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Article in Wiley interdisciplinary reviews. Cognitive science · February 2015
DOI: 10.1002/wcs.1346

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Avian Cognition: Examples of Sophisticated Capabilities in Space and Song

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<td>COGSCI-563.R1</td>
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<td>Advanced Review</td>
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<td>Date Submitted by the Author:</td>
<td>n/a</td>
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<td>Complete List of Authors:</td>
<td>McMillan, Neil; University of Alberta, Psychology Hahn, Allison; University of Alberta, Psychology Spetch, Marcia; University of Alberta, Psychology Sturdy, Christopher; University of Alberta, Psychology</td>
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<tr>
<td>Keywords:</td>
<td>Birds, Cognitive ethology, Spatial cognition, Birdsong, Concepts and categories</td>
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<td>Choose 1-3 topics to categorize your article:</td>
<td>Comparative Psychology (BEAD) &lt; Psychology (BEAA)</td>
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Article type: Advanced Review

Article title: Avian Cognition: Examples of Sophisticated Capabilities in Space and Song

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Abstract

Though birds have traditionally and colloquially been considered less cognitively complex than mammals, and especially primates, more recent research has consistently refuted these assumptions. We argue that the impressive abilities of birds to navigate and communicate require considerable information-processing capabilities. These capacities include collecting, organizing, and selecting from a wide variety of navigational cues to orient toward and find a goal location in the spatial domain, and utilizing open-ended categorization and possibly even abstract reasoning to discriminate species-specific acoustic features of songs and calls. Further, these abilities may be present across many avian species, providing evidence for domain-general cognitive facilities. We provide examples of processes in spatial learning and communication in birds, and locate them within the general literature, as evidence that the term “bird-brain” should not be considered a pejorative.
As the derogatory term “bird-brain” suggests, the traditional view of avian intelligence is that it falls somewhere between that of a rat and a mosquito. Although it has long been known that some birds display exceptional behavioral feats, such as migrating or homing over long distances, building elaborate nests, fashioning and using tools, or singing complex songs, these behaviors were assumed to be primarily innate, requiring little in the way of flexible cognitive capabilities. Recent research in comparative cognition and neuroscience has dispelled this dismissive view of avian cognition. We now know that learning and memory play a significant role in many of these and other remarkable behavioral feats and that some species of birds have sophisticated cognitive abilities that rival those of mammalian species. Here we will describe a select few examples from the domains of spatial cognition and communication that provide a sample of the array of abilities that birds possess.

The sheer number and diversity of bird species (approximately 10,500 species) that live across a wide range of climates and ecosystems worldwide provides scientists with innumerable examples of how different species can adapt, survive, and ultimately reproduce, under many, varied conditions. These adaptations provide researchers with opportunities to examine just how birds, and their cognitive abilities, have evolved to solve the problems with which nature confronts them. For example, because flight is the primary means of locomotion for many birds, they face spatial navigation challenges of a larger scale than do most mammals. Depending on the species and season, many bird species navigate in migrations of thousands of kilometers each year, obtain food from many disparate foraging patches and return home to the nest, and establish and defend large territories. Birds are also commonly very social animals, with the vast majority of species being socially monogamous and many species living in small family groups or large flocks. Birds communicate using a variety of visual and auditory signals, but this particular ability for communication is perhaps best exemplified by the songs of oscines in the order Passeriformes (colloquially, ‘songbirds’). Field observations of birds’ spatial memory and communication abilities provide valuable insight into the ecological uses of some birds’ amazing spatial memory or intricate singing that aids in their survival. Unfortunately, determining the cognitive mechanisms underlying these feats under field conditions can be more of a challenge; it is difficult to uncover the mechanistic bases of spatial memory or song learning, production, or perception abilities without directly manipulating the environment and controlling for alternate cues. Although manipulation of environmental cues has sometimes been accomplished in field studies (e.g., see Maury, Mauch, Hammer and Bingman), for these questions we often need to turn to laboratory studies, which allow us to expand the breadth of species studied, and also facilitate the search for general processes in spatial, communicative, and cognitive abilities.

This review will focus on the particular abilities of birds to use cognitive systems to solve the problems inherent in navigation and communication. Though there are some overlapping problems requiring use of both domains (e.g., a bird determining the boundaries of its territory based on the spatial locations of neighbour songs), our primary contention is that birds show remarkable sophistication in two disparate areas, each critical to their survival, that may point to domain-general advanced cognition.

**SPATIAL COGNITION**
Like other mobile organisms, virtually all bird species need to learn about and remember spatial information for critical daily activities such as foraging for food, finding mates, and returning to the home nest. Reliable and efficient navigation to sources of food can be a determining factor in whether an individual lives or dies. One would thus expect that birds should share with many other organisms basic processes for orienting in the world, for encoding and remembering places, and for navigating efficiently to a goal. However, there is also tremendous diversity among avian species. Many migrating birds navigate over vast distances and have evolved mechanisms for long-distance navigation that continue to amaze scientists and naturalists. Other species have adapted to harsh environments and scarce resources by scatter hoarding food and developing extraordinary spatial memory abilities to recover their caches. An incredible spatial memory for cached food in scrub jays (Aphelocoma coerulescens), magpies (Pica pica) and black-capped chickadees (Poecile atricapillus) extends not only to the location of caches, but also the food type and time of caching. Nectar feeding birds have adapted to the dynamic replenishment of resources by using internal timing mechanisms to track spatial and temporal information. Thus, avian species provide a rich source of information for researchers to study general and specialized processes of spatial cognition.

Much of the research in spatial cognition uses a “transformational” approach pioneered by Tinbergen in his classic studies demonstrating that digger wasps (Philanthus triangulum) use visual landmarks to remember and locate their nest. In this approach, cues are experimentally provided during learning of a location and then they are transformed (displaced, altered or removed) on subsequent tests. For example, Cheng and Sherry used the transformational approach with both pigeons (Columba livia) and black-capped chickadees to test use of a discrete visual landmark and the edge of an extended surface for locating a hidden goal. During training the goal was located at a fixed location near an edge and close to a small object. On tests, the landmark was shifted in a direction that was parallel, perpendicular, or diagonal to the edge. Both pigeons and chickadees altered their search locations when the landmark was shifted parallel to the edge but not when it was shifted perpendicular to the edge. When it was shifted diagonally, their search shifted in the parallel direction only. This suggested that the birds used the landmark to determine where along the edge to search, but not how far from the edge to search. Spetch, Mondloch, and Cheng found the same pattern of results when the landmark and edge were presented as graphic stimuli on a computer touch screen for pigeons, suggesting that distance from an edge is a generally salient spatial cue for birds. As discussed by Cheng and Spetch, the transformational approach provides a powerful experimental method to investigate the cues animals use to remember places.

One critical step in returning to a distant or hidden goal is to maintain or re-establish a directional frame of reference. This is variously referred to as orienting in the environment, determining heading, or getting one’s bearings. Numerous avian species have been shown to be capable of using many different sources of information to orient, including self-generated cues such as path integration, celestial and magnetic cues, landmarks or features of the environment, and geometric properties of an environment. Use of the latter two types of cues – features and geometry – have been particularly well studied in birds in recent years and will be the focus of our discussion.

In this review, we emphasize two themes regarding birds’ use of landmarks and geometry to orient and navigate. The first is hierarchical redundant encoding: Birds, and many other organisms, seem to encode more information than is strictly needed to relocate the goal, although they show...
preference hierarchies for how the cues are weighted if the cues are in conflict. The second theme is flexibility and adaptability in cue preference: hierarchies differ across species and can change as a function of ecological niche or individual experience. There are several reasons why it can be adaptive to encode multiple redundant sources of information: it may improve accuracy in locating a goal (e.g., the multiple bearing hypothesis\(^{27}\); cues may also differ in their value for different components of navigation (e.g. one cue may be most useful for navigating to the general area and another for pinpointing the goal; one cue may be most useful for determining distance and another for computing direction); and it allows the goal to be located even if one or more of the cues is absent or obscured, such as by seasonal or other changes in the environment.

Although encoding redundant information can be valuable, encoding all information in the environment to remember a goal location would be cognitively cumbersome. Encoding all cues would also increase the likelihood of errors arising from the encoding of unreliable or unstable cues that result in conflicting information at the time of test. Not surprisingly then, preferences among potential spatial cues are typically observed. Preference hierarchies may reflect properties of the natural environment (e.g., large geometric properties of space cues may typically be more stable than small features), or properties of the sensory system or evolutionary histories of the species. But preference hierarchies can also vary flexibly depending on individual experiences. We will present a few examples of this flexibility in avian species.

**Orienting in space: Where am I?**

Orientation within an environment can sometimes be lost for a variety of reasons, including taking too many twists and turns (such as exiting from a spiral staircase), distraction (such as moving through space while being engrossed in a conversation or being chased by a predator), or loss of direct contact with the environment being navigated (such as when waking from sleep or emerging from a tunnel or cave). When this happens, the organism must use sensory information to regain a sense of direction. To simulate this process, researchers commonly use some version of a reorientation task that was pioneered by Cheng\(^{28}\). In Cheng’s study, rats (Rattus norvegicus) found food in a particular location within a rectangular chamber and then searched for the location again after they were disoriented. The rats frequently made rotational errors by searching at the wrong but geometrically equivalent location, suggesting that they used geometric shape to regain their sense of direction. Rotational errors occurred even when the chamber included distinctive visual features that could be used to disambiguate the geometry. Since Cheng’s original study, the use of geometry to reorient has been demonstrated in species ranging from insects to humans (see Cheng, Huttonlocher, and Newcombe\(^{29}\) for a recent review), and has been extensively studied in both domestic chicks\(^{26}\) (Gallus gallus domesticus) and pigeons\(^{25}\). Like rats, both chicks and pigeons readily use the geometric shape of enclosed environments to reorient, but unlike rats, pigeons also readily encode the featural information (such as colors, patterns, and textures) and they typically weight featural information more heavily than geometric information on conflict tests\(^{25}\). Kelly\(^{30}\) found that for Clark’s nutcrackers (Nucifraga columbiana), features even facilitated the encoding of geometry.

It is perhaps not surprising that birds would be more likely than rodents to attend to featural information for orientation. Many species of birds are highly visual creatures\(^{31-34}\). Pigeons, for example, have an excellent ability to discriminate colors\(^{35}\), remember fine details in pictures\(^{36,37}\) and recognize objects\(^{38}\). What is interesting is that the relative attention to features or geometric shape
appears to depend on both phylogeny and experience. For example, Kelly and colleagues trained pigeons to find food in one corner of a rectangular enclosure. Pigeons were disoriented before each trial and only cues within the enclosure could be used to reorient. Some pigeons were initially trained with no distinct features, so that only geometry could be used, and then features (patterns in each corner) were added for the remainder of training. Other pigeons were trained with the features present from the outset. Both groups of pigeons encoded the geometry, as evidenced by equivalent choice of the correct and geometrically equivalent corners when the features were removed (see Fig. 1, panel A). However, on conflict tests in which the features were shifted so that correct features were located at geometrically incorrect corners, group differences were apparent: the group trained with features from the outset primarily chose the featurally correct corner, whereas the group trained initially with geometry split their choices between the featurally and geometrically correct corners (see Fig. 1, panel B). Thus, features dominated unless the birds first learned to reorient on the basis of geometry alone.

To determine whether natural history or pre-experimental experiences might alter the use of geometry or features, Gray and colleagues tested wild-caught mountain chickadees (Poecile gambelli) on the reorientation task in a rectangular enclosure with one distinctive wall. When the distinctive wall feature was adjacent to the goal corner, the feature dominated choice on conflict tests and overshadowed control by geometry - the first demonstration that geometry is not always automatically encoded. In a subsequent study, Batty and colleagues used a slightly modified procedure and found that some mountain chickadees encoded geometry despite the presence of an adjacent feature wall, but others did not. Black-capped chickadees, whether reared in the lab or in the wild, showed a greater tendency to use geometry than mountain chickadees.

Whether rearing experience affects geometry use appears to depend on species. Chiandetti and Valltorigara found strong and equivalent use of geometric information for reorientation by newborn chicks whether they were raised in circular or rectangular cages from hatching until testing. Thus, chicks were able to re-orient on the basis of geometry even without prior experience with rectilinear geometry. This may not be the case for non-avian species. Brown, Spetch, and Hurd found that convict cichlid fish (Archocentrus nigrofasciatus) reared in circular tanks were more likely to follow features on conflict tests than those reared in rectangular tanks. Likewise, Twyman, Newcombe, and Gould found that mice (Mus musculus) raised in rectangular cages showed evidence of encoding geometry even when it was redundant with featural information, whereas mice raised in circular cages did not show evidence of encoding redundant geometry and instead used it only when it was the only cue available. The authors suggested that the malleability of cue use for spatial reorientation may reflect the length of the juvenile period. More avian species need to be tested to determine whether the lack of dependence on early experience for use of geometry by chicks is representative of avians in general, or whether it reflects the extreme precocial development of these birds.

When features are used to reorient, an interesting question is whether they are used only as a beacon to approach, or whether they can be used as directional cues. Research with most animals has found that only the features near the goal are used (Bumblebees, Bombus terrestris; chicks, redtail spinefin fish, Xenotoca eiseni), suggesting that they may serve as beacons. Pigeons, however, can use the features at distal corners in the reorientation task (see Fig. 1, panel C), suggesting a sophisticated use of featural information. Their use of geometric information is also
sophisticated. For example, pigeons can use relative geometric shape extracted away from exact sizes\textsuperscript{47}, and they can orient on the basis of floor slope\textsuperscript{48}. Chicks\textsuperscript{49}, pigeons\textsuperscript{50,51} and Clark’s nutcrackers\textsuperscript{52} can also use the angular amplitude of corners to orient. In nature, celestial cues and path integration play an important role in avian navigation\textsuperscript{53}, but even in constrained artificial environments, birds can make use of many different sources of information to regain orientation.

**Cue use for goal localization**

Orienting in an environment is often not the only step necessary to find a goal; the location of the goal within the environment must still be determined. If distinctive cues are present at the goal, directly approaching these cues (i.e., “beaconing”) may be sufficient to find the goal. However, if the goal is not directly marked by distinctive cues, then its location may be remembered on the basis of more distant cues. Navigating on the basis of distant cues is referred to as piloting. These processes have been extensively studied in many avian species.

As with the use of cues to orient, birds appear to be flexible in which cues they use to locate a goal, but they show preferences in their cue use when confronted with conflicting information. For example, Spetch and Edwards\textsuperscript{54} trained pigeons to find food in the middle of three cartons that were aligned in a fixed location along one wall of a room; this provided redundant local cues (position in array of cartons) and global uses (location in the room). Subsequently, the birds were given three kinds of unreinforced tests: local-only (the cartons were moved to a new location in the room to negate the global information), global-only (one carton was removed to eliminate the local position information) and conflict (cartons shifted so that the local and global cues indicated different cartons). The pigeons significantly chose the correct carton on the basis of global or local cues alone, but the conflict tests showed dominance by the local positional cues. They interpreted these results in terms of hierarchical redundant cue use, in which one source of information is preferred but others are also encoded as backups if the preferred one is not available. This type of hierarchical redundant cue use has also been proposed for other aspects of spatial behavior such as homing behavior in pigeons, in which the sun serves as the primary compass cue but other cues serve as a backup when skies are fully overcast\textsuperscript{55}.

The specific cue that dominates depends upon many organismic and stimulus factors. For example, using a similar procedure of training with redundant cues followed by conflict tests, Brodbeck\textsuperscript{56} found that black-capped chickadees showed dominance of global location over local feeder cues, whereas dark-eyed juncos (*Junco hyemalis*) showed no preference. Legge, Spetch and Batty\textsuperscript{57} tested pigeons on a touch-screen task with local (middle position in array), and global cues (location on screen) and found that local cues dominated when the array was aligned horizontally but the dominance reversed when the array was aligned vertically. Healy and Hurly\textsuperscript{58} found that hummingbirds showed dominance by the position in an array when the feeders were spaced close together but showed dominance by the absolute location in the field when the array of feeders was spaced farther apart. Cue preferences were found to be lateralized for chicks\textsuperscript{59}: when trained to find a goal in the center of enclosure by a beacon, chicks followed the beacon on subsequent beacon-shift tests if using their right eye (left hemisphere) but continued to search in the center if using their left eye (right hemisphere). Birds also show experiential flexibility in their use of different sources of information. For example, Gould-Beierle and Kamil\textsuperscript{60} reported that Clark’s nutcrackers showed dominance of global location
over a local nearby landmark, but the nutcrackers showed good control by the local landmark if the goal was moved during training, thereby negating the global information. Similarly, pigeons\textsuperscript{61} and nutcrackers\textsuperscript{62} showed preferential control by absolute over relational distances when both were reliable cues in training, but used relational distance when absolute distance was not a reliable cue\textsuperscript{63,64}. Finally, within the same general class of cues (local discrete landmarks), preference depends on factors such as proximity to the goal\textsuperscript{65}.

The above examples indicate that birds preferentially respond to whichever cues are most salient, reliable or informative, but they attend to other sources of information as well. Interestingly, although birds show hierarchical preferences in situations demanding a discrete choice among search locations, their behavior in situations that allow search within a continuous space suggests that even more sophisticated integration processes may operate. For example, birds often shift their search only partway toward a shifted landmark\textsuperscript{20,21}, suggesting a compromise between the shifted cues and other non-shifted cues. Legge\textsuperscript{66} found that a model of Bayesian integration in which the spatial cues are weighted by their reliability\textsuperscript{67} fit pigeons’ search behavior better than models based on independent cue use. Interestingly, pigeons have even been shown to integrate both temporal and spatial information to determine a single criterion for when to respond\textsuperscript{68}; this finding revealed an ability to centrally integrate information from fundamentally different sources, one based on an internal sense of time and one based on visual perception of a location in space.

It is thus readily apparent that birds’ orientation and navigation depend heavily on the flexible use of multiple sources and elements of information. How birds organize information and learn relationships between stimuli is also critical to the development of categories and concepts, especially in vocal-learning birds that may serve as a non-human analog of language learning and communication, which will be the focus of the next section.

**VOCAL COMMUNICATION AND CATEGORY LEARNING**

For more than 50 years, songbirds have been an increasingly popular species to use as a model for human speech, owing to the remarkable similarities between humans and songbirds during vocal acquisition\textsuperscript{69,70}, including that songbirds learn their songs (and other vocalizations) from adult conspecifics. Songbirds’ singing and calling behaviour (collectively referred to as vocal communication) is critical to their survival as individuals and as species. Males produce song to attract a mate and to defend their territory, while females attend to these songs and singing contests to select a mate\textsuperscript{71}. In addition, females of tropical species commonly produce song\textsuperscript{72}, and there is increasing evidence that females of many temperate songbird species produce songs as well\textsuperscript{73-75}. Both sexes also produce calls (some learned and some not) that are critical to their survival, as these vocalizations provide information about predators, food, and the whereabouts of other members of their species. Likewise, songbirds can attend to other individuals’ vocalizations to identify and discriminate between individuals\textsuperscript{76-78}, flocks\textsuperscript{79,80}, and territory neighbours or strangers\textsuperscript{81}.

Some songbird species, such as song sparrows (\textit{Melospiza melodia}), have repertoires of song types\textsuperscript{82}; that is, they sing several different songs that can be sorted into types with similar acoustic structure. Not only do birds produce acoustically distinct song types, but they also produce variants of these types. Playback experiments with song sparrows have shown that singing birds respond more aggressively when songs of matching types are presented to them (i.e., songs similar to the song the
focal bird is currently singing), compared to playback of songs that are produced by the same bird, but are not a type-match. This elegantly demonstrates category perception, wherein stimuli are sorted into groups based on perceptual similarity, in a wild population of birds performing biologically relevant behaviours (i.e., territorial defense).

We and others have used operant conditioning to probe perceptual and cognitive abilities in laboratory-based experiments, allowing us to study behaviour and perception without the uncontrolled variables experienced by field researchers (e.g., acoustic disturbances), and to also allow us to test the perception of vocalizations by males and females out of breeding season. Our operant methodology has been specifically adapted to assess perception and cognition in small bird species, and songbirds in particular. Briefly, we train birds to wait on a request perch until a stimulus plays. Once the stimulus has been selected and played, over many trials, birds learn through trial and error which stimuli are positive (rewarded with access to food) and which stimuli are negative (unrewarded and resulting in the houselights being extinguished; see Sturdy and Weisman for a detailed description of the operant apparatus). A primary focus for the past several years has been to use this operant go/no-go procedure to illuminate how songbirds perceive natural, open-ended categories that are biologically-relevant. This has led us to design experiments aimed at understanding how songbirds discriminate conspecific (same species) and heterospecific (other species) vocalizations, and how these discriminations may be at the level of categories or even abstract concepts.

Open-ended categorization

One key function that animal signals serve is that of species marker; that is, the signal receiver can differentiate animal signals by species. That an acoustic signal can perform this function is advantageous for many reasons; for example, acoustic signals can function over long distance, and in habitats that contain physical barriers for visual signals. Animals that can rapidly and accurately discriminate signals on the basis of the species emitting such signals can avoid lost time devoted to signals produced by heterospecifics and instead attend to, and act upon, signals from conspecifics. This need for speed and accuracy in decision making is what initially led us to investigate how birds performed such discrimination tasks. How could animals both perform such an important skill expeditiously and accurately? To begin to answer this question, researchers can use operant conditioning to test auditory perception in birds, and examine cognitive mechanisms for quickly sorting “objects” into classes (i.e., open-ended categorization).

Open-ended categorization is the ability, once thought to be the domain only of humans, to classify items flexibly into categories. Once an animal perceives the bounds of class membership (what defines a class, and which stimuli fit in that class), they can then sort new instances of members from that class quickly and easily without the need to continually learn contingencies for each new stimulus. Birds that can identify the species of signaller from an acoustic signal through this mechanism can, for example, avoid unnecessary conflicts by classifying the signaller as either conspecific or heterospecific. Using one of our main study species as an example, black-capped chickadees that identify a bird call as “black-capped chickadee” in an open-ended manner do not require experience with every possible call produced from a bird of every species; once the species-category “black-capped chickadee” is learned, newly-encountered calls can be sorted and acted upon as appropriate. This ability may even allow birds to identify individuals. Using an operant
discrimination task, Weary and Krebs$^{85}$ demonstrated that great tits (*Parus major*), when trained to discriminate between the songs produced by two males, continued to discriminate based on individual when tested with novel songs produced by the same two males. These results suggest that in the wild, birds would be able to identify a singing male, even without learning all of his song types; in other words, birds could use categorization to identify individuals.

Early research on categorization in songbirds analyzed individual components of zebra finch (*Taeniopygia guttata*) songs, with three main goals: (1) sort song notes into types, (2) confirm that birds perceived the vocal categories contained in their songs and calls in a manner consistent with how human scientists had sorted them, and (3) determine whether songbirds, like other species tested, perceived categories in an open-ended manner$^{86,87}$. These studies provided a proof of concept that, at the level of the individual song and call notes, birds could perceive their own species vocal classes as open-ended categories.

**Chickadees as a model system for communication**

Open-ended classification would be important for many species, but especially for black-capped chickadees that produce several variants of their *chick-a-dee* call with differences in note composition thought to relate to different contexts. North American chickadees serve as an excellent model for understanding learning, cognition, and behaviour; by approaching communication in this species from several, convergent avenues, including the fundamental aspects of their vocalizations (bioacoustics), researchers have begun to piece together chickadees’ communication systems and the proximate mechanisms underlying them. This is critical to further studies aimed at deciphering the mechanisms that figure most prominently in discrimination and classification of conspecific and heterospecific vocalizations.

In describing the *chick-a-dee* call produced by black-capped chickadees (see Fig. 2a), Ficken, Ficken, and Witkin$^{88}$ noted four distinct note types: A, B, C, D. Since this description by Ficken and colleagues, additional studies using various bioacoustical and other statistical procedures and neural networks have provided evidence that the *chick-a-dee* call notes produced by black-capped chickadees are natural categories$^{89-91}$. Additionally, bioacoustic analyses have been used to describe the *chick-a-dee* call notes produced by other North American chickadees (mountain chickadees$^{92}$, Carolina chickadees$^{93}$, *Poecile carolinensis*; chestnut-backed chickadees$^{94}$, *Poecile rufescens*; Mexican chickadees$^{95}$, *Poecile sclateri*; boreal chickadees$^{96}$, *Poecile hudsonicus*). These studies provide a description of *chick-a-dee* call notes, and results from operant conditioning studies$^{97}$ confirm that chickadees sort black-capped chickadee *chick-a-dee* notes into the same four categories as bioacousticians.

Being able to categorize the calls (and call notes) based on which species produced the vocalization would benefit individuals by saving time and energy trying to mate with the wrong species. This leads logically to examining if chickadees can discriminate and categorize the calls of different species. To this end, much recent work has focused on two species that live sympatrically: black-capped and mountain chickadees. Previous research$^{98}$ showed that black-capped and mountain chickadees perceived conspecific and heterospecific calls as separate, open-ended categories. Even black-capped chickadees hand-reared with exposure to only conspecific or heterospecific (mountain chickadees) adult birds were able to perform this categorization$^{99}$. When trained on a similar task to discriminate individual note types of the two species’ calls, chickadees learned the D note.
discrimination faster than B and C notes. Though all four notes appear to carry discriminable acoustic features between subspecies, there are elements of D notes that appear to make them easier to discriminate. Together, these data illustrate that chick-a-dee calls contain species-based information, and that chickadees can perceive these differences and form open-ended categories based on whole calls or individual call notes.

These results with the discriminable features of chick-a-dee calls have been extended in studying whether other bird species can perceive and discriminate between features of those calls. Zebra finches, distant relatives to chickadees, have been trained to discriminate black-capped and mountain chickadee call notes, learning the discrimination of D notes faster than A, B, or C notes. Unlike the chickadees tested on the same task, the finches did not have prior experience with calls produced by chickadees; it is important to note, however, that both finches and chickadees are vocal-learning songbirds. Further studies observing discrimination of chick-a-dee calls by pigeons preliminarily found that the birds were better at discriminating calls that varied between- rather than within-species, suggesting that even a non-vocal-learning species could perceive differences in the acoustic features of calls produced by different chickadee species. These results underline that species-specific information carried by the chick-a-dee call are based on acoustic features, rather than genetics or experience alone. Importantly, though there were subtle differences in the discrimination of D and A notes by zebra finches relative to chickadees, the ability to discriminate between species based on calls does not seem to be only a genetically-prebuilt construct for biologically-relevant information. Rather, this learning may reflect a general ability to form perceptual categories, especially when the features of those categories are particularly relevant to the animal. A remaining question is whether an ability for open-ended category learning may also reflect an ability for abstract concepts and relations.

**Songs, Concepts, and Abstract Relationships**

The fundamental difference between concepts and categorization is the formation of a representation more complex than simple perceptual similarities between stimuli, which may be made even more complex by forming abstract relationships between concepts such as bigger, faster, or simply the same as. A common procedure to test for abstract concept formation in animals is the same/different task, in which the subject must identify whether a number of items presented together are “same” or “different”. For example, subjects are rewarded for responding to a test stimulus (e.g., a picture of a tree) only if it is conceptually the same as the sample stimuli that came before it (e.g., pictures of trees, rather than pictures of houses). Importantly, the same sets are used across same and different trials, and typically procedures also incorporate transfer tests involving brand new sets of stimuli; to succeed at this task, animals must learn the same/different relational rule, rather than memorize the correct or incorrect stimuli. Extensive studies with pigeons show that they can learn to acquire same/different visual discriminations and transfer these concepts to novel presentations of stimuli. More recent interest has been in whether songbirds might show same/different discrimination in the auditory domain, especially given the ecological relevance of such a discrimination for duets and countersinging contests.

In contrast to their namesake chick-a-dee call, which contains multiple notes, the song produced by black-capped chickadees is a relatively simple, two-note whistled song. Called the fee-bee song, the first note (fee note) is produced at a higher frequency compared to the second note.
Although the tonal acoustic structure appears simple, the fee-bee song and birds’ singing behavior is actually a complex communication system. For example, males will shift the pitch of their songs to match those of rival males\textsuperscript{107}, and one signal of dominant status in chickadees is the ability to maintain a consistent relative frequency between the two notes while shifting the songs’ absolute frequency up or down\textsuperscript{109}. This relative frequency between the two notes (referred to as the interval ratio) is a species-typical feature within the song, with the interval ratio remaining seemingly invariant across individuals\textsuperscript{110}. In an operant go/no-go task, chickadees solved a discrimination with the species-typical interval ratio in fewer trials compared to abnormal interval ratios\textsuperscript{111}, when the stimuli “songs” were composed of sine-wave tones. There was no difference in the birds’ discrimination performance for stimuli comprised of natural notes, even when the interval ratio was altered, suggesting an advantage for learning a discrimination task with biologically-relevant stimuli.

Although birds may be more adept at discriminating natural stimuli, like those they would encounter in the wild, birds can also discriminate artificial stimuli. Hoeschele and colleagues\textsuperscript{112} showed that chickadees could discriminate between sequences of artificial sounds based on whether those sequences were the same or different; crucially, they transferred this learning to tests with novel stimuli. Similar results have been shown for auditory same/different discriminations in pigeons\textsuperscript{113} and budgerigars\textsuperscript{114} (Melopsittacus undulates). Together, these results suggest that many bird species have the capacity to judge the abstract relations between stimuli, an ability which is considered essential for language development\textsuperscript{115} and considered to be at the upper levels of categorization capability\textsuperscript{103}.

**BIRD-BRAINS? HARDLY**

Spatial cognition and categorization in communication are only two examples of the impressive array of cognitive skills presented by birds. Perhaps the most striking examples of behaviors normally thought reserved to apes are those of the Corvidae family. New Caledonian crows (Corvus moneduloides) show highly complex tool use in the wild\textsuperscript{3,4} and in experiments in captivity\textsuperscript{5,6}. Ravens (Corvus corax) have been suggested to use ‘tactical deception’ to protect their caches from potential pilferers by hiding their food out of sight of conspecifics\textsuperscript{116} and by leading them away from food\textsuperscript{117,118}. Pinyon jays (Gymnorhinus cyanoccephalus) have been suggested to utilize transitive inference to rank unknown conspecifics within a dominance hierarchy, with subsequent changes in social interactions with those individuals\textsuperscript{119}. Eurasian magpies show self-directed behaviors in the mirror test\textsuperscript{120}. Indeed, it is difficult to find examples of ‘highly intelligent’ behaviors in non-human apes that cannot also be observed in corvids, despite incredibly divergent brain architecture in the two groups.

Compelling as their ‘cognitively complex’ behaviors might be, however, the feats of corvids exist on a continuum of high-level processing in birds. Here we have discussed the extensive encoding of spatial information by birds, in line with other species; we have also argued that songbirds leverage categorization in auditory discrimination to produce one of the most impressive learned communication systems present in non-human animals. In both cases, birds appear to have extensive capabilities for processing information and applying decisions flexibly based on systems including hierarchical organization and categorization. To dismiss avians as mere bird-brains is to ignore a wealth of research showing how resourceful and intelligent they are, and the myriad ways that birds use cognition to solve the problems they have faced throughout their evolutionary history.
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Figure captions

**Figure 1.** Schematic of the layout used by Kelly et al. (1998) to study reorientation by geometry and feature in pigeons. Food was consistently located in one corner during training (shown here as the top left corner; the actual corner varied across birds). Some birds were initially trained with features (distinct landmarks) in each corner (Feature group), whereas other birds were first trained with no features (Geometric group) and features were added later. Control trials that were identical to training but contained no food confirmed that birds did not use cues from the food to find the correct corner. Both groups showed strong control by geometry, as evidenced by choices to both geometrically equivalent corners on tests in which the features were absent (Panel A). On conflict tests in which the correct landmark was moved to a geometrically incorrect location, the Feature group was more likely than the Geometry group to choose the corner that contained the correct feature, indicating that initial experience mattered. Both groups (Panel C, data collapsed) chose the correct corner more often than the geometrically equivalent corner when the proximal features were removed, indicating that the pigeons could use the distal landmarks to disambiguate the geometry. Figures are adapted from Kelly DM, Spetch ML, Heth CD. Pigeons' (*Columba livia*) encoding of geometric and featural properties of a spatial environment. Journal of Comparative Psychology 1998 112:259-269. Copyright, American Psychological Association.

**Figure 2.** Sound spectrogram (FFT window = 512 points; -35 to 0 dB relative to peak amplitude) of a black-capped chickadee (a) chick-a-dee call with notes A, B, C, D, D, D and (b) fee-bee song showing fee and bee notes.

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