Are Clark’s Nutcrackers (*Nucifraga columbiana*) Able to Discriminate Knowledge States of Human Experimenters during an Object-Choice Task?

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**Abstract:** Corvids and primates have been shown to possess similar cognitive adaptations, yet these animals are seldom tested using similar procedures. Object-choice tasks, which have commonly been used to test whether an animal is able to infer the mental state of a human experimenter based on a gestural cue, provide one potential means of testing these animals using a similar paradigm. The current study used an object-choice task to examine whether the corvid, Clark’s nutcracker (*Nucifraga columbiana*), is able to use a cognitive strategy to discriminate between the knowledge states of two human experimenters. One experimenter was informed, and the other uninformed, as to the location of a food reward hidden inside one of two opaque containers. During the Uninformed Gesture condition, the nutcrackers were given probe tests during which only the person performing as the uninformed experimenter provided a gesture. Thus, the nutcrackers could not use the experimenter’s gesture to reliably find the food. During the Gesture Conflict condition, the nutcrackers were presented with a cue conflict. During probe tests, both the informed and the uninformed experimenter gestured to separate containers. Thus, to find the food the nutcrackers had to use the gesture from the informed experimenter and refrain from using the gesture of the uninformed experimenter. Our results showed that when the uninformed experimenter’s gesture was presented alone, the birds continued to follow the gesture even though it was not consistently predictive of the food’s location. However, when provided with two conflicting gestures, as a group the nutcrackers responded to the gesture of the informed experimenter at above chance levels. These results suggest that the birds had learned that the gesture was informative, perhaps by associative learning, yet when this mechanism was not reliable the nutcrackers were able to use either the human experimenters’ presence/absence during the baiting process, or possibly their knowledge states, to determine which gesture to rely upon.

**Keywords:** object-choice task, knowledge states, Clark’s nutcracker, complex cognition
Introduction

Research indicates that corvids may share many cognitive abilities with primates, suggesting a convergent evolution of mental abilities (Emery and Clayton, 2004). These cognitive similarities include many aspects of their social cognition. As evidence for their complex social cognitive abilities, primates have been reported to take into account various aspects of an observer to guide their own behavior, including: sensitivity to others’ attentional state (Flombaum and Santos, 2005; Hare, Call, Agnetta, and Tomasello, 2000; Hare, Call, and Tomasello, 2006; Maclean and Hare, 2012; Santos, Nissen, and Ferrugia, 2006), knowledge state (Hare, Call, and Tomasello, 2001; Kaminski, Call, and Tomasello, 2008; Marticorena, Ruiz, Munkerj, Goddu, and Santos, 2011), or dominance status (Hare et al., 2000, 2001). Likewise, research examining the caching-related behaviors of corvids has shown these birds to be capable of similar social cognition. Corvids modify their caching and retrieval behavior depending on whether or not they have been observed, both in natural settings (Bugnyar and Kotrschal, 2002; Heinrich and Pepper, 1998; James and Verbeek, 1983) and laboratory settings (Bugnyar, 2011; Bugnyar and Heinrich, 2005, 2006; Emery, Dally, and Clayton, 2004). When another individual is present, many corvids will cache in areas where the observer would have reduced visual access to the cache location, such as behind obstructions (ravens: Bugnyar and Kotrschal, 2002) or in shaded areas (scrub jays: Dally, Emery, and Clayton, 2004). Ravens also preferentially cache when an observer is distracted or inattentive (Heinrich and Pepper, 1998). Additionally, if witnessed making a cache, corvids have been shown to re-cache their food when the observing bird has left the area (scrub jays: Emery et al., 2004) or to preferentially retrieve caches when a competitor is knowledgeable of the cache location (ravens: Bugnyar, 2011; Bugnyar and Heinrich, 2005; Clark’s nutcrackers: Clary and Kelly, 2011; scrub jays: Dally, Emery, and Clayton, 2006). These strategies have been shown to be flexible as they are differentially applied depending on the identity and dominance status of the specific observer. Ravens, for instance, delay pilfering cached food in the presence of a dominant caching bird (Bugnyar and Heinrich, 2006). Scrub jays show increased cache protection when in the presence of dominant birds and preferentially engage in cache protection from individuals that witnessed their caching (Dally et al., 2006). Furthermore, the cache protection behaviors of scrub jays have been shown to depend on the initial acquisition of experience as a pilferer, potentially representing a form of experience projection (Emery and Clayton, 2001).

These findings suggest that corvids are sensitive to what other individuals see and know, and also recognize that other individuals may have intentions to steal their food. These cognitive skills may be similar to those shown by primates. However, research investigating the complex social cognition abilities of corvids has primarily focused on the domain of food caching (Grodzinski and Clayton, 2010), with few studies using the same experimental procedures as those with primates. Thus, it is not clear whether the abilities shown by corvids are indeed convergent to the abilities shown by primates or if they are limited to food-caching contexts. If corvid social cognition is a more general process, then corvids should be able to use these skills when challenged in non-ecologically relevant contexts and tasks more commonly used to examine primate social cognition.
Object-choice tasks provide one approach for exploring whether the abilities shown by corvids are in fact indicative of flexible cognitive processes (as opposed to associative mechanisms). Typically, during the object-choice task, the subject is required to infer the underlying knowledge state of a human experimenter through the use of the experimenter’s gestural cue to find a food reward hidden under an opaque container (e.g., primates: Byrnit, 2004; Call and Tomasello, 1994; Itakura and Anderson, 1996; Itakura and Tanaka, 1998; Nieworth, Burman, Basile, and Lickeig, 2002; Peignot and Anderson, 1999; canids: Soproni, Miklósi, Topál, and Csányi, 2002; Virányi et al., 2008; cetaceans: Pack and Herman, 2004; Tschudin, Call, Dunbar, Harris, and van der Elst, 2001; bats: Hall, Udell, Dorey, Walsh, and Wynne, 2011).

Recent studies have begun to examine corvid cognition using non-caching procedures such as the object-choice task. However, results from using this approach have been conflicted. Using a pointing cue, for example, Schloegl, Kotrschal, and Bugnyar (2008) presented ravens with an array of five containers and a human experimenter pointed to one previously baited container with his ipsilateral arm. The birds did not choose the container being pointed to more often than if no cue was given. Conversely, von Bayern and Emery (2009) showed that jackdaws were able to use a pointing cue. However, in this study the experimenter extended the contralateral arm to indicate which of two containers was baited. It is not known whether this seemingly subtle gestural difference may account for these results. When non-avian species have been tested with both an ipsilateral and contralateral gesture, the results indicate similar comprehension with either gestural form (dogs: Soproni et al., 2002; dolphins: Pack and Herman, 2004; Herman et al., 1999; seals: Shapiro, Janik, and Slater, 2003). If non-avian species are any indication, then the difference between ravens and jackdaws represents a species difference for gesture use rather than a methodologically driven difference.

Eye gaze has also been used as a directional cue during object-choice tasks with corvids. Thus far, studies using static eye gaze have shown that corvids may not use this cue to guide choices (ravens: Schloegl et al., 2008; rooks: Schmidt, Scheid, Kotrschal, Bugnar, and Schloegl, 2011; jackdaws: von Bayern and Emery, 2009). However, studies using alternating gaze have produced more accurate choice performance (jackdaws: von Bayern and Emery, 2009; Clark’s nutcrackers: Tornick, Gibson, Kispert, and Wilkinson, 2011).

Tornick et al. (2011) reported that Clark’s nutcrackers were proficient at using a variety of gestural cues (each examined independently) to find a food reward hidden in one of two containers. The nutcrackers were able to use a touch gesture (a baited cup was touched using the ipsilateral arm and picked up by the experimenter) and a pointing gesture (the experimenter’s ipsilateral arm and finger were directed to a baited cup) to locate the food reward at above chance levels early in testing. With additional training, the nutcrackers were also able to use eye gaze as a cue (the experimenter’s eyes and head were alternated between the bird and the baited cup).

In addition to being able to examine gesture use, the object-choice paradigm has the potential for investigating whether animals can discriminate between experimenters with different knowledge states (e.g., Povinelli, Nelson, and Boyson, 1990; Povinelli, Parks, and Novak, 1991; Povinelli, Rulf, and Bierschwale, 1994). Povinelli et al. (1990) allowed
chimpanzees to view a situation in which one experimenter witnessed a food reward being hidden under an opaque container, whereas a second experimenter was not afforded this experience. The two experimenters then gestured to one of the containers so that the informed experimenter always indicated the correct container and the uninformed experimenter an incorrect container before allowing the chimpanzee to make a choice. The chimpanzees preferred the gesture of the informed experimenter. However, this preference was not shown to be present for younger chimpanzees (Povinelli et al., 1994) or rhesus monkeys (Povinelli et al., 1991).

Although corvids have been studied for their ability to use experimenter-given cues, they have not been examined for their ability to use knowledge states during the object-choice task (such as conducted by Povinelli et al., 1990). However, recent critiques of the object-choice paradigm have posited that the original “mind-reading” interpretation of this task are confounded by the alternative explanation that the animal need only to attend to the experimenter’s behavioral states to respond correctly (e.g., presence/absence or eye orientation, see Povinelli and Vonk, 2003, 2004). This criticism is valid. However, the object-choice task still requires an animal to make sophisticated social judgments and therefore remains an informative procedure. We used the object-choice task as a way to examine corvid cognition using a paradigm that is typically administered to primates, as well as to present the birds with a social cognition problem outside of their ecological niche of food caching. This affords the opportunity to examine whether corvid social cognition is flexible or domain specific. Thus, the current study examined whether Clark’s nutcrackers are able to discriminate human experimenters based on their knowledge or behavioral states during an object-choice task.

The experiment was conducted in two phases. During Phase 1, nutcrackers were required to locate a hidden food reward by using a combined look→point→touch gesture (from here on referred to simply as “gesture”) from both a familiar and a novel human experimenter. Phase 1 was conducted to establish that the birds could learn the gesture that would be used in Phase 2.

During Phase 2 of this experiment, the same nutcrackers were required to discriminate between an informed and uninformed human experimenter, and use only the gesture from the experimenter that was informed on any given trial to locate a hidden food reward. Therefore, this modified object-choice task was used to examine whether nutcrackers are sensitive to the knowledge state or behavioral state of the experimenter. If the nutcrackers’ cognitive abilities are indeed representative of flexible and complex cognition, then they should be able to solve the social problem presented, despite the non-ecologically relevant (i.e., non-caching) nature of the task.

**Materials and Methods**

**Subjects**

Ten (five male and five female) wild-caught, sexually mature Clark’s nutcrackers (*Nucifraga columbiana*) were used in the experiment. Birds had been in captivity for 8-16 years and were housed in individual cages (73 cm high x 48 cm wide x 48 cm deep) throughout the experiment. The birds were provided a diet consisting of turkey starter,
parrot pellets, sunflower seeds, pine seeds, mealworms, oyster shells, and a vitamin supplement. Each individual was food restricted to 85% of its ad libitum weight for the duration of the experiment. All birds had previous experience with spatial and functional lateralization tasks. The colony room maintained a 12:12 light-dark cycle with light onset at 07:00 and a temperature of 21°C. All housing and experimental conditions were approved by the local animal care committee and met the guidelines of the Canadian Council on Animal Care.

**Apparatus**

Birds were tested in an experimental cage (66 cm high x 48 cm wide x 48 cm deep) surrounded by curtains to create a uniform environment (200 cm long x 175 cm wide). The experimental cage allowed the birds to make choices through two openings at the front of the cage (see Figure 1). Birds could insert their heads through one opening at a time to obtain a food reward from a container situated on a tray (51 cm long x 23 cm wide) outside the cage. Two laterally positioned containers (8.5 cm diameter) were placed in this tray. A swivel lid was attached to each of the containers such that the contents could be occluded. To control for odor cues, each container had a layer of pine seeds along the bottom. The rest of the volume was filled with grit so that a single pine seed could be placed on the surface of the grit, in view of the test subject, when the container’s swivel lid was open. The tray was attached to a pulley system operated by an experimenter located outside of the testing room. This system allowed the experimenter to pull the tray away from the cage once the subject had made a choice. Each trial was viewed and recorded using a Sony Mini DV digital videocassette recorder attached to an EverFocus 1/3” color digital camera mounted on the ceiling above the test cage.

**Procedures**

**Habituation.** Prior to the experiment, the birds were given one container, filled with grit and a food reward, in their home cages so that they could explore the container and learn how to remove the lid to obtain the pine seeds inside. Once birds were readily approaching and reliably opening the containers in their home cage, the birds were individually placed in the experimental cage and allowed to select freely from the containers which were placed flush against the two openings of the experimental cage with the swivel lids opened. On the following 4 days the swivel lids were closed and the birds were allowed to explore the containers and open the lids to retrieve a hidden pine seed from each container. Once birds were consistently opening the containers in less than 30 seconds they began participating in the experiment.
Figure 1. The front of the experimental cage

Notes: Two openings were located on either side of the cage to allow the bird access to either of the containers positioned laterally on the tray outside the cage.

Phase 1

i) Training. Training procedures for Experiment 1 were similar to those used by Tornick et al. (2011). During training, birds received one daily session consisting of eight trials (with sessions conducted Monday through Friday each week). During half of the trials the gesture was performed by an experimenter familiar to the birds (herein referred to as the “familiar experimenter”). The familiar experimenter had extensive history (~6 months) both feeding and handling the birds. During the other half of the trials the gesture was performed by an experimenter unfamiliar to the birds (herein referred to as the “novel experimenter”). The birds had not encountered the novel experimenter prior to the experiment. The trials were counterbalanced and pseudo-randomized so as not to have the same experimenter gesturing during more than two consecutive trials. Familiar and novel experimenters were used to assess whether the birds would show a preference for following the communicative gesture of a known, as opposed to unknown, experimenter as shown by von Bayern and Emery (2009).

During training, an experimenter entered the enclosure and stood at a central location behind the tray. The experimenter then placed an opaque barrier against the front of the bird’s cage so that the bird could not see the experimenter who proceeded to bait one
of the two containers. During half of the trials, the pine seed was placed in the left container and during the other half of trials, in the right container. The container was baited equally by the familiar and unfamiliar experimenter. The baited side was counterbalanced across trials within each session and pseudo-randomized so that the seed was never baited in the same container for more than two consecutive trials.

After baiting one of the containers from behind the barrier, the experimenter closed both of the containers, removed the barrier, and proceeded to show the bird the contents of each container, one at a time. To do so, the experimenter opened the lid of one of the containers for three seconds (or until the bird looked at the open container), closed the lid, and then proceeded to do the same for the other container. The location (left or right) of the container that was opened first was counterbalanced across trials. After this presentation the experimenter pushed the tray flush against the cage. The experimenter immediately left the experimental room to allow the bird to make a choice in private. Birds were allowed to make a single choice, which was defined by the bird making contact with either one of the containers. If the bird chose the rewarded container it was allowed to obtain the seed before the tray was pulled away. If the bird chose the unrewarded container, a 10-second blackout ensued (experimental room lights extinguished) and the tray was pulled away from the cage. After the bird’s choice, a 30-second inter-trial interval was instituted. Once a bird was reliably making a choice within 30 seconds or less, and this choice was correct during seven of the eight trials for 5 consecutive days, the bird was presented with the testing sessions.

**ii) Testing.** Testing was conducted over 20 days (with sessions conducted Monday through Friday each week) with one session per day consisting of eight trials: six training trials and two test trials. The procedures for the six training trials were exactly as described above. The two test trials occurred randomly between trials two through seven (trials one and eight were always training trials), but were never presented consecutively. One test trial was conducted by the familiar experimenter, and the other test trial was conducted by the novel experimenter. For each test trial, the experimenter baited one container as during training. However, once the barrier was removed the experimenter gestured to the baited container, which now had the swivel lid closed, by looking (orienting his head and eyes towards the container), pointing (extending his ipsilateral arm towards container), and touching (making contact with container using his finger tip). This gesture was held for 3 seconds or until the bird attended to the gesture by tilting its head in each direction to view the situation with each eye. If the bird correctly chose the rewarded container, defined as removing the swivel lid, it was allowed to retrieve the seed. However, if it chose the unrewarded container the tray was pulled away. Unlike the training trials, blackout periods were not presented for incorrect choices during testing to reduce the potential for associative learning.

**Phase 2**

During Phase 2 the birds were challenged to use the knowledge states of two experimenters simultaneously in order to find the reward. To accomplish this, we needed to ensure that the birds were able to reliably use the gesture; therefore, during Phase 2 all of the birds from Phase 1 were now explicitly trained to use the gesture. A new person was
used as the novel experiimenter during Phase 2.

i) Training. Birds were trained in three stages. During stage one, the training procedures were the same as those of testing during Phase 1 with the exception that once the barrier was removed the experimenter baited one of the containers in full view of the bird. The experimenter then gestured to the open and baited container for 3 seconds before the bird was allowed to make a choice. Once a bird made a correct choice during seven of the eight trials for 2 consecutive days, the bird was presented with stage two.

Stage two was identical to stage one with the exception that after the container was baited the experimenter closed both containers before gesturing to the baited container. Once a bird made a correct choice during seven of the eight trials for 2 consecutive days, the bird was presented with stage three.

During stage three the visual barrier was erected and from behind this barrier the experimenter repositioned the containers so that they were vertically aligned on the tray (at this point neither of the containers were baited; see Figure 2). This alignment prevented the birds from being able to use the experimenter’s arm position during the baiting process as a reliable cue for the position of the baited container (see below). Once the containers were aligned, the barrier was removed and the experimenter positioned a cardboard stand (28.5 cm x 45 cm) in front of the tray. This stand allowed the experimenter to bait one of the two containers without the bird seeing which of the containers was baited. After the container was baited, the experimenter moved both containers back to their lateral positions, removed the cardboard stand, and proceeded to gesture to the baited container (the location of the baited container now unknown to the bird). The tray was placed flush against the cage and the experimenter left the room permitting the bird to make a choice in private. The bird was allowed to retrieve the seed after making a correct choice, whereas an incorrect choice was followed by a 10-second blackout period. Once a bird was reliably making a choice within 30 seconds or less, and this choice was correct during seven of the eight trials for 5 consecutive days, the bird was presented with the testing sessions.

ii) Testing. Testing was conducted over 16 days (with sessions conducted Monday through Friday each week) with one session per day consisting of eight trials: six stage-three training trials and two test trials. The procedures for the six training trials were exactly as described above for stage three. The two test trials occurred randomly between trials two through seven (trials one and eight were always training trials), but were never presented consecutively. There were two testing conditions: the Uninformed Gesture condition and the Gesture Conflict condition. One test trial of each condition was administered during a daily session. Testing involved two knowledge states: the “Informed Experimenter,” during which the experimenter baited the container and therefore was informed as to the location of the reward, and the “Uninformed Experimenter,” during which the experimenter was not involved in the baiting process and therefore uninformed of the location of the reward. The familiar and novel experimenters performed both roles equally often—i.e., the familiar experimenter acted as the Informed Experimenter and the Uninformed Experimenter, and the novel experimenter also acted as the Informed Experimenter and the Uniformed Experimenter. Thus, the birds could not use the identity of the person to reliably find the food.
Figure 2. Stage 3 training during Phase 2

Notes: 1) Both containers placed centrally on the tray outside the cage. 2) A cardboard stand was introduced to occlude bird’s view of containers. 3) The containers were returned to the lateral positions. 4) The cardboard stand was removed and the containers were placed in their final locations prior to making the gesture.

During the Uninformed Gesture condition, the Informed Experimenter presented the trial as in stage three, except after removing the cardboard stand the Informed Experimenter left the experimental room and was replaced by the Uninformed Experimenter. Prior to this point, the Uninformed Experimenter was in an adjacent room. The Uninformed Experimenter gestured to a predetermined container; during half of the trials this container was the rewarded one and during half of the trials it was the unrewarded one. The gesture was held for 3 seconds after which the tray was pushed flush against the cage and the experimenter left the room, allowing the bird to make a choice in private. This condition allowed us to examine whether the birds would use the gesture information even when it was uninformative, in which case the birds should follow the gesture of the Uninformed Experimenter, or whether the birds would refrain from using the uninformative gesture and either choose randomly between the two containers or adopt a side preference.

During the Gesture Conflict condition, the Informed Experimenter prepared the trial as in stage three, except once the cardboard stand was removed the Uninformed Experimenter also entered the enclosure. As in the Uninformed Gesture condition, the Uninformed Experimenter was in an adjacent room during the baiting process. Both experimenters proceeded to gesture (simultaneously) to a predetermined container. The
Informed Experimenter gestured to the rewarded container whereas the Uninformed Experimenter gestured to the unrewarded container. The gesture was held for 3 seconds, after which the tray was pushed flush against the cage and both experimenters left the room, allowing the bird to make a choice in private. In order to choose correctly, the bird had to use some aspect of the experimenters’ knowledge or behavioral states. Conversely, choosing equally between the two experimenters would indicate that an associative process guided the birds’ choices, and that the associative learning gained from the training trials supersedes any potential preference for an experimenter based on familiarity.

For both test conditions, if a bird chose the rewarded container it was allowed to recover the seed prior to the tray being pulled away, whereas if the unrewarded container was chosen the tray was pulled away (but no blackout period was administered) and a 30-second inter-trial interval ensued.

Statistical analysis
For all analyses alpha was set at 0.05. Choice accuracy was analyzed using repeated measures ANOVAs with Experimenter and Testing Blocks as variables. Although the testing trials were conducted consecutively, for the purpose of analyses we divided them into two equal blocks to examine any learning effects. One-sample t-tests were used to compare the choice accuracy against chance (0.50).

Results

Phase 1
Eight birds progressed to testing after an average of 27 training days. Two birds failed to reach training criterion after 60 days and did not progress to testing during Phase 1.

A repeated measures ANOVA examining choice accuracy with Experimenter (Familiar and Novel) and Testing Blocks (1 and 2) did not show a main effect of Experimenter (Familiar: $M = 0.57, SE = 0.02$; Novel: $M = 0.61, SE = 0.05$; $F(1, 7) = 1.62, p = 0.244$), showing that the birds’ accuracy was similar regardless of which experimenter was performing the gesture. The birds’ accuracy was also similar across Testing Blocks (Block 1: $M = 0.57, SE = 0.05$; Block 2: $M = 0.61, SE = 0.03$; $F(1, 7) = 0.61, p = 0.460$). Although choice accuracy was low, a one-sample t-test showed that the birds were choosing the correct container significantly more than expected by chance, supporting that the birds had learned to use the gesture ($M = 0.59, SE = 0.03; t(7) = 2.59, p = 0.044$).

Phase 2
Four birds met the training criterion after an average of 43.5 days of stage three training, and therefore progressed to testing. The remaining six birds did not meet the training criterion after 85 training days, and did not progress to testing.

Uninformed Gesture condition. A repeated measures ANOVA examining choice accuracy with Experimenter (Familiar and Novel) and Testing Blocks (1 and 2) did not show a main effect of Experimenter (Familiar: $M = 0.84, SE = 0.06$; Novel: $M = 0.84, SE = 0.03$; $F(1, 3) = 0.00, p = 1.000$), showing that the birds’ accuracy was similar regardless of
which experimenter was performing as the Uninformed Experimenter. The birds’ accuracy was also not significantly different across Testing Blocks (Block 1: $M = 0.78, SE = 0.06$; Block 2: $M = 0.91, SE = 0.03; F(1, 3) = 6.00, p = 0.092$).

The nutcrackers followed the Uninformed Experimenter’s gesture at above chance levels ($M = 0.84, SE = 0.04; t(3) = 8.52, p = 0.003$). The birds’ choice accuracy during the Uninformed Gesture Condition was not significantly different from training trials (test trials: $M = 0.84, SE = 0.04$; training trials: $M = 0.93, SE = 0.01; t(3) = -1.82, p = 0.177$). Individually, three of four birds used the gesture at above chance levels (Sid: 13/16 trials, 0.81, binomial: $p = 0.02$; George: 14/16 trials, 0.88, binomial: $p = 0.004$; Tanthalas: 15/16 trials, 0.94, binomial: $p = 0.001$) and one bird missed significance by one response (Tasha: 12/16 trials, 0.75, binomial: $p = 0.08$; see Figure 3). Thus, the birds continued to rely on the experimenter’s gesture to guide their choices despite the gesture not providing reliable information as to the goal’s location.

**Figure 3.** Comparison of each bird’s choice accuracy and overall choice accuracy to chance responding during the Uninformed Gesture condition.

Notes: * $p < 0.05$; ** $p < 0.01$

**Gesture Conflict condition.** A repeated measures ANOVA examining choice accuracy with Experimenter (Familiar and Novel) and Testing Blocks (1 and 2) did not show a significant main effect of Experimenter (Familiar: $M = 0.53, SE = 0.08$; Novel: $M = 0.62, SE = 0.09; F(1, 3) = 0.32, p = 0.608$), showing that the birds’ accuracy was not significantly different depending on which experimenter was performing as the Informed Experimenter. The birds’ accuracy was also similar across Testing Blocks (Block 1: $M =$
Overall, the nutcrackers chose the Informed Experimenter’s gesture significantly more often than would be predicted by chance (\(M = 0.58, SE = 0.02; t(3) = 5.00, p = 0.015\)) and this choice accuracy was not significantly different across Testing Blocks (Block 1: \(M = 0.66, SE = 0.06; \text{Block 2: } M = 0.50, SE = 0.09; t(3) = 1.06, p = 0.377\)). During Block 1, the birds’ performance was above chance, albeit not significantly (\(t(3) = 2.61, p = 0.08\)), whereas during Block 2, the birds’ performance declined to chance levels (\(t(3) = 0.00, p = 1.000\)). Three of the four birds chose the Informed Experimenter’s gesture on the first trial (Sid, George, and Tanthalas). Individually, however, none of the nutcrackers chose the Informed Experimenter’s gesture significantly greater than chance overall (Sid, Tanthalas, and Tasha: 9/16 trials, 0.56, binomial: \(p = 0.80\); George: 10/16 trials, 0.62, binomial: \(p = 0.454\); see Figure 4). Choice accuracy remained very high on training trials (\(M = 0.93, SE = 0.01; t(3) = 32.97, p < 0.001\)).

**Discussion**

**Gesture use**

Learning to reliably use the gestures from two experimenters was clearly a difficult task for the nutcrackers as only four of the 10 birds were able to acquire the training
criterion during Phase 2. The birds showed that they could use the gesture at above chance levels from Phase 1, but many of the birds could not improve this accuracy in order to achieve the accuracy criterion needed for Phase 2 testing. This finding seems to be at odds with those recently reported by Tornick et al. (2011). The nutcrackers in this previous study learned to use gestural cues to locate a food reward quickly and effectively, whereas the majority of our birds were unable to learn to use the human-based gesture despite being explicitly trained to follow the gesture through additional training trials and the implementation of correction procedures after incorrect choices.

Several procedural differences were introduced in our study (e.g. combined gesture, multiple experimenters) compared to that of Tornick et al. (2011), which may account for some of the differences in gesture learning. The results of our study do not support the likelihood that the nutcrackers were learning to use the gesture cue through local enhancement strategies (Tornick et al., 2011; Schloegl et al., 2008). Tornick et al. suggested that this simpler strategy may have accounted for subjects’ superior performance with pointing and touch cues over eye gaze because these cues reduce the distance between the cue and the goal location. However, in our current study, both the point and touch cue of our gesture were presented together and offered no distance between the cue and the container, yet the nutcrackers struggled to learn to follow the gesture. Thus, even though we increased the physical contact with the rewarded container, arguably increasing local enhancement, the nutcrackers were not able to use this local information to improve choice behavior. Alternatively, Mulcahy and Hedge (2012) have suggested that primates (and possibly the nutcrackers in the current experiment) struggle in the object choice task because of their proximity to the choice containers, which interferes with the subject’s ability to attend to the experimenter’s cue.

It has been proposed that early developmental experience with humans may explain the successful use of human-given gestures in some species (e.g., bats: Hall et al., 2011; Canids: Udell and Wynne, 2010; Udell, Dorey, and Wynne, 2010; scrub jays: von Bayern and Emery, 2009). This hypothesis might explain the difficulty the nutcrackers had in learning to reliably use the gesture. However, this would not explain the contradictory results of Tornick et al. (2011) and our experiment, as the birds in these studies were wild-caught as adults and experienced similar laboratory environments and experimental histories.

Knowledge states

The birds that did proceed to testing after learning the gesture tended to use the gestural information from the Uninformed Experimenter during the Uninformed Gesture condition. This suggests that when the birds did learn the gesture, the use of this gesture was robust and persisted even when it did not provide reliable information as to the reward’s location. However, when the gestures from the two experimenters provided conflicting information as to the location of the rewarded container, overall the birds chose the Informed Experimenter more often than would be expected by chance, showing that they were able to distinguish between the two experimenters.

The birds could have made this discrimination by either using the experimenters’ knowledge states (i.e., informed and uninformed) or behavioral states (i.e., presence and
Human knowledge state discrimination in Nucifraga columbiana

The birds’ choices did not seem to be driven by an associative process during the Gesture Conflict condition, since the birds showed discrimination despite receiving equivalent reinforcement from both experimenters during training. Additionally, the birds’ performance was better during the first block of testing (albeit not significantly) with three of the four birds choosing correctly on the first trial, suggesting that the birds were not using a learned rule to solve the task. Using behavioral states would likely require the learning of such a rule, as by itself the behavioral state is not immediately informative unless linked to a knowledge state (e.g., presence during an event leads to an informed knowledge state) and would not explain the first block performance.

The birds’ behavior was not affected by an experimenter’s absence during baiting, as shown by their reliance on the gesture during the Uninformed Gesture condition. Therefore, it seems unlikely that the birds avoided choices to the Uninformed Experimenter during the Gesture Conflict condition simply due to this experimenter’s initial absence during baiting. Instead, the birds used some other aspect of the Informed Experimenter, either his presence during baiting, thus facilitating a greater association between that experimenter and the food, or his informed knowledge state, allowing the bird to reason that the experimenter “knew” the food’s location. At this point, we cannot clearly dissociate these two alternative explanations, yet it seems that the information provided by the Informed Experimenter was used most for the birds’ choices.

Flexible cognition?

To determine whether corvid social cognition is a flexible ability, we argue that it is important to challenge corvids in non-ecologically relevant tasks, which is a reason for choosing the object-choice task in the current study. Researchers have expressed concern over using tasks that are low in ecological validity (e.g., Tomasello, Call, and Hare, 2003). However, examining species in both ecologically relevant and non-ecologically relevant contexts can reveal the potential, and equally as important, the limits of a given species’ cognitive abilities. Furthermore, when used with multiple species, this approach can elucidate how the underlying mechanism responsible for the animal’s behavior (i.e., associative and/or cognitive processes) vary in relation to phylogeny, and thus, how cognitive abilities may have developed over evolutionary time (see also Vonk and Subiaul, 2009).

Overall, the nutcrackers chose the gesture of the Informed Experimenter despite a number of components of the task that could be considered non-ecologically relevant. Aside from explicitly testing the birds outside of a food-caching context, the experiment also required the birds to use the gestures of a distantly-related species. Kaplan (2011) documented how Australian magpies “point” referentially by aligning their body, both horizontally and vertically, toward a predator. Therefore, the important feature of avian gestural exchanges may be body orientation, an aspect not manipulated in this experiment. Considering the different forms that the gestures of primates and birds take (e.g., beak versus limb pointing), the nutcrackers may have had difficulty recognizing that a referential gesture was being presented. This would explain the difficulty the birds experienced during training with a human gesture. Additionally, combining different task components (e.g., gesture use, multiple experimenters, using knowledge states) likely would have increased
the task’s difficulty, an idea proposed by Call and Tomasello (1999), who suggested the object-choice task is difficult in that “the subject is asked to master both the logistics of the task and to display an understanding of other minds at the same time” (p. 382).

Object-choice tasks have also been argued to be a cooperative task (Hare, 2001), which may be less ecologically relevant and consequently less intuitive for a relatively non-social species like the Clark’s nutcracker. Clary and Kelly (2011) made a similar argument when describing the different cache protection strategies nutcrackers use compared to social species. After experiencing cache theft, nutcrackers were found to decrease the number of caches made over time, the opposite pattern of the more social Western scrub-jay (Emery et al., 2004), which increased caching behavior after experiencing pilferage. Thus, the authors suggested that nutcrackers view caching interactions as competitive, whereas social species view them as cooperative. If less social species view social interactions as competitive, this may explain why the majority of the nutcrackers had difficulty consistently following the cooperative communicative gesture during our current study (see also Hare and Tomasello, 2004; Herrmann and Tomasello, 2006). This could explain the above chance, yet low accuracy performance of the nutcrackers in Phase 1 and the inability of many birds to achieve maximum accuracy in Phase 2.

Convergent evolution

Specifically because the object-choice task is difficult and non-ecologically relevant for corvids (perhaps especially so for less social species), the evidence that corvids can succeed in these tasks is particularly revealing as to the extent of their cognitive capabilities. The results presented here highlight the potential flexibility and complexity underlying nutcracker cognition. If the nutcrackers are capable of making judgments about the mental states of others in this difficult context (although strictly speaking, a behavioral account cannot be excluded—see Penn and Povinelli, 2007), then it is possible, although speculative, that these birds are using these abilities proficiently in natural situations (e.g., during caching interactions) and are examples of complex cognition.

Unlike nutcrackers’ ability to interpret human gestures, using knowledge states may be an ecologically relevant skill for corvids and represents a convergence of mental abilities with primates, as the circumstances leading to knowledge acquisition are likely similar (e.g., presence during events leads to informed knowledge states; corvids: Bugnyar, 2011; primates: Hare et al., 2001) and not necessarily cache dependent. The nutcrackers may have been able to use the experimenter’s knowledge state, but were not proficient in using the gesture because the birds could not easily extract the information conveyed due to the divergent forms of avian and human (primate) gestures. Therefore, although it seems that the nutcracker’s ability to generalize gestural forms of communication is limited, their social cognitive processes may be more easily generalized to non-ecologically relevant (i.e., non-caching) contexts.

Our investigation provides an initial step in testing corvids in social cognition tasks more typically utilized with primates. This study indicates that nutcrackers may share with chimpanzees the ability to discriminate between experimenters based on whether the experimenter had previously baited a container and possibly evaluate some aspects of the knowledge states of other individuals—further suggesting that the similarities in behavior
and cognition between corvids and primates represents evidence for convergent evolution.

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