



A case of quick problem solving in birds: string pulling in keas, *Nestor notabilis*

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Keas are extremely inquisitive birds that explore and manipulate objects with their beak and feet when foraging or at play. We investigated how captive keas face a problem that they have never encountered before: food objects suspended from a long string. Using this well-probed test for means–end comprehension, our aim was to see whether, and how, the keas solved the task. The seven subjects showed immediate interest in the string and, with the exception of a fledgling, reached the food by repeating combined actions of pulling up the string with the beak and holding loops of it against the perch with a foot. Four keas completed the first trial within a few seconds, by showing only goal-directed behaviour, thus executing the solution in a manner that could not be improved upon in nine further trials. The behaviour of the fledgling shows that the crucial element of the string-pulling competence is the beak–foot coordination. We then conducted four different two-string discrimination tests varying in the attachments and the spatial relationship of the strings to assess the keas' level of understanding of the functional properties of the task. The subjects' performance suggests that their attention is drawn very quickly to the relevant properties of the strings, that is, their connection between perch and food. These findings contribute to the ongoing debate on the distribution of higher cognitive skills in the animal kingdom by showing high levels of sensorimotor intelligence in animals that do not use tools.

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For many decades, researchers have tried to get a glimpse into the 'folk physics' of animals, that is, their common-sense understanding of how the world works, as well as why it works in the way it does (Köhler 1921; reviewed in Beck 1980; Tomasello & Call 1997; Povinelli 2000; Matsuzawa 2001). Many researchers now believe that it is not only humans but also many large-brained animals that develop an increasing ability to understand causal relationships with increasing experience, with language being only a powerful accelerator of this process, rather than a prerequisite (Rumbaugh et al. 2000).

Causal understanding requires assigning cause–effect or means–end relationships to the physical or social world through either observation or insight. Such causal relationships between objects might lead to the representation of abstract concepts, such as 'connectivity' (Hauser 1997), or the construction of a chain of responses that lead to a goal, or simply the generalization of responses

to similar situations. Only experimental work can elucidate which perceptual-motor abilities are involved and which steps of the solution are achieved in cases where animals appear at first sight to behave creatively or insightfully. The apprehension of a cause–effect relationship between two or more physical objects determines how objects are manipulated, which of several alternative objects are used, and how the individual responses are assembled into a coherent whole.

The ability to gain access to food that is out of reach has long been regarded as a valid example of apprehension of a cause–effect relationship (Köhler 1921; Piaget 1954). Many experiments testing birds' abilities to use a physical object to obtain food that is out of reach have involved the string-pulling task. Known since ancient times and used in animal research for many decades (reviewed in Seibt & Wickler, in press), this task involves the presentation of food suspended by a string or thread fixed to a perch, not accessible from the ground or from flight (Dücker & Rensch 1977). The most effective and intelligent solution to this problem has been described by Heinrich (1995, 2000) with common ravens, *Corvus corax*. It requires that the bird repeats the following sequence several times: reaching down from the perch, grasping the

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string with the beak, pulling the string up, placing the pulled-up loop of string on the perch, then pressing a foot down on the loop and letting go with the beak so that the bird can reach down to pull up another loop (Fig. 1). If a bird has achieved this solution spontaneously, and the complete act has been accomplished in a rapid and smooth manner without any fumbling, we would probably agree with Thorpe (1956) in seeing nothing suggestive of trial-and-error learning. However, out of more than 15 species of birds initially tested with the string-pulling task only ravens seem to understand the cause-effect relationship between food, string and perch, use effective techniques instantaneously, in contrast to a number of other species that do not, and generalize the solution to various situations (Heinrich 2000).

Besides corvids (Emery & Clayton 2004), parrots are especially well known for performing amazing cognitive tasks. Recently, Funk (2002) reported some string-pulling competence in yellow-crowned parakeets, *Cyanoramphus auriceps*, and Pepperberg (2004) in language-trained grey parrots, *Psittacus erithacus*. A parrot species that has received public attention because of its alleged intelligence

and curiosity is the kea (Diamond & Bond 1999). This bird's explorative attitude, combined with its persistent and rigorous destructiveness and almost total lack of neophobia, makes it the ideal candidate for the study of means-end comprehension and sensorimotor intelligence in birds (Huber et al. 2001; Gajdon et al. 2004).

Despite the obvious problems of controlled testing in field situations, Johnston (1999) successfully addressed the string-pulling abilities of wild keas. Of 19 freely participating keas six solved the problem in their first trial, with the median time to completion being 50 s. Other individuals did not instantly master the task or never solved it, suggesting that responses are not innate.

In our experiments we attempted to examine the keas' sensorimotor intelligence under controlled laboratory conditions by using a set-up that allows a distinction between (1) finding the solution by chance, (2) executing innate responses, (3) trial-and-error learning, and (4) means-end comprehension. Because we were interested in the goal directedness of the actions and were aware that keas may learn from even a few errors, we performed a detailed analysis of the initial steps they took to achieve success in



Figure 1. Six frames of a video clip (a–f) showing a kea performing string pulling in the first test.

their first attempt to secure the food reward. To examine the behavioural variability and the amount of learning we compared the performance across trials. Furthermore, following Heinrich's (1995, 2000) comprehensive attempt to examine the cognitive aspects of string pulling in ravens, we devised four patterned string-pulling problems. By varying shape, colour, length and weight of the strings as well as their spatial relationship to each other we assessed the keas' level of understanding of the functional properties of the task.

METHODS

Study Animals

Seven captive keas at the Konrad Lorenz Institute for Ethology in Vienna, Austria, participated in this study. One group consisted of the female Kima (6 years) and the males Bigo (4 years), John (3 years), Knut (2 years) and Bruce (7 months) and the other of the female Tiffany (6 years) and the male Mismo (3 years). All individuals were born in captivity and reared by their parents. They were fully habituated to humans who interacted with them as feeders or experimenters.

The subjects were kept in two large aviaries, providing outdoor conditions year round. The aviary for the large group (15 × 10 m and 4 m high) and the aviary for Tiffany and Mismo (5 × 4 m and 3 m high) could both be divided into three compartments. Both aviaries were equipped with tree trunks, rocks, pieces of wood, perches and wooden shelters and the ground was covered with sand. Chains holding heavy branches were present in the aviary, but could not be lifted by the keas. Except for these items, no string-like objects had been presented to them. Water and food, which contained a mixture of vegetables, fruits, seeds, margarine, ox heart and vitamin supplements every day, were available *ad libitum*. Individual recognition of the birds was facilitated by coloured leg bands. No licence was required for this study.

Apparatus

We conducted the experimental tests in a visually separated corner of the aviary, using a wooden perch and different objects attached to one or more vertical strings (Fig. 2). The perch (170 cm long, 5 × 5 cm in cross-section) was supported by two poles (170 cm high) that were screwed into wooden bases measuring 60 × 60 cm. One or two plastic strings were nailed to the underside of the perch. In the various tests we used strings that differed in colour, length and spatial relationships. We used thin wire attached to the poles at a height of 115 cm to cross the strings or to bring them into a slanted position (Fig. 2). Fixed to the ends of the strings were objects of different shape, texture and weight, such as a yellow toy car (25 g), a black Kodak film canister (20 g), a piece of wood (50 g) and a stone (2000 g). Baiting one of the objects with a mixture of butter and egg yolk provided a food reward.

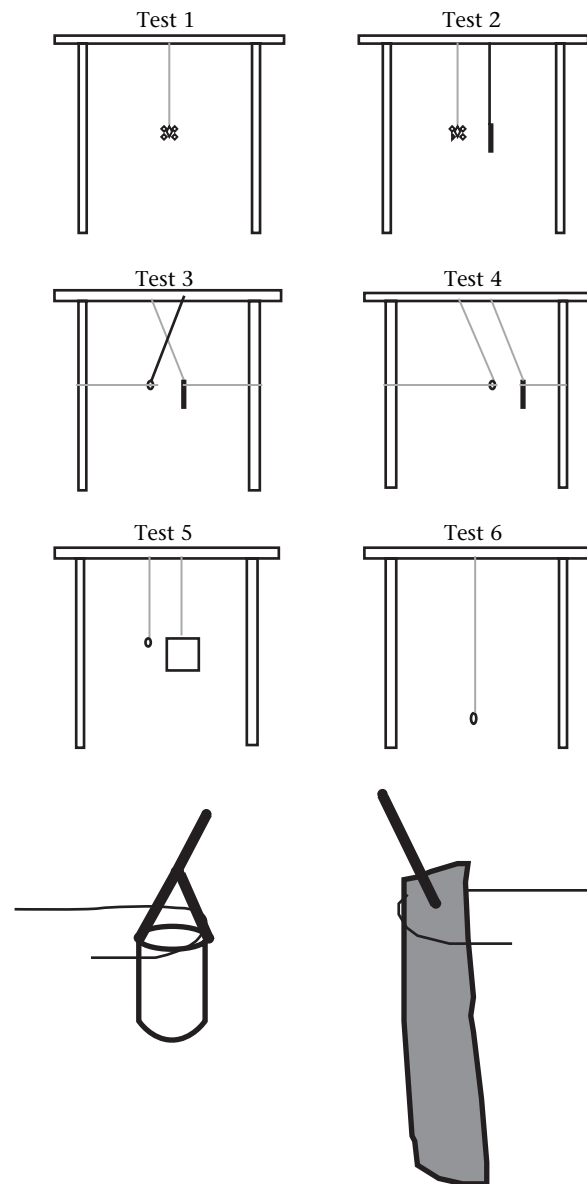


Figure 2. Diagrams showing the single string in tests 1 and 6 and the spatial relationships between the two strings in tests 2–5. The way in which the crossed and the slanted strings were kept in position by thin wires is also shown.

Procedure

The keas received six string-pulling tests. Before starting the experiment we allowed the keas to investigate the wooden perch without the string for 1 h on 3 consecutive days. None of them had ever experienced rewards on a string and they received no string-pulling training prior to the experiments. They were tested individually with the same number of trials in the same sequence of tests, but we changed the order in which they participated every day. Usually we conducted two sessions per day, one in the morning (from 0900 hours) and one in the afternoon (from 1500 hours). Video recording enabled us to analyse the details of the keas' behaviour.

Test 1: single string-pulling task

This initial task tested the keas' ability to pull up a baited toy that was suspended 70 cm from the horizontal perch by a single yellow string. Before the experiment, the preselected individual was lured into the test compartment and the other individuals locked into another compartment of the aviary, from which they could not see the test subject. The subjects received 10 trials in immediate succession. During the intertrial interval (20–30 s), the experimenter (D.W.) baited the object on the string while the bird flew to another perch in the aviary.

Test 2: object discrimination task

To see how the object on the string controlled the keas' pulling behaviour, we presented in three consecutive sessions of 10 trials each two strings, one with the baited object attached, as before, and one with a piece of wood attached. The three sessions differed in the baited object (the toy of test 1 in the first session, a film canister in the other two) and the colour of the strings (both yellow in the first two sessions; the string with the baited object was red in the third one). In this test, as in all other patterned string problems, we determined the position of the rewarded string for each session in an arbitrary manner by tossing a coin. The subjects could investigate both objects for about 10 s before the first trial. Test 2 followed immediately after the last trial of test 1.

Test 3: crossed strings task

By crossing the strings we wanted to assess whether the keas' choice was determined by the spatial or the functional relationship between string and reward, that is, if they pulled at the string directly above the baited object as in the 40 trials before or based their choice on the functional connection between food and string. The food container was now suspended 20 cm laterally to where it was located before (Fig. 2). We conducted two 30-trial sessions to examine improvement of performance. While in these sessions we used strings of different colour to ensure that the birds could follow the strings from one end to the other, we used two yellow strings in a further 20-trial session.

Test 4: slanted strings task

In this task, the two yellow strings were bent off to the same side (Fig. 2). Although the food container was again directly below where the unbaited string was attached to the perch, the strings did not cross. We conducted one 20-trial session.

Test 5: overload string task

In a 20-trial session, the keas could choose between two yellow strings, one with the food container and the other with a heavy (2000-g) stone baited with a large amount of butter. This task tested whether the choices were influenced by relevant physical properties of the attached objects (their weight).

Test 6: overlength string task

In this 20-trial task we wanted to test the flexibility of problem solving in keas. Over the preceding 160 trials, the

keas were trained to pull up the string from the perch they were sitting on but in this task the length of the string was 140 cm, enabling the subject to reach the reward from the ground.

RESULTS

Performance in the Single String-pulling Task

All keas showed immediate interest and flew directly to the perch. None tried to obtain the reward by flying directly at the toy or by jumping up to it from the ground. With the exception of the fledgling (Bruce) they solved the task in their first trial.

Table 1. Action list and action sequences in the keas' first attempt to secure the reward

| Action number | Efficient actions | N | Inefficient actions | N | Exploratory actions |
|---------------|---|----|---|----|---------------------|
| 1 | Lands on perch | 12 | Tries to place string on perch but does not succeed | 17 | Nibbles string |
| 2 | Reaches for string with beak | 13 | Tries to place foot on string but does not succeed | 18 | Nibbles perch |
| 3 | Pulls up string with beak | 14 | Drops string after having pulled it up | 19 | Touches string |
| 4 | Places string on perch | 15 | Sits on perch | | |
| 5 | Uses one foot to hold string on perch | 16 | Flies off perch | | |
| 6 | Uses both feet to hold string on perch | | | | |
| 7 | Pulls up string until body is upright and therefore gains more string | | | | |
| 8 | Grabs string directly with foot | | | | |
| 9 | Takes one or more steps sideways on perch holding string with beak | | | | |
| 10 | Lets go of string with beak to reach down again | | | | |
| 11 | Gains reward after having pulled up string | | | | |

Table 2. Action sequences of individual keas in their first attempt to secure the reward

| Subjects | Action sequence |
|----------|---|
| Bigo | 1-2-17-3-4-5-6-10-2-3-4-5-10-2-3-4-5-10-2-3-4-5-10-2-3-4-5-10-2-3-4-5-11 |
| John | 1-2-17-3-5-10-2-3-5-9-6-10-2-3-5-10-2-3-9-6-10-2-3-4-5-11 |
| Kima | 1-2-3-5-10-2-3-6-10-2-3-5-10-2-3-9-5-11 |
| Mismo | 1-2-17-3-9-5-10-2-3-9-5-10-2-3-9-5-10-2-3-5-10-2-3-5-11 |
| Knut | 1-2-17-17-10-18-2-17-17-10-2-17-2-3-5-10-2-3-5-10-2-3-9-5-10-2-3-10-14-2-17-10-2-3-5-10-2-3-9-5-10-14-16-1-2-3-9-5-10-2-3-5-10-14-2-3-9-5-10-2-3-14-2-3-5-10-2-3-9-5-10-2-3-9-5-10-2-3-5-10-2-3-5-11 |
| Tiffany | 1-2-17-3-5-10-2-3-5-10-2-3-5-17-14-18-18-18-2-3-14-2-17-2-17-17-17-18-18-18-15-18-18-16-1-16-1-2-17-2-17-2-3-6-10-14-2-19-2-3-6-10-2-3-5-3-4-17-3-9-5-10-2-3-8-10-17-10-14-18-15-2-17-3-10-14-2-3-6-10-2-3-9-5-10-2-3-5-10-2-3-5-10-2-3-9-6-11 |
| Bruce | 1-2-17-17-3-13-14-2-17-3-3-12-14-2-3-3-12-13-14-2-3-3-13-7-13-14-18-18-18-18-18-2-3-4-5-17-14-2-3-13-14-2-3-14-2-3-17-3-13-14-2-17-3-4-13-14-2-3-13-14-2-3-4-5-17-4-13-14-2-3-4-5-17-4-6-10-14-2-3-4-5-7-5-4-13-14-2-3-4-13-4-5-17-13-4-6-17-8-17-7-13-14-2-3-4-5-7-13-14-2-3-7-13-7-9-4-5-10-2-3-3-9-4-13-14-2-3-3-7-9-4-5-7-5-7-14-2-3-3-7-14-2-3-3-7-9-4-13-14-2-3-7-9-4-5-10-2-3-4-5-6-11 |

See Table 1 for list of actions. Exploratory and inefficient actions are in bold. The action sequence of Bruce was recorded during his second test 1 month after his first (unsuccessful) attempts (see text).

A detailed analysis of the actions of the keas in their first attempt revealed that they fell into three subgroups with regard to their goal directedness in the single string-pulling task (Tables 1, 2). Four subjects showed mostly efficient, rather than exploratory, actions, including the key elements of pulling up and stepping on the string (see Table 1 for the categorization of actions). Given that the birds were facing the problem for the first time, they found this solution very rapidly (9–15 s; Table 3). Even more striking, these ‘immediate solvers’ did not show any improvement across the further nine trials of the task. They also never attempted to fly off with the food object once it was recovered.

Although taking the group as a whole, there was also no significant difference in latency or number of pull-ups between the first and the second trial (Wilcoxon test: latency: $T = 7$, $N = 7$, $P = 0.24$; pull-ups: $T = 10$, $N = 7$, $P = 0.5$) or the first and the 10th trial (latency: $T = 3$, $N = 7$, $P = 0.06$; pull-ups: $T = 1.5$, $N = 7$, $P = 0.06$), it is evident that the two remaining subgroups behaved differently from the immediate solvers. The juvenile Knut and the adult Tiffany showed many exploratory actions (nibbling), executed the efficient actions more slowly and

left the perch once or more before completing the task. They dramatically improved their methods in the second trial, but not thereafter (Table 3). The fledgling Bruce was the only bird that was completely unable to secure the food toy in his first attempts. Only after 1 month and three further trials did he solve the string-pulling task.

One obvious measure of string-pulling skill is how often the string is dropped (Table 3). In fact, the 7-month-old fledgling’s (Bruce) bad performance in the first trial is reflected by the large number of drops. In his first trial he pecked at the string and pulled it up with his beak a few centimetres. Only twice was he able to hold the string with his foot but he seemed unable to coordinate his movements and to repeat the correct sequence several times. After three unsuccessful sessions (each of 10 min on 3 consecutive days) we stopped testing him for 1 month. When tested again he became successful only after three further 10-min trials. The obvious challenge was to move the beak holding the string towards the foot and thereby place the string directly underneath the foot. When he managed to do this, he could hold the string with the foot more accurately and repeat the necessary movements until he reached the reward. In

Table 3. Performance in the single string-pulling task

| Trial | Subjects | | | | | | | | | | | | | | | | | | | | |
|-------|----------|---|---|--------|----|----|------|---|---|------|---|---|------|----|---|-------|---|---|---------|----|---|
| | Bigo | | | Bruce* | | | John | | | Kima | | | Knut | | | Mismo | | | Tiffany | | |
| | T | P | D | T | P | D | T | P | D | T | P | D | T | P | D | T | P | D | T | P | D |
| 1 | 12 | 5 | 0 | 369 | 30 | 19 | 15 | 4 | 0 | 9 | 4 | 0 | 120 | 16 | 4 | 13 | 6 | 0 | 330 | 17 | 5 |
| 2 | 10 | 6 | 0 | 24 | 4 | 2 | 11 | 7 | 0 | 21 | 7 | 1 | 18 | 9 | 1 | 26 | 9 | 1 | 32 | 11 | 2 |
| 3 | 9 | 5 | 0 | 17 | 3 | 0 | 4 | 5 | 0 | 15 | 5 | 0 | 10 | 5 | 0 | 13 | 5 | 1 | 17 | 6 | 0 |
| 4 | 17 | 7 | 1 | 33 | 4 | 1 | 6 | 5 | 0 | 11 | 5 | 0 | 10 | 6 | 0 | 16 | 5 | 1 | 15 | 8 | 0 |
| 5 | 7 | 3 | 0 | 40 | 8 | 4 | 6 | 6 | 0 | 16 | 6 | 0 | 11 | 6 | 1 | 26 | 5 | 1 | 14 | 6 | 1 |
| 6 | 10 | 4 | 0 | 13 | 4 | 2 | 13 | 5 | 1 | 13 | 5 | 0 | 13 | 6 | 1 | 24 | 6 | 3 | 29 | 11 | 2 |
| 7 | 22 | 6 | 1 | 120 | 10 | 3 | 6 | 7 | 0 | 17 | 7 | 0 | 17 | 8 | 1 | 15 | 3 | 1 | 18 | 5 | 0 |
| 8 | 13 | 8 | 0 | 13 | 1 | 0 | 8 | 7 | 0 | 17 | 7 | 1 | 9 | 5 | 0 | 8 | 3 | 0 | 14 | 4 | 0 |
| 9 | 10 | 4 | 0 | 86 | 8 | 5 | 9 | 5 | 0 | 11 | 5 | 0 | 10 | 5 | 0 | 14 | 4 | 2 | 25 | 10 | 0 |
| 10 | 13 | 5 | 0 | 65 | 21 | 7 | 6 | 6 | 0 | 12 | 6 | 0 | 10 | 5 | 0 | 6 | 1 | 0 | 11 | 5 | 0 |

T: time to completion (s); P: number of pulls; D: number of drops.

*For Bruce data are given not for his first session, but for the session including his first successful trial (see text).

his previous attempts, he held the string with the beak in an upright position and tried to place the foot on the vertically dangling string. While in this first successful trial the step-on method emerged slowly, it was executed in a quick and fluent manner in the next trial.

The female Tiffany also showed some improvement with respect to the number of drops. In contrast, the remaining keas showed small numbers of drops from the beginning of the task (Table 3). These five individuals had no problem holding the string with their claws or by stepping on it; four of them never dropped the string with the food in the first trial.

Methods Used to Obtain the Reward

Although the task seemed to require straightforward solutions, we found a considerable variation in the techniques shown and in the frequency of their usage. Taken together, the group of keas performed nine different techniques when confronted with the various tests (Table 4). Combinations of up to five different methods per trial occurred. Only four methods, loop making, side walking, turn and upright pull, were shown by all individuals. The variation in methods used in alternation remained consistently high across tasks.

Performance in the String Discrimination Tasks

An analysis of the subjects' individual performances in the four discrimination tests revealed some variation between tests and subjects. We scored their choice in a trial as 'correct' if they started with a clear pulling action at the baited string. Note that at the onset of test 2, all birds were proficient at the string-pulling task.

In test 2, which required a discrimination between the baited and the unbaited object, all seven subjects performed extremely well. Only two (Kima and Mismo) failed in the first trial, but none in the following two trials. The

string with the baited toy was chosen by the group in 86% of all 10 trials, in 83% of all further 10 trials with the food container, and in 84% of the 10 trials with strings of different colour.

In the crossed strings task, the birds faced much greater problems. Only one bird (John) chose the correct string in the first trial (as well as in 27 of the 29 following trials, with the failures occurring in the second and 25th trials). Three birds (Bruce, Knut and Mismo) learned quickly after the failure in the first trial (with 24, 25 and 25 correct trials thereafter), one bird only after a number of failures (Bigo, with two correct choices in the first 13 trials and 14 correct choices in the remaining 17 trials), and two birds (Kima and Tiffany) remained at chance level throughout the 30 trials (12 and 16 correct trials). In the repetition phase (further 30 trials), all birds were overwhelmingly correct, with a minimum of 26 correct trials out of 30 trials (group performance: 91%). When we used the same colour for both strings, four birds failed in the first trial, and four birds remained confused during 19 further trials. Only Bruce, John and Knut performed significantly well (binomial test: $P < 0.02$).

In the slanted strings task, all birds performed well. Only Bigo failed in the first trial. The percentage of correct choices in the first 10 trials of the whole group was 87% and in the next 10 trials 86%. In the first trial of the overload test, three birds (John, Knut and Tiffany) failed. Some learning occurred thereafter, as the percentage of correct choices in the first 10 trials of the whole group was 81% and in the next 10 trials 93%.

In the final overlength string task, the birds could easily obtain the reward by flying to the ground near the food container. However, after 160 trials in which they were required to pull up the string from the perch, six birds continued to use their pulling technique, although it sometimes took them almost 1 min or 20 correct pulls. Only one female (Tiffany) changed her behaviour. After 11 pulling trials she flew some distance away from the perch, then returned to the apparatus by successively climbing

Table 4. The relative frequencies of methods used to solve the tasks

| Subjects | Methods | | | | | | | | |
|----------|---------|-----------|--------------|-------------|--------------|------|--------------|------|------|
| | Flip | Foot grab | Foot stretch | Loop making | Side walking | Turn | Upright pull | Wrap | Down |
| Bigo | 0.4 | 0.7 | 0.3 | 58.9 | 32.4 | 1.1 | 6.2 | 0.0 | 0.0 |
| Bruce | 0.7 | 2.3 | 0.0 | 5.6 | 60.0 | 2.6 | 28.3 | 0.4 | 0.0 |
| John | 2.3 | 1.0 | 0.4 | 54.6 | 28.3 | 0.4 | 13.0 | 0.0 | 0.0 |
| Kima | 0.0 | 6.6 | 0.0 | 7.6 | 57.8 | 2.0 | 26.0 | 0.0 | 0.0 |
| Knut | 2.0 | 0.0 | 0.0 | 22.5 | 66.5 | 5.9 | 3.1 | 0.0 | 0.0 |
| Mismo | 0.0 | 0.8 | 0.0 | 9.7 | 76.6 | 3.8 | 9.0 | 0.0 | 0.0 |
| Tiffany | 0.5 | 3.8 | 3.3 | 23.2 | 32.4 | 7.1 | 27.7 | 0.0 | 2.1 |
| Total | 0.8 | 2.2 | 0.6 | 26.0 | 50.6 | 3.3 | 16.2 | 0.1 | 0.3 |

Flip: reaching down and flipping the string to the other side of the perch; Foot grab: grabbing the string with the foot and placing it on the perch; Foot stretch: standing on the string with both feet, moving the foot with the loose end of the string laterally on the perch and thereby pulling the string up; Loop making: reaching down, pulling up string with the beak, placing the foot on the string, letting go of the string with the beak, remaining in place, reaching down again; Side walking: reaching down, pulling up the string with the beak, walking to the side of the perch, placing the foot on the string, reaching down again; Turn: turning the whole body 180° while holding the string and stepping on the additional string with the feet; Upright pull: pulling up the string till the body is in a completely upright position and thus gaining more string; Wrap: pulling up the string, letting go at the other side of the perch, pulling up at the other side and by repeating these steps wrapping the string around the perch; Down: taking the food container from the ground (only possible in test 6).

down branches and finally got close to the string on the ground, from where she easily obtained the reward. In all further trials she flew directly to the ground near the food cup.

DISCUSSION

Inspired by Heinrich's (1995, 2000) studies with ravens, and in accord with findings obtained from wild keas (Johnston 1999), our experiments with captive keas indicate that these parrots are very efficient at finding a solution to a nontrivial technical problem and at discriminating between stimuli based on the functionality of an object and its relationship to other objects. So far, only grey parrots and ravens have proved to behave similarly well in such means–end object retrieval tasks (Pepperberg 2004; Heinrich & Bugnyar 2005). Several characteristics of our keas' performance invite discussion in comparison to other published experiments and to the existing theories of the cognitive processes underlying problem solving in animals.

First, all keas except the fledgling solved the string-pulling task by coordinating beak and a foot in their first trial. Four of those successful keas retrieved the food object dangling on a string instantaneously and without showing exploratory or ineffective methods (such as flying up from the ground or pecking at the string as ravens did; see Heinrich & Bugnyar 2005). This is, to our knowledge, by far the quickest manner in which the string-pulling problem has been solved by birds. Perhaps they had worked out a solution to the retrieval problem even before their first trial run.

Second, it is remarkable that from the first trial of the initial single string-pulling task onwards there was no significant improvement of the group across the test. Neither the time to completion nor the number of pulls or drops decreased in our whole bird sample in a significant manner. In contrast, in all other birds tested so far, including ravens (Heinrich 1995; Heinrich & Bugnyar 2005), improvement in performance was on the whole gradual and intermittent. We might therefore argue that the overt construction, rather than the explicit training, of a sequence of actions in order to bring about an effect was the key achievement in the keas' string-pulling behaviour.

Third, the keas' behaviour remained flexible, as they used different techniques throughout all string-pulling tests, that is, for about 180 trials. Although there was some evidence of an increase in the efficiency of particular action elements, the keas did not eliminate techniques. We suggest that the elimination of methods is hampered in keas by their strong inclination towards object exploration and object play. Nevertheless, as is evident from the short task completion times, the majority of their actions were food directed and guided by some understanding of the key functional features or affordances of the task. Only in the test with the extra long string did they behave stubbornly. However, 160 rewarded pull-ups of the string might have narrowed their attention towards the end of the string. Only tests with naïve animals may elucidate the true problem-solving capacities of keas in this task.

Finally, the keas showed very high success rates in the discrimination tasks, thereby demonstrating attendance to the end and the configuration of the strings. The two-string choice experiments showed that the birds instantaneously distinguished between strings with baited and unbaited objects. Such immediate solutions were obviously not achieved in the crossed and slanted strings tasks. Except for one raven in Heinrich's study (1995) there are no reports to our knowledge of birds solving this problem. Even for primates the solution is not always immediate and may require an extended period of learning (reviewed in Tomasello & Call 1997; Povinelli 2000).

The most advanced solution in the crossed and slanted strings tasks would require the possession of a 'concept of connectedness' (Piaget 1954). However, without presenting in probe trials strings that vary in the visual salience of connectedness, it remains unclear to what extent an understanding of 'contact' is grounded in a genuine appreciation of physical connection (Hauser 1997; Povinelli 2000). A less advanced although equally effective solution would require attendance to the perceptually tangible cues of the strings, particularly the continuity of the paths, as opposed to causally imperceptible physical factors. However, tracing the paths of the strings is difficult when facing a crossing at some distance. The much better performance in the slanted strings task than in the crossed strings task might be counted as evidence that tracing the paths of the strings was the critical element in the keas' discrimination performance.

How does this study contribute to the ongoing discussion about the evolution of cognition? In the past, the string-pulling task has been used to examine whether animals apply an evolutionarily 'programmed' solution, or learn by trial and error (instrumental conditioning), or show means–end behaviour. However, it is unlikely that these alternatives constitute exclusive options for an animal in the string-pulling situation. Obviously, the execution of the motor acts involved rests on preprogrammed action elements. The real challenge in the string-pulling task, of course, is the assembling of the actions into a coherent whole. Gradual improvement was obviously not the dominant process underlying the keas' performance. In addition, the collection of the necessary proprioceptive experiences is arguably not sufficient for the construction of an action sequence that is appropriate for the task at hand. The early failures of the fledgling and the great variability of techniques applied render an explanation in terms of 'preprogrammed' solutions unlikely.

Instead, there is increasing evidence that the apprehension of cause–effect relationships between two or more physical objects, including the subject's own body, guides the covert assembly of the response sequence, the exact manner in which objects are manipulated, and which of several alternative objects are used (Hauser 1997; Heinrich 2000; Rumbaugh et al. 2000). Perhaps this is what Thorpe (1956) called insight in contrast to trial-and-error learning, in which actions are selected through reinforcement. We believe that our keas' string-pulling behaviour can be best explained by such apprehension of a cause–effect relationship and the adaptive reorganization of experience.

Our study supports the hypothesis that keas manage to solve complex technical tasks by some kind of understanding of means–end relationships and by attending to the functional properties of objects. Captive keas in Vienna have shown an ability to manipulate group members in a cooperation task (Tebbich et al. 1996), to understand the affordances of locking devices through observation of a conspecific (Huber et al. 2001), and to solve difficult technical tasks quickly (Gajdon et al. 2004). An interesting feature of these studies is the striking difference in performance of wild and captive keas. When tested under controlled conditions, wild keas failed to show convincing forms of social learning and horizontal transmission of technical innovations (Gajdon et al. 2004, *in press*), and also performed less convincingly in the string-pulling task (Johnston 1999) than the birds in the present study. However, we should not make strong claims about this difference before determining the effects of group arousal, neophobia and the presence of humans in the wild. Furthermore, string-pulling behaviour, and most probably the performance in all problem-solving tasks, depends on the experience and skill of the individual acquired prior to the experiment and on social strategies, as has been shown recently in grey parrots (Pepperberg 2004). In that study, those birds with little training in referential English requests succeeded in string pulling, whereas birds that could request the suspended item failed to obtain the object but engaged in repeated requesting. The wild keas in Johnston's (1999) study might also have been engaged in social strategies and therefore might have shown less goal-directed string-pulling behaviour than our individually tested keas.

In conclusion, the findings from parrot studies have shown that neither extensive tool use and manufacturing, as in New Caledonian crows, *Corvus moneduloides* (Hunt 1996), nor food caching and feeding in the vicinity of dangerous predators, as in ravens (Heinrich 1999; Bugnyar & Kotrschal 2002), are the evolutionary recipe for advanced intelligence in birds. For primates, numerous researchers have proposed that intelligence is a correlate of having a complex social system and a long life (the so called 'social function of intellect' hypothesis put forward first by Jolly 1966 and Humphrey 1976). Marler (1996) and later Emery & Clayton (2004) have suggested similar selection processes for birds, and Pepperberg (1999) added emphasis on the combination of intelligence and advanced communication skills in parrots. Indeed, parrots may rival corvids and primates not only in relative brain and telencephalic volumes (Iwaniuk et al. 2005), but also in some cognitive abilities.

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