Current Biology

Report

New Caledonian Crows Behave Optimistically after Using Tools

Highlights

- Wild New Caledonian crows are optimistic after tool use, indicating positive affect
- Crows appear to enjoy, or be intrinsically motivated by, tool use
- Effort cannot explain this; crows are less optimistic after an effortful task
- Intrinsic enjoyment may shape the evolution of complex actions like tool use

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In Brief

McCoy et al. find that wild New Caledonian crows are optimistic after tool use. Optimism is an indicator of positive mood; in other words, crows appear to enjoy using tools. This suggests that intrinsic motivation (enjoyment) is a fundamental proximate cause in the evolution of tool use and other complex behaviors.

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New Caledonian Crows Behave Optimistically after Using Tools

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SUMMARY

Are complex, species-specific behaviors in animals reinforced by material reward alone or do they also induce positive emotions? Many adaptive human behaviors are intrinsically motivated: they not only improve our material outcomes, but improve our affect as well [1–8]. Work to date on animal optimism, as an indicator of positive affect, has generally focused on how animals react to change in their circumstances, such as when their environment is enriched [9–14] or they are manipulated by humans [15–23], rather than whether complex actions improve emotional state. Here, we show that wild New Caledonian crows are optimistic after tool use, a complex, species-specific behavior. We further demonstrate that this finding cannot be explained by the crows needing to put more effort into gaining food. Our findings therefore raise the possibility that intrinsic motivation (enjoyment) may be a fundamental proximate cause in the evolution of tool use and other complex behaviors.

RESULTS AND DISCUSSION

People feel happy when performing certain behaviors. For example, humans improve their affective state by giving altruistically [1], playing sports [2–5], and striving for concrete goals [6–8]. Do animals also feel happy after carrying out certain actions? Despite strong arguments for evolutionary continuity between humans and animals [24–26], research in this area has often been critiqued for being overly anthropomorphic. However, researchers now have the tools to objectively measure the affective state of an animal. The cognitive bias test is based on the finding that animals, like humans, will treat an identical ambiguous stimulus differently depending on their affective state: individuals in a positive state will interpret an ambiguous stimulus as more positive than individuals in a negative state [9, 14, 19, 27–32]. That is, individuals in a positive state act optimistically, and those in a negative state act pessimistically. The terms optimism and pessimism in this context are short-hand labels for responses made to ambiguous cues from which, respectively, positively and negatively valenced affective states (“dimensional” emotions and/or moods) [32] can be inferred without implying that these are consciously experienced.

To date, studies that have used the cognitive bias test have generally focused on changing the circumstances of an animal by manipulating their environment or the animal themselves. Environmental enrichment is associated with optimism: rats [9–14], starlings [12, 13], and pigs [14] housed with enrichment are optimistic, and those housed without environmental enrichment are pessimistic. Similarly, unpredictable or aversive environmental experiences cause pessimism, such as in rats subject to chaotic housing conditions [28]. Manipulation of animals themselves also changes their cognitive state. Pessimism emerges when peccaries are trapped [15], piglets are handled roughly [16], calves are painfully disbudded [17] or separated from their mothers [18], honeybees [19] and flies are shaken [20], rats are given experience of chronic social defeats [21], chicks are socially isolated [22], and ravens observe a peer in a negative state [33]. Positive manipulation also appears to cause optimism, as exemplified by work showing that tickled rats are more optimistic than peers handled normally [23].

The effect of performing complex, species-specific behavior on animal emotion has received comparatively little attention, despite suggestive evidence that it improves mood in humans [1–5, 8, 34, 35]. To date, only two studies have directly examined whether animals show more positive affect after carrying out complex species-specific behaviors [36, 37]. These studies have found mixed results. When given experience searching for food randomly placed within a maze arena, dogs actually behaved more pessimistically [37]. However, this may have been an artifact of the study design; dogs were interrupted during their search of the maze, which could have promoted a negative affective state (because they were prevented from eating the rest of the food). In another study, when dogs practiced nosework (searching for food using olfactory cues, a species-specific behavior), they became more optimistic, and dogs who practiced heelwork (walking behind their owner) did not change their affective state [36]. Although these results raise the possibility that complex, species-specific behaviors can improve animal affective states, the nosework group were trained to search for food, and the heelwork group were trained not to move freely. This difference may have led the nosework dogs to approach the ambiguous stimulus faster rather than because of a change in their affective state.

Figure 1. Spatial Cognitive Bias Test

(A) Experimental aviary setup.

(B–D) Box is placed in one of three locations on the table, along with a wooden marker that does not change location. Birds learned that the box on one side (B) had a large reward (3 meat cubes); the box on the other side (C) had a small reward (¼ of a meat cube). The box in the middle (D) was ambiguous and used to test optimism.

(E–G) Crows (E) fly or walk to table, (F) remove box lid, and (G) retrieve meat from inside.

At present, therefore, it is not yet clear whether complex, species-specific behaviors lead to positive affective states in animals, as they do in humans. One way to test this hypothesis is to focus on tool-using animals. Previous research suggests that tool-using animals like chimpanzees and New Caledonian crows are intrinsically motivated to use tools [38, 39], but no study has yet directly tested this hypothesis by examining whether tool use leads to a positive affective state. Here, we tested whether tool use—a complex, species-specific behavior in New Caledonian crows—instills positive affect, as indicated through approach speed toward an ambiguous stimulus.

We presented a spatial cognitive bias test [9, 28–31] to fifteen wild New Caledonian crows captured and temporarily housed in an aviary before re-release. These crows had no previous experience in the laboratory before capture. We trained these crows that a box placed on one side of a table contained a large reward and the same box, when placed on the opposite side of the table, contained only a small reward (Figure 1). They had 30 s maximum to approach and open the box. The crows approached the large reward box quickly, anticipating the large reward (mean latency: 3.79 s; SEM = 0.18 s) but moved slowly or not at all to the small reward (mean latency: 25.20 s; SEM = 0.79 s). To measure affective state, we recorded crows' approach times to an ambiguous stimulus: the same box placed halfway in between where the large and small reward boxes had been (Figure 2D). Quicker approaches imply a relatively more positive affective state, and slower approaches imply a relatively more negative affective state.

We compared latency to approach the ambiguous box after crows encountered one of four conditions, each of which resulted in the same reward amount (Figure 2). We compared (1) tool use, using a stick tool to extract one piece of food from an apparatus (Figure 2A), with (2) no tool, extracting one piece of food with their beak from the front of the same apparatus (Figure 2B). This tested whether crows were more optimistic after using a tool rather than simply after gaining food. It also controlled for the presence of the apparatus itself. However, differences between these two conditions might also be due to the fact that tool use took more effort than no tool use (the crows were slower to extract meat with a tool than with just their beaks). We therefore also compared (1) effort, traveling to four separate locations in the aviary to get four ¼ pieces of food (Figure 2C), with (2) easy, taking four ¼ pieces of food directly from the table (Figure 2D). This tested whether approach speed changed when crows had to put more effort into getting food. If tool use led to increased positive affect, we predicted that birds would be more optimistic after using a tool, rather than just their beak, to gain food, but not when putting more effort into gaining food compared to receiving it easily.

We found that recent experiences significantly impact New Caledonian crow affective state, as measured through latency to approach an ambiguous stimulus. We found that the statistical model containing the factors condition (consisting of four levels: tool use, no tool, effort, and easy) and trial order as main effects (with no interaction) was the best fit for the data (repeated-measures Bayesian ANOVA: BF = 17.89; see Table S1 for details on all models fitted). To assess the relative importance of condition and trial order, we compared the fit of the condition-only and trial-order-only models to the condition + trial order model. For this comparison, where we remove a single factor, a BF = 1 indicates no difference in model fit, BF > 3 indicates a substantial improvement, and BF < 0.33 indicates a substantial decrease in model fit. Removing trial order from the model led to no substantial difference in the model's fit to the data (BF = 0.96). This implies

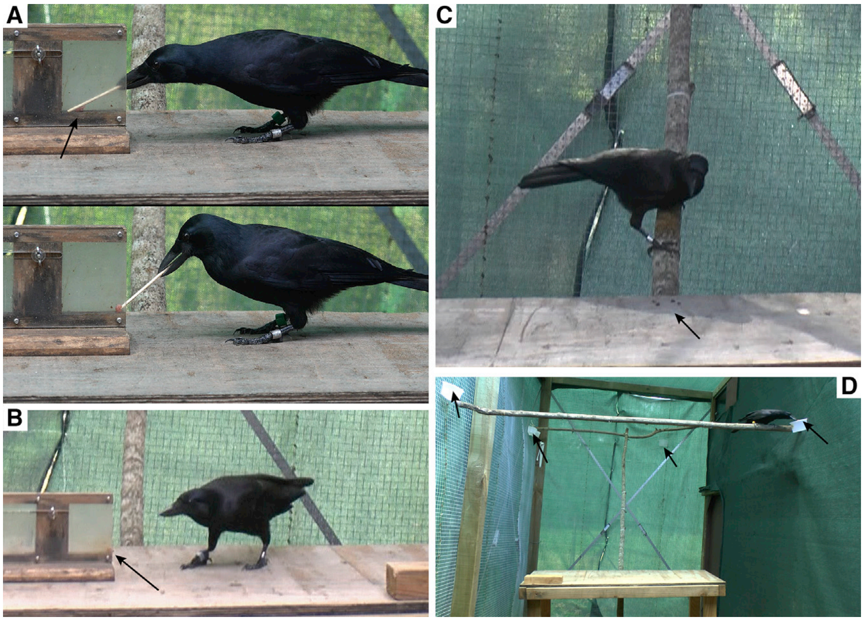

Figure 2. Test Conditions

Optimism was tested after four different experiences (arrows indicate food location).

(A) "Tool" condition, in which birds used a tool to extract one block of meat from a wood and plexiglass apparatus.

(B) "No tool" condition, in which birds used their beak to extract one block of meat from within reach in the same apparatus.

(C) "Easy" condition, in which birds retrieved four ¼ block pieces of meat from one location.

(D) "Effort" condition, in which birds traveled to four locations in the aviary to retrieve four ¼ block pieces of meat, placed within sight on the rims of the white dishes.

that the birds did not change their attitude toward the ambiguous stimuli because of repeated exposure (each bird saw the ambiguous stimulus four times total). In contrast, removing condition from the model led to a substantial reduction in the fit of the model (BF = 0.045). As such, condition appears to be the main factor driving approach latency to the ambiguous stimulus in crows (see STAR Methods and Table S1).

Crows differed in their approach speed between our paired conditions. Crows approached the ambiguous stimulus significantly faster in tool use condition trials, where they used a tool to extract a meat block from an apparatus, than in no tool trials, where they extracted a meat block from the same apparatus using only their beak (Figure 3; Bayesian paired t test: BF = 28.70). Crows were also significantly faster after the easy condition, where they retrieved four meat ¼ blocks from a single location on the table, compared to the effort condition, where they traveled to four locations in the aviary to retrieve four meat ¼ blocks (Figure 4; Bayesian paired t test: BF = 7.62). These results show that New Caledonian crows approached ambiguous stimuli faster after (1) using a tool to gain food rather than just their beak and (2) gaining freely available food from one location rather than collecting it from multiple locations.

Our study shows that tool use leads to New Caledonian crows approaching an ambiguous stimulus faster, as do "windfalls," where an animal gains freely accessible food. In contrast, crows approached an ambiguous stimulus more slowly after extracting food from an apparatus with their beak and after flying to collect food across their aviary. Reward processing includes multiple dissociable components (liking, wanting, and learning) [40, 41]. Measuring approach speed in this spatial paradigm specifically reveals the "wanting" component, from which we can infer affective "liking" [9, 28–31]. Quicker approaches suggest that the crows had liked a prior experience more and so were in a more positive affective state, and slower approaches suggest crows had not liked a prior experience as much, leading them to be in a relatively more negative affective state. These results therefore suggest that tool use, rather than effort or activity in general, led to increased positive affective state in our study species. This demonstrates that complex, species-specific activities can influence the positive affect of an animal above and beyond the affect generated by being active or gaining a material reward. Interestingly, we also found that crows acted more optimistically after collecting food from an easily accessible location. This finding supports anecdotes reporting that animals receiving windfalls of food often show an elevated affective state [42].

Our results suggest that intrinsic motivation (internal feelings and predispositions) influences the evolution of tool use. That is, we propose that mechanisms of intrinsic reward evolved to support tool use and have shaped its evolution and development over time. Past work has claimed that both chimpanzees and New Caledonian crows are intrinsically motivated to use tools [38, 39]. This claim is based on two observations, namely (1) the higher rates of unrewarded object-related behavior by individuals of tool-using species compared to related non-tool-using species [38, 39] and (2) the lack of correlation between the presence of tool behavior and ecological resources requiring tool use [38]. This research suggests that, at a behavioral level, reinforcement of tool use is not only derived from external motivators, such as reward, but also from intrinsic, psychological motivators as well. Our results suggest that, at least in New Caledonian crows, positive affect is a key mechanism in creating intrinsic motivation for this species to use tools. That is, because positive affect increases in New Caledonian crows after tool use, above and beyond that created by simply gaining food (i.e., crows gain intrinsic enjoyment from this behavior), they are then intrinsically motivated to perform more of this behavior in the future. Given the evolutionary distance between New Caledonian crows and humans, this therefore suggests that intrinsic motivation is a fundamental proximate cause in the evolution of tool use. However, further work is needed to confirm this. First, in terms of the results here, due to the need to run four conditions, we used only one ambiguous stimulus (middle), rather than three (near-small, middle, and near-large), as has been used in many other studies (e.g., [9, 12, 17, 19, 43]). The five-point methodology is preferred, because it validates that animals view the ambiguous stimuli

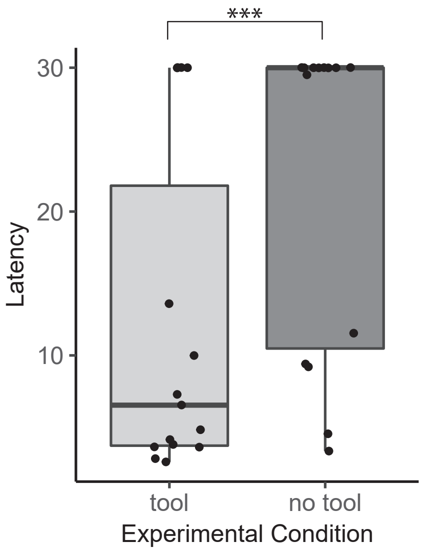

Figure 3. Crows Are Optimistic after Using a Tool to Extract Food

Crows (n = 15) were exposed to one of two experiences just prior to the cognitive bias test (presentation of an ambiguous stimulus): tool refers to using a tool to extract meat from an apparatus and no tool refers to retrieving meat from within reach within the same apparatus (no tool required). Crows were significantly more optimistic (faster to the ambiguous stimulus) in the tool condition versus no tool (Bayesian paired t test; BF = 28.70). In each boxplot, the horizontal bar is the median, the box ranges from the 25th to 75th percentile, and the whiskers show the range of data points. See Data S1 for all latency times and Figure S1 for mean latencies (±SEM) for all trials.

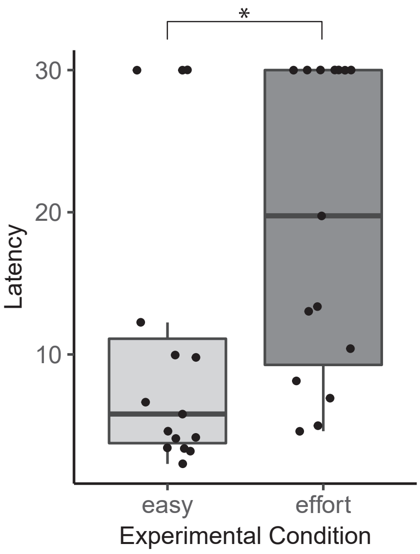

Figure 4. Crows Are More Optimistic after Receiving an Easily Accessible Meat Reward Rather Than a Reward Requiring Effort

Crows (n = 15) were exposed to one of two experiences just prior to the cognitive bias test (presentation of an ambiguous stimulus): easy refers to retrieving meat from the table and effort refers to flying around the aviary to retrieve meat from four locations. Crows were significantly more optimistic (faster to the ambiguous stimulus) in the easy condition versus effort (Bayesian paired t test; BF = 7.62). In each boxplot, the horizontal bar is the median, the box ranges from the 25th to 75th percentile, and the whiskers show the range of data points. See Data S1 for all latency times and Figure S1 for mean latencies (±SEM) for all trials.

as relating to the training stimuli (the response curve along a distribution of expected rewards has five, rather than three, points). Logistical considerations led us to use the three-point methodology (STAR Methods). Future testing with this rigorous five-point methodology would therefore be useful to validate these results. Second, although humans are intrinsically motivated to perform many behaviors [44–48], no study has yet examined whether humans are intrinsically motivated to use tools.

Previous work on animals has shown that circumstantial change impacts affective state, such as through environmental enrichment or aversive manipulation. The results reported here show that tool use—a complex, species-specific activity performed by the animals themselves—can improve the affective state of animals. Our research therefore suggests that ‘‘occupational’’ enrichment [49], which encourages animals to exhibit complex, species-specific behaviors, could significantly improve captive animal welfare by increasing the positive affect of animals. Cognitive bias protocols have already been used to test simple welfare interventions, from pharmacological treatment for separation anxiety in dogs [50] to environmental enrichment in a wide variety of animals [12–14, 51, 52]. This work could be extended to test the impact of not only species-specific behaviors but also active, goal-directed enrichment on captive animals with repetitive or negative behavior, akin to problem-solving therapy for humans suffering from depression [53]. Our research, therefore, opens up a promising line of enquiry for future research: the effect of executing complex, species-specific behaviors and goal-directed actions on animal welfare.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- LEAD CONTACT AND MATERIALS AVAILABILITY
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS
- DATA AND CODE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2019.06.080.

A video abstract is available at https://doi.org/10.1016/j.cub.2019.06.080#mmc5.

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AUTHOR CONTRIBUTIONS

Conceptualization, D.E.M. and A.H.T.; Methodology, D.E.M., M.S., and A.H.T.; Formal Analysis, P.N. and A.H.T.; Investigation, D.E.M., M.S., and R.H.; Resources and Funding Acquisition, A.H.T. and R.D.G.; Writing – Original Draft, D.E.M. and A.H.T.; Writing – Review & Editing, D.E.M., M.S., P.N., R.H., R.D.G., and A.H.T.; Visualization, D.E.M.; Supervision, A.H.T. and R.D.G.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and Algorithms		
R	The R Foundation	https://www.r-project.org/

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Dakota E. McCoy (dakotamccoy@g.harvard.edu). All latency times recorded in this study are available in the Supporting Information file Data S1, and all code used for statistical analyses are available in the Supporting Information file Methods S1.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Fifteen wild New Caledonian crows (*Corvus moneduloides*; n = 7 in 2016, n = 8 in 2018) were captured and housed in an aviary on Grand Terre, New Caledonia for temporary behavioral research purposes before being released back into the wild. Birds were housed in family groups with substantial natural enrichment (logs, bushes, seashells, etc). The birds' daily diet consisted of meat, dog food, eggs, and fresh fruit, with water available *ad libitum*. They were not food-deprived, and birds were maintained at or above their weights at capture. After the research studies were completed, birds were released at their capture sites. Previously, researchers observed that crows housed temporarily in captivity (similarly to the present study) successfully reintegrated into the wild after release [54]. Experiments were conducted in a solo "experimental" aviary, where birds had ample room to fly about but were screened from viewing other birds. The test took place on a table at the front of the experimental aviary, and multiple high perches allowed the birds to remain at the back of the aviary (or elsewhere) when they did not want to participate. One bird, "Jupiter," exhibited signs of nervousness in other experiments and thus was tested in his home compartment. Our work was carried out under the approval of the University of Auckland Animal Ethics Committee (reference no. 001823).

METHOD DETAILS

Birds were trained on a protocol [28, 30, 31] designed to test whether they demonstrate optimistic behavior. The bird's affective state, whether positive or negative, motivates their latency toward an ambiguous stimulus after different experiences. We used a spatial protocol [9, 29] where birds were trained to know that a small tub with a lid contained a large reward if it was placed on one side of the table and a small reward if it was placed on the other side (Figure 1). The large reward was 3 cubes of meat, while the small reward was ¼ of a cube of meat. We provided a small reward as contrast, rather than no reward or an aversive stimulus, because these are wild birds who are fed *ad libitum* and participate in our tasks on a voluntary basis. We placed a marker on the table to assist with location memory (since some birds use landmarks for location memory in the wild [55, 56]. We counterbalanced this protocol across birds (half of the birds learned that left was the large reward and right the small reward, and half learned the opposite).

In all phases, birds were given a maximum of 30 s to open the box. During training birds were (i) habituated to the apparatus (ii) given 10 trials of the large reward side and 10 trials of the small reward side (pseudorandomized in blocks of five of the same trial) and (iii) given blocks of 8 trials where trial type (large reward and small reward) was pseudorandomized across trials. We repeated (iii) until birds achieved criterion for two blocks in a row (defined as approaching faster in the final three large reward pseudorandom trials of each block than the final three small reward pseudorandom trials [29]), after which time the bird proceeded to the test phase.

At test, we examined how optimistically a bird behaved after having a particular experience, where relative optimism is indexed by quicker approaches to the ambiguous box and relative pessimism is indexed by slower approaches. For each test block, the bird received 4 refresher trials (two large reward and two small reward presented pseudorandomly), followed by three trials of one of four experience types ("Conditions" in Figure 2), followed by a test trial where the "ambiguous" stimulus was presented (the same box placed in the middle of the table, Figure 1D).

Often in studies using the ambiguous-stimulus framework, researchers present three ambiguous stimuli: near-positive, near-negative, and middle. This rigorous five-point methodology ensures that the animals perceive the ambiguous stimuli as relating to the stimuli from training, because it generates a response curve with five, rather than three, points along a distribution of expected rewards. Here, we used a three-point methodology with only one ambiguous stimulus (middle) because of the logistical constraints of our experimental design, which required testing wild-caught, temporarily captive birds on four conditions (Tool, No Tool, Effort, and Easy; see details below). The crows' average approach time in the refresher trials of the large reward baseline was 3.79 s (SEM = 0.18) and in the refresher trials of the small reward baseline was 25.20 s (SEM = 0.79), demonstrating that the crows continued to distinguish between the large reward and small reward locations before the test trials. The average approach time for ambiguous trials was 16.19 s (SEM 1.52), which falls almost exactly halfway in between the small and large reward baselines (Figure S1). This suggests that the crows perceived the ambiguous stimulus as relating to the small and large stimuli, but this does need to be validated with a 5-point methodology.

Each experience trial yielded one large total block of meat (equivalent in size to two normal blocks). In the "Tool" condition, the birds conducted standard tool use with a block apparatus to retrieve a single large block of meat. We placed the tool on the table during the test phase when the experience started, and we did not remove it until after the test was concluded. In the "No Tool" condition, crows used their beaks to retrieve a single large block of meat from the tool-use apparatus, without needing nor receiving a tool. In the "Easy" condition, birds retrieved four ¼-block pieces of meat from the table directly, while in the "Effort" condition, birds traveled around the aviary to four locations to retrieve four ¼-block pieces of meat placed within sight. It was necessary to split the meat in this way so it could be distributed around the aviary for the Effort condition. We paired the conditions as Tool – No Tool and Effort – Easy for analysis because the birds received one large block of meat in the former two conditions and four ¼-block pieces of meat in the latter two conditions; although the total reward size was the same, the presentation was not strictly comparable. Additionally, the same tool apparatus was present in both the Tool and No Tool conditions but was not in the other two conditions. Finally, these comparisons directly tested the hypotheses we were interested in. We pseudorandomized the order of these experiences for each bird, but ensured that Tool and No Tool were always adjacent, while Effort and Easy were always adjacent. Prior to the experience trials (at least one half-day before) birds were given one sample trial of each experience to ensure that they were able to complete the experience task.

During test trials, after the "ambiguous" stimulus was presented, we interrupted the bird the moment their beak touched the lid so that they would retreat from the table and thus could not thoroughly explore the box. This ensured the bird did not learn whether the ambiguous stimulus contained food or not across test trials. To ensure that the Test Phase did not confuse the bird's understanding of the protocol, we repeated the stage (iii) of training between each test trial; that is, after their first test the birds had to achieve criterion for two blocks in a row before they continued with their second test, and so on. We repeated the test protocol four times; that is, each bird saw the ambiguous stimulus four times total, separated by criterion protocols in between each test protocol. We hypothesized that they would not develop negative associations with the ambiguous trial and a lack of reward given that they would only receive four total trials; a similar methodology with chimpanzees found no change in response to ambiguous stimuli over five trials [57]. We included Trial Order as a predictor in our statistical modeling to control for the potential effect of seeing the ambiguous stimulus four times, but it had no explanatory power in the model (see Quantification and Statistical Analysis). This shows that the ambiguous stimulus did not become aversive to the crows over the 4 test trials due to these trials being interrupted.

We measured optimism by scoring the trial in which birds were given an ambiguous stimulus after an experience. We recorded the time it took the bird to approach the stimulus (with a maximum option of 30 s). To ensure consistency of our timing method, we controlled the crows' approach trajectory by placing a small piece of meat between their upper back perch (a preferred resting location) and the table (the test location). Therefore, birds would consistently fly to this baited portion, pause, and then either go down to the table or not. Using Solomon Coder, we timed the bird's delay between (i) landing on the perch to retrieve the bait and (ii) descending to the table to open the box and retrieve the reward inside. The moment the bird landed on the table was used as the "end" time, because that is the point at which the bird had decided to investigate the stimulus. If birds chose not to descend to the table after 30 s had elapsed, we assigned a latency time of 30 s [58]. All latency results during test trials are reported in Data S1. To measure interobserver reliability, a second coder unaware of test condition coded 20% of the videos and we calculated intraclass correlation coefficient (ICC, oneway, consistency) using the function icc in R package irr [59]); there was high agreement (ICC = 0.954, 95% CI = [0.921,0.974]).

QUANTIFICATION AND STATISTICAL ANALYSIS

All analyses were carried out using the "Bayes Factor" [60] package in R using the lmBF and ttestBF functions (see Methods S1 for code). We tested n = 15 crows, each on the four experimental conditions. In order to analyze whether the crows differed in their approach latency across the four different experimental conditions, we constructed several Bayesian repeated-measures ANOVA models with differing fixed effects (Condition-Only, Trial Order-Only, Condition+Trial Order, and Condition*Trial Order). All models also contained Participant as a random effect to account for the within-subjects nature of the experiment design. Each of the models were compared to a simple model which just included Participant as a random factor, and we selected the model which best explained the data (i.e., had the highest Bayes Factor (BF)). In Bayesian analysis, BF > 3 indicate substantial/significant support for the alternative hypothesis whereas BF < 0.333 indicate substantial/significant support for the null hypothesis [61]. Each model was constructed with objective priors of prior width r = 1 for fixed effects and r = 0.5 for random effects. Having established that the Condition+Order model was the best fit for the data (with no interaction; see Table S1 for all models fitted), we directly compared the fit of the Condition-Only model and the Order-Only model to the Condition+Order model. If one factor of these factors was having a larger effect on the crow's approach latency, removing that factor from the model should reduce the fit of the model to the data more substantially.

To explore our pairwise comparisons, we used Bayesian paired t tests to test between the crows' approach latencies in the Tool-No Tool conditions and the Easy-Effort conditions. For both t tests, a negative half-Cauchy distribution with r = 0.707 and an effect size centered on 0 was used an objective prior distribution. t test results can be found in Figures 3 and 4 and in the Results and Discussion.

DATA AND CODE AVAILABILITY

All data and code is available as Supporting Information. Data S1 is an excel spreadsheet of crow latency times, and Methods S1 is an annotated HTML document of the code used to run statistical analyses.