Journal of Comparative Psychology

Can Grey Parrots (Psittacus erithacus) Succeed on a "Complex" Foraging Task Failed by Nonhuman Primates (Pan troglodytes, Pongo abelii, Sapajus paella) but Solved by Wrasse Fish (Labroides dimidiatus)?

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Can Grey Parrots (*Psittacus erithacus*) Succeed on a "Complex" Foraging Task Failed by Nonhuman Primates (*Pan troglodytes, Pongo abelii, Sapajus paella*) but Solved by Wrasse Fish (*Labroides dimidiatus*)?

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Linking specific cognitive abilities of nonhuman species on a laboratory task to their evolutionary history-ecological niche can be a fruitful exercise in comparative psychology. Crucial issues, however, are the choice of task, the specific conditions of the task, and possibly the subjects' understanding or interpretation of the task. Salwiczek et al. (2012) compared cleaner wrasse fish (*Labroides dimidiatus*) to several nonhuman primate species (capuchins, *Sapajus paella*; chimpanzees, *Pan troglodytes*; orangutans, *Pongo abelii*) on a task purportedly related to the ecological demands of the fish, but not necessarily of the nonhuman primates; fish succeeded whereas almost all of the nonhuman primates that were tested failed. We replicated the two-choice paradigm of the task with three Grey parrots (*Psittacus erithacus*), whose ecology, evolutionary history, and cortical capacity are arguably more like those of nonhuman primates than fish. Greys succeeded at levels more like fish than all the nonhuman primates, suggesting possible alternative explanations for their success. Fish and nonhuman primate subjects also experienced a reversal of the initial conditions to test for generalization: Greys were similarly tested; they performed more like fish and capuchins (who now succeeded) than the apes (who continued to fail).

Keywords: Grey parrots, avian cognition, fish-primate-parrot comparisons, comparative cognition, reversal learning

Supplemental materials: http://dx.doi.org/10.1037/a0036205.supp

The cognitive capacities of nonhuman species have often been linked to their evolutionary history and ecological niche. Specifically, researchers (see Humphrey, 1976; Jolly, 1966) have long argued that primate intelligence is a correlate of complicated social and ecological systems and long lives; that is, an outcome of selection processes favoring animals that flexibly transfer skills across domains, and remember and act upon knowledge of detailed intragroup social relations and the complexities involved in finding and sharing resources over long time periods. Similar arguments have been made for the cognitive abilities of corvids and parrots (Emery, 2004; Marler, 1996; Pepperberg, 1999; Pepperberg et al., 2013). Other researchers have further refined this approach, using laboratory tests to compare whether relative ability to solve specific types of tasks relates to a species' behavior in the wild. Olson, Kamil, Balda, and Nims (1995), for example, showed that operant tests scores on spatial, but not color, memory tasks for four species of corvids were correlated with their relative caching abilities. In a similar vein, Salwiczek et al. (2012) suggested that the abilities of cleaner wrasse fish (*Labroides dimidiatus*) and nonhuman primates (*Pan troglodytes*, *Pongo abelii*, *Sapajus paella*) on a two-choice paradigm—both choices leading to a single immediate reward but only one choice leading to a subsequent second reward—were correlated with their feeding behavior patterns in the wild. In nature, the wrasse fish generally choose to clean visiting

("ephemeral") clients first, because resident reef clients will likely still be around afterward; if the wrasse choose the resident clients first, they lose out on the chance to service the additional visiting client. The various nonhuman primates species tested in the Salwiczek et al. (2012) experiment are not faced with such a choice in the wild, and in the laboratory task, wild caught adult (but not juvenile) fish outperformed all the nonhuman primates. Were the task based simply upon general cognitive capacities, one would expect the nonhuman primates, with their advanced problem-solving skills and (relatively) large cortical areas (Reader, Hager, & Laland, 2011), to have performed at least as well if not better than the fish.

An ecological approach to cognition would thus seem to have validity, but sometimes the conditions of the task, rather than the underlying cognitive mechanism(s) being studied, are what correlate to evolutionary history and ecological niche (note, e.g., Beck, 1967; Bolhuis & Macphail, 2001). In those cases, reconfiguration of the task may allow species to show comprehension of the underlying mechanism. Take, for example, ravens' success and keas' failure on a task testing understanding of exclusion (Schloegl et al., 2009)—inferring where a reward must be by excluding the places it is not. The results purportedly made sense based on ravens' propensity for, and keas' lack of, caching, but may have been less a consequence of the presence or absence of caching abilities than a matter of experimental design. With tasks more comparable to those given to noncaching nonhuman primates, Grey parrots, also a noncaching species, succeeded (Mikolasch, Kotrschal, & Schloegl, 2011; Pepperberg et al., 2013; note, however, related studies on other noncaching corvids, Mikolasch, Kotrschal, & Schloegl, 2012a; Schloegl, 2011; and the possible effects of local enhancement on both Grey parrots and jackdaws, Mikolasch, Kotrschal, & Schloegl, 2012b). Interestingly, Grey parrots' success or failure on an acoustic exclusion task depended upon whether the action of the experimenter did or did not replicate parrot-head bobbing, an activity indicative of feeding and thus the presence of food (Schloegl et al., 2012). These studies demonstrate the difficulties inherent in transferring an ecologically based task from the field to the laboratory in a way that tests the actual underlying mechanism in question, that separates the ability to deal with specific initial conditions from the ability to solve the basic task, and that does indeed allow researchers to infer a nonhuman species' cognitive capacity for understanding an underlying mechanism from its success or failure on a given task.

Such concerns led us to replicate the Salwiczek et al. (2012) task with Grey parrots. Grey parrots have demonstrated a number of cognitive capacities once thought limited to nonhuman primates (e.g., Pepperberg, 1999; Pepperberg & Shive, 2001) or young humans (Pepperberg & Carey, 2012), including a form of vocal mutual exclusivity (Pepperberg & Wilcox, 2000) and solving tasks involving numerical induction (Pepperberg, 2006; Pepperberg & Carey, 2012). Grey parrots' evolutionary history, ecological niche, and even cortical organization appear to be closer to those of nonhuman primates than wrasse cleaner fish (Iwaniuk, Dean, & Nelson, 2005; Jarvis et al., 2005; May, 2004; Pepperberg, 1999), with the exception that Grey parrots are more often prey items than are the great apes; Greys are probably more similar in that regard to the capuchins studied by Salwiczek et al. (2012). We thus set out to determine if Grey parrots would act more like fish or nonhuman primates, and what their data might suggest with re-

spect to the claims made by Salwiczek et al. (2012). Experiment 1 replicated the initial Salwiczek et al. (2012) two-choice task, and Experiment 2 replicated their reversal task.

Experiment 1

We tested whether Grey parrots could solve a task where, according to Salwiczek et al. (2012), success purportedly relates to abilities that arose from the specific evolutionary history and ecological niche of wrasse cleaner fish, but not nonhuman primates. Specifically, could these birds quickly learn to differentiate and choose the site of an immediate reward that allows for a subsequent reward over the choice of the site of an immediate reward that leads to withdrawal of another? We provided two identical pieces of food in two distinct locations; choice of one (the "resident" or "permanent" site in Salwiczek et al., 2012) allowed consumption of only that piece of food, whereas choice of the other ("ephemeral" in Salwiczek et al., 2012) allowed subsequent consumption of the second. Thus, the initial reward is the same whatever the choice; the question is whether the subject will recognize the future consequences of the choice and quickly learn to opt for the one leading to the second reward.

Method

Subjects. Three Grey parrots (*Psittacus erithacus*) were tested. One had considerable laboratory experience whereas the other two, pet birds, had little such experience. The pet birds were tested to determine if laboratory experience (e.g., reward-based questioning on cognitive tasks) would affect the outcome and also to expand the number of available subjects for study.

One Grey parrot to be studied, Griffin, was tested in a laboratory at Brandeis University. He was a subject of continuing studies on comparative cognition and interspecies communication (e.g., Pepperberg & Nakayama, 2012; Pepperberg & Wilcox, 2000; Pepperberg & Wilkes, 2004), including a two-choice task on exclusion (Pepperberg et al., 2013) and another task requiring choice of one of four colored cups, each of which had different reward consequences (Péron et al., 2013). He was 18 years old at the time of the current experiment and had been in the lab since he was 7.5 weeks old. Housing and general feeding conditions are described in Pepperberg and Wilkes (2004). He was not food or water deprived at any time. Testing occurred on a T-stand outside his cage; he could move to and from the T-stand at will; testing was thus conditional on his willingness to participate.

A different set of Greys, Pepper and Franco, lived in a suburban household (Hartsfield) with two adult humans who had previously been trainers in the Brandeis lab and who could be relied upon to follow protocols exactly. Both birds had participated in the previous study on exclusion (Pepperberg et al., 2013), but had had no other formal testing. Pepper, a female, was 17 years old and had lived with the Hartsfields since she was about 3 months old; Franco, a male, was 12 years old and had joined the household when he was 7 years old, having lived with another family previously. Pepper had received considerable training on referential communication (e.g., Pepperberg, 1981) but had not been formally tested on production or comprehension; Franco had entered the Hartsfield household with the capacity to produce some human speech, but his referential knowledge was unknown. He subse-

quently had about 5 years of referential training, but no formal testing. Again, neither bird was food nor water deprived. Trials occurred on parrot stands atop their cages.

Materials. The Brandeis apparatus consisted of two identically shaped strips of construction paper (cut from the same template), roughly 4 × 20 cm, one white, one black, placed on a felt-covered tray about 4.5 cm from each other and equidistant from the parrot's beak; rewards (halves of a cashew nut, equated for size equality) were placed about 1.5 cm from the edge of each paper strip (see Figure 1). Construction paper had been an exemplar for training the label "paper" (e.g., Pepperberg, 1999), and the tray had been used in various ways in previous experiments (e.g., Pepperberg et al., 2013; Péron et al., 2013); thus all materials were familiar. Identical pieces of construction paper and a clipboard, equally familiar to the Hartsfield birds, were used in their trials. Rewards for the Hartsfield birds were various treats such as single pieces of popcorn, walnut halves, and so forth, always chosen to be as identical in size as possible. For all three birds, the food rewards were items that were reserved for use as treats rather than as part of their staple diet. Reward type was consistent throughout for each bird, but differed among birds based on individual preference to motivate their participation. For each bird, one color was chosen consistently to represent "ephemeral" rewards. Right–left positions of the black and white pieces of paper were randomized, for an equal number of presentations on each side, and such that no position was repeated more than three consecutive times.

Procedure. In the Brandeis lab, trials began when the tray was placed on a wooden stool in front of Griffin such that the paper strips with their nut rewards were equidistant from his beak; the stool was a fixture in the laboratory and on which the tray was often placed during other studies (e.g., Pepperberg et al., 2013). The tray was slid toward Griffin until he could reach and make a choice. Following choice of the "permanent" strip, the tray was gently slid away from Griffin so that the second reward was still visible but no longer in reach; following choice of the "ephemeral" strip, the tray was left in place so that Griffin could finish consuming his first reward and then obtain the second. Griffin immediately took nuts off of the paper strips and thus needed no habituation to the apparatus.

In the Hartsfield home, the clipboard was presented manually to each bird, again ensuring that the strips were just within grasp, but equidistant from their beak. Following choice of the "permanent" strip, the clipboard was gently withdrawn so that the second reward was still visible but no longer in reach; following choice of

the "ephemeral" strip, the clipboard was left in place so that the bird could finish consuming the first reward and then obtain the second. Sometimes the bird was handed the second reward. Pepper, who has a congenital toe disfigurement that causes a slight bias in her balance, could not initially reach both paper strips equally at the distance at which the clipboard was presented; after we noticed her consistent left-side bias (after her fifth session, see below), the board was brought a few centimeters closer to her beak (but paper strips were still equidistant) so that she could choose without bias. Pepper and Franco also immediately took treats off of the paper strips; thus, again, no habituation to the apparatus was necessary.

In both situations, experimenters carefully stared at the birds' beaks during presentation of the apparatus to avoid potential cuing of side choice. Notably, earlier studies had already demonstrated that Greys do not use human cues in choice experiments unless the cues are deliberate and obvious. Specifically, parrots did not previously respond to human gaze direction when objects on a tray were closely spaced (<5 cm) and the human head was about 30 cm away from the tray (Pepperberg, 1990, 1999), which was also the case here. In the Giret et al. (2009) study in which Grey parrots did respond to human gaze, the two objects of interest were 1.6 m apart and the human face was deliberately turned in the direction of one of the objects; thus the bird could easily distinguish the line of sight, unlike the situation in the current study. Further evidence about unlikelihood of cuing comes from specific controls in a two-choice exclusion study (Pepperberg et al., 2013) that found neither visual nor olfactory cues using a similar configuration of rewards.

A second human experimenter, out of the parrot's range of sight, independently viewed the trials in the Brandeis lab and noted Griffin's choices. Observations were compared for interobserver reliability. A small subset of trials was videotaped for viewing by persons not involved in the experiment to check for "dithering" (vacillating, moving between options before making a choice; note Barlow, 1968) and possible cuing. Hartsfield videotaped trials and sent them to the Brandeis lab for independent scoring.

As was the case for the primates in the Salwiczek et al. (2012) study, we generally separated trials by about 90 sec from the time of choice. We chose that time interval rather than the longer one used for the fish because we expected the parrots to behave more like the nonhuman primates. Because Griffin could come and go at will, and often would not participate for a full 10 trials in a given session, some of his trials within sets of 10 were actually separated by up to 3 days (see below); he never had more than one session/day. The Hartsfield birds would participate for 10 trials in a given session and had no more than one session/day each. Griffin's tests occurred April and May 2013; Franco's and Pepper's tests occurred May and June 2013.

Notably, the physical set up of the task was as similar as possible but not identical to either that of the fish or the nonhuman primates. For each species, rewards were species-appropriate and identical and did not differ with respect to familiarity/novelty as would likely be the case, for example, with respect to resident versus visiting client fish; thus, as in the Salwiczek et al. (2012) study, the task did not exactly replicate a natural situation, but rather used the laboratory adaptation. Here, too, adaptations were made to be consistent with the biology of the subjects. The parrots neither had to move any considerable distance toward the rewards
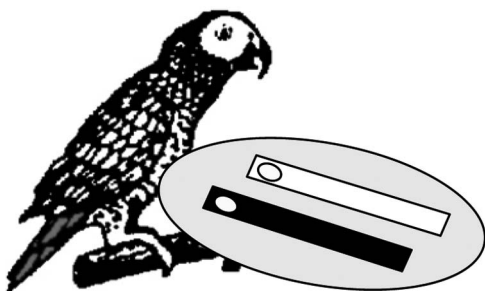

Figure 1. Schematic of parrot and tray, with black and white paper strips and treat placement.

(like the fish), nor reach into another chamber (like the primates); they simply had to bend down to pick one of the two rewards. Unlike the primates that had to grasp the rewards in their hands, but like the fish that grasped the rewards in their mouths, the parrots grasped the reward in their beaks.

Learning criterion. We based our criteria as closely as possible on those used by Salwiczek et al. (2012): Significance, as in that study, was considered to be reached when a subject made correct choices (the "ephemeral" reward) on ≥9/10 consecutive trials, ≥8/10 on two sets of consecutive trials, or at least ≥7/10 trials on three consecutive sets of trials (significance on a binomial test, $p < .05$, for chance of [1/2]). Again, because Griffin could come and go at will, and often would not participate for a full 10 trials in a given session, we lumped his trials into sets of 10, which could occur over several days, and were sometimes separated by up to 3 days. As in Salwiczek et al. (2012), the plan was that once an individual reached the first, second, or at least the third criterion, we would switch to Experiment 2 (reversal trials). As it turned out, however, two parrots succeeded so quickly that we decided to do two (Griffin) and one (Franco) additional postcriterion sessions in Experiment 1 before switching to Experiment 2 to ensure that the data were solid.

Results

Data are reported for each bird independently because Griffin's history and experimental conditions differed from those of Franco and Pepper, and Franco and Pepper differ with respect to sex and Pepper's slight disability. Data are summarized in Figure 2. The three parrots' data are, however, pooled for statistical comparison with the fish and nonhuman primates. No significant difference existed between parrots and the adult wrasse fish (Mann–Whitney U test, $U = 12.5$, $p = .38$), but significant differences existed between the parrots and the nonhuman primates (capuchins:

Mann–Whitney U test, $U = 24$, $p = .012$; apes: Mann–Whitney U test, $U = 23.5$, $p = .012$).

Griffin. Griffin's "ephemeral" choice was set as white. He succeeded (choosing white on nine of 10 trials) in his third set of 10 trials. He never dithered, but made a choice immediately upon presentation and then watched what occurred next. Toward the end of the experiment, he sometimes started to stretch toward the correct choice even before the tray was in place. He never protested when the tray was withdrawn (e.g., never said "Want nut"; see Péron et al., 2013) but might request a nut a few seconds before a subsequent trial was to occur. His score was 6/10 on the first set of trials, 7/10 on the second set, and 9/10 on the third set. Thus his data compared favorably with those of wrasse fish and his success rate exceeded that of all primates tested. We did, however, continue to test him for two more sets of trials to ensure that his data were solid; he scored 7/10 on the fourth set and 8/10 on the fifth set. He completed his trials over the course of 11 days. Separation of some sets of trials by long periods did not seem to affect his responses.

Franco. Franco's "ephemeral" choice was also set as white. He completed 10 trials in each session, with sessions separated by one day, completing his course of trials in two days. He initially (on the first set of 10 trials) seemed to have a left side bias, but after choosing black twice in a row and receiving only a single reward, figured out the system and no longer responded with respect to side. He never dithered but, like Griffin, chose immediately and watched what happened as a consequence. He succeeded (choosing white on nine of 10 trials) on his second set of 10 trials. He, too, was given another session to see if his data were solid; he again achieved 9/10 correct. Thus his data also compared favorably with those of the fish and his success rate exceeded that of the nonhuman primates tested.

Pepper. To control for a Grey parrot's possible affinity for black versus white, Pepper's "ephemeral" choice was set as black. Her trials initially were disappointing. She scored 6/10, 5/10, 6/10, 4/10, and 5/10 on her first five sessions, each session being 10 trials/day for consecutive 5 days. On observing her videos, however, it became clear that she had an almost 100% bias to choose whatever was on her left side; furthermore, her left-sided choice appeared to be a consequence of her inability to balance properly on her disabled foot at the distance at which the clipboard was being presented to her. When the tray was, on her sixth session, 4 days later, presented several centimeters closer, she immediately achieved 9/10 correct, reaching criterion on her first physically possible session. Her understanding of the task thus likely preceded her physical ability to complete it, and she should probably be considered comparable to the other two Greys. She also never dithered. One could, of course, argue that her experience in the earlier trials assisted her in attaining a near-perfect score the first time the apparatus was at an appropriate distance, but success even on the sixth set puts her closer to the fish than to most of the nonhuman primates.

Discussion

The key conclusion is that three Grey parrots performed at levels comparable to the wrasse fish, at levels significantly better than the (lumped) apes tested in the Salwiczek et al. (2012) studies, and at a slightly better level than the chimpanzees (small sample
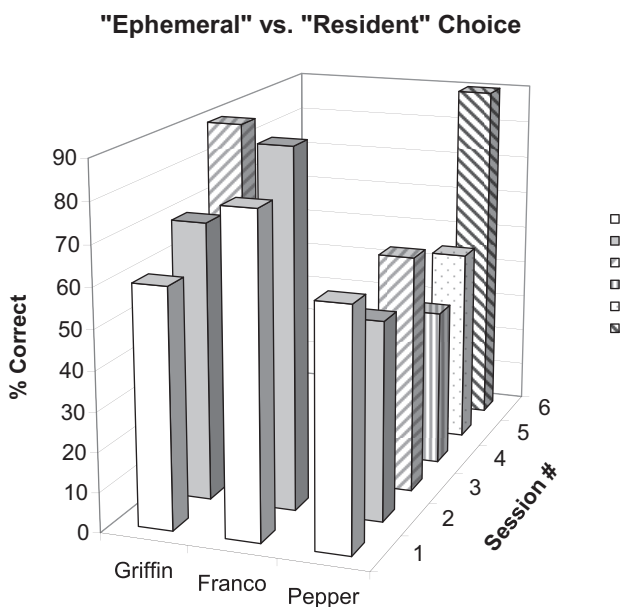

"Ephemeral" vs. "Resident" Choice

Figure 2. Results for Experiment 1, showing percentage of correct ("ephemeral") choices for each bird for each session.

numbers precluded statistical comparison). All of the capuchins and orangutans and two of the four chimpanzees failed to reach criterion in fewer than 10 sessions; only after those 100 trials, with significant changes in the experimental design, and with a number of subsequent sessions, did most of them learn the task. Experience in a laboratory setting did not give Griffin any advantage over Pepper and Franco, nor did separating trials by several days within the 10-set sessions seem to affect Griffin's results.

Given that Grey parrot feeding ecology, evolutionary niche, and relative cortical size is more similar to that of the nonhuman primates than the fish, we question whether the task actually does relate solely to the conditions of the wrasse foraging context. According to Salwiczek et al. (2012), the task specifically involves the ability to take not only immediate but also future consequences into consideration; that is, understanding that although either choice provides the same immediate reward, one choice leads to a second, subsequent reward. Thus the task can be framed as a conditional discrimination, with the results of the first choice leading to either the positive act of gaining access to the second visible reward or the negative act of seeing that second visible reward being moved out of reach. (According to Thomas, 1996, the task might also be seen as a conjunction of conditional tasks, but the complexity is roughly equivalent.) Apes can indeed learn conditional discriminations, although Nissen, Blum, and Blum (1948) argued that a minimum of hundreds of trials are needed (but note Premack, 1976); such data then lead to the question of why nonhuman primates would be so much slower than fish and parrots to learn the given task. Possible reasons for these findings will be saved for the General Discussion.

Experiment 2

As in the Salwiczek et al. (2012) study, once our subjects succeeded on the primary task, we tested how they would fare on a reversal, in which the former "ephemeral" choice became the "resident" choice and vice versa. If solving the primary task had engendered a general understanding of the conditions, then reversal should proceed relatively quickly. Although Grey parrots have not previously been faced with reversal learning tasks, their cortical capacities are presumed similar to those of nonhuman primates (e.g., Iwaniuk et al., 2005), who generally perform rather well in such studies (e.g., Rumbaugh & Pate, 1984). Given the poor showing of the nonhuman primates in the Salwiczek et al. (2012) study, despite previous research demonstrating correlations between brain (cortical) size and reversal learning (Deaner, Van Schaik, & Johnson, 2006), we were not sure what to predict for the parrots. If reversal learning reflects general cognitive capacity, however, we expected that the birds would have little trouble with reversals after solving the initial task.

Method

Subjects, materials, procedures, learning criteria. Other than the reversal of the conditions for reward (black and white now indicating the reverse of what they indicated in the first experiment for each parrot), the subjects, materials, procedures, and learning criteria were generally the same as in Experiment 1. The only difference was that on the first reversal session, Griffin's possible choices were not controlled randomly with respect to side; we kept the white paper on the right for 80% of trials (only for the third and fifth trials was white on the left). We wished to determine if lack of side changes would hinder or improve his reversal learning compared to that of Franco and Pepper, whose placements were randomized.

Again, Hartsfield sessions were videotaped and sent to the Brandeis lab for independent analysis, and a sample of Griffin's choices were taped as well. See online Supplement materials, for example, Video S1 and Video S2.

Results

Data are again reported independently for each bird. A summary of the results is in Figure 3. The parrots' data are, however, pooled together for statistical tests. Overall, the parrots' data looked more like the best of the wrasse fish and capuchins than the great apes. The parrots' data were, however, significantly different from all of the species studied by Salwiczek et al. (2012) according to statistical tests (parrots and wrasse fish, Mann–Whitney U test, $U = 18$, $p = .024$; parrots and capuchins, Mann–Whitney U test, $U = 24$, $p = .012$; parrots and apes, Mann–Whitney U test, $U = 15$, $p = .036$). As in Salwiczek et al. (2012), who include the first 10 trials (when errors were expected) in the number needed to achieve reversal (R. Bshary, personal communication, 2014), we similarly included the first 10 for our birds when analyzing and comparing the data.

Griffin. As before, Griffin often would not participate in 10 consecutive trials for a given session. We again clumped trials into groups of 10, even if they were separated by several days. As expected, Griffin failed on his first reversal session, scoring 3/10. He consistently chose the right side, where white was placed 80% of the time, until the final trial when he finally chose left and black (i.e., he chose the right side consecutively the first 9 trials; thus he
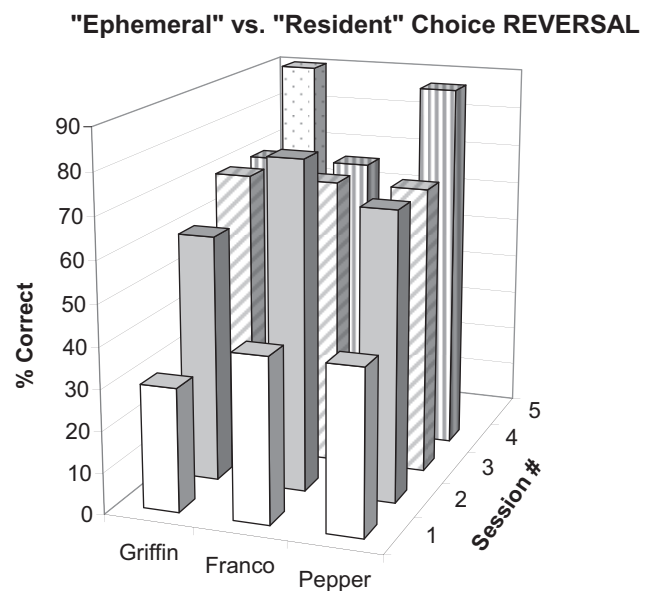

"Ephemeral" vs. "Resident" Choice REVERSAL

Figure 3. Results for Experiment 2, showing percentage of correct ("ephemeral") choices for each bird for each session after the color of the paper denoting the correct choice was switched.

was correct on Trials 3 and 5, where black was on the right, but possibly only because of his consistent choice of right). Three days later, on his next session, when placement of the white and black choices were now counterbalanced with respect to side, he scored 6/10. On the next three sessions, held over the course of a week, he scored 7/10 on Sessions 3 and 4, and 9/10 on his fifth and final session. He did not dither in his first reversal session, but after several trials stopped reaching for the white side before the tray was fully in place. He tried to change his choice once in his last session, when, on one trial, he chose the nut residing on the side that provided a single reward, quickly dropped the nut, and began to reach for the other side. We did not let him make the change and counted the behavior as an error; it was his only error in that set of trials. Overall, he was thus comparable to the wrasse fish and the capuchins, the best of which needed six sessions and outperformed the apes.

Franco. As before, Franco completed 10 trials/session on every session. Like Griffin, he failed, as expected, on his first reversal session, scoring 4/10 correct. He did however seem to learn more quickly than Griffin, scoring 8/10 and 7/10 on each of the next two sessions, and, after a 4-day hiatus, 7/10 on his last session. He dithered only in the last few trials of his first session, as if realizing that his previous strategy was no longer leading to the expected outcome, but not yet being sure what to do. He outperformed the wrasse fish and all nonhuman primates, needing only four sessions to achieve criterion.

Pepper. Pepper, like Franco, again completed 10 trials/session for each of her sessions. As did the other two birds, she failed—as expected—on her first reversal session, scoring, like Franco, 4/10 correct. On the next day, she scored 7/10; 3 days later she scored 7/10 and 9 days later scored 9/10; she therefore needed only four sessions to succeed. She never dithered in any of her choices. The last session occurred 9 days after the previous session because of scheduling conflicts at the Hartsfield home. Pepper, like the other two Greys, also outperformed the fish and the nonhuman primates.

Discussion

The key point is that the Grey parrots again performed better than most of the nonhuman primates and even somewhat better than the fish. Lack of control for right-left placement in Griffin's first set of trials did not seem to help and may have hindered his learning, as he needed one more set of sessions than Pepper and Franco. Overall, the parrots' propensity to understand how to respond when the contingencies were reversed was exceptionally good. The data suggest that not only ecological niche and evolutionary history might be involved in success, but also that some degree of generalized cognitive processing is required, as reversal is not common in nature. Still, it is not clear why parrots responded in a manner somewhat more like fish and capuchins than great apes, succeeding in a surprisingly few number of trials. The Grey parrots were not at ceiling, so the task obviously presented some level of challenge, but they all quickly understood the "win-stay/lose-shift" nature of the task.

General Discussion

Why, given that fish solve the initial task faster than nonhuman primates and acquire reversals faster than most nonhuman pri-mates, do Grey parrots, that are far more similar to nonhuman primates than to fish, act—in general—more like fish? The answer cannot lie solely in that Experiment 1 recreates the evolutionary history and ecology of wrasse fish more closely than that of nonhuman primates; then parrots would perform more like non-human primates. Grey parrots, like nonhuman primates, have more K-selected species traits than wrasse fish: longer lives (over 30 years in captivity), longer maturation periods, larger body size, fewer young. Like the apes, they forage over wide distances (~60 km/day; May, 2004), likely have some form of dominance hierarchy if their behavior in lab is representative (I. M. Pepperberg, personal observation), and likely store and update ecological and social information over their long lifetimes. Even their suscepti-bility to predation would be similar at least to the capuchins. Moreover, foods used by Greys that might be considered "ephem-eral"—for example, seasonal fruits (May, 2004)—are also likely in the nonhuman primates' diet. Nor can the answer lie simply in having a large and more complexly organized brain; then the nonhuman primates should have succeeded at levels similar to parrots and to have outperformed the fish. We first discuss some explanations suggested by Salwiczek et al. (2012) to elucidate the fish performance, then examine additional possibilities.

In terms of reinforcement contingencies, Salwiczek et al. (2012) suggested that removal of the second reward in Experiment 1 upon an incorrect choice was a stronger punishment for fish than pri-mates—that is, removal acted as both a social and foraging pun-ishment for the fish, given their ecology, and that the stronger punishment encouraged learning. Such an argument is unlikely to hold for parrots, who would likely view the conditions as do the nonhuman primates, not as the fish.

In terms of cognitive mechanisms, Salwiczek et al. (2012) discussed possible backward induction, that is, starting from the endpoint and figuring out which steps lead to the desired outcome. No data exist to suggest that Grey parrots are particularly good at backward induction, though a recent study (Auersperg, Kacelnik, & von Bayern, 2013) suggested the possibility of such behavior in another parrot, Goffin's cockatoos (*Cacatua goffini*): The cocka-toos solve a five-step lock box problem and did equally well when lock order was altered, showing they understood the interrelated nature of the various locks. Grey parrots have not been tested on such tasks, but evidence exists for their general inductive behavior: One Grey, Alex (not part of this study), induced the ordinality of his number labels (Pepperberg, 2006) and inferred the cardinal value of novel number labels from their ordinal positions on the numeral list, a behavior not yet demonstrated in chimpanzees (Pepperberg & Carey, 2012). Nonhuman primates innovate while solving multistep problems (e.g., Tomasello & Call, 1997), but not at the same level as the cockatoos, where no training or observa-tional learning existed for at least one bird (Auersperg et al., 2013). The need for backward induction for parrot or nonhuman primate foraging is unclear. Possibly, evolution of complicated foraging patterns, such as termite fishing or nettle processing (e.g., see Byrne, 2009), would require such backward induction; if so, that might explain why two chimpanzees did succeed in the initial Salwiczek et al. (2012) task. The authors suggest, however, that the immediate rewards present in the task seemed, on the whole, to block the apes' option to used backward induction.

Another suggestion by Salwiczek et al. (2012) for the fishes' successes and nonhuman primates' failure in Experiment 1 has less

to do with foraging strategies per se than with possible species-specific physical traits and their influence on success or failure. Fish and parrots (for the most part) eat by putting food directly in their mouths/beaks, acquiring and consuming items sequentially, as in this task. Nonhuman primates, in contrast, can gather food independently and simultaneously with both hands; possibly the presence of two identical food pieces that could not be simultaneously acquired triggered their reported level of frustration/stress (Salwiczek et al., 2012). For many tasks given nonhuman subjects in which choices must be made, symbols represent positive or negative choices in the absence of the hedonic presence of the reward, or the actual reward differences are obvious (e.g., one vs. two pieces of food). Here, the hedonic presence of two identical food rewards may have diverted attention from the distinguishing features indicating whether subsequent rewards were possible; an inability to recognize and then act on the appropriate contingencies may have contributed to stress. Stress may negatively affect learning speed (Yerkes & Dodson, 1908; note Ciompi, 1991). Negative effect of stress on reversal learning in nonhuman primates has specifically been examined (Judge, Evans, Schroepfer & Gross, 2011; see Premack, 1976), and might be responsible for the relatively poor showing of the apes in Experiment 2; the capuchins, which succeeded fairly well on reversal, were not described as frustrated. As stated above, parrots and fish, used to sequential eating, may have been affected less, thus succeeding more easily. Notably, chimpanzees (Boysen & Berntson, 1995; Boysen, Berntson, Hannan, & Cacioppo, 1996; Boysen, Mukobi, & Berntson, 1999) but not orangutans (Shumaker et al., 2001) are distracted by hedonic values of food in a reversed reinforcement contingency task (where they receive the smaller reward if they choose the larger). Neither Greys nor capuchins have been tested on such tasks, but neither evinced frustration in the current experiments.

The Experiment 1 task, though based on wrasse fish feeding ecology, could be interpreted as a conditional discrimination, if a somewhat unconventional one, which nonhuman primates and Grey parrots would both seem likely to solve; Salwiczek et al. (2012) suggested it requires considerable processing power. Other tasks, reviewed in Salwiczek et al. (2012), that also seem to require considerable processing power, appear to be selected for in so-called "lower" organisms (e.g., detour behavior in spiders, Jackson & Wilcox, 1993). Salwiczek et al. (2012) thus appeared to argue that traditional predictions of processing power—overall brain/body ratios (see Overinton, Morand-Ferron, Boogert, & Lefebvre, 2009)—are less important than the possibility that particular brain areas may be enhanced in a species for exploitation of a particular niche (e.g., hippocampus size and caching, Basil, Kamil, Balda, & Fite, 1996). How that idea explains the Grey parrots' success is unclear, unless one argues that Greys are exceptionally good generalists, proficient in solving many cognitive tasks (Pepperberg, 1999; Pepperberg & Carey, 2012; Pepperberg et al., 2013). Given that reversals in nature are not common, Experiment 2 likely does test processing power rather than ecological relevance; that is, once the Experiment 1 task has been solved, and the underlying principle understood, subjects in Experiment 2 should recognize the reversal and revise their behavior fairly quickly, even if they were slow in Experiment 1.

Interestingly, criteria for success in the Salwiczek et al. (2012) task is not simply finding the solution, but rather finding it quickly. Nissen et al. (1948) argued that apes need a minimum of several hundred trials to manage conditional discrimination tasks, which corroborates the finding of Salwiczek et al. (2012). Rumbaugh and Pate (1984), in contrast, found reversal trial levels in apes that would qualify as comparable to the wrasse using the Salwiczek et al. (2012) criteria; however, Rumbaugh and Pate's tasks were not reversals of conditional discriminations, but of simple associations (A+/B- to A-/B+). Wrasse fish and Grey parrots, notably, solve both the original task and the reversal more quickly than the apes in the Salwiczek et al. (2012) study, and capuchins also succeed on the reversals fairly quickly. Might the ecology of a species create a need to select for speed as well as accuracy in information processing: for the parrots and possibly the capuchins, the issue of being small prey animals, which must constantly monitor for attack; for the species of wrasse studied, the need to act quickly when a new potential client appears? Interestingly, Salwiczek et al. (2012) note that in preliminary studies, a different cleaner fish, the *L. bicolor*, which actively pursue ephemeral clients, does poorly on both the task and the reversal, possibly because they do not have to distinguish and choose quickly between types of clients.

Alternatively, whereas wrasse may succeed in Experiment 1 because the task correlated with their feeding strategies, such a correlation may have had nothing to do with the behavior of Grey parrots and nonhuman primates; that is, different mechanisms may be involved for fish, parrots, and nonhuman primates. Possibly, parrots saw the task as using symbolic representation (e.g., "white" equals two, "black" equals one). If so, Griffin, with his extensive training and testing in referential communication, and Pepper and Franco, by extension, with their similar training albeit lack of testing, might have had an advantage over some of the nonhuman primates with respect to the number of trials needed to acquire the original association; again, success was not based on eventual accuracy, where nonhuman primates might have outperformed the parrots, but rather on speed of acquisition. Although one orangutan in the Salwiczek et al. (2012) study did have some experience in human sign language, no orangutan succeeded on the initial task; whether it was the sign language-trained ape or the one with extensive computer experience that succeeded on the reversal task is not stated. Interestingly, Premack (1976) reported that Sarah, his chimpanzee that was extensively trained in symbolic representation, succeeded in a conditional discrimination task and reversal after only about 35 trials. Such reasoning does not, however, explain why two chimpanzees did moderately well on the initial task and capuchins succeeded so well on the reversal task.

In sum, we cannot argue that the particular foraging ecology and evolutionary history of a particular species are solely what prepare it for success on this task; we can, however, support Salwiczek et al. (2012) by suggesting that such aspects may be sufficient but not necessary for success. Notably, the different results for the two closely related cleaner fish species with differing feeding strategies speak to this point. Grey parrots, who have more in common with nonhuman primates than fish, succeed at levels more like the fish and, on the original task (Experiment 1), outperform the capuchins and even the great apes (faster on an absolute basis than even the two chimpanzees that succeeded; Salwiczek et al., 2012). Other contingencies in Grey parrot ecology and evolutionary history might be involved in their success. Possibly specific conditions of the task, that is, the simplified choice options and use of their beaks to obtain reward immediately upon choice, contributed to their success. Also, in addition to selection related to complicated

social and ecological systems and long lives, maybe being small prey items further select for a need to evaluate and act on information more quickly than apes, who have fewer predators and may be equally resourceful but have the luxury of taking longer to acquire a fruitful behavior pattern. In addition, small animals (fish, parrots, capuchins) generally have higher metabolisms than larger ones and would pay a higher energetic price for making a wrong choice. Possibly, a constellation of characteristics together enable the Grey parrots' success. We suggest that care must be taken before conclusions are drawn about how success or failure on a specific task relate to a single aspect of a species' ecology and evolutionary niche.

References

Auersperg, A. M. I., Kacelnik, A., & von Bayern, A. M. P. (2013). Explorative learning and functional inferences on a five-step means-end problem in Goffin's cockatoos (*Cacatua goffini*). *PLoS One, 8,* e68979. doi:10.1371/journal.pone.0068979

Barlow, G. W. (1968). Dither: A way to reduce undesirable fright behavior in ethological studies, *Zeitschrift für Tierpsychologie, 25,* 315–318.

Basil, J. A., Kamil, A. C., Balda, R. P., & Fite, K. V. (1996). Differences in hippocampal volume among food storing corvids. *Brain, Behavior, & Evolution, 47,* 156–164. doi:10.1159/000113235

Beck, B. B. (1967). A study of problem solving by gibbons. *Behaviour, 28,* 95–109. doi:10.1163/156853967X00190

Bolhuis, J. J., & Macphail, E. M. (2001). A critique of the neuroecology of learning and memory. *Trends in Cognitive Science, 5,* 426–433. doi:10.1016/S1364-6613(00)01753-8

Boysen, S. T., & Berntson, G. G. (1995). Responses to quantity: Perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes, 21,* 82–86. doi:10.1037/0097-7403.21.1.82

Boysen, S. T., Berntson, G. G., Hannan, M. B., & Cacioppo, J. T. (1996). Quantity-based interference and symbolic representations in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes, 22,* 76–86. doi:10.1037/0097-7403.22.1.76

Boysen, S. T., Mukobi, K. L., & Berntson, G. G. (1999). Overcoming response bias using symbolic representations of number by chimpanzees (*Pan troglodytes*). *Animal Learning & Behavior, 27,* 229–235. doi:10.3758/BF03199679

Byrne, R. W. (2009). Animal imitation. *Current Biology, 19,* R111–R114. doi:10.1016/j.cub.2008.11.027

Ciompi, L. (1991). Affects as central organising and integrating factors. A new psychosocial/ biological model of the psyche. *The British Journal of Psychiatry, 159,* 97–105. doi:10.1192/bjp.159.1.97

Deaner, R. O., Van Schaik, C. P., & Johnson, V. (2006). Do some taxa have better domain general cognition than others? A meta-analysis of nonhuman primate studies. *Evolutionary Psychology, 4,* 149–196.

Emery, N. J. (2004). Are corvids 'feathered apes'? Cognitive evolution in crows, jays, rooks and jackdaws. In S. Watanabe (Ed.), *Comparative analysis of minds* (pp. 181–213). Tokyo, Japan: Keio University Press.

Giret, N., Miklósi, A., & Kreutzer, M. (2009). Use of experimenter-given cues by African grey parrots (*Psittacus erithacus*). *Animal Cognition, 12,* 1–10. doi:10.1007/s10071-008-0163-2

Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 303–317). Cambridge, UK: Cambridge University Press.

Iwaniuk, A. N., Dean, K. M., & Nelson, J. E. (2005). Interspecific allometry of the brain and brain regions in parrots (*Psittaciformes*): Comparisons with other birds and primates. *Brain, Behavior and Evolution, 65,* 40–59. doi:10.1159/000081110

Jackson, R. R., & Wilcox, R. S. (1993). Observations in nature of detouring behaviour by *Portia fimbriata,* a web-invading aggressive mimic jump-ing spider from Queensland. *Journal of Zoology, London, 230,* 135–139. doi:10.1111/j.1469-7998.1993.tb02677.x

Jarvis, E. D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., Medina, L., . . . Butler, A. B. (2005). Avian brains and a new understanding of vertebrate evolution. *Nature Reviews Neuroscience, 6,* 151–159. doi:10.1038/nrn1606

Jolly, A. (1966). Lemur social behaviour and primate intelligence. *Science, 153,* 501–506. doi:10.1126/science.153.3735.501

Judge, P. G., Evans, D. W., Schroepfer, K. K., & Gross, A. C. (2011). Perseveration on a reversal-learning task correlates with rates of self-directed behavior in nonhuman primates. *Behavioural Brain Research, 222,* 57–65. doi:10.1016/j.bbr.2011.03.016

Marler, P. (1996). Social cognition: Are primates smarter than birds? In V. Nolan, Jr. & E. Ketterson (Eds.), *Current ornithology* (vol. 13, pp. 1–32). New York, NY: Plenum Press. doi:10.1007/978-1-4615-5881-1_1

May, D. (2004). *The vocal repertoire of Grey parrots* (Psittacus erithacus) *living in the Congo Basin*. PhD thesis, University of Arizona.

Mikolasch, S., Kotrschal, K., & Schloegl, C. (2011). African grey parrots (*Psittacus erithacus*) use inference by exclusion to find hidden food. *Biology Letters, 7,* 875–877. doi:10.1098/rsbl.2011.0500

Mikolasch, S., Kotrschal, K., & Schloegl, C. (2012a). Is caching the key to exclusion in corvids? The case of carrion crows (*Corvus corone corone*). *Animal Cognition, 15,* 73–82. doi:10.1007/s10071-011-0434-1

Mikolasch, S., Kotrschal, K., & Schloegl, C. (2012b). The influence of local enhancement on choice performances in African Grey parrots (*Psittacus erithacus*) and jackdaws (*Corvus monedula*). *Journal of Comparative Psychology, 126,* 399–406. doi:10.1037/a0028209

Nissen, H. W., Blum, J. S., & Blum, R. A. (1948). Analysis of matching behavior in chimpanzees. *Journal of Comparative and Physiological Psychology, 41,* 62–74. doi:10.1037/h0061040

Olson, D. J., Kamil, A. C., Balda, R. P., & Nims, P. J. (1995). Performance of four-seed caching corvid species in operant tests of nonspatial and spatial memory. *Journal of Comparative Psychology, 109,* 173–181. doi:10.1037/0735-7036.109.2.173

Overinton, S. E., Morand-Ferron, J., Boogert, N. J., & Lefebvre, L. (2009). Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Animal Behaviour, 78,* 1001–1010. doi:10.1016/j.anbehav.2009.06.033

Pepperberg, I. M. (1981). Functional vocalizations by an African Grey parrot (*Psittacus erithacus*). *Zeitschrift für Tierpsychologie, 55,* 139–160. doi:10.1111/j.1439-0310.1981.tb01265.x

Pepperberg, I. M. (1990). Cognition in an African grey parrot (*Psittacus erithacus*): Further evidence for comprehension of categories and labels. *Journal of Comparative Psychology, 104,* 41–52. doi:10.1037/0735-7036.104.1.41

Pepperberg, I. M. (1999). *The Alex studies*. Cambridge, MA: Harvard University Press.

Pepperberg, I. M. (2006). Ordinality and inferential abilities of a Grey Parrot (*Psittacus erithacus*). *Journal of Comparative Psychology, 120,* 205–216. doi:10.1037/0735-7036.120.3.205

Pepperberg, I. M., & Carey, S. (2012). Grey Parrot number acquisition: The inference of cardinal value from ordinal position on the numeral list. *Cognition, 125,* 219–232. doi:10.1016/j.cognition.2012.07.003

Pepperberg, I. M., Koepke, A., Livingston, P., Girard, M., & Hartsfield, L. A. (2013). Reasoning by inference: Further studies on exclusion in Grey parrots (*Psittacus erithacus*). *Journal of Comparative Psychology, 127,* 272–281. doi:10.1037/a0031641

Pepperberg, I. M., & Nakayama, K. (2012, November). *Recognition of amodal and modally completed shapes by a Grey Parrot* (Psittacus erithacus). Oral presentation, Psychonomic Society Annual Meeting, Minneapolis, MN.

Pepperberg, I. M., & Shive, H. A. (2001). Simultaneous development of vocal and physical object combinations by a Grey Parrot (*Psittacus*

erithacus): Bottle caps, lids, and labels. *Journal of Comparative Psychology, 115,* 376–384. doi:10.1037/0735-7036.115.4.376

Pepperberg, I. M., & Wilcox, S. E. (2000). Evidence for a form of mutual exclusivity during label acquisition by Grey parrots (*Psittacus erithacus*)? *Journal of Comparative Psychology, 114,* 219–231. doi:10.1037/0735-7036.114.3.219

Pepperberg, I. M., & Wilkes, S. R. (2004). Lack of referential vocal learning from LCD video by Grey parrots (*Psittacus erithacus*). *Interaction Studies: Social Behaviour and Communication in Biological and Artificial Systems, 5,* 75–97. doi:10.1075/is.5.1.05pep

Péron, F., Johns, M., Sapowicz, S., Bovet, D., & Pepperberg, I. M. (2013). A study of reciprocity in Grey parrots (*Psittacus erithacus*). *Animal Cognition, 16,* 197–210. doi:10.1007/s10071-012-0564-0

Premack, D. (1976). *Intelligence in ape and man*. Hillsdale, NJ: Erlbaum Associates.

Reader, S. M., Hager, Y., & Laland, K. N. (2011). The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society, London B, 366,* 1017–1027. doi:10.1098/rstb.2010.0342

Rumbaugh, D. M., & Pate, J. L. (1984). Primates' learning by levels. In G. Greenberg & E. Tobach (Eds.), *Behavioral evolution and integrative levels* (pp. 221–240). Hillsdate, NJ: Erlbaum.

Salwiczek, L. H., Prétôt, L., Demarta, L., Proctor, D., Essler, J., Pinto, A. I., Wismer, S., Stoinski, T., Brosnan, S. F., & Bshary, R. (2012). Adult cleaner wrasse outperform capuchin monkeys, chimpanzees, and orang-utans in a complex foraging task derived from cleaner-client reef fish cooperation. *PLoS One, 7,* e49068. doi:10.1371/journal.pone.0049068

Schloegl, C. (2011). What you see is what you get–Reloaded: can jackdaws (Corvus monedula) find hidden food through exclusion? *Journal of Comparative Psychology, 125,* 162–174. doi:10.1037/a0023045

Schloegl, C., Dierks, A., Gajdon, G. K., Huber, L., Kotrschal, K., & Bugnyar, T. (2009). What you see is what you get? Exclusion performances in ravens and keas. *PLoS One, 4,* e6368. doi:10.1371/journal.pone.0006368

Schloegl, C., Schmidt, J., Boeckle, M., Weiss, B. M., & Kotrschal, K. (2012). Grey parrots use inferential reasoning based on acoustic cues alone. *Proceedings of the Royal Society B, 279,* 4135–4142. doi:10.1098/rspb.2012.1292

Shumaker, R. W., Palkovich, A. M., Beck, B. B., Guagnano, G. A., & Morowitz, H. (2001). Spontaneous use of magnitude discrimination and ordination by the orangutan (*Pongo pygmaeus*). *Journal of Comparative Psychology, 115,* 385–391. doi:10.1037/0735-7036.115.4.385

Thomas, R. K. (1996). Investigating cognitive abilities in animals: Unrealized potential. *Cognitive Brain Research, 3,* 157–166. doi:10.1016/0926-6410(96)00003-1

Tomasello, M., & Call, J. (1997). *Primate cognition*. New York, NY: Oxford University Press.

Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit formation. *Journal of Comparative Neurology & Psychology, 18,* 459–482. doi:10.1002/cne.920180503