



Social learning affects object exploration and manipulation in keas, *Nestor notabilis*

LUDWIG HUBER*, SABINE RECHBERGER* & MICHAEL TABORSKY†

*Institute of Zoology, University of Vienna

†Konrad Lorenz-Institut für Vergleichende Verhaltensforschung (KLIVV), Austrian Academy of Sciences

(Received 5 March 2001; initial acceptance 25 April 2001;
final acceptance 6 July 2001; MS. number: 6870)

Both the pattern of exploration and the manipulation efficiency of young keas attempting to open a complex food container proved to be influenced by the observation of an experienced group member. Five individuals were allowed to observe a trained conspecific that iteratively demonstrated several techniques to open a large steel box. The lid of the box could be opened only after several locking devices had been dismantled: a bolt had to be poked out, a split pin had to be pulled, and a screw had to be twisted out. The observers' initial manipulative actions were compared with those of five naïve control subjects (nonobservers). Although the observers failed to open the box completely and thus to get the reward in their first attempts, they explored more, approached the locking devices sooner and were more successful at opening them. Although their initial attempts did not match the response topography or the sequence of the model's actions (movement or sequence imitation), their improved efficiency at unlocking the devices seemed to reflect the acquisition of some functional understanding of the task through observation (emulation learning).

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Besides socially acquired food preferences (Galef 1988; see also Heyes & Galef 1996), ethologists have studied foraging (Palameta & Lefebvre 1985), mate choice (Dugatkin 1992), song learning (West & King 1985) and tool use (Tomasello et al. 1987; see also Tomasello & Call 1997) as primary candidates for social learning. A less frequently studied behaviour for which social learning may be particularly adaptive is exploratory or curiosity behaviour (see Miklosi 1999). A high variance in the abundance of different food types favours opportunistic generalism, which is functionally linked to learning and cognition (Lefebvre 2000). Opportunistic resource exploitation may increase and diversify the tendency of animals to explore their environment (Gray 1981), interact with new stimuli (neophilia; Greenberg 1990; Heinrich 1995), taste new foods (Daly et al. 1982) or feed in the vicinity of large species that are normally avoided (Lefebvre & Giraldeau 1996).

Except in studies of primates (see reviews in Byrne 1995; Tomasello 1996; Tomasello & Call 1997; Byrne & Russon 1998; Whiten, in press), the majority of recent studies of social learning have used very simple

manipulations of simple objects. Rats, *Rattus norvegicus*, pushed a joystick either to the left or to the right (Heyes et al. 1992); pigeons, *Columba livia*, and quails, *Coturnix japonica*, pecked or stepped on a treadle (Akins & Zentall 1996, 1998; Zentall et al. 1996); starlings, *Sturnus vulgaris*, pulled up or pushed down a plug (Campbell et al. 1999); ravens, *Corvus corax*, pulled at a flap or levered a gliding lid (Fritz & Kotschal 1999); and marmosets, *Callithrix jacchus*, pushed or pulled a pendulum door (Bugnyar & Huber 1997) or removed a lid from a plastic canister either by hand or mouth (Voelkl & Huber 2000).

Among birds, ravens are often-cited examples of exploratory animals (Heinrich 1995, 1999; Ratcliffe 1997). A species with comparable behavioural flexibility is the kea. This New Zealand parrot has been used as an example of curiosity in birds for a century. The rapidly changing environment in New Zealand during Pleistocene glacial climates and the relatively low food abundance of the kea's natural habitat is thought to have led to the evolution of extreme behavioural flexibility (Temple 1996). Their explorative attitude combined with their persistent and rigorous destructiveness results in 'open' (Mayr 1974; Lorenz 1977) and opportunistic (Diamond & Bond 1999) foraging.

Keas remain in family groups and flocks until they are sexually mature (males at about 5 years, females at about

Correspondence: L. Huber, Department of Theoretical Biology, Institute of Zoology, University of Vienna, Biocenter, Althanstrasse 14, A-1090 Vienna, Austria (email: ludwig.huber@univie.ac.at). M. Taborsky is now at the Division of Behavioural Ecology, University of Berne, Wohlenstrasse 50a, CH-3032 Hinterkappelen, Switzerland.

4 years; Jackson 1960) and show a variety of social behaviours, including elaborate play (Keller 1975) and cooperation through social manipulation (Tebbich et al. 1996). Object exploration is firmly bound to the general activities of the group (Diamond & Bond 1999; Johnston 1999).

Extended association with parents, extreme iteroparity and long potential life span seem to favour social learning and other forms of time-consuming skill acquisition (Richerson & Boyd 2000). Also, group foraging as a strategy to cope with spatially and temporally clumped, highly unpredictable food may favour learning from others in the group (Klopfer 1959; Brown 1964), especially by providing information about the location and appearance of high-quality resources (Turner 1965; Clayton 1978; Diamond & Bond 1991).

We investigated the effects of horizontal (within-generation) transmission of information between a model and an observer by comparing the performance of observers and naïve group members at their first encounters with an attractive object (artificial fruit). Specifically, we expected that observations of skilled actions of a trained conspecific would affect the initial patterns of exploration and manipulation of the complex food container through social learning.

Three successive manipulations were necessary to dismantle locking devices of a box containing attractive rewards. In such a complex task the keas may benefit from the model's demonstration in several ways. Compared with nonobservers they might (1) show more vigorous exploration after being 'energized' by the observation of the model's activity (social facilitation; Zajonc 1965; see also Clayton 1978, for a definition), (2) be attracted to the locus or the object at which the model executed highly salient manipulations (local or stimulus enhancement; Spence 1937; Thorpe 1956), (3) be engaged in similar species-typical behaviour as the conspecific model (contagion; Thorpe 1963), (4) learn about the relationship between a given stimulus and reinforcement (observational conditioning, Cook et al. 1985); (5) learn about the properties or potential uses (the so called 'affordances', Gibson 1979) of a stimulus (emulation learning; Tomasello 1990), (6) or learn some part of the form or the sequence of the demonstrated technique (movement and sequence imitation; Thorpe 1956; Whiten 1998). These effects are not mutually exclusive but may synergistically support actions of the observer.

Our experimental design was aimed at determining any social-learning effect and at dissociating the various types of influences. Therefore it included a nonobserver control group to dissociate social effects on motivation, perception or learning in the observers. We also used the 'two-action test' (Dawson & Foss 1965; Whiten & Ham 1992; Heyes 1996) to determine whether observers copied the demonstrated behaviour; two groups of observers were permitted to watch one of two conspecifics demonstrating one of two alternative opening techniques on each device. Finally, to detect sequence imitation, one of two alternative opening sequences was shown to the observers.

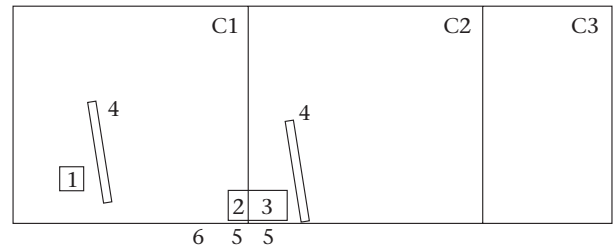


Figure 1. The experimental set-up in two compartments (C1 and C2) of the aviary, seen from above: 1=training table; 2=observer platform; 3=model table; 4=wooden walls; 5=positions of the digital video camera; 6=position of the VHS camera.

METHODS

Study Animals

We used 12 captive keas, five males and seven females, between their first and sixth summer since fledging. We had two adult males (5 and 4 years of age), one adult female (4 years), one subadult male (2 years), three subadult females (2, 3 and 3 years), one juvenile male and three juvenile females (1 year), and one male fledgling. They were all full siblings bred at the Konrad Lorenz-Institut für Vergleichende Verhaltensforschung in Vienna (KLIVV), and kept with each other since fledging. All birds were habituated to humans who interacted with them as feeders or experimenters.

Holding Conditions

All 12 subjects were kept together in an outdoor aviary at the KLIVV, Vienna, year round. The aviary measured 15 × 10 m and was 4 m high and could be flexibly divided into three compartments of equal size, each measuring 5 × 10 × 4 m (see Fig. 1); it was equipped with branches at different heights and with tree trunks and rocks on the ground. Water was available ad libitum. The keas were fed daily a mixture of vegetables, fruits, seeds, margarine and ox heart, and were kept at a constant weight. We used coloured rings to identify the birds. Before the experiment we used information on the direction of agonistic interactions at the food tray to rank them (see Tebbich et al. 1996).

Apparatus and Opening Techniques

The design of the experimental apparatus was adapted from the artificial fruit invented by Whiten et al. (1996) to investigate imitation of foraging techniques in chimpanzees, *Pan troglodytes*. As in this study, and in a recent study with capuchins, *Cebus apella* (Custance et al. 1999), no attempt was made to make the artificial fruit resemble real fruit but only functionally to mimic a resource that needed various types of manipulations to open it and extract an edible or otherwise attractive core. The box consisted of Plexiglas walls that were held in position by a blue-painted stainless steel frame, measuring 40 × 25 × 25 cm and weighing 13 kg. The top of the box consisted of a hinged lid made of Plexiglas framed in

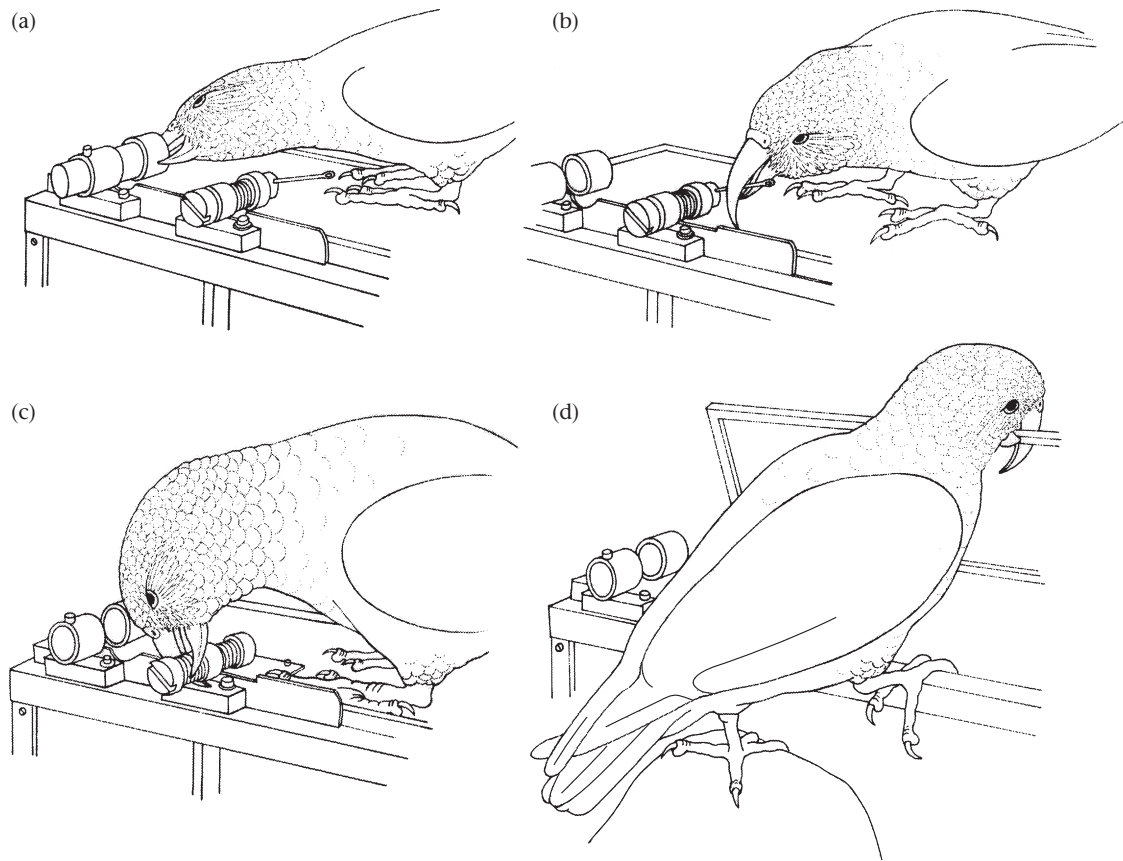


Figure 2. Schematic representations of the actions of model Blue-Blue opening the artificial fruit during observer training: (a) poking the bolt out of the rings; (b) pulling the metal split pin out of the screw; (c) rotating the screw; (d) raising the lid.

aluminium (weight 0.5 kg), and fixed to the steel frame by two hinges.

Before the lid could be opened, three sets of locking devices had to be removed (see Fig. 2): a screw, a split pin and a bolt. The white plastic (Polyamid 6) screw (2 cm diameter; 8 cm long) passed through a steel ring on the steel frame of the box and through a steel ring on the aluminium frame of the lid. The screw was threaded so that one full rotation moved it outwards by 2.5 mm. The protruding end of the screw was enlarged (2.6 cm diameter) and a groove made it easy for a kea to grasp this part of the screw with its bill. Attached to the rear end of the screw was a safety bolt that prevented the screw from being rotated. It consisted of a metal split pin, 9 cm long, which was firmly wedged in a hole in the screw and which required some force (range 0.5–1.5 N; mean 1.0 N) to be pulled out of the screw. Finally, a bolt latch was mounted on the upper-left edge of the box. A red plastic bolt (2.8 cm diameter, 5.3 cm long) passed through a metal ring on the lid and a metal ring on the frame of the box. This bolt was not threaded and could thus be poked out of the rings without twisting it.

Two of the three locking devices were designed so that two different techniques could be used to dismantle them (two-action condition). The screw had to be twisted either clockwise or anticlockwise, as we used two screws that were identical in all aspects except their thread; the bolt had to be poked out either from the front of the box

over the lid or from the rear side of the lid towards the front (a tiny screw in the metal ring, inserted either in the front or the rear part, served as a one-way blocker). Furthermore, the three locking devices had to be dismantled sequentially. This requirement was achieved by a safety bolt mechanism with a spring leaf that mutually blocked either the screw or the bolt latch; the metal split pin, in the rear of the screw, could be removed at any time.

Wooden tables were used as platforms for the experimental apparatus and wooden walls were erected to separate visually particular places in the aviary. We placed a large paving stone (10 × 10 × 10 cm) in front of the box as a step from which the birds could manipulate the lid.

The experiment was conducted in two of the three compartments of the outdoor aviary. In compartment 1 (see Fig. 1), the two models were trained on a training table (50 × 50 cm and 100 cm high) in the corner furthest from the adjacent compartment. This corner was visually separated from the two other compartments by a wooden wall (2 × 2 m). During the observer training, the models were transferred to compartment 2, where they opened the box on the model table (80 × 60 cm and 100 cm high). This table was placed directly at the wire-mesh separation between compartments 2 and 1, and was visually isolated by a wooden wall (2 × 2 m) from compartment 3, in which the remaining birds of the group were kept. During the observer training, one observer

was put into compartment 1. The observer platform (40 × 60 cm and 100 cm high) was placed in compartment 1 adjacent to the model table, at the same height and directly at the wire mesh.

The apparatus was put in place, and the data were collected manually on a prepared checksheet, by the experimenter (S.R.) who was positioned close to the front of the aviary near the observation window of the video camera (see Fig. 1). All observer and test sessions were recorded simultaneously by a digital video camera (Sony DCR-VX1000E), supported on a tripod and focused through a glass window (30 × 20 cm) that was inserted in the wire mesh of the front wall. This camera was directed towards the box at a distance of ca. 1 m. In addition, a VHS camcorder (Panasonic MC5) was positioned in front of compartment 1 during observer sessions capturing the events on both the observer and the model table.

Procedure

The experiment involved four distinct phases: model training, observer training, observer testing and control tests.

Model training

We selected as models the dominant and oldest male (Black) and a male of middle rank (Blue-Blue). These two birds proved to be the most manipulative and curious birds in the group during the winter before the experiment. They were held during the time of model and observer training (about 3 months) in compartment 1, separated from the group only through a wire mesh. Here they could be trained as models in isolation, to which they habituated well (daily separation from and reintegration into the group would have been very stressful).

Both birds received training by the method of successive approximation to the task of opening the apparatus. The experimenter was present at all times and led the birds through several successive steps of training. First, the box was presented without any locking devices and with the lid lying loosely on the box. The birds learned to push the lid away to reach into the box for food (butter plus egg yolk) or toys. The lid was then mounted on the steel frame at the rear of the box, and the birds learned to open the box by raising the hinged lid with their beak.

A further training step began by fixing the lid to the frame by mounting the screw device. First, the screw was twisted into the ring only about 2 mm so that only one rotation was required to remove the screw from the latch. As the birds became proficient in twisting and removing the screw, the screw was twisted into the ring to increasing depths until it was inserted 12.5 mm. At this final stage, complete removal required five full rotations. The birds acquired different techniques of removing the screw. While Black sat on the paving stone in front of the box and grasped the screw by inserting his mandible into the groove, Blue-Blue used to sit on the lid and grasp the middle part of the screw which was visible between

the two rings (see Fig. 2). At the end of screw training, Black performed between 20 and 25 rotating actions to remove the screw completely, while Blue-Blue performed between 25 and 35 actions, because his technique seemed to allow at best only a revolution of 90° at a time.

The last three steps involved training to pull the metal split pin out of the screw, thereafter to poke the red bolt out of the rings, and finally to dismantle all the devices in the given sequence. Black learned the following sequence: split pin, screw (anticlockwise), bolt (from the rear side of the lid towards the front); Blue-Blue learned the sequence bolt (from the front of the box over the lid), split pin, screw (clockwise). After the sequence was learned, the models were separately trained for 1 more week (about 20 openings) to perfect the opening techniques. The birds were used as models after they had dismantled all devices and opened the lid in less than 1 min from the first action.

Observer training and testing

We used equal numbers of birds as observers and nonobservers (controls). From the five observers, three were allowed to observe model Black (the subadult female Oldred, the juvenile female Green-Silver and the juvenile male Goldi), while two were allowed to observe Blue-Blue (the adult male Confetti and the juvenile female Red). The remaining five birds (one adult female, Yellow; two subadult females, Green and Red-Yellow; one juvenile female, Blue; and one male fledgling, Blue-Red) served as controls and were not allowed to observe a model before being presented with the apparatus during control tests.

The observer training involved three demonstration phases and three test phases for each observer after 1 day of habituation. During this time, all birds except one model and one observer were kept in compartment 3. One day before the start of the observer training, we placed one arbitrarily selected observer in the observer compartment and its model in the model compartment. After an observer passed through all phases of observer training and testing, we removed it from the observer compartment and released it back into compartment 3. The model remained in the model compartment until all its assigned observers had completed the observer training. Table 1 gives the sequence in which the observers were used and other details of the procedure.

The design of the observation training was intended to give the observers a maximum of observation opportunities within an overall time frame of 3 consecutive days. Because of the high interindividual differences in adapting to novel situations and the stress of isolation from the group we decided to be flexible in how long the observers attended the model's demonstrations. Instead of forcing them into strictly limited observer sessions, we terminated daily observer training only when the model stopped working. We counted the number of observed opening actions performed by the model (Table 1).

The mean duration of observer training prior to the tests was 132, 44 and 40.4 min for the first, second and third tests, respectively. The first test commenced

Table 1. Durations of observation and test phases, and the number of opening actions observed prior to each test

	Minutes of observation prior to			Actions observed prior to			Test duration (min)		
	Test 1	Test 2	Test 3	Test 1	Test 2	Test 3	Test 1	Test 2	Test 3
Observers									
Goldi	140	50	30	14	21	24	10	45	30
Oldred	190	40	60	10	15	23	30	30	65
Green-Silver	125	45	42	14	23	30	70	25	75
Confetti	120	55	50	12	17	24	25	75	20
Red	85	30	20	8	17	23	30	15	20
Controls									
Green							50	10	40
Yellow							315	20	180
Blue-Red							25	20	30
Red-Yellow							25	20	15
Blue							25	65	15

immediately after the observation session in which the 80th complete model sequence had been observed by the observer. At least 15 and 23 additional observed model sequences were required to start the second and the third test sessions, respectively. Independent of the presence of an observer at the observation platform, the models opened the apparatus repeatedly without considerable variations between repetitions. On average, model Blue-Blue opened the box quicker than model Black (ca. 60 versus ca. 90 s, respectively).

We tested each observer three times. Because of individual differences in perseverance of exploration, tests lasted for a variable amount of time (Table 1). Test sessions were terminated after a bird stayed away from the apparatus for more than 5 min continuously.

While the apparatus remained in place, the two birds in action (the model and the observer) were exchanged between compartments 1 and 2. After a habituation phase of 30 min we refilled the apparatus with food and the observer candidate was allowed to manipulate it. During the observer and control tests a white plastic bolt was used instead of the screw. This 'non-functional screw' was identical to the real screws except that it was not threaded so that it could be poked out of the rings without twisting it. The red bolt could be poked out in both directions instead of one. These modifications were done to see if the observers copied the actions that had been demonstrated by the models.

Control testing

The control birds were individually tested in compartment 2 at the model table on 3 consecutive days. One day before the test we placed one arbitrarily selected control in compartment 2 to habituate it to the new situation. On the subsequent test days it was presented with the artificial fruit at the model table and allowed to investigate the apparatus until it left the apparatus voluntarily for more than 5 min. Before the control bird could investigate the apparatus S.R. filled it with attractive food. If a control bird lost interest after less than 10 min (stayed away

from the apparatus for more than 5 min continuously), we tested it again on the next day. Table 1 lists the test duration for each bird.

Observer reliability and statistical analysis

The behavioural sequences were analysed by S.R. from the videotapes by recording the occurrences of events on an all-occurrence basis over the entire test. Using the Observer software (Noldus Inc., Wageningen, The Netherlands) we coded from the videotapes the first touch of the apparatus and the first touch of a locking device in each test, as well as all manipulations with the apparatus. Specifically we coded twisting, pushing and pulling actions and the object at which they were executed. Opening success was defined for each locking device as complete removal of the removable part (bolt, pin and screw) from the fixed part (the metal rings or the screw, respectively). We specifically coded the duration of unsuccessful manipulation of the bolt as duration of manipulation until a bird either succeeded or gave up. In addition, we recorded the fine-grained pattern of the action sequence of the most successful observer and the most successful control during the first test session on a purely descriptive level. These additional recordings were not used for statistical analysis.

To control for any experimenter bias, eight independent ethologists from the Institute of Zoology, as well as S.R., were asked to score a tape that showed the first test session of observer Green-Silver. We asked them to identify the exact time when the bird's beak touched the bolt and then compared the scores ($N=11$) of every rater with the scores of S.R. The mean squared error was 0.5 s. A paired t test (one tailed) showed that S.R.'s ratings did not deviate significantly from the independent raters' codings ($t_{10}=0.73$, $P=0.48$).

We used nonparametric, two-tailed tests (Mann-Whitney U test) and a 0.05 level of significance (α) to compare means between groups. The results are given as the median and quartiles Q1 and Q3.

RESULTS

Exploration Time

Observers and control individuals differed in their time spent at or near the apparatus and in their perseverance of object exploration. The observers spent a median of 714 s (537.8–920.8 s) over the three test phases exploring the apparatus and its devices, while the control birds were active at the apparatus for only 171 s (61.5–308 s; Mann–Whitney U test: $U=25$, $N_1=N_2=5$, $P<0.01$). Observer and control birds did not differ in the time they spent at the apparatus until they left the table in the first test session (observers: $N=5$, median 255 s, 122.5–455 s; control birds: $N=5$, median 60, 51–184.8 s; Mann–Whitney U test: $U=20$, $N_1=N_2=5$, $P=0.15$). Observers used between 93 and 100% of the complete exploration time in the first test for tactile activities, while control birds used only between 0 and 7% of time for tactile exploration (Mann–Whitney U test: $U=24.5$, $N_1=N_2=5$, $P<0.02$). Because neither observers nor control birds succeeded in opening the lid and reaching the desired reward, differences in persistence of exploration cannot have been due to reinforcement effects.

Time until First Contact

The median latency from the first contact with the apparatus to the first contact with one of the locking devices (screw, split pin, or bolt), calculated across all three test sessions, was 0 s (0–3.8 s) for observers and 17 s (3.5–22.5 s) for controls (Mann–Whitney U test: $U=23.5$, $N_1=N_2=5$, $P=0.02$). This difference also became obvious in the individual analyses of time periods (Fig. 3).

Because control birds were initially more interested in looking at the apparatus and nibbling at the frame, lid and walls of the box, they spent relatively little time manipulating the locking devices (screw, split pin, or bolt). Perseverance at manipulating all three devices during tests was much higher in observers than in controls (observers: median 372 s; 107.3–534.5 s; controls: median 33 s; 11.8–148.3 s; Mann–Whitney U test: $U=25$, $N_1=N_2=5$, $P<0.01$). When separated for the five different parts of the box, a difference between observers and controls appeared to be significant only for the screw (more exploration in observers) or approached significance for the lid (more exploration in controls; Table 2).

Opening Success

Although neither observers nor control birds ever succeeded in opening all the devices and the lid, thus reaching the desired reward, there was a striking difference between members of the observer and control groups in their success at opening the three locking devices. All five observers opened at least one device in each test phase while only one control bird did so in the first and second tests, and two control birds opened one device in the third test. Two observers (Oldred and Green-Silver) were able to dismantle all three devices but no control bird opened more than one device (Table 3). The number of successfully opened locks (range 0–3) was

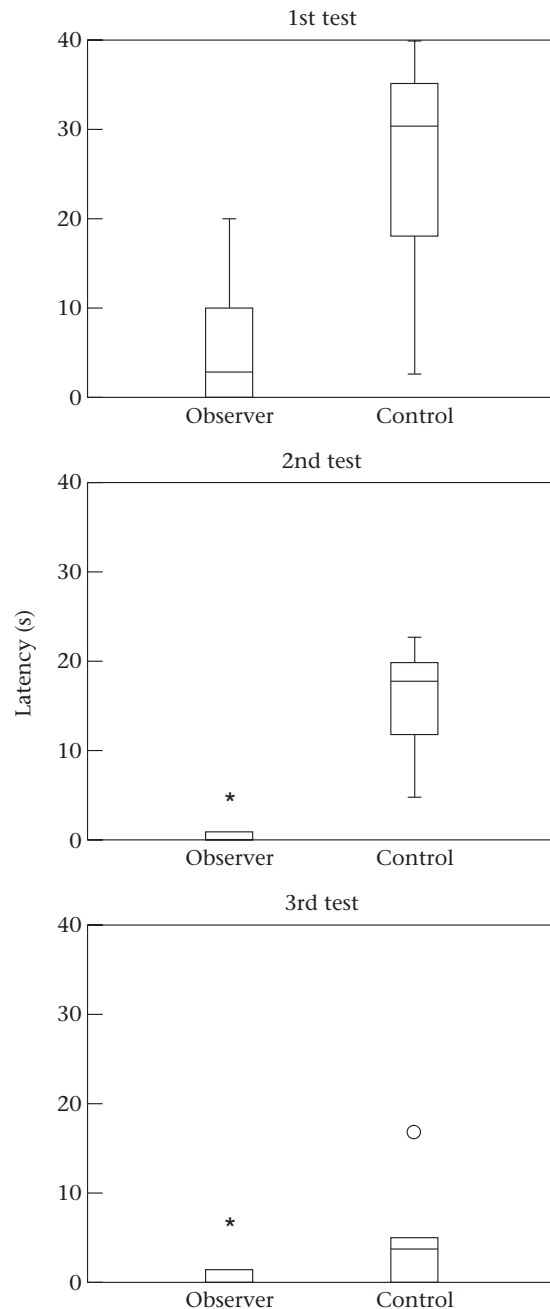


Figure 3. Latency from the first contact with the apparatus to the first contact with one of the three locking devices (screw, split pin and bolt). The two experimental groups are compared separately for each of the three test phases. If the first contact with the apparatus was made with one of the devices instead of any other part of the box, we scored the latency as zero. The bottom, middle and top horizontal lines of each box show the 25th, 50th (median) and 75th percentiles, respectively. The whiskers extend to the 90th percentile. The circle indicates data values between 1.5 times and 3 times the interquartile range above the 75th percentile and asterisks values more than 3 times the interquartile range above the 75th percentile.

significantly different between observers and controls for the first test session (Mann–Whitney U test: $U=23$, $N_1=N_2=5$, $P=0.015$), and for the whole test (Mann–Whitney U test: $U=22$, $N_1=N_2=5$, $P=0.031$).

Table 2. Relative time ($\bar{X} \pm SD$) spent at the different parts of the apparatus across three tests

	Observers	Controls	<i>U</i>	<i>P</i>
Box	27.3±7.0	25.0±10.4	13.0	0.92
Lid and rings	24.6±15.6	41.1±12.4	20.5	0.09
Screw	35.1±13.9	12.8±8.0	24.0	0.02
Bolts	8.8±2.6	13.3±7.5	7.5	0.29
Split pin	4.3±3.8	7.8±8.3	10.0	0.60

The relative time is given as percentage of the total exploration time in each of three tests, averaged over five individuals in each group. The probability of accepting the null hypothesis is derived from a Mann–Whitney *U* test.

Overall, of all locking devices the bolt mechanism was opened most successfully. Four of five observers achieved bolt opening in the first test session and one control bird (Green) eventually removed the bolt in the third session. The duration of unsuccessful manipulation of the bolt varied considerably between individuals, but not significantly between the experimental groups (observers: median 36 s; 29.8–102 s; controls: median 80 s; 54.8–106.5 s; Mann–Whitney *U* test: $U=7$, $N_1=N_2=5$, $P=0.31$). The variation appeared to be closely related to the individuals' success; the four successful observers manipulated the bolt only for 37 ± 18 s ($\bar{X} \pm SD$) until they removed it in the first session, whereas the one unsuccessful observer manipulated it for a total of 225 s over all three test sessions.

Table 4 compares the sequence of actions in the first test between the most successful bird in each group. The female observer Green-Silver achieved quick success with the locking devices because her opening actions appeared to be not completely arbitrary, as they were in the control bird, but included several long sequences of poking and pulling. Therefore, the observer required as few as 34, 10 and 17 s to open the bolt, the split pin and the screw, respectively. In contrast, the most successful control bird (the female Blue), although showing greater patience than the observer in probing and manipulating the three devices, seemed to sample from the whole repertoire of foraging and play actions to see what worked, and only by chance arrived at an efficient means of manipulating the chosen object. Therefore, forceful pulling actions appeared only late in the course of manipulating the split pin, eventually leading to its complete removal after 77 s.

Response Matching

To check for evidence of imitation we compared the frequencies with which the observers and controls performed twisting, pushing and pulling, regardless of the target object. Sometimes observers attempted to twist the 'screw' or the bolt, but such attempts appeared sporadically in the control group, too. In each experimental group, observer and control, one bird engaged in twisting actions frequently (24 and 9 times, respectively), but there was no significant difference in twisting frequencies between groups (both medians 1). Pushing movements were shown more often by observers than controls

(medians 15 and 10; Mann–Whitney *U* test: $U=22$, $N_1=N_2=5$, $P=0.046$). Pulling movements were shown about equally often in both groups (both medians 10).

There was also no indication of model-consistent manipulation of the three devices by the observers, that is, the response topography, the twisting direction and the opening sequence did not differ between the two observer groups (two-action test) nor between experimental groups. All observers began to investigate the bolt (demonstrated by the model Blue-Blue). No observer of model Black began with the pin. Three control birds began with the bolt, two with the screw. In all 10 birds the pin was manipulated third.

Observational learning could also have led to the birds knowing at which object which manipulation is appropriate. However, such object-movement dependency is only worth considering in the case of twisting, because the bolt could not be pulled before being poked and the pin could not be poked or pushed but just pulled. If imitation occurred, observers should have demonstrated a higher frequency of screw twisting than bolt twisting, and this proportion should be higher in observers than in controls. From the 28 twisting actions performed by observers in the first test session, the screw/bolt proportion was 21/7. However, it was 11/2 in the controls, so there was no significant observational effect to be detected.

DISCUSSION

Keas that observed the skilled performance of a trained conspecific showed, in comparison with birds of a non-observing control group, (1) faster approach to the locking devices, (2) extended persistence in their manipulative actions, (3) relatively more tactile exploration, and (4) greater success in opening the locking devices. Altogether, these results provide strong evidence for social effects on object exploration in this species.

The highly significant effects of observing a model on approach and manipulation persistence point to mechanisms of social facilitation and stimulus enhancement. As far as we are aware, social effects on object exploration have never been studied under tight experimental conditions. The models' extraordinarily repetitive and persistent activities at the empty box during model training appeared to depend on a very powerful, intrinsic motivation. This may reflect an innate preference for object play and exploration, which are both highly facilitative (Diamond & Bond 1999). We suggest that the combination of a highly active conspecific and a novel object increased significantly the keas' curiosity.

Our results also suggest that the keas learned something during observation. Perceptual factors may lead to learning about the environment as a result of the behaviour of others. Such learning can be highly advantageous whether response matching is involved or not. The observers' performances indicated that the enhancement effects were relatively fine tuned, thus drawing the observers' attention to the specific parts of the object with which the model was interacting. The keas were attracted not only by the box as such (generalized

Table 3. Locking devices that were successfully opened during the test phases of observer and control birds

	Test 1	Test 2	Test 3
Observers			
Goldi	Bolt	Bolt	Bolt
Oldred	Bolt	Bolt	Bolt, Split pin, Screw
Green-Silver	Bolt, Split pin, Screw	Bolt, Split pin	Split pin
Confetti	Bolt	Bolt	Bolt
Red	Split pin	Split pin	Split pin
Controls			
Green	—	—	Bolt
Yellow	—	—	—
Blue-Red	—	—	—
Red-Yellow	—	—	—
Blue	Split pin	Split pin	Split pin

Table 4. Action sequences of the most successful observer (Green-Silver) and the most successful control (Blue) during the first test session until success

Subject	Time (min)	Action list
Green-Silver	0	tB gS tB pB pB pB pB pB rB rB tRB gB rB tB gB gB tS gS tRS gS gB gRB tB gS gS nS
	1	gR gR pB pB pB pB plB thB thB tBO tB tS gS gS gP mP mP iP pIP pIP pIP thP gS iS pS gS pIS thS
Blue	0	tRB tB gRB tB gRB taRB tL gP tBO tBO nBO tL gL gS
	1	taS nS gS gRS gS tL gS tBO nS gS rS nS taRS tP taP tL gB gRB taRB tRB NL gL gL
	2	tL gB tRB tB taB gS taS taRS taS tL gS gRS gS gP mP
	3	tL tB tB taL gB taB tRB tL tP gS gRS iP gS tP mP iP gP pIP iP gP taP gP
	4	gRS tL tP tP gP iP mP iP mP pIP mP gP gS gRS gP tL gRS tL
5	tB tL tBO tL gL gP pIP iP iP pIP mP pIP pIP pIP thP	

The actions are coded by a symbol for the action (lower case) and a symbol for the object (upper case) at which the action was executed. Forceful movements (see text) are given in bold. Actions: touch (t), taste (ta), grasp (g), rotate/twist (r), push/poke (p), pull (pl), throw (th), nibble (n), insert the upper or the lower bill into the ring of the split pin (i), move the split pin up and down (m). Objects: bolt (B), split pin (P), screw (S), lid (L), metal rings of either screw (RS) or bolt (RB), frame, walls, and all other parts of the box (BO).

stimulus enhancement), but specifically by the screw, bolt and split pin (localized stimulus enhancement; see Caldwell et al. 1999), which was reflected by short approach latencies to these locks, and great persistence at manipulating them.

There was no evidence of true imitation, that is, the copying of the response topography of the opening technique shown by the models. It might be argued that the alternative directions of manipulation were too similar at the observers' distance to have such fine-grained effects, or that the differences between the alternatives had no special meaning for the observers that would lead them to copy them. One further reason for the failure to find imitation is that the observers in this experiment saw 'too much too fast' during demonstration sessions. That is, the demonstrated skill might have been too complex, and too swiftly executed, for the observers to learn the actions in the available time, and without prior experience of manipulating the apparatus themselves.

One salient alternative explanation is that the kea's propensity for exploration, object play and demolition runs counter to the exact reproduction of movements demonstrated by others. It may be a chief characteristic of explorative and playful animals to use their own, idiosyncratic methods to manipulate attractive objects. In the

keas, this has been suggested from field observations (Diamond & Bond 1999). Being attracted by a conspecific to explore a novel object does not necessarily lead to slavish copying, but may lead to learning what parts of the object are worth exploring (Huber 1998).

The striking difference between observer and control groups in terms of opening success of the locking devices suggests additional, social-learning effects. The observers' superiority in this respect cannot be accounted for by simple attraction to the box or its parts and subsequent trial-and-error learning. Note that, for instance, the observers were not always first attracted to the bolt mechanism but opened it (with one exception) in the first test session after 30 s of manipulation on average. A closer look at the behaviour of the most successful bird of each experimental group during the first test session further supports our conclusion that opening success did not result from mere trial-and-error-learning.

Two arguments in favour of stimulus enhancement as an explanation of the observers' opening superiority must be considered. First, the activities of the models might have made those parts of the removable objects attractive at which the pulling or poking action should be executed. The split pin, for instance, had two clearly distinctive ends. Only at the one with the loop were pulling actions

successful. If the observers were attracted towards the loop and thus directed their initial manipulations to the 'correct' locus of the objects, manipulation efficiency should be increased. However, the observers did not prefer the 'correct' parts of the devices. Green-Silver, for instance, began nibbling at the 'incorrect' part of the split pin, began nibbling at the screw head but then poked it out from behind, and made first contact with the bolt at the part that was visible between the tunnels.

Second, by seeing a model manipulating a removable object, observers may be subject not only to attentional shifts, but also to specific motivational shifts towards the execution of species-typical movements. For instance, Palameta & Lefebvre (1985) found that observer pigeons were sufficiently motivated to pierce through a paper lid on a dish of food only when they saw the whole sequence of pecking through the lid and then eating the seed beneath. Observer birds who saw (1) models peck through the lid to an empty dish or (2) eating through an already made hole in the lid did not learn to peck through the lids themselves. In the keas, the highly salient activities of the models might have been particularly powerful enhancers so that, even if all birds were likely to explore the removable objects, only observers were sufficiently motivated through stimulus enhancement to direct sustained and vigorous actions towards these parts of the box, and then learned the actions through their own efforts.

The striking asymmetry in the opening efficiency between the experimental groups could be a result of the observers' acquisition of specific information about the function or the potential use of the locking devices. Rather than learning that the split pin, for instance, is a signal for food, or is attractive as a manipulandum, or has an attractive loop end, the observer may have learnt that the split pin 'can be removed' or 'can be pulled out'. Such information about the functional significance of objects may be acquired during a process of 'action-outcome contingency learning' (Heyes 1993). However, this would imply that the observer formed an association between an object and the particular action the model used to produce a specific change of state in the environment. At least at a detailed level such response matching (e.g. twisting the screw) was not found. An alternative formulation in the sense of what can be done (declarative, e.g. removing) with the object rather than what must be done (procedural, e.g. twisting) is implied if we think of 'affordance' (Gibson 1979) learning or 'object movement reenactment' (Custance et al. 1999). From detailed observation in the wild, Diamond & Bond (1999, page 79) concluded that the keas' 'interest in objects for demolition is related more to the objects' affordances than to its potential for providing food resources'.

In contrast to imitative learning, observers used what they learned in devising their own behavioural strategies, what Tomasello (1990) called emulation learning. Chimpanzees who observed a conspecific using a rake to obtain food were much more efficient in using the tool on their own than nonobserver animals (Tomasello et al. 1987). Although our observers did not copy their model (e.g. by twisting), they obviously learned something

important about the task. Having seen an object used in some way, the observer knows that this functional use is possible for this sort of object (e.g. 'the white screw can be removed'). Perhaps understanding the change in the world produced by the manipulations of another individual may be the observer's only way of learning that such a change of state is possible (Tomasello 1996).

With respect to the acquired representation, we regard emulation learning as being cognitively quite demanding. Just looking in the direction of environmental changes is not sufficient to learn about and reproduce them. Capuchins, for instance, were unable to learn to use efficiently a tool they had repeatedly observed being used by others (Visalberghi 1993). Emulation learning may involve not only some understanding of affordances of objects but also causal understanding of some sort (M. Tomasello, personal communication). How these two relate or, if indeed they are part of the same basic cognitive skill, is an important question for future research.

Acknowledgments

Financial support was provided by the Jubiläumsfonds of the Austrian National Bank (grant P-6289). We are grateful to Cecilia Heyes, Michael Tomasello, Andrew Whiten and Thomas Zentall for their comments on the manuscript, to Johannes Fritz, Thomas Bugnyar, Bernhard Voelkl, Sabine Tebbich and Michaela Ritzmeier for their contributions in discussion, to Christine Grabmayer for help with kea handling, and to Heidemarie Grillitsch for drawing Fig. 2.

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