Kea, *Nestor notabilis*, produce dynamic relationships between objects in a second-order tool use task

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Creating sophisticated object relationships to achieve a goal has been considered to be one of the defining features of intelligent species (van Schaik et al. 1999; Reader & Laland 2002). The more complicated object relationships created by animals often involve the use of tools as a means to reach a desired item. Tool use was defined by Beck (1980, page 10) as ‘the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool’. Tool use competences can be categorized in terms of levels of complexity: Fragaszy et al. (2004a) described the relationships produced when a subject acts on an object and an action on a second object occurs by default as zero-order relations, as, for example, pulling a piece of cloth with a food reward resting upon it (Auersperg et al. 2009). Acting with object A in relation to object B (for example pounding a nut with a stone) is classified as a first-order relation. Finally, acting with object A in relation to object B following a placement of object B in relation to a third object C would be a second-order relationship. Wimpenny et al. (2009, page 2) also described ‘second-order tool use’ as ‘using one tool on another object to access it or modify it for the use as a tool’.

Secondary tool use has rarely been observed in nonhuman animals other than primates. There is, however, increasing evidence of elaborate consideration of object relationships in two corvid species. The New Caledonian crow, *Corvus moneduloides*, which routinely uses tools within its natural environment, has recently shown secondary tool manipulation in the laboratory in the form of meta-tool use (Taylor et al. 2007; Wimpenny et al. 2009). There is also evidence that these birds have some causal understanding about the effects that objects may have on one another (von Bayern et al. 2009; Taylor et al. 2009). Recently, there have also been impressive demonstrations of first- and second-order tool use in a nontool-using corvid, the rook, *Corvus frugilegus* (Bird & Emery 2009). To our knowledge, there has been no investigation of secondary tool use in any bird species other than corvids.

There is currently debate on whether tool use stimulated the evolution of intelligence in tool-using species or whether it is more likely to be a by-product of general-purpose intelligence (Bird & Emery 2009). It has also been argued that most birds are routinely establishing more complicated object relationships during nest building than during tool use and that tool use might merely have evolved to replace morphological adaptations (Hansell & Ruxton 2008; Kacelnik 2009). It would therefore be interesting to test complex levels of tool use in species that lack sophisticated nest construction.

The kea is a parrot, resident in the mountain region of New Zealand. This species is not known to build complex nest cups but...
to breed in simple burrows (Jackson 1963). As a consequence of a scarcity of predators and a seasonality of food availability, kea are highly neophobic. Similar to other destructive foragers, such as the New World capuchin monkeys, *Cebus libidinosus*, which use tools in the laboratory as well as in the wild (Fragaszy et al. 2004a, b), kea display an extremely strong urge to manipulate and dismember novel objects (Diamond & Bond 1999, 2004). This ‘haptic neophilia’ may expose the animals to functional object characteristics that are unavailable to more neophobic species. It is likely that such behaviour enhances innovativeness and facilitates learning.

Observations of kea in the laboratory have shown remarkable learning capacities about their physical environment (Werdenich & Huber 2006). They also show intense combinatorial activity during object play, in particular when inserting objects into hollow spaces (G. K. Gajdon, M. Lichtenegger & L. Huber, unpublished data). Since combinatorial actions may allow access to otherwise inaccessible resources and require an ability to coordinate objects relative to each other, they can be considered as precursors of tool use in nontool-using species (Fragaszy et al. 2004a).

To examine the kea’s sensitivity to different orders of object relationships, we devised an experimental set-up in which subjects had to establish increasingly complicated levels of spatial relationships between objects by themselves. Our subjects had previously participated in an ‘inserting as means paradox’ (G. K. Gajdon et al., unpublished data), in which they had learned to drop the smaller of two differently sized cubes into an opaque tube. The opaque tube was firmly fixed in a vertically slanted position and contained a reward, which was pasted onto the middle of the tube floor using cream cheese. When an object was inserted into the upper end of the tube it would knock against the reward and cause it to fall out at the lower end of the tube. For the following experiment, we used a similar design but the tubes were lying on the ground without fixation.

In the first ‘tube-lifting’ paradigm, the reward was lying freely on the tube floor and the tube had to be lifted to one end to release it. The object relations produced here are zero-order relations (Fragaszy et al. 2004a). The following ‘spaghetti-breaking’ paradigm investigated whether the animals could combine their tool size expertise with their new experience from the tube-lifting paradigm to master a second-order tool use task. Here, the reward was pinned inside the tube using uncooked spaghetti and could only be attained by inserting the appropriate object (a ball) and thereafter lifting the tube at the side in which the object was inserted to break the spaghetti and release the reward. The object relationships produced in this case are second-order relationships (act with an object A (tube) in relation to an object B (ball) following a placement of object B in relation to a third object C (reward); see Fragaszy et al. 2004a).

**SUBJECTS**

Ten kea participated in the experiment: three juvenile females (Coco, Plume and Rudy), two juvenile males (Gino and Tammy) and five adult males (Mismo, Luke, Frowin, Knut and Kermit). They were all bred in captivity. The juveniles as well as the adult Kermit were hand raised. All subjects were kept together in a large outdoor aviary (15 × 10 m and 4 m high) at the Konrad Lorenz Institute for Ethology in Vienna, Austria. The aviary was equipped with breeding cabins, wooden shelters, foraging tables, a pond, a climbing wall as well as heavy branches that were suspended from the ceiling. Additional environmental enrichment was provided daily (leafy branches, halved coconuts, cardboard boxes and other objects). The floor of the aviary was covered with sand.

Food was spread every day at 1200 and at 1700 hours and consisted of a mixture of seeds, vitamin supplement, various fruits and vegetables as well as a daily protein source (boiled eggs, cottage cheese with yogurt, corn or minced beef). The amount of food was balanced weekly to keep the birds at their free feeding weights. Fresh drinking water was available ad libitum. The subjects were visually isolated from their groupmates, by an opaque sliding wall, within an experimental compartment (5 × 10 m) during testing. All subjects that participated in the described experiments were housed in accordance with the Austrian Federal Act on the Protection of Animals. Furthermore, as all kea studies were strictly noninvasive and based purely on behavioural tests, they were classified as nonanimal experiments in accordance with the Austrian Animal Experiments Act.

**TUBE LIFTING**

**Task 1: Tube Lifting**

**Methods**

A consolidation phase was designed to control whether the animals were motivated by the reward rather then by a more general interest in playing with the apparatus. Two transparent Plexiglas tubes (outer diameter: 4 cm; inner diameter ca. 3.8 cm; length 22 cm) were arranged next to one another in line at a distance of about 20–25 cm (see Task 1 in Table 1, Fig. 1). One, both or neither of the tubes was baited with a peanut. The birds were not allowed to observe the baiting of the tubes. A trial started as soon as the subject entered the experimental compartment and ended as soon as the food was retrieved. The reward could be attained by lifting the baited tube and, hence, causing the peanut to fall out at the other end. Subjects had to walk approximately 1.5 m towards the apparatus. The birds received five sessions of four trials (left tube baited, right tube baited, both tubes baited and no tube baited) in random order.

**Results**

All data investigated followed a normal distribution (Kolmogorov–Smirnov test). No subject made more than two incorrect

<table>
<thead>
<tr>
<th>Condition</th>
<th>Correct sequence of actions</th>
<th>Trial no./session</th>
<th>Session no.</th>
<th>No. of stoppers</th>
<th>Reward pierced</th>
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<tr>
<td>SB</td>
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<td>8</td>
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<td>0</td>
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<td>2</td>
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<td>2</td>
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<tr>
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<td>Choose correct tube; insert at correct end; lift same end; lift opposite end</td>
<td>0.25</td>
<td>2</td>
<td>15</td>
<td>3</td>
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| Tube lifting (TL), side-restricted tube-lifting (TLA–D), spaghetti-breaking (SB) and side-restricted spaghetti-breaking tasks (SBA–C); P<sub>c</sub> — hypothesized mean; trial no./session — number of trials per session; session no. — number of sessions; no. of stoppers — the total number of stoppers on both of the two tubes; reward pierced — the state of the reward (pierced by a piece of spaghetti or free inside the tube).
choices within the 10 trials in which just one of the two tubes was baited (binomial test: \( P = 0.044 \)). All subjects except Frowin stopped lifting tubes in the ‘none’ condition after five sessions.

Task 2: Side-restricted Tube Lifting

Methods

Two transparent tubes were arranged as in Task 1. The tubes were fitted with wooden stoppers at one or both ends. The four possible test conditions A–D are detailed in Fig. 1 and Table 1. In all conditions except D and C, in which one of the tubes had stoppers at both ends, the peanut was available by lifting a reward-baited tube at the end sealed with a stopper so the food would roll out at the open end. Subjects received 15 sessions of eight trials. Each session comprised each condition twice, and, thus, each subject received a total of 30 trials of each condition. The side of the correct tube in conditions A, B and C, as well as the side of the baited tube in condition D, was pseudorandomized. The arrangement of the stoppers (pointing left or right) was randomized. A trial was scored as correct if the subject directly lifted the side of the tube that would lead it to a reward. Condition D was only considered as correct if the subjects did not lift either tube within the experimental time. A trial lasted 2 min or until the reward was recovered.

Results

In the first trial (independent of condition), eight of 10 subjects chose to lift a tube end without a stopper and therefore incorrectly (binomial test: \( P = 0.044 \)).

The subjects developed three different techniques during testing. Most subjects lifted the tube directly at the stopper end. Gino grabbed the middle of the tube, lifted it up in a horizontal position and finally poured its content out at one side. Frowin grabbed the lower rim of the open end of a baited tube and lifted it very high above his head until the food fell out towards his bill. His technique became consistent after his fifth session.

In condition D the kea always tried to open the baited tube with the unavailable reward with their beak and never stopped doing so, as was expected because of their extreme curiosity and their unrestrained play instinct (Diamond & Bond 1999).

We divided the remaining results into three session blocks (sessions 1–5; sessions 6–10; sessions 11–15). Within each session block, a subject participated in 10 trials of each condition (A, B, C and D). We set the hypothesized mean at 0.5 in conditions A and B and at 0.25 in condition C. The data followed a normal distribution (Kolmogorov–Smirnov test). Performance improved throughout the first two session blocks: We found a significant difference between blocks 1 and 2 (mixed-model analysis: mean ± SE = \(-2.67 ± 0.53, P < 0.001\)), but no difference between blocks 2 and 3 (mixed-model analysis: mean ± SE = \(-0.77 ± 0.52, P = 0.14\)). We also performed one-sample t tests for each session block for each condition. The group mastered each of the conditions A, B and C in the second session block \((t\_A = 2.844, P = 0.02; t\_B = 4.65, P = 0.002; t\_C = 4.009, P = 0.004\).

Kermit and Gino were very successful in all trials of blocks 2 and 3 (82% and 78%, respectively) and Mismo even reached 93% correct choices by that time (for individual data see Table 2).

Discussion of Tube Lifting

The consolidation phase demonstrated that the reward was clearly visible as well as the primary motivation for the birds.

**Figure 1.** Constellation examples for the four different tasks: the horizontal lines represent the tubes, the bold vertical lines the stoppers and the small circles the food reward. In Task 3 the three black images represent the three objects offered. The thin vertical lines in Task 4 represent the spaghetti on which the reward is pierced.

<table>
<thead>
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<th>Task 1: training tube lifting</th>
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<table>
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<tr>
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<td>Rudy</td>
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<tr>
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<td>5</td>
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<td>2</td>
<td>7</td>
<td>9</td>
<td>6</td>
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</table>

* Statistically significant according to a binomial test with hypothesized mean for TLA and TLB = 0.5 and for TLC = 0.25.
The group succeeded in all conditions of Task 2 in the second session block. On their very first trial subjects lifted the tube at the open end, causing the reward to fall towards the stopper at the opposite end. This could result from a transferred preference to lift the tubes at the rim, which was rewarding in Task 1. There are possible associative rules that could relate features of the tubes to the food reward: For example, birds may always lift a rewarded tube at the stopper end in condition A and B, or always lift a rewarded tube that only has one stopper at the stopper end in condition C. Some birds accomplished either condition A or B at the same time as condition C. It would be more plausible to learn to lift at the stopper end first and only later attend to the number of stoppers in a tube. An alternative explanation would therefore be that they developed an apprehension about the nature of the stoppers (blockage). This will be the subject of future studies.

Frowin used the simplest possible solution to the task: since he consistently grabbed the tubes at the open end and poured the content towards his face he did not have to attend to the number of stoppers in condition C. Gino always lifted the tube in the middle and poured the content out. Therefore, after choosing a rewarded tube with only one stopper, he simultaneously had to attend to the position of the stopper and to the direction of his pouring.

**SPAGHETTI BREAKING**

**Task 3: Spaghetti Breaking**

**Methods**

The same nine subjects as in Tasks 1 and 2 (Gino had died) participated in a short preference test on three unfamiliar wooden objects: a big ball (2r = 8 cm), a small ball (2r = 3.5 cm) and a small cube (4 × 4 cm). Each bird was allowed to explore the objects for 5 min individually while being visually isolated from its groupmates.

The following day, the same objects were placed in a triangular arrangement (ca. 1 m side length) around two transparent Plexiglas cubes that were aligned next to each other as in Tasks 1 and 2 (see Task 3 in Fig. 1). The big ball and the small cube (because of its shape) did not fit into the tube opening. The small ball matched the diameter of the tube opening and could carefully be inserted. One of the tubes was baited with a reward (a piece of rice waffle); the other tube was empty. The reward was pierced by a piece of uncooked spaghetti (Barilla No. 1), which was inserted through a small hole in the middle of the tube. The surplus spaghetti was broken off at the upper surface of the tube and transparent adhesive tape was put over the small hole. If an appropriately sized object was inserted into the tube and if the tube was subsequently lifted at the same end, the object would dash against the spaghetti, break it and release the reward at the opposite end (see Supplementary Material).

Subjects received five sessions of eight trials in this task. The baiting was pseudorandomized (four right and four left baited trials). Trials ended when the reward was recovered or after 5 min. To investigate whether subjects used the most efficient order of actions, we scored a trial as correct if the subject (1) carried the correct object (small ball) to the correct tube, (2) inserted it into the tube and (3) then lifted at the same end. Trials including attempts to lift the tubes before inserting or attempts to insert the wrong objects were scored as incorrect.

**Results**

Object preference. In the initial exploratory phase (in which only the three objects and no tubes were available to the subjects), the data for the frequencies of manipulations were normally distributed for each object (Kolmogorov–Smirnov test). There were no traceable differences in the frequency of the manipulation between the big ball (bb) and the small ball (sb; mixed-model analysis: mean difference ± SE = −0.33 ± 0.56, P = 0.56). Both ball objects were, however, touched more often than the small cube (sc; mixed-model analysis: mean differencebb−sc ± SE = 1.55 ± 56, P = 0.013; mean differencebb−sc ± SE = 1.22 ± 0.56, P = 0.04).

**Spaghetti breaking.** Seven of nine subjects inserted objects into the tubes in the first trial. Two juvenile females, Plume and Ry (Pl and Ry), were excluded from testing after not inserting any object over three sessions. All remaining subjects except Knut stopped lifting the tubes before fetching an object in the first session. Mismo only lifted a tube once in the first trial and then immediately fetched the correct object (sb) and consistently used the correct sequence of actions to retrieve the reward.

In session 1, the mean frequency of lifting tubes before the tool was fetched in the first four trials was 2.95 and in the last four trials 0.2. The group data within each session were normally distributed (Kolmogorov–Smirnov test).

The choices were consistently correct after the second session, that is, after 16 trials (t = 3.05, N = 7, P = 0.023) and the performance kept improving throughout the sessions (mixed-model analysis: blocks 1−2: mean difference ± SE = −39.78 ± 62, P < 0.001; blocks 2−3: mean difference ± SE = −22.87 ± 62, P < 0.001).

**Object preference during testing.** The mean frequency of touching the small ball was 50 times (8.2 times in the first session). The cube was only touched 9.5 times on average (7.2 in the first session). The big ball, which was as popular as the small ball in the preference test, was only touched 0.8 times on average (all in the first session). The mean frequency of inserting the correct object into the incorrect tube was 0.27 across the experiment.

**Task 4: Side-restricted Spaghetti Breaking**

**Methods**

The reward was pinned onto a Barilla No. 1 piece of spaghetti inside the tube, as previously, but the tubes contained wooden stoppers. The stoppers were shifted inside the tubes at ca. 1.5 cm from the tubes’ end. It was still possible to insert an object into a stopper end, but the movement of the object would eventually be blocked. The arrangement of the stoppers was the same as in conditions A, B and C in Task 2 (see Task 4 in Fig. 1). The tubes were arranged as previously and only one object (small ball) was placed in between them at a distance of about 30 cm towards the entry of the subject. Subjects received 15 sessions of eight trials. Each session comprised each condition twice, and, thus, each subject received a total of 30 trials of each condition. The sequence of actions was regarded as correct if the subject (1) carried the object to the correct tube directly (without previous lifting of the tubes), (2) inserted it at the open end, lifted at the open end and (3) lifted at the closed end causing the reward (and the ball) to fall out. Any deviation from this sequence of actions was scored as incorrect (see Fig. 2, Supplementary Material).

Even when the correct sequence of actions had been conducted, the reward was still not always available. There were two possible reasons for this: (1) the tube was not lifted up high enough or too slowly so the object did not break the spaghetti and the reward was still stuck inside the tube (Pierced); and (2) the spaghetti broke but only the ball was poured out of the tube and the reward was still lying loosely inside the tube (Loose). We recorded the next action of the subject after such an occurrence. There were four different possibilities. Reinsert the ball at the open end, insert the object at the stopper end, lift the open end or lift the stopper end. The correct
action if the reward was still pierced was to reinsert the object at the open end; the correct action if the reward was loose inside the tube was to lift the stopper end. The events were divided into the three session blocks (1–5, 6–10, 11–15) as previously.

Results

We set the probability of performing correctly by chance (Pc) conservatively at 0.5 in conditions A and B and at 0.25 in condition C as in Task 2. Within one block, each subject participated in 10 trials of each condition. The data within each block followed a normal distribution (Kolmogorov–Smirnov test). Knut lost motivation during the second block because of poor health. The subjects did not solve condition A in the most efficient order (tA3 = 1.55, P = 0.19), but they did master conditions B and C after the second session block, that is, after 10 trials per condition (tB3 = 2.75, P = 0.05; tC3 = 7.086, P = 0.002). In 79.4% of the incorrect trials of the first session block, the ball was first inserted at the stopper end. The performance improved throughout the blocks (mixed-model analysis: blocks 1–2: mean difference = 39.78 ± 6.19, P < 0.001; blocks 2–3: mean difference = 22.67 ± 6.19, P < 0.001).

Discussion on Spaghetti Breaking

In Task 3, seven of nine subjects obtained the reward on the first trial within the time given. This illustrates that, with experience, nontool-using kea can rapidly generate complex levels of object

### Table 3

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<th>SBC1</th>
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* Statistically significant according to a binomial test with hypothesized mean for SBA and SBB = 0.5 and for SBC = 0.25.

### Table 4

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<tr>
<td>Coco</td>
<td>3/7</td>
<td>9/14</td>
</tr>
<tr>
<td>Kermit</td>
<td>6/15</td>
<td>13/19</td>
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<tr>
<td>Knut</td>
<td>1/6</td>
<td>9/10</td>
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<tr>
<td>Mismo</td>
<td>3/7</td>
<td>4/5</td>
</tr>
<tr>
<td>Luke</td>
<td>8/10</td>
<td>12/13</td>
</tr>
<tr>
<td>Tammy</td>
<td>6/7</td>
<td>14/18</td>
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</table>

* Above chance according to binomial test with hypothesized mean at 0.25.

The adult male Luke mastered conditions B and C after the first session block, Kermit and Tammy solved the task after the second session block (see Table 3).

Additionally, we evaluated events in which the reward was not available after the correct sequence of actions. If 10 or more events occurred within one session block of an individual, we conducted a binomial test with the hypothesized mean set at 0.25 (four possible responses). Knut, Luke and Kermit accomplished correct reactions to the Pierced event in the first block, but Knut later decreased in performance because of his health problems. Most subjects reacted accurately to the Loose event after the second session block (see Table 4). Luke solved the problem in the first session block. We do not have enough data from Tammy in the first session block but he had a tendency to react correctly straightaway (see Table 4).
relationships such as second-order tool use. Initially, the tubes were lifted before searching for a suitable object, which is a plausible outcome given the birds' experience in Tasks 1 and 2. The lifting ceased after only one session, in Mismo's case even after the first trial, and subjects scanned the surroundings for the appropriate object. Hence, the birds were quickly able to infer that a tool was needed.

In contrast to the inserting as means paradigm (as described in the Introduction), tubes were lying freely on the ground and the diameter of the tubes was much smaller. Subjects could not just drop the correct object as before but it had to be carefully fitted into the tube entrance, which was complicated by the tube lying horizontally and being movable. Once the object was inserted, the tube had to be lifted with enough power to create sufficient force in the ball to break the anchorage of the reward. Additionally, subjects had to search for the correct object (the position of which was changed for each trial) at a distance and carry it to the correct tube. This also complicated the task since it required basic planning mechanisms (Visalberghi et al. 2009). Subjects were similarly interested in both ball objects during the preference trial. During the actual test, they immediately preferred the small ball, which indicates that they were able to transfer their tool size expertise spontaneously from the inserting as means paradigm (as described in the Introduction) to the novel context and objects.

The most efficient action sequence in Task 3 was to find the correct object, carry it to a baited tube, insert it and lift the tube at the same end. The adult male Mismo produced this order immediately and continuously, which indicates that he was able to combine spontaneously both his tool size expertise from the inserting as means paradigm and his tube-lifting experience in this context. The rest of the group accomplished consistency of this order after only 16 trials. In sessions 1 and 2, it was a common failure to insert the correct object first into the empty tube. This might be caused by the change in reward; the white rice waffle may appear more cryptic inside the Plexiglas tube than the peanut. Difficulties with avian vision through Plexiglas have been described before (Wimpenny et al. 2009).

In Task 4, all subjects achieved the reward within the time given from the first trial on. Luke used the most efficient sequence of actions possible in conditions B and C after the first session block, hence after 10 trials of each condition. The group also mastered the highly complex multistep action sequences of conditions B and C after the second session block, hence after 20 trials of each condition. Since subjects first inserted the ball at the stopper end in 80% of the incorrect trials in the first session block, it is likely that they were initially induced to go to the stopper end, as this was rewarding in Task 2, and insert the ball (as this was rewarding in Task 3). This is probably a chaining effect that subjects managed to inhibit after the second session block.

The results of Task 4 show that kea can quickly accomplish a highly complicated action sequence in the correct order. Stringing together such elaborate successions (means–means–end sequences) within a few trials can be cognitively demanding since it requires disregarding the final goal in the beginning in order to concentrate on the necessary steps in the sequence according to its order in time and space (Santos et al. 2005). Kea seem to be highly sensitive to the contingencies of reinforcement of these tasks. The performance of some subjects reflects a susceptibility to learning sets (learn how to learn) as shown in primates by Harlow (1949). They seem to be able to learn to execute strategic rules to situations that help to solve problems more efficiently.

We can gain cues about some of the mechanisms involved when looking at the supplementary data collected from the cases when the reward was not available after the correct sequence of actions. The adult male Luke reacted immediately in the most efficient manner if the reason for the unattainability of the reward was that the spaghetti had not broken (reinsert the object at the open end). He also spontaneously reacted correctly when the spaghetti was broken but the reward was still loose inside the tube (lift the closed end and the reward will fall out).

Luke was able to apply his knowledge flexibly from either Task 2 (lift at the stopper end) or Task 3 (insert tool) depending on the state of the reward (Pierced or Loose). To investigate his perception of tool function in further detail, we need to alter the weight of the object in the experiment.

CONCLUDING REMARKS

The tube-lifting paradigm (Task 2) shows that captive kea rapidly develop a sensitivity for stoppers in a set-up testing for zero-order relationships.

The results of the spaghetti-breaking paradigm (Task 3) indicate that they can flexibly apply previous experience about tool size assessment and their tube-lifting experience (Tasks 1 and 2) to a new context that even involves simple planning mechanisms (Visalberghi et al. 2009). Most importantly, captive kea, which are not natural tool users, are the first noncorvid birds to be shown to be capable of mastering a second-order tool use paradigm (Fragaszy et al. 2004a; Taylor et al. 2007; Bird & Emery 2009; Wimpenny et al. 2009). All avian species that have previously been tested on complicated tool use tasks are, to our knowledge, nest builders. The kea, in contrast, breeds in simple burrows and does not construct complex nests (Jackson 1963). It has been debated whether tool use can be explained by low-level processes, since most birds are already routinely establishing more complex object relationships during nest building (Hansell & Ruxton 2008). Although we cannot determine the cognitive prerequisites of complex tool use in birds, the present findings suggest that sophisticated nest construction is not crucial here.

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Supplementary Material

Supplementary material associated with this paper is available, in the online version, at doi:10.1016/j.anbehav.2010.08.007.

References


