominance, with birds from different geographic areas, inspired our work in examining geographic differences in black-capped chickadee song more fully. Pooling song statistics based on dominance status and attempting to use statistical techniques like discriminant function analyses (DFAs) to sort bird songs based on dominance rank initially failed. We deduced that this failure was due to geographic-based differences in song structure that, although dominance was perceived by birds irrespective of geographic origin, nonetheless impaired other data-driven approaches. When we instead analyzed acoustic parameters of songs based on their geographic origin, we found clearer results. When we structured our statistical techniques to classify songs based on geography rather than based only on dominance, our accuracy significantly improved and our results were sensible and interpretable: Within a population, dominance cues were consistent and songs could be sorted thusly. Combining songs from different populations impaired this ability because of consistent geographical differences in acoustic structure (Hahn, Guillette, et al., 2013).

Following our bioacoustic studies, we designed an operant discrimination study (Hahn et al., 2016) to verify that birds did perceive geographic differences as functional open-ended categories, and then to further test the mechanisms underlying this perception. In common with other similar tasks we trained birds in either a true category discrimination in which all rewarded songs were from one geographic region, or a pseudo category discrimination, where songs were randomly assigned with half coming from each region. When comparing acquisition performance in two experiments, true category discrimination birds were faster (compared to pseudo category) in one experiment but not in the other. Similar to our study examining sex-based open-ended categorization of songs (Hahn et al., 2015), we did not find consistent evidence for faster learning for a true category discrimination of geography-based differences in song. As previously found in sex categorical discrimination, where acquisition of the true category also did not exceed the pseudo category, when birds in the true category group were tested with untrained songs they responded appropriately based on their training, providing evidence that birds perceived the geographic origin of songs as functional category. When birds were tested with manipulated signals, it appeared that song duration was a primary factor for categorizing based on geographic location, which was consistent with our previous bioacoustic analyses (Hahn, Guillette, et al., 2013). Our results suggest that duration is the primary factor that distinguished geographical origin of songs. There may well be other features that have yet to be determined. Similar to the perception of dominance, perception of geography can be encoded as open-ended categories. We have shown (Hahn et al., 2016) that birds transfer their training to novel vocalizations and also show intermediate responding to vocalizations in which the controlling variable (duration) was intermediate between the different geographic locations. Identifying the other acoustic features relevant to geographic differences will be the focus of subsequent work.

The preceding examples show how a seemingly simple song signal can effectively encode many biologically relevant features, such as sex, dominance status, and geographic origin. Also important is that birds seem to treat these signals and classes as open-ended categories, a mechanism that would be advantageous when encountering and responding to such signals in nature. Another perceptual task where speed of processing is likely important is that of species discrimination. We next turn to a consideration of how chickadees perform such a task using their species-universal *chick-a-dee* call as a species classifier.

Species: Categories and Mechanisms

Our very earliest work examined chickadee *chick-a-dee* call notes in an attempt to discern whether the birds agreed with human classification of their call notes. As we have already detailed, this work was largely successful and served as confirmation that we and others were tapping into meaningful vocal categories in the *chick-a-dee* calls. One of the many follow ups from this work included describing and defining the note types in the *chick-a-dee* calls of other chickadee species and determining whether birds can discriminate among species and whether they treated signaler species as open-ended categories. Finally, we wanted to identify what call notes or other acoustic features might allow birds to discriminate among the calls of different species.

To date we have examined this ability in black-capped and mountain chickadees using black-capped, Carolina (*P. carolinensis*), and mountain chickadee (*P. gambeli*) calls as stimuli. The most comprehensive of these studies involved black-capped and mountain chickadees both serving as subjects, discriminating among each other's calls. We also compared sympatric black-capped and mountain chickadees with allopatric black-capped chickadees. To establish that birds treated species as an open-ended category, we trained birds on simultaneous between- and within-category discriminations. In this design birds would, for example, learn which black-capped chickadee calls were rewarded and discriminate these from both unrewarded black-capped and mountain chickadee calls. If the species calls were perceived as categories, birds were expected to learn the easier between-species discriminations faster than the within-species discriminations. This pattern of responding was observed for both study species and both species' calls, and held irrespective of what population the birds originated from (Bloomfield & Sturdy, 2008). To understand the mechanism underlying this ability, we trained birds on a between-category discrimination, where they were rewarded for responding to one species' calls and not the other. Following successful acquisition and transfer to novel calls, we presented birds with several variations of manipulated call stimuli. These tests revealed that the terminal dee portion controlled species classification to a greater extent that the initial chick-a portion of the calls (Bloomfield, Farrell, & Sturdy, 2008a). Our ecological explanation for this result was that these portions of the call have a particular frequency structure that transmits well through the wooded areas that these birds inhabit**.**

Separate experiments were designed to test the impact of differential auditory experience during development. To do so we hand-reared nestling black-capped chickadees with either adult, wild-caught black-capped or mountain chickadees, and then tested them on a species-based discrimination task. This task used a standard true category/pseudo category discrimination in which one group of birds was trained to respond to one species' calls and withhold responding to the other species' calls (true category), while another group was trained to respond to calls from both species, half rewarded and half unrewarded (pseudo category). We found a difference in acquisition performance between true and pseudo category groups, that is, we observed a category-specific advantage leading to faster acquisition for birds in the true over the pseudo category group. Testing with untrained calls revealed that true category birds did respond in a manner consistent with their training, providing a replication of species-based categories seen in our previous studies. Moreover, we observed no effect of altered social environment of cross-fostering birds with a different species (Bloomfield, Farrell, & Sturdy, 2008b).

The studies just described add to the many examples of perceptual and functional vocal categories that chickadees, and presumably all songbirds and indeed most animals, perceive (e.g., Katz et al., 2002; Lea, 1984; Wasserman et al., 1988). From low level note categories through categories based on sex, dominance, geography, and species, birds have demonstrated a remarkable ability to perceive their vocalizations as categories. Next, we will describe two recent examples in which we have extended these studies beyond perceptual/functional categories to examining abilities thought to be even more exclusive to the realm of humans.

Same-Different Concept Discrimination

The idea of perceiving abstract relations, that is, knowing the relations among stimuli that are not bound by perceptual features, or abstract concepts such as *same* or *different*, has for many years been believed to be an ability only possessed by humans and the main feature that set humans apart from other non-human animals. Many experiments with nonhuman animals have refuted this archaic belief.

For example, Cook and Brooks (2009) trained pigeons in an auditory discrimination with training stimuli that were comprised of either many identical auditory stimuli (termed same) or many different auditory stimuli (termed different). Birds were only rewarded if they responded following the presentation of *different* stimuli. Pigeons learned how to perform this task to a high level of accuracy and generalized the abstract concept to many different dimensions.

In collaboration with Cook, we (Hoeschele, Cook, Guillette, Hahn, & Sturdy, 2012) trained black-capped chickadees in a version of this task. Chickadees, like pigeons, learned to discriminate based on the abstract concept of same/different. Further, chickadees also transferred their training to novel stimuli along many dimensions. Interestingly, chickadees' ability to generalize was limited to the pitches of stimuli experienced during training. This suggested that songbirds, such as chickadees, that rely heavily on pitch perception may be constrained and perform more poorly in relational auditory based tasks such as the same/different discriminations because their frequency perception expertise is such that they fail to generalize to pitches other than those used in training. Clearly, chickadees are among the many nonhuman animals that have abilities beyond perceptual categorization.

Threat Perception

Same/different tasks assess conceptual knowledge of a very general ability, that is, to demonstrate the ability to discriminate *sameness*. In a more species-specific demonstration of conceptual knowledge, Templeton, Greene, and Davis (2005) exposed black-capped chickadees to aerial predators of different sizes, and hence different levels of threat. Paradoxically, smaller raptors pose a greater risk to chickadees than do larger birds simply because these smaller predators are more maneuverable and as a result more likely to successfully predate chickadees. Chickadees seemed to systematically alter their *chick-a-dee* call structure such that the number of D notes contained in calls increased in a linear manner as the threat posed by the predator increased. Subsequent work refining this result points to the duty cycle, or the amount of call per unit time being the critical factor for communicating threat level (Wilson & Mennill, 2011), something that producing more D notes accomplishes.

We (Avey, Hoeschele, Moscicki, Bloomfield, & Sturdy, 2011) exposed black-capped and mountain chickadees to high-threat saw-whet owl mounts and low-threat great-horned owl mounts to obtain the birds' vocal responses to later use as stimuli. Following this step, and using different chickadees, we exposed birds to either mobbing calls made in response to high- or low-threat predators, or to the calls produced by high- and low-threat predators. When IEG expression was quantified, high-threat stimuli elicited significantly more gene expression than low-threat stimuli. Interestingly, it did not matter whether the birds were exposed to *chick-a-dee* mobbing calls made in response to a predator or the vocalizations that the predators themselves produce, the high/low pattern held true. Presenting a subset of these stimuli to hand-reared birds without experience with predators or mobbing elicited less IEG expression to predator vocalizations, suggesting that birds required experience with predator vocalizations, mobbing behavior and vocalizations, or some combination of these conditions in order to respond in a species-typical manner.

Using behavioral and/or neurobiological techniques, these final two examples provide clear and compelling evidence that the cognitive abilities of nonhuman animals, in this case chickadees, is likely far more sophisticated than normally believed. Our work demonstrates the perceptual mechanisms used by nonhuman animals, including chickadees, to navigate a socially dynamic world; it also clearly shows not only that these abilities are sophisticated, but that they also share much in common with human perception. Research for abstract concepts is still in its infancy, but will surely lead to more remarkable findings repeatedly demonstrating the breadth of similarities in cognitive abilities shared between human and nonhuman animals.

Summary and Conclusions

Our aim in this brief review was to highlight the rich, hierarchically-organized suite of categories that exist in songbird vocalizations. We have covered a large swath of our research program from perceptual categories through to abstract concepts, starting with the building blocks (notes) and ending with abstract concepts (same/different and threat). To make our case the most compelling, we have invoked different modes of representation from behavioral studies of discrimination ability to neurobiological examining the locus and neurobiological bases for the cognitive abilities our behavioral work explores.

We can make some clear conclusions. First, category perception is pervasive in songbirds and other nonhuman animals. In making this claim, or more specifically, in standing with Herrnstein, Wasserman, Lea, and those who came before us, we suggest that it is best to verify the generality of perceptual and conceptual categorization across species, levels, representation type, including both behavioral and neurobiological.

Second, category perception in songbirds, at least with respect to their vocalizations, can be considered to occur as both perceptual and functional categories. Third, songbirds and in our case chickadees, have been shown to perceive vocal categories of many types, from vocal class, to sex, dominance, and geographic location. Fourth, we have shown that songbirds can perceive abstract concepts of same and different, an ability once thought not to be possessed by songbirds. Finally, there are many avenues of investigation to explore in the future in this rich and exciting research area of which we are excited and privileged to play a part.

References

Astley, S. L. & Wasserman, E. A. (1992). Categorical discrimination and generalization in pigeons: All negative stimuli are not created equal. *Journal of Experimental Psychology: Animal Behavior Processes*, *18*, 193-207.

Avey, M. T., Hoeschele, M., Moscicki, M. K., Bloomfield, L. L., & Sturdy, C. B. (2011). Neural correlates of threat perception: Neural equivalence of conspecific and heterospecific mobbing calls is learned. *PLoS ONE*, *6*(8), e23844.

Avey, M. T., Kanyo, R. A., Irwin, E. L., & Sturdy, C. B. (2008). Differential effects of vocalization type, singer and listener on ZENK immediate early gene response in black-capped chickadees (*Poecile atricapillus*). *Behavioral Brain Research*, *188*, 201-208.

Bloomfield, L. L., Farrell, T. M., & Sturdy, C. B. (2008a). All “chick-a-dee” calls are not created equally: Part II. Mechanisms for discrimination by sympatric and allopatric chickadees. *Behavioral Processes*, *77*, 87-99.

Bloomfield, L. L., Farrell, T. M., & Sturdy, C. B. (2008b). Categorization and discrimination of “chick-a-dee” calls by wild-caught and hand-reared chickadees. *Behavioural Processes*, *77*, 166-176.

Bloomfield, L. L., & 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. *Behavioural Processes*, *77*, 73-86.

Charrier, I., Bloomfield, L. L., & Sturdy, C. B. (2004). Note types and coding in parid vocalizations. I: The chick-a-dee call of the black-capped chickadee (*Poecile atricapillus*). *Canadian Journal of Zoology*, *82*, 769-779.

Charrier, I., Lee, T. T. Y., Bloomfield, L. L., & Sturdy, C. B. (2005). Acoustic mechanisms of note-type perception in black-capped chickadee (*Poecile atricapillus*) calls. *Journal of Comparative Psychology*, *119*, 371-380.

Christie, P. J., Mennill, D. J., & Ratcliffe, L. M. (2004). Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees. *Behavioral Ecology and Sociobiology*, *55*, 341-348.

Cook, R. G., & Brooks, D. I. (2009). Generalized auditory same-different discrimination by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *35*, 108-115.

Gray, C. B. (1995). Categorization of artificial and natural auditory stimuli by the European starling (*Sturnus vulgaris*). *Dissertation Abstracts International: Section B: The Sciences and Engineering*, *56*(6-B), 3498.

Goelet, P., Castelucci, V., Schacher, S., & Kandel. E. (1986). The long and the short of long-term memory-a molecular framework. *Nature*, *332*, 419-422.

Ficken, M. S., Ficken, S. R., & Witken, S. R. (1978). Vocal repertoire of the black-capped chickadee. *The Auk*, *95*, 34-48.

Hahn, A. H., Guillette, L. M., Hoeschele, M., Mennill, D. J., Otter, K. A., Grava, T., Ratcliffe, L. M., & Sturdy, C. B. (2013). Dominance and geographic information contained within black-capped chickadee (*Poecile atricapillus*) song. *Behaviour*, *150*, 1601-1622.

Hahn, A. H., Hoang, J., McMillan, N. A., Campbell, K., Congdon, J., & Sturdy, C. B. (2015). Biological salience influences performance and acoustic mechanisms for the discrimination of male and female songs. *Animal Behaviour*, *104*, 213-228.

Hahn, A. H., Hoeschele, M., Guillette, L. M., Hoang, J., McMillan, N., Congdon, J. V., Campbell, K. A., Mennill, D. J., Otter, K. A., Grava, T., Ratcliffe, L. M., & Sturdy, C. B. (2016). Black-capped chickadees categorize songs based on features that vary geographically. *Animal Behaviour*, *112*, 93-104.

Hahn, A. H., Krysler, A., & Sturdy, C. B. (2013). Female song in black-capped chickadees (*Poecile atricapillus*): Acoustic song features that contain individual identity information and sex differences. *Behavioural Processes*, *98*, 98-105.

Herrnstein, R. J. (1990). Levels of stimulus control: A functional approach. *Cognition*, *37*, 133-166.

Herrnstein, R. J., & Loveland, D. H. (1964). Complex visual concept in the pigeon. *Science*, *146*, 549-551.

Hill, B. G., & Lein, M. R. (1987). Function of frequency-shifted songs of black-capped chickadees. *Condor*, *89*, 914-915.

Hoeschele, M., Cook, R. G., Guillette, L. M., Hahn, A. H, & Sturdy, C. B. (2012). Auditory same/different concept learning and generalization in black-capped chickadees (*Poecile atricapillus*). *PLoS ONE*, *7(10)*, e47691

Hoeschele, M., Moscicki, M. K., Otter, K. A., van Oort, H., Fort, K. T., Farrell, T. M., Lee, H., Robson, S. W. J., & Sturdy, C. B. (2010). Dominance signalled in an acoustic ornament. *Animal Behaviour*, *79*, 657-664.

Hulse, S. H., & Cynx, J. (1985). Relative pitch perception is constrained by absolute pitch in songbirds (*Mimus, Molothrus,* and *Sturnus*). *Journal of Comparative Psychology*, *99*, 176-196.

Katz, J. S., Wright, A. A., & Bachevalier, J. (2002). Mechanisms of same/different abstract-concept learning by rhesus monkeys. *Journal of Experimental Psychology: Animal Behavior Processes*, *28*, 358-368.

Lea, S. E. G. (1984). In what sense do pigeons learn concepts? In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), *Animal cognition* (pp. 263-276). Hillsdale, NJ: Erlbaum.

Mello, C. V., Vicario D., & Clayton D. F. (1992) Song presentation induces gene expression in the songbird forebrain. *Proceedings of the National Academy of Sciences USA*, *89*, 6818–6822.

Mennill, D. J., Ramsay, S. M., Boag, P. T., & Ratcliffe, L. M. (2004). Patterns of extrapair mating in relation to male dominance status and female nest placement in black-capped chickadees. *Behavioral Ecology*, *15*, 757-765.

Nickerson, C. M., Bloomfield, L. L., Dawson, M. R. W., & Sturdy, C. B. (2006). Artificial neural network discrimination of black-capped chickadee (*Poecile atricapillus*) call notes. *The Journal of the Acoustical Society of America*, *120*, 1111-1117.

Njegovan, M., Hilhorst, B., Ferguson, S., & Weisman, R. (1994). A motor-driven feeder for operant training in song birds. *Behavior Research Methods, Instruments, & Computers*, *26*, 26-27.

Nowicki, S. & 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.

Otter, K. & Ratcliffe, L. (1996). Female initiated divorce in a monogamous songbird: abandoning mates for males of higher quality. *Proceedings of the Royal Society of London B: Biological Sciences*, *263*, 351-355.

Otter, K., Ratcliffe, L., Michaud, D., & Boag, P. (1998). Do female black-capped chickadees prefer high-ranking males as extra-pair partners? *Behavioral Ecology and Sociobiology, 43*, 25-36.

Park, T., Okanoya, K., & Dooling, R. (1985). Operant conditioning of small birds for acoustic discrimination. *Journal of Ethology*, *3*, 5-9.

Phillmore, L. S., Bloomfield, L. L., & Weisman, R. G. (2003). Effects of songs and calls on ZENK expression in the auditory telencephalon of field- and isolate-reared black-capped chickadees. *Behavioral Brain Research*, *147*, 125-134.

Ratcliffe, L., Mennill, D. J., & Schubert, K. A. (2007). Social dominance and fitness in black-capped chickadees. In K. A. Otter (Ed.), *The ecology and behavior of chickadees and titmice* (pp. 131-146). New York, NY: Oxford University Press.

Ribeiro, S., Cecchi, G. A., Magnasco, M. O., & Mello, C. V. (1998). Toward a song code: Evidence for a syllabic representation in the canary brain. *Neuron*, *21*, 359-371.

Roberts, L. A., Higgins, M. J., O'Shaughnessy, C. T., Stone, T. W., & Morris, B. J. (1996). Changes in hippocampal gene expression associated with the induction of long-term potentiation. *Molecular Brain Research*, *42*, 123-127.

Smith, S. M. (1991). *The black-capped chickadee: Behavioral ecology and natural history.* Ithaca, NY: Cornell University Press.

Sturdy, C. B., Bloomfield, L. L., Charrier, I., & Lee, T. T. -Y. (2007). Chickadee vocal production and perception: An integrative approach to understanding acoustic communication (pp. 153-166). In K. A. Otter (Ed.), *Ecology and behaviour of chickadees and titmice: an integrated approach*. New York, NY: Oxford University Press.

Sturdy, C. B., Bloomfield, L. L., Farrell, T. M., Avey, M. T., & Weisman, R. G. (2007). Auditory category perception as a natural cognitive activity in songbirds. *Comparative Cognition & Behavior Reviews, 2*, 93-110. Retrieved from http://psyc.queensu.ca/ccbr/index.html DOI:10.3819/ccbr.2008.20006

Sturdy, C. B., Phillmore, L. S., & Weisman, R. G. (1999). Note types, harmonic structure, and note order in the songs of zebra finches (*Taeniopygia guttata*). *Journal of Comparative Psychology, 113*, 194-203.

Sturdy, C. B., Phillmore, L. S., Price, J. L., & Weisman, R. G. (1999). Song-note discriminations in zebra finches (*Taeniopygia guttata*): Categories and pseudocategories. *Journal of Comparative Psychology*, *113*, 204-212.

Sturdy, C. B., Phillmore, L. S., & Weisman, R. G. (2000). Call-note discriminations in black-capped chickadees (*Poecile atricapillus*). *Journal of Comparative Psychology, 114,* 357-364.

Sturdy, C. B., & Weisman, R. G. (2006). Rationale and methodology for testing auditory cognition in songbirds. *Behavioral Processes*, *72*, 265-272.

Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science*, *24*, 1934-1937.

Wasserman, E. A., Kiedinger, R. E., & Bhatt, R. S. (1988). Conceptual behavior in pigeons: Categories, subcategories, and pseudocategories. *Journal of Experimental Psychology: Animal Behavior Processes*, *14*, 235-246.

Weisman, R., Njegovan, M., & Stephen, I. (1994). Frequency ratio discrimination by zebra finches (*Taeniopygia guttata*) and humans (*Homo sapiens*). *Journal of Comparative Psychology*, *108*, 363-372.

Wilson, D. R., & Mennill, D. J. (2011). Duty cycle, not signal structure, explains conspecific and heterospecific responses to the calls of black-capped chickadees (*Poecile atricapillus*). *Behavioral Ecology*, *22*, 784-790.

Wilson, D. R., Ratcliffe, L. M., & Mennill, D. J. (2016). Black-capped chickadees, *Poecile atricapillus*, avoid song overlapping: Evidence for the acoustic interference hypothesis. *Animal Behaviour*, *114*, 219-229.

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