Animal Behaviour 223 (2025) 123166

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Stimulus enhancement in kea, *Nestor notabilis*, in an object choice task

Elisabeth Suwandschieff [a, *], Yasmin M. Gräter [a, 1], Remco Folkertsma [b, c, 2], Amelia Wein [a, 3], Raoul Schwing [a, 4]

[a] Haidlhof Research Station, Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine, Vienna, Austria
[b] Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine, Vienna, Austria
[c] Platform Bioinformatics and Biostatistics, University of Veterinary Medicine, Vienna, Austria

ARTICLE INFO

Article history:
Received 9 August 2024
Initial acceptance 13 September 2024
Final acceptance 15 January 2025
Available online xxx
MS. number: 24-00492R

Keywords:
kea
local enhancement
Nestor notabilis
object choice task
social learning
stimulus enhancement

Previous studies illustrated that kea, *Nestor notabilis,* can apply socially acquired information to solve both simple and complex tasks. However, evidence of which social learning mechanisms kea utilize is still vague. Therefore, in this study, we investigated the role of stimulus versus local enhancement as mechanisms of social learning in an object choice task. We presented 10 kea individuals with objects of four different shapes and nine different colours and tested whether observer kea would copy the object and/or apparatus choice of two demonstrator kea, which were given free choice. This experimental set-up significantly decreased training rotations for demonstrators and led to randomization across trials, thus presenting a promising new technique for future studies. Overall, observer kea chose the same objects more often than expected by chance, suggesting some evidence for stimulus enhancement as the primary social learning mechanism. Meanwhile, we find no evidence for local enhancement. These results are in line with kea behavioural ecology as an inquisitive island species that spends a lot of time gathering information about objects (i.e. stimuli). Additionally, highly fluctuating resource availability and depletion rates in their natural environment could make the information of locality less valuable to them. This study helps explain ambiguous results from past experiments and supports distinguishing the different processes at play in the social learning of kea. To understand the full picture of social learning in kea, less complex mechanisms, such as stimulus enhancement, will need to be tested and excluded in future experiments.

Social learning is the acquisition of information from an individual through observation (Heyes, 1994). It can be defined as ‘learning that is facilitated by observation of, or interaction with, another individual (or its products)’ (Heyes, 1994; modified by Hoppitt & Laland, 2013, p. 4). It requires observers, those individuals watching an interaction of another individual with the environment, to identify this interaction or behaviour as a source of information for their behaviour. Learning from conspecifics can have adaptive advantages over individual learning, as it minimizes the cost associated with information acquisition, making it less dangerous and time-consuming than trial-error learning (Reader, 2016). Through social learning, (naïve) individuals can learn about foraging behaviour that is, what to eat, when and where (Galef & Giraldeau, 2001), learn about predators (Griffin, 2004) and/or how to move through their habitat safely, without having to explore the whole habitat itself (Mörchen et al., 2023). For a long time, social learning was considered a special skill unique to humans (Heyes, 2016; Meltzoff, 1988). However, experimental evidence has illustrated social learning in numerous species across the animal kingdom (Auersperg et al., 2014; Brown & Laland, 2003; Call et al., 2005; Custance et al., 1999; Funk, 2002; Galef, 2002; Huber et al., 2001; Huber & Gajdon, 2006; Slagsvold & Wiebe, 2011; Suwandschieff, Wein, et al., 2023).

Social learning can be differentiated into different mechanisms (Zentall, 2006). Following Hoppitt and Laland (2013), individual mechanisms can broadly be broken down into action- or context-specific effects, that is, are the specific actions of a demonstrator learned, or alternatively, does learning occur in a specific context such as location or response to a specific stimulus (Logan et al., 2016)? Social learning mechanisms that are action-specific describe the direct copying of others or their products, that is, imitation (Thorpe, 1963) and emulation (Tomasello et al., 1987). This

---

* Corresponding author.
E-mail address: Elisabeth.Suwandschieff@vetmeduni.ac.at (E. Suwandschieff).
[1] *E-mail address*: yasmin@graeter.de (Y. M. Gräter).
[2] *E-mail address*: Remco.Folkertsma@vetmeduni.ac.at (R. Folkertsma).
[3] *E-mail address*: ameliawein@gmail.com (A. Wein).
[4] *E-mail address*: Raoul.Schwing@vetmeduni.ac.at (R. Schwing).

https://doi.org/10.1016/j.anbehav.2025.123166

study focuses on the context-specific mechanisms that are associated with locality or stimuli, such as local and stimulus enhancement. For a detailed specification of all the different social learning mechanisms see Hoppitt and Laland (2013) and Zentall (2022).

Local enhancement (Thorpe, 1963) occurs when the observer's attention is drawn to a specific location because of the demonstrator's behaviour in that location (Zentall, 2006). In the classic example by Lorenz, ducks (species unspecified), only learned an escape location (hole in the pen) after seeing another duck escape through this location (Lorenz, 1935). Atlantic canaries, *Serinus canaries*, however, specifically used the information provided by their fathers concerning foraging locations (Cadieu et al., 1995). Stimulus enhancement (Spence, 1937) occurs when the observer's attention is drawn to a stimulus, or features thereof, because of a demonstrator interacting with it (Zentall, 2006). For example, house sparrows, *Passer domesticus,* used the information on food colour provided by a demonstrator to select novel food types (Fryday & Greig-Smith, 1994). Graylag geese, *Anser anser*, however, who received a demonstration showed increased attention (and solving success) to a wooden bar in a lid-opening experiment (Fritz et al., 2000).

Stimulus enhancement, in contrast to local enhancement, also requires ‘generalization since the observer's attention is drawn not only to the object with which the model is interacting but also to objects of the same type at other locations and the same object at other times' (Fritz et al., 2000, p. 1120; Giraldeau, 1997; Spence, 1937). Thus, the observer must remember the object and form associations between similar objects in different locations. In contrast, local enhancement ‘occurs when, after or during a demonstrator's presence or interaction with an object at a particular location, an observer is more likely to visit or interact with the object at that location’ (Hoppitt & Laland, 2013 cited in Wild & Hoppitt, 2022, p. 6519), hence it is locally bound.

Local and stimulus enhancement are often referred to as simpler mechanisms as they are associated with indirect contextual learning, that is, they ‘influence the probability of learning’ (Fritz et al., 2000, p. 1123), but need not result in direct actions being learned. Nevertheless, they can play a pivotal role in action-specific social learning mechanisms (Heyes, 1994; Hoppitt & Laland, 2008; Zentall, 2011) as local and/or stimulus enhancement may facilitate action learning by initially increasing the salience of the location or stimulus (Zentall, 2011). Additionally, both local and stimulus enhancement can occur simultaneously and are not always distinguishable from one another, especially if the stimuli in question are in a set or fixed location (Zentall, 2011). While there is plenty of experimental evidence for social learning in avian species (Akins & Zentall, 1996; Auersperg et al., 2014; Dawson & Foss, 1965; Fawcett et al., 2002; Heyes & Saggerson, 2002; Huber et al., 2001; Loretto et al., 2020; Nguyen et al., 2005), the exact differentiation between the mechanisms at play often remains ambiguous. This is in part due to the experimental set-ups aimed at testing for action-specific mechanisms such as imitation. As it can be difficult to distinguish between the different social learning mechanisms and several mechanisms may be at play simultaneously, local and/or stimulus enhancement may appear as byproducts of the experimental design. For an overview of experimental evidence of action-specific social learning mechanisms resulting in ambiguous results as well as potential alternate explanations see Zentall (2006).

Kea parrots, *Nestor notabilis,* were tested on their imitative and nonimitative social learning capacities (that is, action-specific mechanisms) in several experiments (Huber et al., 2001; Suwandschieff, Huber, et al., 2023; Suwandschieff, Wein, et al., 2023) that showed such ambiguous results about context-specific mechanisms. Kea failed to show imitative behaviour when solving an artificial fruit task, yet did show fine-tuned enhancement effects, as both generalized (test box) and localized (individual locking devices) stimulus enhancement (Huber et al., 2001) could be demonstrated. Suwandschieff and colleagues illustrated that both social facilitation and local enhancement may explain the results of a simple two-choice task experiment consisting of removing stoppers from a test box (push—pull actions) as observer birds were faster in their initial response to the box compared with nonobserving control group birds (Suwandschieff, Wein, et al., 2023). The results of the final study suggested that kea solved a two-step sequence task via emulation as individuals showed pronounced exploration and behavioural flexibility; however, no evidence for imitation could be found, despite clear social learning effects in the observer group. While all three studies could find evidence for social learning in these experiments, the exact mechanisms that were associated with task acquisition remained inconclusive. This is in part due to simpler mechanisms, such as stimulus and/or local enhancement, not being directly tested, that is, to be able to focus on the effects of the demonstration, all options presented, and all actions that led to these were rewarded. As the importance of local and stimulus enhancement as potential mechanisms for social learning was not directly tested, basic knowledge about these mechanisms in kea is missing to date. The study at hand aims to close this gap.

Kea are parrots endemic to the mountains of the South Island of New Zealand. Kea have many characteristics that support social learning (Gajdon et al., 2004). Low predation rates during their evolution along with the uncertainties of their natural habitat, which is marked by seasonal and local fluctuations in food availability, have resulted in a highly exploratory species that shows strong behavioural flexibility and curiosity (Diamond & Bond, 1999; Huber et al., 2001; Smith et al., 2022; Suwandschieff, Huber, et al., 2023). Kea apply social learning; however, limited evidence for the social learning mechanisms at play could be illustrated in this species to date. To bridge this gap and understand which context-specific social learning mechanisms could potentially be relevant for kea, the study at hand, therefore, specifically tested first for stimulus enhancement and then local enhancement as mechanisms underlying social learning in kea.

Using an object choice task within a demonstrator and observer experiment (Gajdon et al., 2004; examples include Huber et al., 2001; Kis et al., 2015; Klein & Zentall, 2003) provided a promising experimental design to investigate whether information such as stimulus and later location are used by kea when solving a task. Object choice tasks are often found in the cognition and behaviour literature and have mostly been used to study animals' abilities to interpret human or conspecific cues (Kaminski et al., 2005) or test cognitive abilities in an experimental setting (Bastos & Taylor, 2020; O'Hara et al., 2015). By adding an object selection to the demonstrator—observer set-up, we aimed at narrowing down on and separating the effects of local versus stimulus enhancement. The object choice task provided the opportunity to test several different stimuli simultaneously and also add different locations across different experimental conditions (see details on individual conditions below). Kea have illustrated in the past that they are very good at adapting to changing reinforcement contingencies in within-session reversal learning tasks (Laschober et al., 2021). In addition, the novel set-up allowed us to overcome one of the main hurdles when using conspecific demonstrators: the time-consuming training of reliable action demonstration. Previous social learning experiments with kea had limitations because each demonstrator could only perform a single action or sequence of actions. Here we presented a demonstrator with a choice of different objects to insert into a box and rewarded any demonstrator choice. We addressed the effects of stimulus and local enhancements on the observers' choice by varying the objects and providing alternative box positions.

Our main research question was whether kea could learn to select the same stimulus as a conspecific demonstrator in an object choice task. We hypothesized that observing a conspecific solving an object choice task, that is, interacting with a specific stimulus (object), would affect the stimulus choice of an observer bird. We predicted that observers would significantly choose the demonstrated object choice over other available options. We tested this by having a demonstrator choose from two or four objects and inserting the chosen object into a box in conditions 1 (two objects, one box), 2 (four objects, one box) and 3 (four objects, two boxes). Furthermore, we hypothesized that adding a demonstrated location would affect the location choice of the observers. We predicted that the location of the demonstrator's box would influence the observer's box location choice. We tested this by having a demonstrator choose either one or between four objects and insert the chosen object into one box with differing locations in conditions 3 (four objects) and 4 (one object).

METHODS

Ethical Note

The study was approved by the ethics and animal welfare committee of the University of Veterinary Medicine Vienna (ETK-178/11/2022), Austria, following good scientific practice guidelines and national legislation. The housing conditions comply with the Austrian Federal Act on the Protection of Animals (Animal Protection Act; § 24 Abs.1 Z 1 and 2: § 25 Abs. 3; TSchG, BGBl. I Nr. 118/2004 Art. 2). As the study was strictly noninvasive, according to the Austrian Animal Experiments Act (TVG 2012), it was not classified as an animal experiment.

Housing

All testing took place at the Kea Lab, located at the Haidlhof Research Station (HHR) in Bad Vöslau, Austria. The Kea Lab is a group of 29 captive kea parrots permanently housed in a large outdoor aviary (52 × 10 × 4 m, L × W × H; Fig. 1), which is equipped with hanging branches, shelters for resting and protection against the weather, ponds, feeding tables and environmental enrichment that is renewed regularly. The aviary contains two breeding compartments, which are closed during the breeding season, two experimental compartments (10 × 6 × 4 m) on opposite ends of the aviary, and a large central area that serves as the main living quarters. Outside of testing times, the experimental compartments are left open, as they serve as additional living space.

The experimental compartments can be divided into two equally-sized subcompartments with a sliding, see-through wire-mesh door. All testing took place in the experimental compartments.

Kea are fed three times daily with a mixture of fruit, vegetables, seeds and protein (cooked meat or eggs). Water is available ad libitum in bowls and ponds. Kea subjects are never food-deprived for experiments, and rewards are highly valued treats (in this case peanuts), which were shown to be preferred over food items that are part of their regular diet (Schwing et al., 2017). All participation in experiments is voluntary, and only positive reinforcement is used. Subjects are trained to enter experimental compartments on command and can refuse to work by ignoring the command. Once inside the experimental compartment, they can end a session early by retreating to shelters, lying down on the ground, or otherwise refusing to participate. If this happens, the subject is directed back into the main aviary, and testing is attempted another time. If a subject refuses to work three times in a row, that subject is dropped from the experiment.

Kea are a gregarious species that live in fission–fusion social flocks (Diamond & Bond, 1999). While a dominance hierarchy is maintained, this hierarchy is nonlinear (Diamond & Bond, 1999). Twelve adult kea participated in this study: five females and seven males. Their ages ranged from 6 to 23 years (Table 1). To remove age group as a factor, no juveniles were included in the study. To prevent disruption during the breeding season (which affects females significantly; see below) and to modulate the effect of rank, which is assumed to influence task acquisition in, for instance, vervet monkeys, *Chlorocebus aethiop* (van de Waal et al., 2013), two high-

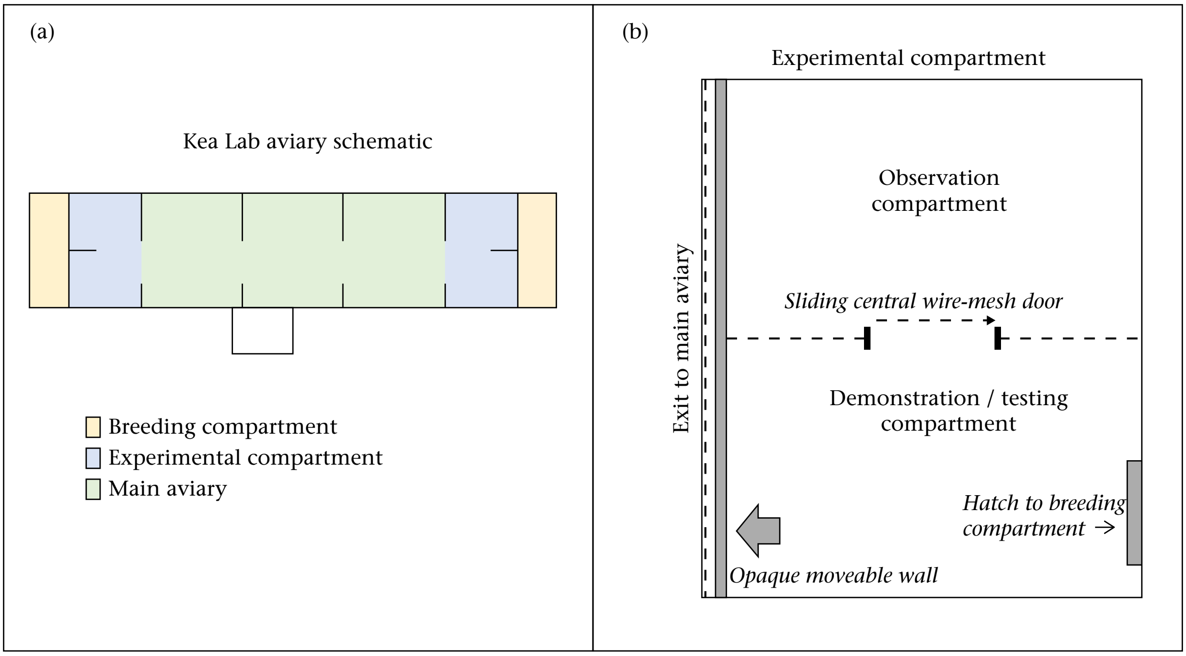

Figure 1. (a) Schematic of the whole kea aviary, as well as a detailed view of the experimental compartments where all testing took place. Outside of testing times, the experimental compartments were left open as part of the main living space for the kea. (b) Observers stayed in the observation compartment and watched the demonstration through the central sliding wire-mesh door. After the demonstration was complete, the demonstrator was sent out, and the observer was given access to the demonstration/testing compartment.

Table 1
List of subjects, age, sex, role in experiment and condition participated

Subject	Age	Sex	Role	Conditions			
				1	2	3	4
Diana	6	F	Observer	y	y	y	y
Kiri	8	F	Observer	y	y	x	x
Lilly	16	F	Observer	y	y	x	x
Mali	9	F	Observer	y	y	x	x
Plume	16	F	Observer	y	y	x	x
Jean Luc	8	M	Observer	y	y	y	y
John	23	M	Observer	y	y	y	y
Odo	8	M	Observer	y	y	y	y
Pancake	6	M	Observer	y	y	y	y
Skipper	6	M	Observer	y	y	y	y
Frowin	19	M	Demonstrator	y	y	x	x
Kermit	19	M	Demonstrator	y	y	y	y

F: female; M: male. y: yes; x: no.

ranking males served as demonstrators and the 10 remaining individuals participated as observers.

Breeding season plays an important role in territorial behaviour in kea, with breeding pairs showing increased aggressive behaviour and low tolerance towards others (conspecifics and heterospecifics) during the reproductive season (Orr-Walker & Jenkinson, 2024). Especially females show increased aggressive behaviour and ‘elevated concentrations of faecal glucocorticoid metabolites (fGCMs)’ (Donelan et al., 2022, p. 107). Due to the aggression rates and stress on the breeding pair in captivity, they are typically separated into breeding compartments for this time (Wein et al., 2021). Breeding pairs remain separated until eggs are laid and incubation has started, at which point male breeding partners return to the group (main aviary) and receive 1 h daily access to the female in the breeding compartment (Wein et al., 2021). This approach facilitates the continued integration of the males in the group while mimicking natural male breeding behaviour; the males typically forage during the day and only briefly return to the female to feed them. The breeding–brooding season can last 5–7 months, between November and May (ex-situ northern hemisphere adaptation; Donelan et al., 2022). The final rearing period for kea chicks is quite long: ‘approximately four months from the start of incubation to chicks fledging’ (Pullar, 1996, p. 9). Altogether, this is a considerable amount of time influencing kea (especially female) behaviour, which needs to be considered when interpreting the results of this study that took place during the breeding and brooding season. Due to restraints placed by university terms, the study had to take place in the winter term (between October and February) with a potential extension into the summer term (March–September), that is, overlapping with the breeding–brooding season.

Test Apparatus

Two identical wooden boxes were custom-built for this experiment (27 × 16 × 27 cm). Each box had a square opening on the top (8 × 8 cm) for the subject to drop in an object (object descriptions below); see Fig. 2. The boxes were tall enough that the kea could easily drop the objects in, but deep enough that they could not take them out again. A black polyvinyl chloride tube protruded from the top of the box and reached through it to the reward tray (10 × 8 cm). To reward the subjects, the experimenter dropped one-fourth of a peanut seed into the tube, which fell through and landed in the reward tray for the subjects to access.

Stimuli

The objects consisted of four shapes (cylinder, cube, sphere and pyramid), each handmade from 28.5 g modelling clay (FIMO, Staedtler, Wien, Austria, https://www.staedtler.com/at/de/). They were made in the following nine colours: brown, green, orange, violet, white, blue, red, yellow and black (Fig. 3). The colour, shape and size of the objects were chosen so that they could easily be distinguished from any angle, and manipulated with the kea's beak.

Figure 3. Stimuli were small objects made from exactly 28.5 g of modelling clay. The objects were handmade in four shapes (cylinder, cube, sphere, pyramid) and nine colours (brown, green, orange, violet, white, blue, red, yellow and black).

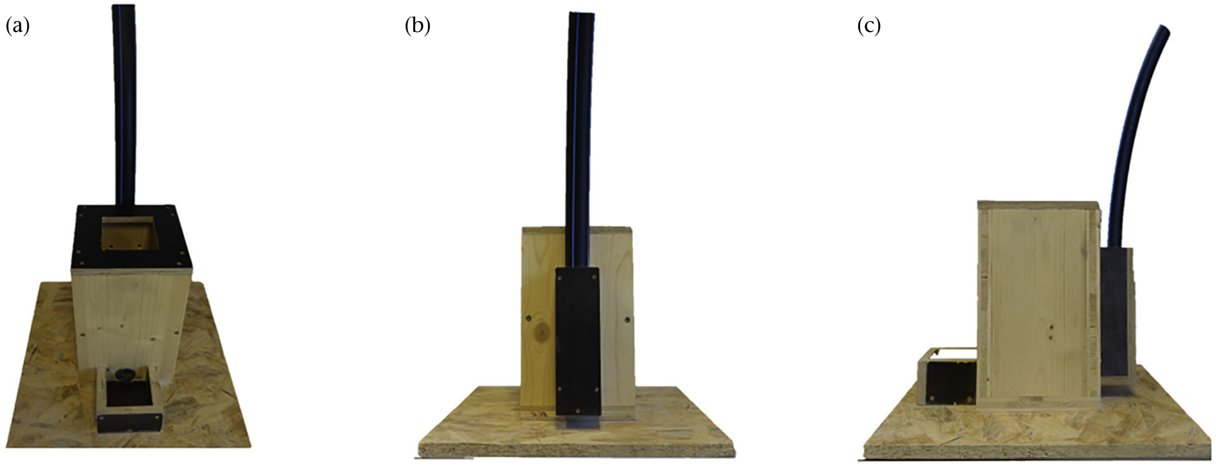

Figure 2. Test apparatus: example of one of the two identical test boxes: (a) front view of reward tube, square opening for the object and feeding tray; (b) back view with reward tube; and (c) side view both feeding tray and reward tube.

Procedure

Training

Each training session consisted of ten trials, and all subjects received one training session per day. In training step one, all 12 subjects (demonstrators and observers) were trained to perform the required action: they had to drop a neutral object (a small wooden ring) into the square opening of the box. The neutral object, which was not used during testing, consisted of a different material and had a different colour and shape than the test objects. The criteria for completing training step one was 10 out of 10 in a single session. All individuals required three training sessions to complete the first training step.

Once an individual met the criteria in training step one, they moved on to training step two, where they learned the chosen task. Here, they were offered a second ring, which was wrapped in dark green yarn to distinguish it from the original ring. Subjects were required to choose between the two rings and were rewarded for dropping the original unwrapped wooden ring into the box. The criteria for completing training step two were 10 out of 10 correct choices in a single session. On average, individuals took two and a half training sessions to complete the second training step. Ten individuals required two sessions to complete this step, while two individuals required five training sessions to reach the criterion.

Once training was completed, two subjects (Fr and Ke) received additional demonstrator training. This consisted solely of training entering and exiting the training compartment, through either the door to the main aviary or the hatch to the breeding compartment; see Fig. 1. Altogether, demonstrators received three training sessions each. Each demonstrator's choice was rewarded regardless of the object's colour or shape; therefore, no additional training for demonstrators was necessary. This novel approach was applied to reduce training rotations for the demonstrator individuals.

Testing

The general procedure was identical for all four test conditions, with all individuals receiving them in the same order. Each observer received ten test sessions per condition. Each session consisted of five trials and took around 15 min. Observers received one test session per day, regardless of condition. A trial comprised one demonstration followed by the test. Each trial ended after an object was placed into the box or after 1 min had passed with no interaction with the objects. Object colour, shape and side assignment were randomized across trials and all demonstrator choices were rewarded.

Each trial began with the observer separated in the observation subcompartment of the experimental compartment and the demonstrator outside the testing compartment; see Fig. 1. The experimenter set up the apparatus and stimuli in the demonstration/test compartment, and once they were in place, the experimenter gave the demonstrator access. After the demonstration, the demonstrator left the compartment, and the stimuli and apparatus were reset, and the sliding wire-mesh door to give the observer access was opened. The observer was allowed to make any choice, and based on that choice, was either rewarded or not, then sent back to the observation compartment. This procedure was repeated for a total of five trials.

The experimental compartments at the Haidlhof Research Station are equipped with two entry and exit points, shown by the arrows in Fig. 4. There is an opaque sliding wall that separates the experimental compartment from the rest of the aviary, as well as movable wire-mesh doors dividing the compartment into two sections, in our case, an observation and demonstration/test compartment. In all conditions, demonstrators entered and exited the demonstration/test compartment either via the door to the main aviary or via the hatch to the breeding compartment; see Fig. 4. They received additional training on those two entry/exit points to guarantee reliable demonstrations regardless of approach angle. Each condition had its own unique set-up to ensure that the observers had a clear view of both the objects and the box(es) and that the demonstrator could enter and exit the compartment smoothly. The conditions were as follows.

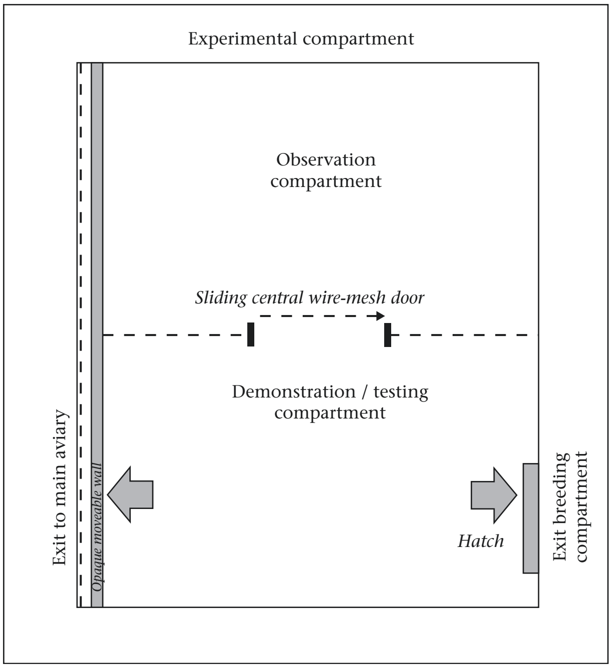

Figure 4. Schematic of the experimental compartment. The experimental compartment can be separated into an observation and a demonstration/test compartment via wire-mesh sliding doors. The entry and exit to the main aviary are indicated on the left (behind the opaque movable wall). A hatch on the right-hand side of the demonstration/test compartment functions as an additional entry and exit.

(1) Condition 1: pretest for stimulus enhancement. Two objects were placed in front of one box for both demonstrators and observers. Observers were rewarded only for the demonstrated object (Fig. 5).

(2) Condition 2: test for stimulus enhancement. Four objects were placed in front of one box for both the demonstrator and observer. Observers were rewarded for choosing the same object as was demonstrated (Fig. 6).

(3) Condition 3: test for stimulus versus local enhancement. The demonstrator received two objects and one box, while the observers received four objects and two boxes. For observers, novel objects were placed in front of the old box (old location) while old objects were placed in front of the novel box (new location). Observers were rewarded for choosing the same object as was demonstrated (Fig. 7).

(4) Condition 4: test for local enhancement. The demonstrator received one object and one box, while the observers received one object and two boxes (the old box in the old location and the new box in the new location). The object was placed centred in front of the observer (wire-mesh separation) and remained constant for both the demonstration and the test. Observers were rewarded for choosing the same box/location as was demonstrated (Fig. 8).

The different experimental set-ups resulted in different probabilities to make a correct choice for the observers by chance. In the first condition, observers chose between two objects and had to put one into the box (identical to training), resulting in a probability of

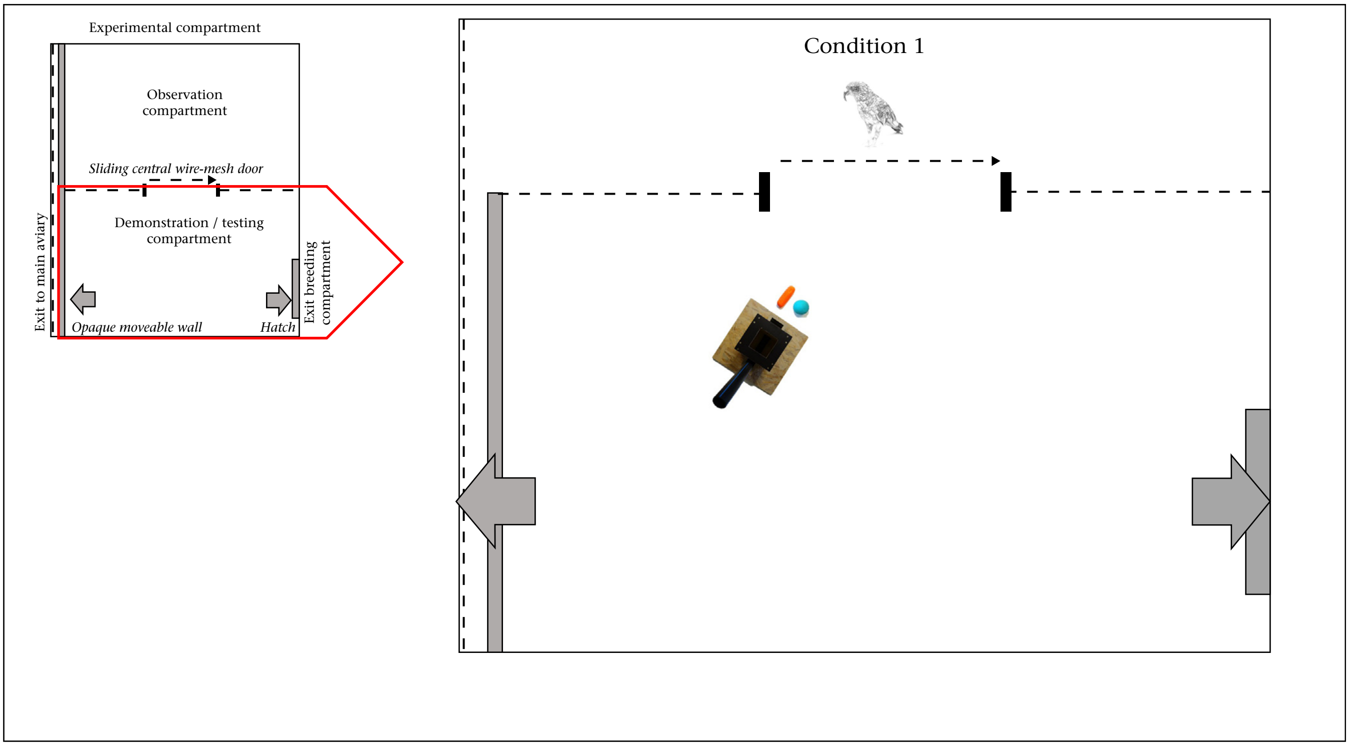

Figure 5. Schematic of condition 1 experimental set-up. One box with two objects right in front of it, facing the observer behind the sliding central wire-mesh door.

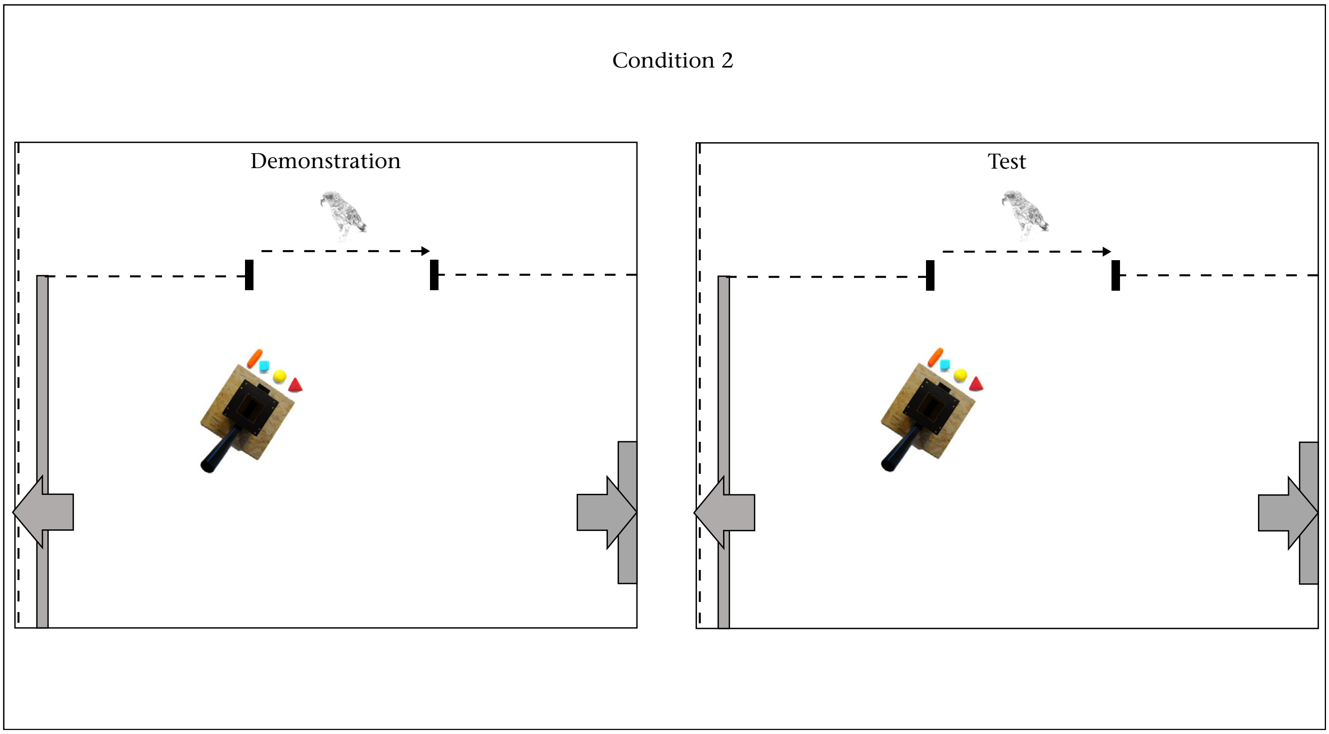

Figure 6. Schematic of condition 2 experimental set-up. The demonstration depiction shows the set-up for the demonstrator, of one box and four objects, facing the observer behind the sliding central wire-mesh door. The test depiction shows the set-up for the observer of one box and four objects, facing the observer behind the sliding central wire-mesh door.

50 % for choosing the same object at random as the demonstrator. In the second condition, four objects were offered reducing the probability of choosing the same object at random to 25 %. The third and fourth conditions aimed to disentangle local and stimulus enhancement. For this reason, in the third condition, four objects and two boxes were offered, to the observers, resulting in a 25 % probability of choosing the correct object and a 50 % probability of choosing the same box at random. In the fourth condition, a single

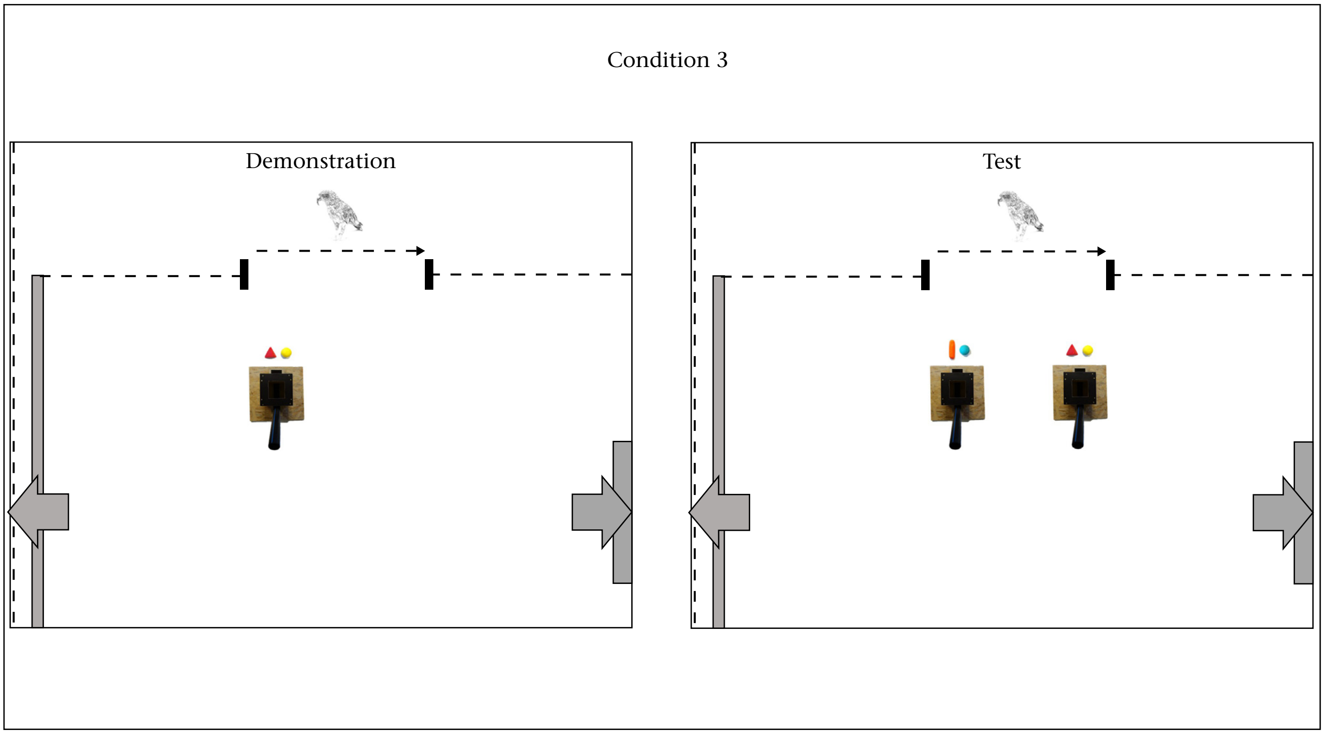

Figure 7. Schematic of condition 3 experimental set-up. The demonstration depiction shows the set-up for the demonstrator of one box and two objects. The test depiction shows the set-up for the observer of two boxes with two objects right in front of each box, facing the observer behind the sliding central wire-mesh door.

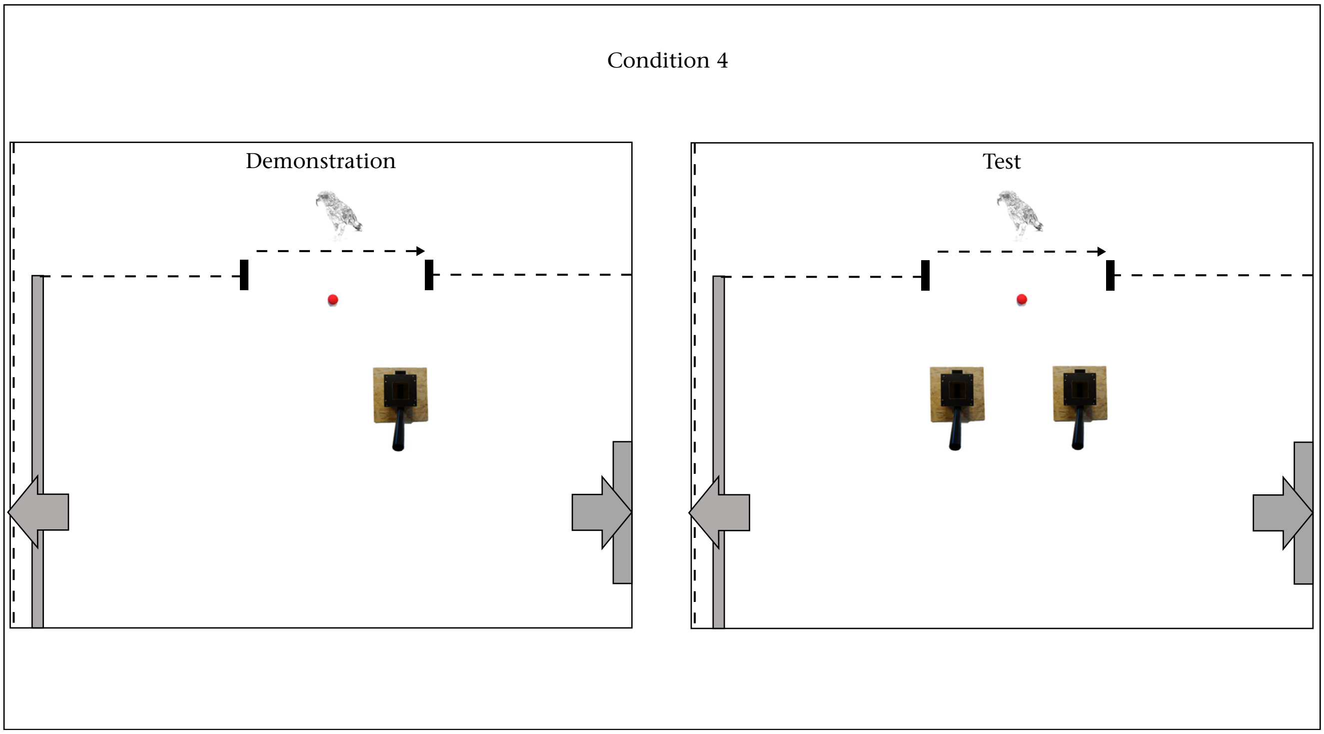

Figure 8. Schematic of condition 4 experimental set-up. The demonstration depiction shows a set-up for a demonstrator of one box and one object 1 m away from one box, centred towards the observer. Test depictions show a set-up for observers of two boxes 1 m apart with one object 1 m in front and in between the two boxes, facing the observer behind the sliding central wire-mesh door.

object was offered in front of two boxes again, resulting in a 50 % probability level of making a correct choice by chance.

In all conditions, the objects were semirandomly assigned and differed in colour and shape over all trials to reduce biases.

Data Collection

All trials were filmed with a video camera (JVC, EverioR). The number of correct and incorrect object choices per session for each observer was recorded. In the case of the third and fourth conditions, it was additionally noted in which box the object was put. Furthermore, the number, colour and shape of objects offered; objects chosen by the demonstrator and observer; and whether an object was put into the box at all were documented for each trial.

Analysis

To test whether the observer kea chose the same object as the demonstrator, we fitted several generalized linear mixed models with a binomial error structure and a logit link function (Baayen, 2008). In each of these models, we used 'correct_choice' as the response variable (binary with no/yes). In each model, we fitted the following variables as control predictors to remove any potential influence on the observer's choice: trial number, observer sex, demonstrator (in the model for conditions 1 and 2), object shape and object colour. Before being included in the model, we z-transformed the trial number to achieve easier interpretable coefficients. To account for repeated measurements in each model, we included the subject as a random effect and the random slope for the trial number within the subject. We then used the 'emmeans' package (Lenth, 2024) to obtain the estimated marginal mean for the value of the intercept (averaged over the levels of each predictor) and corresponding SEs and 95 % confidence intervals. Using these we then calculated the z-scores and corresponding P value for significant deviation of the intercept from zero, which in a logistic model represents a probability at chance level. A probability of 0.5 was the null hypothesis for the responses for conditions 1 and 4; however, for the responses for conditions 2 and 3, the chance level to be correct was 0.25. For these conditions, we, therefore, tested for a significant deviation from the chance level of 0.25 by subtracting the logit-transformed chance value of 0.25 from the estimated intercept value and recalculated the corresponding z-scores and P values of these adjusted estimates (Hosmer & Lemeshow, 2013). Additionally, we tested the significance of the control predictors by dropping them from the model one at a time and comparing the simpler model with the more complex model using likelihood ratio tests. Across all data sets, we removed data where individuals did not make a choice. Models were fitted in R (version 4.2.3; R Core Team, 2024) using the 'glmer' function of the lme4 package (Bates et al., 2015) using the optimizer 'bobyqa' (Powell, 2009). Factors such as colour, shape or side preferences, that could potentially influence the results, were analysed. The demonstrators (Kermit and Frowin) were free in their choice of shape/colour, and their choice informed the rewarded stimuli for observers. Consequently, we assumed that colour and/or shape preferences in the demonstrators could affect our results. We, therefore, examined whether the demonstrator's choice of colour or shape differed from chance level. Condition 4 only presented one object per trial, and therefore no preference testing was possible. In all conditions (1–3), the presentation of shape and colour was randomized across trials and sessions, and no more than four colours were presented at once (in any given trial). This meant that some shapes and colours (and their combination) were presented more often than others. To account for this, only trials where the demonstrator's chosen colour was presented together with 1 (condition 1 and 3 consisting of two objects) or 3 (condition 2 consisting of four objects) other colours were considered (e.g. ensuring in each trial a colour was only presented once). Irrespective of what the colours of the other objects in that particular trial were, we then used binomial tests to investigate whether the demonstrator's choice differed from chance level (condition 1 and 3, $P = 0.5$; condition 2, $P = 0.25$; see Table S1 in the Supplementary Material). To investigate any demonstrator preference for shape in condition 1 and condition 3 we tested whether demonstrator shape preference differed from chance for each pairwise comparison using binomial tests. Similarly, we used a chi-square test for each observer in condition 2 to investigate if the ratio of choice for shapes differed from chance level ($P = 0.25$; see Table S2 in the Supplementary Material). The results indicated that the two demonstrators showed varying degrees of preference for either colour or shape depending on the condition (Tables S1 and S2). Since only one box was presented during demonstrations, it was not necessary to test for a demonstrator side bias for box position. However, as observer individuals received two boxes in both conditions 3 and 4, a potential side bias was tested in those two conditions, and none could be found (condition 3 $P = 0.36$ and condition 4 $P = 0.48$). For more information on the results of these factors, see the Supplementary Material (Table S3).

During the first and second conditions, all 12 kea completed the full test, 10 observers and two demonstrators. In the third and fourth conditions, four observers and one demonstrator kea were excluded from the study. Two of the individuals entered breeding during the study; one was first injured during a conflict and then also entered breeding and could not be further tested. Additionally, one observer and one demonstrator exhibited a lack of motivation and were excluded. Consequently, conditions three and four were completed with six observers and a single demonstrator; see Table 1. Therefore, conditions 1 and 2 were separated in the analysis, with one model (per condition) including all individuals participating in the conditions and one model (per condition) including only motivated individuals (see Table 1), so those six individuals completed all conditions. In most cases, individuals selected the object directly as soon as they reached it. Only once did an observer kea not select an object within the time frame of 1 min. Two objects instead of one were selected 16 times in 1600 trials in total (including all conditions). The selection of two objects was recorded as a false response. All the above factors were considered in the analysis.

RESULTS

First Condition: Two Objects and One Box (Chance Level 0.5)

The analysis for all individuals ($N = 10$) revealed that, overall, observers chose the same object as the demonstrator at the chance level (52.5% ± 3.4% correct, $z = 0.73$, $P = 0.464$). There were individual differences in performance, with the best individual (Diana) choosing the same object as the demonstrator 76% of the time (38/50 correct choices), and the least successful individual (Mali) choosing the same object 44% of the time (22/50 correct choices); see Fig. 9. The analysis of the motivated individuals ($N = 6$) showed that, overall, observers chose the same object as the demonstrator significantly more than expected by chance (67.3% ± 4.8% correct, $z = 3.29$, $P < 0.001$). There was an effect of colour ($\chi^2_8 = 23.89$, $P < 0.01$) and shape ($\chi^2_3 = 11.93$, $P < 0.01$) for all individuals ($N = 10$). For the motivated individuals ($N = 6$) we found an effect of colour ($\chi^2_8 = 28.76$, $P < 0.001$) but not shape ($\chi^2_3 = 4.88$, $P = 0.18$). For detailed results, see the Supplementary Material (Tables S4 and S5).

Second Condition: Four Objects and One Box (Chance Level 0.25)

The analysis for all individuals ($N = 10$) revealed that, overall, observers chose the same object as the demonstrator significantly more than expected by chance (35.9% ± 3.7% correct, $z = 3.18$, $P < 0.01$). The highest score of an individual choosing the same object as the demonstrator over all 50 trials was 56% (28/50 correct choices), the lowest was 14% (7/50 correct choices), and on average, 39.4%. The analysis of the motivated individuals ($N = 6$) showed

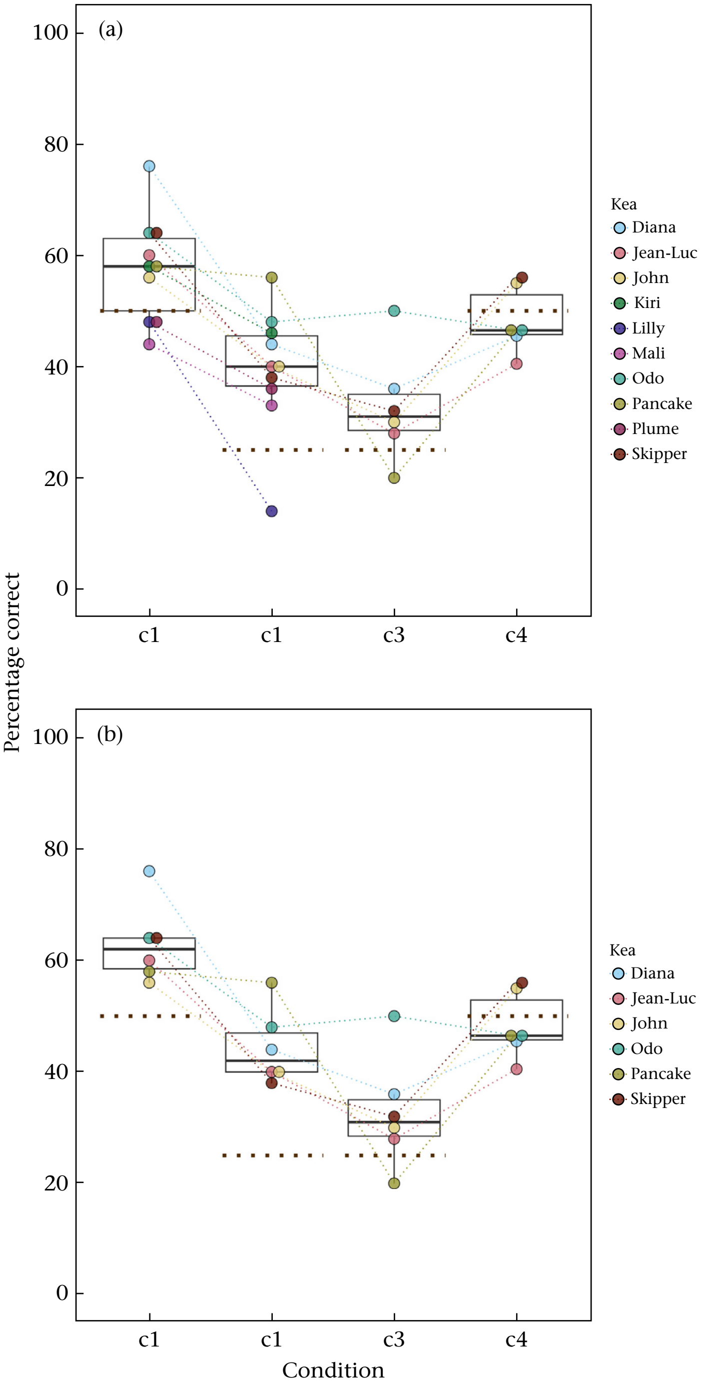

Figure 9. Percentage correct per condition. (a) The percentage of demonstrated object choices in conditions 1–3 and the percentage of demonstrated box choices in condition 4 for all individuals ($N = 10$). (b) The same information for the motivated individuals ($N = 6$) that participated in all four conditions. The box represents the interquartile range (25th percentile - 75th percentile) whereas the thick black line represents the median (50th percentile) for the data. The horizontal dotted lines indicate the chance level for the different conditions to choose the same object or box as demonstrated. Error bars represent model estimates and 95 % confidence limits. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

that, overall, observers chose the same object as the demonstrator significantly more than expected by chance (43.6% ± 4.8% correct, $z = 4.33$, $P < 0.001$). There was an effect of colour ($\chi^2_8 = 23.65$, $P < 0.01$) but not shape ($\chi^2_2 = 1.10$, $P = 0.58$) for all individuals ($N = 10$). Similarly, for the motivated individuals ($N = 6$), we found an effect of colour ($\chi^2_8 = 21.41$, $P < 0.01$) but not shape ($\chi^2_2 = 0.08$, $P = 0.96$). For detailed results, see the Supplementary Material (Table S4 and Table S5).

Third Condition: Four Objects and Two Boxes (Chance Level 0.25)

The analysis of all individuals ($N = 6$) revealed that, overall, observers did not choose the same object as the demonstrator significantly above the chance level (27.4% ± 5.1% correct, $z = 0.48$, $P = 0.633$). Additionally, observers did not prefer the old versus new box/location (49.0% ± 4.1% old, $z = -0.23$, $P = 0.816$). The highest score for choosing the same object as the demonstrator over all 50 trials was 50% (25/50 correct choices), the lowest was 20% (10/50 correct choices), and on average, 32.7%. In 157 out of 300 trials, the observers selected the new (nondemonstrated) box/location to place their object; in 87 out of these 157 trials, the object choice was correct. In 143 trials, they placed the object in the old (demonstrated) box/location; in 11 trials, this was the correct object. No side preference could be found in observer birds (37.2% ± 13.4% right, $z = -0.91$, $P = 0.363$). There was an effect of colour ($\chi^2_8 = 26.04$, $P < 0.01$) and shape ($\chi^2_2 = 9.48$, $P < 0.01$) for all individuals ($N = 6$). For detailed results, see the Supplementary Material (Table S4 and Table S5).

Fourth Condition: Single Object and Two Boxes (Chance Level 0.5)

The analysis of all individuals ($N = 6$) revealed that, overall, the observer's choice of the box did not differ significantly from the expected random chance level (47.7% ± 4.1% correct, $z = -0.55$, $P = 0.581$). Out of the 300 trials, all six observers chose the same box as shown in 142 trials, and in 152 trials, the other nondemonstrated box. There were minor differences in individual performance, with the best individual choosing the same box/location as the demonstrator 56% (28/50 correct choices) of the time, and the least successful individual choosing the same box/location 40% (20/50 correct choices) of the time; see Fig. 9. No side preference could be found in observer birds (29.4% ± 25.7% right, $z = -0.70$, $P = 0.481$). For detailed results, see the Supplementary Material (Tables S4 and S5). Only one object was offered per trial; hence, no further analysis of object choice and/or preference was conducted.

DISCUSSION

The study provides novel evidence that the object choice of an observer kea is influenced by the object choice of a conspecific demonstrator and likely not by the location. Stimulus enhancement may, therefore, play a significant role whenever kea attempt to solve a demonstrated task. Individual differences in performance were evident in all conditions, with varying shape and/or colour preferences identified across individuals and conditions. The object choice task, which was used within the demonstrator–observer experiment, was a novel approach that has not been employed with kea before and constitutes a promising method for the future.

Breeding season plays a key role in kea's overall motivation to participate in tasks and female participation specifically. Therefore, the results for those conditions that included females that later dropped out due to breeding ($N = 3$) or lack of motivation ($N = 1$) were separated into two. One analysis included the performance of all individuals ($N = 10$), while the second analysis focused only on the motivated individuals ($N = 6$) who completed all four conditions.

Our findings showed that motivated individuals significantly matched their choice of objects in the two conditions where stimulus enhancement was the sole factor (conditions 1 and 2 with two and four objects, respectively). Those conditions that had the additional factor of location (two boxes), however, illustrated that individuals did not perform significantly above the chance level (conditions 3 and 4). Colour and shape continued to have a significant effect in condition 3 (four objects and two boxes), indicating that although all individuals performed at chance level, stimulus remained an important factor. Furthermore, no indication for location matching could be illustrated in the final two conditions, which was particularly pronounced in condition 4 (one object and two boxes), where local enhancement was the sole factor. Our hypothesis that observing a conspecific solving an object choice task will affect the object choice of the observer kea was, therefore, confirmed. Our prediction that the location of the demonstrator's stimulus choice would influence the location of the observer's stimulus choice, could not be validated. Due to the design of our study and the resulting data, we suggest that stimulus enhancement was the predominant learning mechanism: the observer's attention was drawn to an object because of a demonstrator interacting with it.

Our finding is in line with previous studies (Huber et al., 2001; Suwandschieff, Huber, et al., 2023; Suwandschieff, Wein, et al., 2023) and suggests that kea's natural habitat facilitates object-related preferences. They are known to be very interested in the affordance of objects (Diamond & Bond, 1999; Huber et al., 2001; Smith et al., 2022), and, as opportunistic group foragers, may be dependent on the informational value each resource (object in this case) provides (Mettke-Hofmann et al., 2002). While it is clear that kea benefit from a demonstration, and hence social learning is relevant to them, they seem to be more prone to engage with objects than to pay close attention to the location. This predisposition matches their extremely curios, inquisitive and neophilic nature (Diamond & Bond, 1999; Smith et al., 2022; Suwandschieff, Huber, et al., 2023). As an island species that is faced with fluctuating food availability, the exact location of a resource may be less relevant as it is not consistent over time. It would therefore make sense that more attention is paid to the resource itself (affordances) than to the locality of it. This is in line with the characteristics of island-dwelling species, for whom ‘the value of information is high’ (Mettke-Hofmann et al., 2002, p. 267), and a lot of time is spent gathering information about the environment (that is, affordance learning).

Considering these new results, it is plausible to assume that previous studies (Huber et al., 2001; Suwandschieff, Huber, et al., 2023; Suwandschieff, Wein, et al., 2023) had effects of stimulus enhancement that remained undetected. Therefore, when solving more complex tasks, kea could benefit from stimulus enhancement, especially in the first trials, by initially increasing the salience of the stimulus (Zentall, 2011). This result clearly illustrates that stimulus enhancement must be accounted for in any social learning experiment provided to kea.

The object choice task within the demonstrator–observer set-up allowed demonstrators to choose any object. Subsequently, this object became the rewarded stimulus for observers. This set-up decreased the training rotation for demonstrators significantly. Additionally, as multiple objects in different shapes and colours were offered in a randomized manner across trials and conditions, it warranted that observers could not solve the tasks based on previous trial experience. This approach seems like a promising technique for reducing training rotations while providing randomization across trials.

Some aspects of the study should be considered when interpreting the results. The experimental set-up may have primed kea on stimulus enhancement, therefore potentially inhibiting local enhancement. Specifically, condition 3, which targeted contrasting stimulus and local enhancement, might have been affected (1) by the previous two conditions which primed the subjects on the stimulus and (2) by the stimulus remaining the rewarded factor within the condition. The final condition (4) attempted to counter stimulus rewarding; however, it could be that by that time, kea were completely primed on only looking for stimulus enhancement in the task. Going forward, it may be more conducive to testing each mechanism individually rather than pooling them. Future studies will have to be even clearer to delimit the individual social learning mechanisms tested with any specific task. Additionally, the mixed results for the two groups ($N = 10$ versus $N = 6$) indicate that motivation plays a major role in the performance of kea concerning stimulus matching. While kea are generally highly motivated to participate in testing, and object manipulation rates are high in this species, other factors seem to influence individual performance. Breeding can be assumed to have major effects on individual motivation levels, as other activities take priority during this time.

Object-related information seeking may not be as relevant for individuals in periods where reproductive activities take precedence. Intraspecific variation in psittacine cognition and task performance is well documented and is multifactorial; for a full review on the subject see, Cussen (2017). Future studies will have to take factors such as motivation, seasonal fluctuation thereof, and the corresponding data analysis (considering potential motivational intraspecific differences) into account.

In conclusion, while some aspects remain indistinct, the study provides some evidence that kea rely on stimulus enhancement as the main effect in this social learning task, if motivated. The observer's attention was drawn to an object because a demonstrator kea was interacting with it, and such behaviour should be beneficial to kea in their natural habitat. The object choice task, which was used within a demonstrator–observer experiment, constitutes a novel and promising approach that has not been employed with kea before. Overall, the results suggest that less complex mechanisms need to be tested for and excluded when investigating social learning in this species.

Author Contributions

Remco Folkertsma: Writing – review & editing, Formal analysis, Data curation. **Yasmin M. Gräter:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Raoul Schwing:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Funding acquisition, Data curation, Conceptualization. **Elisabeth Suwandschieff:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Amelia Wein:** Writing – review & editing, Supervision, Investigation, Data curation, Conceptualization.

Data Availability

All relevant data and the R script have been uploaded to the Science DB repository at https://doi.org/10.57760/sciencedb.16282 and are publicly available under a CC BY 4.0 licence.

Declaration of Interest

The authors declare that they have no conflicts of interest to disclose.

Acknowledgments

We would like to express our gratitude to Andràs Pèter for his help with devising the test box, the Austrian Science Fund (FWF) for funding the project (P 33507-B), and the entire staff at the research station Haidlhof for their hard work and ongoing support. This research was funded in whole or in part by the Austrian Science Fund (FWF) [grant P 33507-B]. For open access purposes, the authors have applied a CC BY public copyright licence to any author-accepted manuscript version arising from this submission.

Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123166.

References

Akins, C. K., & Zentall, T. R. (1996). Imitative learning in male Japanese quail (*Coturnix japonica*) using the two-action method. *Journal of Comparative Psychology, 110*(3), 316–320. https://doi.org/10.1037/0735-7036.110.3.316

Auersperg, A., von Bayern, A., Weber, S., Szabadvari, A., Bugnyar, T., & Kacelnik, A. (2014). Social transmission of tool use and tool manufacture in Goffin cockatoos (*Cacatua goffini*). *Proceedings of the Royal Society B: Biological Sciences, 281*(1793), 20140972. https://doi.org/10.1098/rspb.2014.0972

Baayen, R. H. (2008). *Analyzing linguistic data: A practical introduction to statistics using R*. Cambridge University Press. https://doi.org/10.1017/CBO9780511801686

Bastos, A. P. M., & Taylor, A. H. (2020). Kea show three signatures of domain-general statistical inference. *Nature Communications, 11*(1), 828. https://doi.org/10.1038/s41467-020-14695-1

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1 SE-Articles), 1–48. https://doi.org/10.18637/jss.v067.i01

Brown, C., & Laland, K. N. (2003). Social learning in fishes: A review. *Fish and Fisheries, 4*(3), 280–288. https://doi.org/10.1046/j.1467-2979.2003.00122.x

Cadieu, J. C., Cadieu, N., & Lauga, J. (1995). Local enhancement and seed choice in the juvenile canary, *Serinus canarius*. *Animal Behaviour, 50*(3), 793–800. https://doi.org/10.1016/0003-3472(95)80139-1

Call, J., Carpenter, M., & Tomasello, M. (2005). Copying results and copying actions in the process of social learning: Chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Animal Cognition, 8*(3), 151–163. https://doi.org/10.1007/s10071-004-0237-8

Cussen, V. A. (2017). *Psittacine* cognition: Individual differences and sources of variation. *Behavioural Processes, 134*, 103–109. https://doi.org/10.1016/j.beproc.2016.11.008

Custance, D., Whiten, A., & Fredman, T. (1999). Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 113*(1), 13–23. https://doi.org/10.1037/0735-7036.113.1.13

Dawson, B. V., & Foss, B. M. (1965). Observational learning in budgerigars. *Animal Behaviour, 13*(4), 470–474. https://doi.org/10.1016/0003-3472(65)90108-9

Diamond, J., & Bond, A. B. (1999). *Kea, Bird of Paradox*. University of California Press.

Donelan, E., Philpott, M., MacKinnon, K., Klosterman, K., & Roth, T. (2022). Faecal glucocorticoid metabolite concentrations associated with illness, sex, age, and season in a kea *Nestor notabilis* population at the Cincinnati Zoo and Botanical Garden. *Journal of Zoo and Aquarium Research, 10*(2), 107–114. https://doi.org/10.19227/jzar.v10i2.654

Fawcett, T. W., Skinner, A. M. J. J., & Goldsmith, A. R. (2002). A test of imitative learning in starlings using a two-action method with an enhanced ghost control. *Animal Behaviour, 64*(4), 547–556. https://doi.org/10.1006/anbe.2002.3092

Fritz, J., Bisenberger, A., & Kotrschal, K. (2000). Stimulus enhancement in greylag geese: Socially mediated learning of an operant task. *Animal Behaviour, 59*(6), 1119–1125. https://doi.org/10.1006/anbe.2000.1424

Fryday, S. L., & Greig-Smith, P. W. (1994). The effects of social learning on the food choice of the house sparrow (*Passer domesticus*). *Behaviour, 128*(3/4), 281–300.

Funk, M. S. (2002). Problem solving skills in young yellow-crowned parakeets (*Cyanoramphus auriceps*). *Animal Cognition, 5*, 167–176.

Gajdon, G. K., Fijn, N., & Huber, L. (2004). Testing social learning in a wild mountain parrot, the kea (*Nestor notabilis*). *Animal Learning & Behavior, 32*(1), 62–71. https://doi.org/10.3758/BF03196007

Galef, B. G. (2002). Social learning of food preferences in rodents: Rapid appetitive learning. *Current Protocols in Neuroscience, 21*(1), 8.5D.1–8.5D.8. https://doi.org/10.1002/0471142301.ns0805ds21

Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour, 61*(1), 3–15. https://doi.org/10.1006/anbe.2000.1557

Giraldeau, L. A. (1997). The ecology of information use. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (4th ed., pp. 42–68). Blackwell.

Griffin, A. S. (2004). Social learning about predators: A review and prospectus. *Animal Learning & Behavior, 32*(1), 131–140. https://doi.org/10.3758/BF03196014

Heyes, C. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews of the Cambridge Philosophical Society, 69*(2), 207–231. https://doi.org/10.1111/j.1469-185x.1994.tb01506.x

Heyes, C. (2016). Homo imitans? Seven reasons why imitation couldn't possibly be associative. *Philosophical Transactions of the Royal Society B: Biological Sciences, 371*(1686), Article 20150069. https://doi.org/10.1098/rstb.2015.0069

Heyes, C., & Saggerson, A. (2002). Testing for imitative and nonimitative social learning in the budgerigar using a two-object/two-action test. *Animal Behaviour, 64*(6), 851–859. https://doi.org/10.1006/anbe.2003.2002

Hoppitt, W., & Laland, K. N. (2008). Social processes influencing learning in animals: A review of the evidence. *Advances in the Study of Behavior, 38*, 105–165. https://doi.org/10.1016/S0065-3454(08)00003-X

Hoppitt, W., & Laland, K. N. (2013). *Social learning*. Princeton University Press. https://doi.org/10.23943/PRINCETON/9780691150703.001.0001

Hosmer, D. W., & Lemeshow, S. (2013). *Applied logistic regression* (2nd ed.). J. Wiley.

Huber, L., & Gajdon, G. K. (2006). Technical intelligence in animals: The kea model. *Animal Cognition, 9*(4), 295–305. https://doi.org/10.1007/s10071-006-0033-8

Huber, L., Rechberger, S., & Taborsky, M. (2001). Social learning affects object exploration and manipulation in keas, *Nestor notabilis*. *Animal Behaviour, 62*(5), 945–954. https://doi.org/10.1006/anbe.2001.1822

Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Animal Behaviour, 69*(1), 11–18. https://doi.org/10.1016/j.anbehav.2004.05.008

Kis, A., Huber, L., & Wilkinson, A. (2015). Social learning by imitation in a reptile (*Pogona vitticeps*). *Animal Cognition, 18*(1), 325–331. https://doi.org/10.1007/s10071-014-0803-7

Klein, E. D., & Zentall, T. R. (2003). Imitation and affordance learning by pigeons (*Columba livia*). *Journal of Comparative Psychology, 117*(4), 414–419. https://doi.org/10.1037/0735-7036.117.4.414

Laschober, M., Mundry, R., Huber, L., & Schwing, R. (2021). Kea (*Nestor notabilis*) show flexibility and individuality in within-session reversal learning tasks. *Animal Cognition, 24*(6), 1339–1351. https://doi.org/10.1007/s10071-021-01524-1

Lenth, R. (2024). *Emmeans: Estimated Marginal Means, aka Least-Squares Means. R package* [Computer software] version 1.10.5. https://cran.r-project.org/web/packages/emmeans/emmeans.pdf.

Logan, C. J., Breen, A. J., Taylor, A. H., Gray, R. D., & Hoppitt, W. J. E. (2016). How New Caledonian crows solve novel foraging problems and what it means for cumulative culture. *Learning & Behavior, 44*(1), 18–28. https://doi.org/10.3758/s13420-015-0194-x

Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels. *Journal für Ornithologie, 83*(2), 137–213. https://doi.org/10.1007/BF01905355

Loretto, M. C., Schuster, R., Federspiel, I. G., Heinrich, B., & Bugnyar, T. (2020). Contextual imitation in juvenile common ravens, *Corvus corax*. *Animal Behaviour, 163*, 127–134. https://doi.org/10.1016/J.ANBEHAV.2020.03.007

Mörchen, J., Luhn, F., Wassmer, O., Kunz, J. A., Kulik, L., van Noordwijk, M. A., van Schaik, C. P., Rianti, P., Utami Atmoko, S. S., Widdig, A., & Schuppli, C. (2023). Migrant orangutan males use social learning to adapt to new habitat after dispersal. *Frontiers in Ecology and Evolution, 11*, Article 1158887. https://doi.org/10.3389/fevo.2023.1158887

Meltzoff, A. N. (1988). The human infant as '*homo imitans*'. In *Social learning: Psychological and biological perspectives* (pp. 319–341). L. Erlbaum.

Mettke-Hofmann, C., Winkler, H., & Leisler, B. (2002). The significance of ecological factors for exploration and neophobia in parrots. *Ethology, 108*(3), 249–272. https://doi.org/10.1046/j.1439-0310.2002.00773.x

Nguyen, N. H., Klein, E. D., & Zentall, T. R. (2005). Imitation of a two-action sequence by pigeons. *Psychonomic Bulletin & Review, 12*(3), 514–518. https://doi.org/10.3758/BF03193797

O'Hara, M., Huber, L., & Gajdon, G. K. (2015). The advantage of objects over images in discrimination and reversal learning by kea, *Nestor notabilis*. *Animal Behaviour, 101*, 51–60. https://doi.org/10.1016/j.anbehav.2014.12.022

Orr-Walker, T., & Jenkinson, T. (2024). *Kea (Nestor notabilis) husbandry manual 2024*. Kea Conservation NZ. https://www.keaconservation.co.nz/wp-content/uploads/2024/09/Kea_Husbandry_Manual_Final_2024.pdf.

Powell, M. J. D. (2009). The BOBYQA algorithm for bound constrained optimization without derivatives. In Cambridge NA Report NA2009/06 (Vol. 26). Cambridge: University of Cambridge.

Pullar, T. (1996). *Kea (Nestor notabilis) Captive Management Plan and Husbandry Manual*. Department of Conservation NZ. https://www.doc.govt.nz/documents/science-and-technical/tsop09.pdf.

R Core Team. (2024). *R:* A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.r-project.org/.

Reader, S. M. (2016). Animal social learning: Associations and adaptations. *F1000Research, 5*(F1000 Faculty Rev), 2120 [version 1; peer review: 2 approved].

Schwing, R., Weber, S., & Bugnyar, T. (2017). Kea (*Nestor notabilis*) decide early when to wait in food exchange task. *Journal of Comparative Psychology, 131*(4), 269–276. https://doi.org/10.1037/com0000086

Slagsvold, T., & Wiebe, K. L. (2011). Social learning in birds and its role in shaping a foraging niche. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 969–977. https://doi.org/10.1098/rstb.2010.0343

Smith, G. E., Bastos, A. P. M., Chodorow, M., Taylor, A. H., & Pepperberg, I. M. (2022). Contrafreeloading in kea (*Nestor notabilis*) in comparison to Grey parrots (Psittacus erithacus). *Scientific Reports, 12*(1), Article 17415. https://doi.org/10.1038/s41598-022-21370-6

Spence, K. W. (1937). Experimental studies of learning and the higher mental processes in infra-human primates. *Psychological Bulletin, 34*(10), 806–850. https://doi.org/10.1037/h0061498

Suwandschieff, E., Huber, L., Bugnyar, T., & Schwing, R. (2023). Kea, bird of versatility. Kea parrots (*Nestor notabilis*) show high behavioural flexibility in solving a demonstrated sequence task. *Journal of Ornithology, 165*(1), 49–55. https://doi.org/10.1007/s10336-023-02127-y

Suwandschieff, E., Wein, A., Folkertsma, R., Bugnyar, T., Huber, L., & Schwing, R. (2023). Two-action task, testing imitative social learning in kea (*Nestor notabilis*). *Animal Cognition, 26*(4), 1395–1408. https://doi.org/10.1007/s10071-023-01788-9

Thorpe, W. (1963). *Learning and instinct in animals*. Methuen.

Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of tool-use by young chimpanzees. *Human Evolution, 2*(2), 175–183. https://doi.org/10.1007/BF02436405

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science, 340*(6131), 483–485. https://doi.org/10.1126/science.1232769

Wein, A., Schwing, R., Yanagida, T., & Huber, L. (2021). Vocal development in nestling kea parrots (*Nestor notabilis*). *Bioacoustics, 30*(2), 142–162. https://doi.org/10.1080/09524622.2019.1705184

Wild, S., & Hoppitt, W. J. E. (2022). Social learning. In J. Vonk, & T. K. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior* (pp. 6518–6527). Springer International Publishing. https://doi.org/10.1007/978-3-319-55065-7_1879.

Zentall, T. R. (2006). Imitation: Definitions, evidence, and mechanisms. *Animal Cognition, 9*(4), 335–353. https://doi.org/10.1007/S10071-006-0039-2, 2006 9:4.

Zentall, T. R. (2011). Social learning mechanisms: Implications for a cognitive theory of imitation. *Interaction Studies, 12*(2), 233–261. https://doi.org/10.1075/is.12.2.03zen

Zentall, T. R. (2022). Mechanisms of copying, social learning, and imitation in animals. *Learning and Motivation, 80*, 101844. https://doi.org/10.1016/j.lmot.2022.101844