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"Motor Imitation in Kea (*Nestor notabilis*) Parrots"

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ODE TO JOY

Kea, guardian of the mountain, clown of the alps, wise counsellor (*Nestor*[1]) so worthy of note (*notabilis*[2]), a treasure (*taonga*[3]) indeed.

"The cheekiest parrots I hear, is the mountains of New Zealand's kea – destroys all it spies this clown from the skies and is smarter than all of its peers" (Liz Brownlee).

[1]Greek mythology: sage, wiseman
[2] Latin: notable, noteworthy but also notorious and memorable
[3] Māori: precious, valuable in different contexts (e.g. culturally)

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AUTHOR CONTRIBUTIONS

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ES contribution: experimental design (in cooperation with YMG and RS) experiments (in cooperation with YMG), writing (original draft in cooperation with YMG) review and editing (in cooperation with all authors).

DECLARATION

I hereby declare that this thesis is my own, autonomous work, which was conducted in accordance with the rules of good scientific practice. All sources and aids used have been indicated as such. I assure that no part of this work has been previously submitted to any other academic institution for the fulfilment of any kind of degree.

Place/ date/ signature



Vienna, August 2024
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SUMMARY

Social learning is widespread in the animal kingdom, it is a cost-effective and, therefore, adaptive way of dealing with complex physical and social environments. Various mechanisms within social learning can be differentiated depending on what information is being processed. Perceptual factors include local or stimulus enhancement while motivational factors include social facilitation or enhancement. Within social learning, one animal copying another is one very specific process within the larger taxonomy of social learning. Imitation is defined as the copying of a novel or otherwise improbable act (Thorpe) and is considered cognitively demanding, as it is associated with high fidelity response matching, includes novelty, and poses the correspondence problem. However, copying can include a variety of processes, as an observer may not copy faithfully or only specific parts of a behavioural sequence. Therefore, the concept of emulation (Tomasello) emerged to differentiate between copying the exact behaviour (imitation) and copying the results that are achieved with that specific behaviour (emulation).

While imitation is considered cognitively demanding, species that are known for their cognitive abilities (e.g. parrots and corvids) and/or are indeed phylogenetically close to humans (i.e. the great apes) do not necessarily show imitation. Furthermore, experimental evidence for imitative behaviour in these species has produced mixed results in the past. Kea (*Nestor notabilis*) have demonstrated physical and technical intelligence and are confirmed social learners. However, past experiments have failed to find imitative behaviour in this highly social and skilled species. Therefore, the aim of this thesis was to examine potential imitative learning in kea, which has never been illustrated before, and thereby adding to the knowledge base for this species.

To start this process, in chapter one (manuscript one) a simple but well established two-action task design was tested, in order to see if response matching could be induced in kea. Due to the lack of response matching that was found in this initial experiment the second experiment was designed to increase complexity and reduce individual learning. The second chapter (manuscript two), therefore, addresses a sequence task that was tested as a continuation of the effort to find imitative behaviour in this species. While the second experiment was successful in inducing response matching, no imitative behaviour could be illustrated. The final chapter (manuscript three), therefore, reduced the complexity to such a degree that perceptual

factors such as stimulus and local enhancement could be distinguished. The thesis is concluded with a brief summary and discussion of all the experiments and findings as well as some ideas for future directions for experiments looking at potential imitative behaviour in kea.

INTRODUCTION

Social learning

Learning comprises interacting with the environment and thereby gaining information, which in turn can shape future interactions with said environment [1]. This environment may be physical or social [2] and it provides cues that, can not only be detected but may predict future events [3]. This process of recognising the "predictive relationships between events" [2 p. 5,4] is commonly referred to as associative learning [5,6]. Specifically, learning via association occurs "when there is a change in an animal's behaviour as a result of one event being paired with another" [3 p. 27]. Associative learning processes have been found in a wide range of taxa (invertebrate and vertebrate species), and "are taxon- and domain-general […] [i.e.] phylogenetically ancient adaptations" [2 p. 5].

Individuals can learn via trial-and-error/experience also referred to as asocial learning, or alternatively, learn from or through others, also referred to as social learning. According to Heyes, both asocial (individual) and social learning depend on the same principle learning mechanisms, both are "mediated by associative processes" [2 p. 8]. While there is no consensus on how much social learning can be explained solely via associative processes (dependent on but not limited to the inclusion or exclusion of language/communication, signalling and teaching) [i.e. 2, vs. 7] there is agreement on the context specificity of social learning. Hence, what is special about social learning is the (social) context in which learning occurs, i.e. the 'input mechanisms' which Heyes calls the "perceptual, attentional, and motivational processes that supply information for learning" [2 p. 6]. As social learning is context specific it has been defined as "learning that is facilitated by observation of, or interaction with, another individual (or its products)" [8, adapted by 9 p. 4]. Social learning requires observers – those individuals watching another's action or interaction with the environment – to associate the behaviour of another individual as a potentially viable source of information for one's own behaviour, and it therefore relies on the experience or action of other individuals (the demonstrator(s)) for information acquisition. Such learning is vicarious [10], in contrast, trial-and-error learning (asocial or individual learning) is enactive [10] and relies on the individual's own experience of the world, which is accurate (as it is directly experienced) but can be quite costly [11] – it may involve superfluousness (time/energy cost/loss), increased effort (opportunity cost/loss), or potential risks (exposure to predation) [7].

Social learning is widespread in the animal kingdom; from insects [12], to fish [13,14] to birds [15,16] to mammals [17,18], and even non-social reptiles [19], many species show this learning variant. It seems to be a cost-effective and, therefore, adaptive way of dealing with complex physical and social environments as it can provide a shortcut to desired resources. Naïve individuals can, e.g. obtain information on what to eat when and where [20], whom to avoid [21] and with whom to mate [22]. On the other hand, indiscriminate replication may not enhance fitness at all [23]. Other individuals may not provide reliable information [24], some individuals might be more reliable than others [25] or may outright try and conceal information for their own benefit [26]. Thus, social learning requires individuals to gauge costs and benefits associated with social information [11], and to utilize social information selectively [27], making sure to rely on both vicarious and enactive information.

Various mechanisms within social learning can be differentiated [28] depending on what information is being processed. Perceptual factors include local [29] or stimulus enhancement [30] while motivational factors include social facilitation or enhancement [31]. The key difference being, what draws the attention or increases the arousal of the observer, and thereby facilitates learning [32]. Local and stimulus enhancement rely on information gained from another individuals' interaction with its environment. They describe the direction of attention of the observer to the most salient place or object. In local enhancement the attention of the observer is drawn to the location or place of activity that is associated with the positive outcome [29 in ,32]. In stimulus enhancement the attention of the observer is drawn to the manipulandum or object (the stimulus or a feature thereof), that is associated with the positive outcome. Local and stimulus enhancement often occur simultaneously and, therefore, the two mechanisms are not always distinguishable from one another [32]. Social facilitation or enhancement, on the other hand, falls under the category of motivational factors and relies on the mere presence of another individual to motivate interaction with the environment. In social facilitation the presence of (an)other individual(s) affects the arousal states of the observer, which can lead to increased activity [32]. This heightened arousal state increases the observers "contact with environmental contingencies" which in turn increases the likelihood of a "high probability response" [31 in ,32 p. 235] to occur. Hence, the chances of advantageous responses (e.g. general exploratory behaviour leading to a successful response) are increased while at the same time the chances of a non-advantageous responses (e.g. fear behaviour inhibiting exploration/activity) are decreased resulting in the facilitation of dominant responses, and hence a better overall performance [33]. It is important to note that several social learning

mechanisms can be at play simultaneously, they are not discrete clusters or components and it can be difficult to disentangle whether perceptual or motivational factors determined the outcome of a given experiment.

Within social learning, one animal copying another is a specific case and lies somewhat outside of the above-described perceptual and motivational factors. Copying in this context is defined as “occurrences of social learning where observers reproduce the behavior, general behavioral organization, or actions of others” [34 p. 1718]. It is, therefore, one very specific process within the larger taxonomy of social learning. Copying, is interesting as it “provides animals with an extra-genetic inheritance system that enables fast and efficient transmission of potentially adaptive information and skills” [34 p. 1721]. It is, therefore, unsurprising that copying has received significant attention within social learning. It is important to remember that copying can take various forms depending on what exactly is being copied and how, and therefore, several terms have been introduced to differentiate between the individual processes.

Copying, in everyday language, is often equated with imitation and imitation in-turn is associated with cognitive complexity. This is not surprising seeing as humans are understood as the great imitators (*Homo imitans*) [as proposed by Meltzoff [35]]. In humans the capacity for imitation is believed to “provide the foundation for language acquisition, skill learning, socialization and enculturation” [36 p. 8], and is considered a special case: it is performed with high-fidelity, sometimes without extrinsic motivation, and can be cross-modal [37]. In order to assess the capacity for imitation in non-human animals an array of studies looking at the mechanisms, functions, and forms of imitation have been conducted over the past decades [38,39]. For the purpose of this thesis Thorpe’s definition of imitation as the copying of a novel or otherwise improbable act [40] has been adopted.

Imitation cannot be explained exclusively by the perceptual and motivational factors described above and it is considered cognitively demanding, as it is associated with high fidelity response topography matching [17], is assumed to include the acquisition of new techniques [40] (or improbable acts), and poses the correspondence problem [39]. In imitation “an observer learns and reproduces something about the topography of body movements — which part of the body to move (e.g., head or foot), or how to move body parts relative to one another (e.g., to bring appendages closer to the trunk or to move them further away)” [8,in 41 p. 44]. An emphasis on topographic features helps differentiate imitation from other forms of social learning, as it is

important to know what exactly is being copied or what information is extracted from a demonstration [17].

The correspondence problem, on the other hand, refers to the difference between the visual feedback of a demonstration and the performance itself. So, those instances where the seen behaviour of others does not visually match the seen actions of oneself. As Meltzoff and Moore described it, “the felt but unseen movements of the self [have to be matched] with the seen but unfelt movements of the other” [42 p. 180]. The discovery of mirror neurons in macaques (*Macaca nemestrina*) [43] seemed to provide a promising explanation for the process of imitative learning in the brain. Mirror neurons play a fundamental role in copying physical response topographies [44] and position this function in the premotor cortex (and not the visual cortex) of the brain. However, while mirror neurons play a causal role in stimulus matching, their relevance for “perceptually opaque imitation” [45] is unclear [32]. Consequently, Rizzolatti [46] stated that mirror neurons are not the sole explanation, and hence they do not render the correspondence problem mute. While mirror neurons make “action observation meaningful by linking it to the observer’s own potential action […] [they are] not sufficient for imitation” [47 p. 3]. They cannot be correlated to opaque imitation, in which the sensory input from the demonstration and action do not match [48].

An alternative explanation was provided by Heyes with ‘Associative Sequence Learning (ASL)’ [49]. Heyes suggested that associative processes link visual and motor representations directly, thus, eliminating the need for “prior cross-modal representations of the observed action” [50 p. 82], i.e. removing the correspondence problem. However, “coding of sequential information” or more specifically “arbitrary sequential information” processing is difficult for most animals [51], including human infants [45]. While associative processes may underlie many social learning mechanisms it is not clear if they can account for more complex information learning, as is the case in true imitation. The exact mechanism by which imitative learning is processed, therefore, to date, remains inconclusive.

Copying can encompass further specificities, as an observer may not necessarily copy all the individual steps (or order) of a demonstrated behaviour but rather reproduce the results of an act without copying the exact behaviours the demonstrator used to achieve said result. Therefore, the concept of emulation [52,53] emerged to differentiate “copying only the results the model achieves” (i.e. emulation) from “copying the actions of another individual” (i.e. imitation) [54 p. 7]. Hence, emulation can be understood as learning about the environment

and changes that occur through the engagement of another individual with this environment [32]. Thus, “in emulation learning the organism learns new things, some of them quite complex; it is just that they are learning about the environment, not about behavior” [52 p. 704]. Nevertheless, emulation is also classified as a copying process and it can be hard to differentiate between imitation and emulation. For instance, “emulation […] could well involve information processing that shares fundamental similarities with the imitation of bodily movements” [55 p. 39]. Hence, similar information could be processed, and the same goal may be achieved in both imitation and emulation, therefore, emulation was further differentiated.

To specify the type of information utilized in emulative learning, three main distinct forms have been defined – *end-state emulation, object-movement-reenactment, and affordance learning* [38]. End-state emulation [38] indicates that individuals can learn about the goal or result of an act without needing to replicate the exact topography used by the demonstrator to achieve said goal. Only the end-state of what has been achieved is copied via idiosyncratic means [38,56]. Object-movement-reenactment [57] refers to solely copying the objects’ movement without any concern for the demonstrator, i.e., those elements of a solution sequence that relate to the physical object in use [38]. And finally, affordance learning refers to the “properties of objects or other aspects of the environment […] such as brittleness, [or] relationships between objects such as containment or functions” [38 p. 2419].

Several experiments clearly evidenced that some species do not utilize all the information provided by a demonstration to obtain a result [e.g. 58–65] and hence engage in emulation rather than imitation. For instance, great apes show strong emulative behaviour when solving a tool-using task [66], and parrots devise their own behavioural strategies when solving a complex multi-lock sequence task [67]. The experimental evidence concerning emulative learning, thus, suggests that “copying is often imprecise” [34 p. 1720] and that distinguishing between the different forms of copying is pivotal for understanding animal learning [35]. While emulation cannot be equated with imitation, it should be noted that learning about the changes in the environment induced by the engagement of another individual with said environment is quite a feat. It may be an equally complex process to imitation [16] and requires “the translation of an observed environmental relationship into behavior that produces the same consequence [and] is a quite remarkable ability” [16 p. 18, 59].

Emulation seems to be quite prevalent in great apes, phylogenetically the closest relatives to humans, on the other hand imitation – at the level of other distantly related species such as

dogs (*Canis familiaris*) [68,69] – does not appear to be as developed. While many species are distinct social learners in general, and show emulation, imitation seems to be less common. Nonetheless, there are some very good examples of imitation in the animal kingdom. Marmoset monkeys (*Callithrix jacchus*), for instance, showed high-fidelity response topography matching in a canister opening task [70,71]. Voelkl and Huber clearly demonstrated, that marmosets that observed a film canister being opened via a specific mouth technique matched the model's action topography. Japanese quail (*Coturnix japonica*), while not as proficient in response topography matching as the marmoset monkeys, illustrated significant matching behaviour in screen direction pushing and could additionally delay the performance of an acquired treadle pecking or stepping response (i.e. deferred imitation) [64,65]. These results suggest that other factors than phylogenetic relatedness, for instance ecology or social structure, may drive imitation [72].

The question, why some animals show copying at high levels of response fidelity (i.e. imitation) and others do not (emulation) is very intriguing. While imitation is considered cognitively demanding, species that are known for their cognitive abilities (e.g. parrots and corvids) and/or are indeed phylogenetically close to humans (i.e. the great apes) do not necessarily show imitation. What is even more intriguing, is that the experimental evidence for imitative behaviour seems to produce mixed results. While psittacine birds are undoubtedly proficient social learners, studies investigating imitation in parrots have largely remained inconclusive with regard to high-fidelity response matching. For instance, Auersperg and colleagues [73] could demonstrate that naïve Goffin's cockatoos (*Tanimbar corella*) learned a tool-using task by observing a trained demonstrator, however, imitation was evident only at very low fidelity levels, leading the authors to suggest emulative learning over imitation.

The limited evidence for imitation in parrots may be an artifact of the testing methodology or experimental design. Huber and colleagues' study on imitation in kea (2001) was designed to control for perceptual factors such as local or stimulus enhancement, motivational factors such as social facilitation, as well as distinguishing between emulative and imitative behaviour. For this purpose, the authors devised a complex task including three sets of locks, an experimental setup comprising control (non-observers) and test (observers) groups, as well as two alternative actions for two of the three and a two-way sequence for all three of the locking devices. This clever design could clearly demonstrate social effects concerning both social facilitation and stimulus enhancement. While the level of copying the demonstrated response topography was low and therefore imitation could not be illustrated, improved task efficiency

and individual behavioural strategies indicated emulative learning. The authors concluded that kea were potentially more interested in affordance learning and thus engaged in emulation rather than imitation. A potential caveat discussed by Huber and colleagues was the task complexity or as they put it, “one further reason for the failure to find imitation is that the observers in this experiment saw ‘too much too fast’ during demonstration sessions” [67 p. 952]. This suggests that, while task complexity is necessary to induce copying behaviour [74] it can potentially impede the copying of an exact response topographies.

In light of the above, it appears pertinent to re-test species that may not have previously demonstrated imitation, and to further refine the testing methodology. Especially in species, that fulfil many of the criteria potentially promoting imitative behaviour, as is the case with kea. Therefore, this thesis was designed to investigate potential imitative behaviour in kea who have been tested on imitation in the past but have failed to demonstrate this behaviour.

Kea (*Nestor notabilis*)

Psittacine birds show complex cognitive abilities such as tool manufacture [73], object permanence [75], and have demonstrated complex social cognition [76,77]. Because of their advanced cognitive abilities, psittacines (along with corvids) are commonly known as the ‘feathered apes’ [78]. [78]. Kea are large gregarious parrots of the *Strigopoidea* family [79], endemic to the Southern Alps of New Zealand. Kea are generalists with a varied, omnivorous diet [81]. They live in fission-fusion social flocks of up to 30 individuals [80] and show high social in-group tolerance. They have extended juvenile periods with maturation occurring around the age of three years for females and four years for males [81]. With an average life expectancy of 30 years (in the wild) this juvenile period is comparable to that of primates.

Their social structure, long lifespans, extended juvenile periods, and the fluctuating food availability in their natural environment along with their foraging styles suggest that they are predisposed to social learning [82]. And indeed, kea show social learning capacities both in the wild [81] and in the lab [67]. However, the complex physical and social environment kea live in and their marked physical and technical intelligence [67,83–89] may indicate that imitative learning could have evolved in this species. Especially for those behaviours that require a high level of technical skill which kea have illustrated a capacity for in the past. Although it is plausible to assume that imitative learning potentially exists in this species, and emulation could be exemplified [67] the existence of imitative behaviour has yet to be verified.

Aims of the thesis

The aim of the thesis was to evidence potential imitative learning in kea, which has never been illustrated before, thereby adding to the knowledge base for this species. As a first step, from the evidence base provided by Huber and colleagues [67], the task complexity was broken down to see if imitative behaviour could be found in a simple two-action task. For this purpose, a study/methodology that has successfully illustrated response matching in another psittacine species [15] seemed like a promising starting point. Heyes and Saggerson tested budgerigars (*Melopsittacus undulatus*) on a two-action task requiring the removal of stoppers, via two equivalent opening methods, from a food box. In order to produce comparative results, the testing protocol of Heyes and Saggerson was closely followed. Consequently, the first manuscript of this thesis details the two-action task experiment conducted with kea. The results indicated that, although, there were strong social effects on exploration in general and the latency of opening success specifically (social facilitation) no evidence of response matching could be illustrated in this task.

The lack of response matching in this simple experimental set-up resulted in a task design with increased complexity by introducing a sequence task, detailed in manuscript two. In this task, a test box was introduced that had to be opened in an exact sequence that included two steps at two different parts of the test box (diagonally placed). Two solving sequences were possible, left to right or right to left diagonal, with mechanics within the test box preventing any other solving solutions. The results illustrated a strong effect of demonstration, with the test group being twice as successful in solving the task as the control group. However, the results could not show motor imitation as no individual matched the exact response topography of the demonstrator, and all individuals engaged in high levels of exploration with variable response topographies indicative of behavioural flexibility.

While the first and second experiment clearly exemplified the incredible exploratory nature and behavioural flexibility of kea, they were less precise in disentangling perceptual factors that may have influenced the results. Perceptual factors such as stimulus properties and location can indicate which information is being attended to and, therefore, a simple object choice task to differentiate between local and stimulus enhancement was at the core of this experimental design, detailed in manuscript three. The task was intended to address the question of which information is being utilised (stimulus *versus* location), while simultaneously honing in on the potential of kea attending to perceptual factors closely, which would be necessary to achieve

high-fidelity response matching. The object choice task included the demonstration of the placement of small objects (of four different shape and nine colour combinations) at varying locations. Across different conditions, first stimulus matching, followed by a differentiation between stimulus and local enhancement, was tested. The results clearly illustrated that kea apply stimulus matching when solving this very simple object choice task. Hence, stimulus enhancement was identified as the primary social learning mechanism that guides their behaviour in this task. Additionally, the final experiment could provide evidence that kea can pay close attention to perceptual factors if necessary, which is a promising result for the study of imitative behaviour in this species.

MANUSCRIPT ONE: Two-action task, testing imitative social learning in kea (*Nestor notabilis*)

Animal Cognition
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ORIGINAL ARTICLE



Two-action task, testing imitative social learning in kea (*Nestor notabilis*)

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ORIGINAL ARTICLE

Two-action task, testing imitative social learning in kea (*Nestor notabilis*)

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Abstract

Social learning is an adaptive way of dealing with the complexity of life as it reduces the risk of trial-and-error learning. Depending on the type of information acquired, and associations formed, several mechanisms within the larger taxonomy of social learning can be distinguished. Imitation is one such process within this larger taxonomy, it is considered cognitively demanding and is associated with high-fidelity response matching. The present study reproduced a 2002 study conducted by Heyes and Saggerson, which successfully illustrated motor imitation in budgerigars (*Melopsittacus undulatus*). In our study, eighteen kea (*Nestor notabilis*) that observed a trained demonstrator remove a stopper from a test box (1) took less time from hopping on the box to feeding (response duration) in session one and (2) were faster in making a vertical removal response on the stopper once they hopped on the box (removal latency) in session one than non-observing control group individuals. In contrast to the budgerigars (Heyes and Saggerson, Ani Behav. 64:851–859, 2002) the present study could not find evidence of motor imitation in kea. The results do illustrate, however, that there were strong social effects on exploration rates indicating motivational and attentional shifts. Furthermore, the results may suggest a propensity toward emulation in contrast to motor imitation or alternatively selectivity in the application of imitation.

Keywords Kea · Nestor norabilis · Social learning · Imitation · Two-action task · Emulation

Introduction

Imitation can be defined as the copying of a novel or otherwise improbable act (Thorpe 1963). It is a process within the larger taxonomy of social learning (Whiten et al. 2009) and presents a specific form of social learning, in which an individual acquires a behaviour through "observation of, or interaction with, a conspecific or its products" (Heyes 1994: 207). Social learning is considered an adaptive way of dealing with the complexity of life as it mitigates the risk of trial-and-error learning. Different learning mechanisms, with varying degrees of fidelity–the degree to which the behaviour of the observer matches that of the demonstrator (Whiten and Ham 1992)–can be identified. While in enhancement the individual orients their attention toward a certain object or location (Whiten and Ham 1992) as the primary source of information, in emulation the individual orients their attention towards the result (Tomasello et al. 1989). Imitation combines both levels of abstraction and therefore represents a "high level cognitive achievement" (Whiten and Ham 1992:271) and can be associated with high-fidelity response matching (Huber et al. 2009). For the study at hand, we maintained the definition of imitation used by Heyes and Saggerson "imitation refers to copying by an observer of a feature of the body movement of a model" (Heyes 2001: 254), for a comprehensive listing of social learning mechanisms see Hoppitt and Laland (2013).

Multiple species have illustrated imitative skills in experimental settings, including two-action tasks (Akins and Zentall 1998; Bugnyar and Huber 1997; Voelkl and Huber 2000; Fawcett et al. 2002; Heyes and Saggerson 2002; Nguyen et al. 2005), bi-directional controls (Akins

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et al. 2002; Heyes et al. 1994; Heyes and Dawson 1994; Mitchell et al. 2018) and Do-as-I-do tasks (Custance et al. 1995; Huber et al. 2009; Fugazza et al. 2015; Tomasello et al. 1993; Call 2001, Topál et al. 2006). However, there are also many studies that failed to provide evidence for imitation (Veit et al. 2023 (*Sus domesticus*); Greco et al. 2013 (*Loxodonta africana africana*); Izawa and Watanabe 2011 (*Corvus macrorhynchos*) to name a view). Although those studies are difficult to explain, it is worth pointing out that they typically do provide evidence for other forms of social learning. For instance, human's closest relatives the great apes (*Pan troglodytes, Pongo pygmaeus, Pan paniscus*) tend to show low levels of motor imitation, particularly when it comes to high-fidelity copying of actions (Clay and Tennie 2018, Horner and Whiten 2005, Nielson and Susianto 2010). Instead, they tend to use their own actions to produce the demonstrated outcome, i.e. show emulation (Tomasello 1998).

Parrots are large-brained birds and renowned for their capacity to solve complex physical problems, which they achieve both spontaneously and through trial-and-error (Auersperg et al. 2009, 2011, 2012, Dawson and Foss 1965, Funk 2002, Miyata et al. 2011, Pepperberg and Funk 1990, Werdenich and Huber 2006). Yet, despite the recognised physical cognitive abilities of parrots, out of the near 400 parrot species only very few have been tested on their motor imitation capacities (Dawson and Foss 1965, Galef et al. 1986, Moore 1992, Huber et al. 2001, Heyes and Saggerson 2002, Gajdon et al. 2004, Auersperg et al. 2012) and even fewer could successfully demonstrate such behaviour, to date only African greys (*Psittacus erithacus*) and budgerigars (*Melopsittacus undulatus*) have been illustrated to show motor imitation conclusively. Goffin's cockatoos (*Tanimbar corella*), have illustrated the ability to spontaneously make and use their own tools, and that naïve observers can learn tool-using tasks by watching a trained demonstrator (Auersperg et al. 2012, 2014). However, even though the authors could show strong evidence for emulation, imitation was at best evident at low-fidelity levels (Auersperg et al. 2014). Although the cockatoos only successfully solved the task after watching a demonstrator, they applied different techniques (levering) to achieve this goal. Furthermore, tool manufacturing and use are highly specialized skill sets, which might suggest a specialized predisposition for the advanced social learning which Goffin's demonstrated.

Heyes and Saggerson on the other hand, tested 28 juvenile budgerigars, which are not known for such specialized technical skills, on imitative and nonimitative social learning using a two-action task. In their test, observer birds saw "a conspecific demonstrator repeatedly remove one of two stoppers from the horizontal surface of a food box, either by pulling the stopper up or by pushing it down into the box" (Heyes and Saggerson 2002: 852). Responses to the demonstrated stopper colours indicate nonimitative social learning whereas responses in line with the extraction topography (pulling vs. pushing) suggest motor imitation (Heyes and Saggerson 2002). Their results illustrated that observer birds preferentially applied the demonstrated opening method and hence engaged in motor imitation.

Kea (*Nestor notabilis*), a large parrot species endemic to the Southern Alps of New Zealand, have well marked technical intelligence (Auersperg et al. 2009, 2011; Gajdon et al. 2004, 2013; Huber et al. 2001; Huber and Gajdon 2006; Miyata et al. 2011; O'Hara et al. 2015, 2016) but have not illustrated motor imitation at the level of other species of the same order (*Psittaciformes*). However, there are only very few studies on the motor imitation capacities of kea. For instance, in 2001 Huber and colleagues tested kea on their ability to "match the response topography or the sequence of (…) [a] model's actions (movement or sequence imitation)" (Huber et al. 2001: 945). Observer birds watched trained conspecifics open a large steel box by manipulating three locking devices (bolt, split pin and screw) in direct succession. Although observer birds compared to non-observers did show increased "efficiency at unlocking the devices (which) seemed to reflect the acquisition of some functional understanding of the task through observation (emulation learning)" (Huber et al., 2001: 945), they did not engage in motor imitation. This raises the question of whether kea are simply more prone to emulation (Huber et al., 2001), as imitation has not provided a selective advantage in the course of their evolution, or whether the right favourable conditions to test imitation in this species have simply not yet been devised (Huber 2002).

In the study at hand, we, therefore, attempted to further investigate kea's ability to motor imitate by closely reproducing a study that has successfully illustrated imitation in budgerigars (Heyes and Saggerson 2002). We present a close replication of the methods applied by Heyes and Saggerson, with minor adjustments to the sample size, experimental group composition and materials to account for kea specificities (i.e. neophilia and larger size), by following an analogous experimental protocol. Through reproducing the experimental protocol of a successful study, illustrating motor imitation in *psittacines*, we hoped to set favourable conditions to test motor imitation in kea. Our hypothesis was that watching a conspecific demonstrator solve a two-action-task will affect the action performed by the test subject (observer). We predicted that kea will show increased use of the demonstrated action over alternative actions and that test group individuals will be quicker to approach and gain access to the test box than non-observing control group individuals.

Methods

Study site and housing

The kea subjects in this study were permanently housed in a flock of 23 birds in an outdoor aviary (52 m × 10 m × 4 m) at the Haidlhof research station in Bad Vöslau, Austria. The aviary in which they were housed was equipped with sand substrate, hanging branches for perching, shelters, and a variety of enrichment which was renewed regularly. The kea had access to water ad libitum and food was provided three times a day and consisted of fruits, vegetables, seeds, and protein once daily (cooked meat or eggs). Subjects were never food restricted for the purposes of experiments, and all research was non-invasive. In contrast, Heyes and Saggerson maintained the test subjects at 90% bodyweight for the test rotation.

Testing took place in one of two testing compartments (10 m × 6 m × 4 m) in the aviary. These compartments were closed off during testing, but remain open otherwise and are part of the main living area for the kea. All subjects have been previously trained to enter and exit the experimental compartments on verbal command, and all participation was voluntary. Subjects could refuse to participate by ignoring the command to enter the compartment, and they could end sessions early by retreating to perches or shelters, laying down on the ground, or otherwise refusing to participate. If a subject ended a session early, it was directed back into the main aviary and tested again another time.

Apparatus and set-up

Heyes and Saggerson trained and tested their budgerigars in a holding room in a metal testing cage with all sides occluded by white cardboard (Heyes and Saggerson 2002). The cage was separated into two compartments, i.e. demonstration/test and observation compartment. Comparably, the testing compartment of the kea aviary is a) visually occluded from the rest of the aviary during testing, and b) can be separated into two sub-compartments by closing a mesh wire door in the centre. The two sub-compartments served as the demonstration/test and observation areas. As the kea test compartment is large compared to the testing cage of the budgerigars, two 1 × 1 × 1 m tunnels made out of semi-opaque (milky) plastic, were added to simulate the testing cage used with the budgerigars. The test cage and tunnels decrease the space available to the individuals and thereby likely funnel and channel the view (via the semi-opaque side walls) and guiding the attention towards the demonstration area by reducing environmental (visual) noise.

As a 'test box' Heyes and Saggerson used a white, rectangular box (22 × 10.5 × 4.5 cm). The box was divided into equally sized sections and two holes in a white lid provided access to the rewards in the sections below. We adjusted the measurements of the budgerigar test box by a factor of 3.8 to account for the larger size of kea (who are on average 3.8 times longer than budgerigars), resulting in a comparable rectangular wooden test box (see Fig. 1). As in the budgerigar study, the lid of the box featured two feeding holes (also adapted by a factor of 3.8) and the box was divided in half to create two feeding sections. In contrast to the budgerigars, who received time-based millet seed rewarding, kea were rewarded with access to ¼ piece of peanut–their preferred reward that is routinely used–and therefore, additional reward trays were integrated inside the box (see Fig. 1). These reward trays were added to mimic the direct availability of the reward upon opening the box and to prevent the kea from having to search the box for a single piece of peanut.

As in Heyes and Saggerson, the test box was placed on the floor at the far end of the tunnel, directly up against the mesh wire, with its long axis facing the mesh wire. The

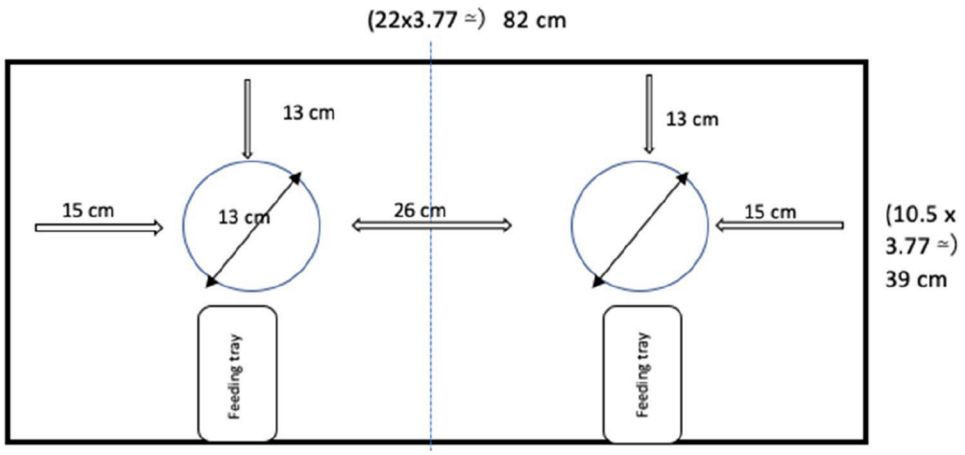

Fig. 1 Kea test box specification, including feeding trays, and removable lid. Adjusted by a factor of 3.8 (incl. test box, feeding holes and stoppers) to the budgerigar test set-up to account for the larger size of kea

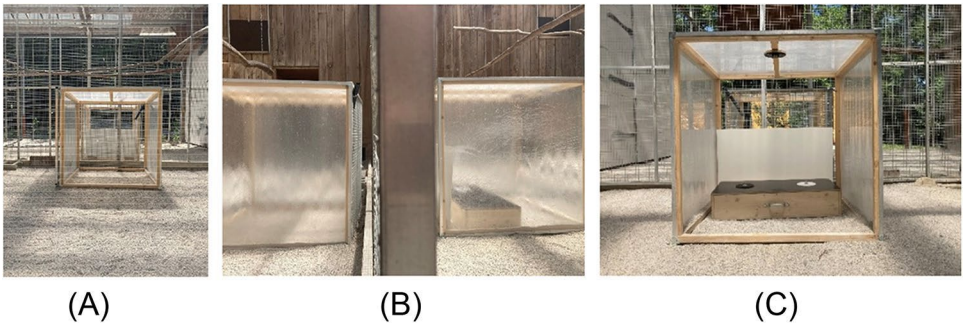

Fig. 2 Kea test cage set-up: **A** observation compartment view, **B** two tunnels up against mesh wire separation and **C** demonstration/test compartment view including test box with stoppers and removable visual barrier

second tunnel was placed directly opposite the test box on the other side of the mesh wire (see Fig. 2).

Stoppers

As stoppers for their box, Heyes and Saggerson used two ping-pong balls cut in half. The open half of the cut ping-pong ball had wire crossed over the top, to allow the birds to grip it. The other side had a smooth surface with no further alteration. The exposed sides of both stoppers were coloured in royal blue or black. Additionally, "the rim of each hole (for the stoppers) was lined with a thin (2 mm) strip of sponge" (Heyes and Saggerson 2002: 853) to provide friction material for the stoppers to stay in place. They used metal brackets, attached to the upper or lower rim of the stopper to prevent all but one removal response on the stoppers in training.

In our set-up, we also provided the kea with circular stoppers of two different colours. In contrast to the budgerigars, the stoppers for the kea were made of durable foam cut into 13 cm diameter disks with a width of 2 cm (see Fig. 3). These stoppers better matched the keas' large size and also had the advantage that they stayed set in the feeding holes without additional friction material. Kea are highly inquisitive, and any additional material in the holes could have been a distraction. A loop that matched the keas' beak size was attached to the exposed side of the stopper, which they could use as a grip. Finally, as in the budgerigar study, two different stopper colours were used, but to make the difference more salient these were black and white, rather than black and royal blue.

For demonstrator training the stoppers were equipped with an additional 17 cm plastic disc attached to the bottom part of the stopper (see Fig. 3). The wider part of the disc was placed inside the hole. This prevented the pulling response and ensured that demonstrators could only solve the task by pushing (see explanation below in the Subjects section). Additional brackets inside the box ensured that only the correct stopper could be removed. The training stoppers were also used in the demonstration sessions to ensure that demonstrations were always solved correctly. Both training and testing stoppers looked identical from the top, making it impossible for the observers to differentiate them on a visual basis.

Subjects

Eighteen of the 23 kea were available to participate in the study (Table 1). Subjects were 9 females and 9 males and ranged in age from four to 22 years old.

There were several important differences in our study design compared to the one we were replicating. First was the number of subjects. Heyes and Saggerson used 36 juvenile budgerigars, eight as demonstrators, and 28 as observers. The kea population at the research station Haidlhof is smaller and therefore fewer individuals were available for testing. We also introduced a control group, with an equivalent sample size to the test group ($N = 9$), which was not present in the Heyes and Saggerson study. This control group was necessary because, based on extensive experience working with the kea, we predicted that they were much more likely to pull the stoppers out of the experimental box, rather than push them. If this were the case, then there would be no need for a test group that observed the "pull" action, as we predicted that kea would solve the task through trial-and-error by pulling. On the other hand, we predicted that "push" would be a much more improbable action for kea. Therefore, we introduced Control Group 1 (CG1, $N = 4$)) to test for this. The results of CG1 confirmed



Fig. 3 Test stoppers: on top and inside the test box; training stoppers with integrated discs from different angles (below and above)

Table 1 Test subject identification (ID), sex, age, rearing method (hand vs. parent), group number, experimental group assigned, colour assigned in bold for demonstrated colours (demonstrators only) and italic for observed colours (test groups only) and demonstrator assigned (only applicable for test groups)

	ID	Sex	Age	Raised	Group number	Experimental group	Colour	Demonstrator
1	Fr	♂	17	Parent	1	Control CG1	*Black*	NA
2	Jo	♂	22	Parent	1	Control CG1	NA	NA
3	Pa	♂	11	Parent	1	Control CG1	*White*	NA
4	Ro	♂	13	Parent	1	Control CG1	*White*	NA
5	Fy	♀	5	Parent	2	Control CG2	NA	NA
6	Sy	♀	14	Hand	2	Control CG2	NA	NA
7	Co	♀	14	Hand	3	Test TG1	*White*	Ro
8	Je	♂	6	Hand	3	Test TG1	*White*	Ro
9	Pl	♀	14	Hand	3	Test TG1	*Black*	Fr
10	Pn	♂	4	Hand	3	Test TG1	*White*	Pa
11	Sk	♂	4	Hand	3	Test TG1	*Black*	Fr
12	Di	♀	4	Hand	4	Test TG2	*Black*	Fr
13	Ke	♂	17	Hand	4	Test TG2	*White*	Ro
14	Pi	♂	17	Hand	4	Test TG2	*Black*	Fr
15	Pu	♀	8	Hand	4	Test TG2	*White*	Pa
16	Ly	♀	14	Hand	5	Control CG3	NA	NA
17	Ti	♀	3	Parent	5	Control CG3	NA	NA
18	Wy	♀	14	Hand	5	Control CG3	NA	NA

our prediction that kea preferentially pull, rather than push, as all subjects pulled the stoppers in every trial, with no instances of pushing. Based on these results, demonstrators were trained only on the "push" action.

The subjects in CG1 were chosen with the intent of re-training them to serve as demonstrators for the test groups. As there was no control group in the Heyes and Saggerson study, this was also a difference in their experimental design. We purposely chose the four highest-ranking adult males in the kea group (Fr, Jo, Pa, Ro), to create as homogenous a group of demonstrators as possible. After completing the control sessions, Jo dropped out of the experiment due to breeding. The remaining three demonstrators (Fr, Pa, Ro) were re-trained on the "push" action. In addition, Pa and Ro were trained that only the white stopper was baited, and Fr was trained that only the black stopper was baited.

Additional control groups (Control Group 2 (CG2, $N = 2$) and 3 (CG3, $N = 3$)) were tested later to create a balanced comparison between the test groups and control groups. Due to availability of individuals (breeding season) these groups had to be split in two (CG2 and CG 3 respectively) and were tested at different times. Control subjects were chosen according to the following criteria: during test sessions, observers had to remain in an observation tunnel for the duration of the demonstration (see the section on Apparatus and setup), but some subjects were hesitant to enter or remain in the tunnels despite extensive training. Therefore, those individuals that could not be trained to remain inside the tunnel were assigned to the control groups. In total, we had three Control Groups (CG) comprising nine individuals.

All individuals that could be trained to enter and remain in the tunnels during demonstration sessions were included in the test groups. Test Group 1 (TG1) was comprised of five individuals and Test Group 2 (TG2) of four individuals, for a total of nine test individuals (see Table 1 for further details).

Habituation and training procedure

As with the budgerigars, the kea were trained and tested in the testing compartment. First, they were target-trained to enter the observation tunnel, and as mentioned above, the subjects who failed this training were assigned to the control groups. All individuals were test box trained, regardless of the experimental group. In test box training, subjects were separated individually into the testing compartment and were allowed to feed from the test box inside the tunnel, or outside for the control group birds which did not tolerate the tunnels. The stoppers were absent during test box training, and both sides were rewarded. Following the budgerigar protocol, once an individual successfully fed from the test box in 100% of trials in 3 consecutive sessions of 10 trials each, their training was considered complete. On average CG individuals spent 3.9 and TG individuals 5.2 sessions in test box training. Feeding bout reduction sessions were not necessary for the kea as they received access to a single piece of peanut. Due to keas' neophilic nature, no habituation to the stoppers was necessary or conducted.

Following Heyes and Saggerson the demonstrators received additional stopper training, where the training

stoppers were fixed to prevent all but one response. This training was more complex and involved four phases, each with its own criterion for advancement (10/10 correct in two consecutive sessions, with no wrong side attempts), for the detailed training protocol see Online Resource 3. Once the demonstrators had successfully reached criterion in all four phases they were ready to perform their demonstration. During testing none of the demonstrators deviated from their assigned opening method or colour.

Testing procedure

Heyes and Saggerson tested two repetitions of the two-action task, with the first repetition using constant stopper positions across trials (blue and black always on the same side) and the second repetition using randomised colour/side assignment of the stoppers. In our current replication study, we tested the kea *only* on the second repetition, so that the side on which the positive stimulus occurred was randomized from trial to trial. Also note that, while the Heyes and Saggerson experiment consisted of four test conditions (black pull, black push, blue pull, blue push), the kea had two test conditions (black push, white push) and one control condition with no demonstration.

Following the test session protocol of Heyes and Saggerson, each CG individual received seven test sessions at 10 trials each over four consecutive days, with sessions taking place in both the morning and afternoon. CG birds that were called into the testing compartment were allowed to approach the test box and manipulate it based on trial and error. All responses were rewarded regardless of colour choice or method. Once an individual chose one response and retrieved their reward, it was called back to the observation compartment. The test box was rebaited, and the stoppers were replaced based on randomised colour-side combinations.

The testing schedule for the kea was exactly the same as that for the budgerigars. Test subjects received ten sessions altogether, one in the morning and one in the afternoon, over five consecutive days. Each session started with the demonstrator in the demonstration compartment with the test box and the test subject (henceforth observer) in the observation compartment. The first three sessions were demonstration-only, in which the observers saw their respective demonstrator open the test box ten times in a row. Starting in the fourth session and continuing to the tenth and final one, observers were given test sessions directly after viewing a demonstration session, in which they gained access to the experimental box. These demonstration/test sessions started with ten demonstration trials, after which the demonstrator was removed from the testing compartment. The observers were then given access to the box for ten consecutive trials, with no other individuals present.

All responses were rewarded for the observers, regardless of colour choice or method. Once a subject gained access to the reward by removing one of the two stoppers, the trial was ended and the subject was called back to the observation compartment. The test box was re-baited and the stoppers replaced based on randomised colour/side combinations.

In contrast to the budgerigars, kea were unrestricted in their movement within the larger demonstration and observation compartments, as they were free to enter and exit the tunnels. To ensure that the observers were present inside the tunnel during the demonstration trials, Experimenter 1 directed the subject inside using target training before each trial began. Once the observer was inside the tunnel, Experimenter 2 gave the demonstrator access to the tunnel with the test box inside. After the demonstrator removed the stopper and retrieved the reward, Experimenter 2 directed him out of the tunnel and re-baited the box for the next trial. For the test sessions, where the demonstrator was not present, observers were given access to the test box when Experimenter 1 opened the door to the demonstration compartment, and they were sent back to the observation compartment using a verbal command when they had solved the task.

Each individual (test and control group) had unlimited time to engage with the task, unless, an individual left the testing compartment or did not engage with the task for more than 15 min the session was terminated. This was the case in four sessions, for three individuals. For examples of demonstration session and test sessions see the videos provided in the supplementary materials (Online Resources). All experimenters present in the test compartment wore mirrored sunglasses in all demonstration and test sessions so that they would not provide any inadvertent cues to the participating subjects.

Data scoring

All experiments were videotaped from two sides, behind the observation compartment and directly above the test box within the test compartment tunnel. All recordings of the test sessions were scored/coded (excluding the observation-only sessions) with Solomon Coder (version beta 19.08.02). Following our hypothesis and predictions the succeeding behaviours were coded for all test sessions: 1) the approach duration from the opening of the gate to hopping onto the test box with both feet touching (to estimate how fast individuals were in approaching the box), which was converted to the approach pace, see below; 2) the removal latency from landing on a test box with both feet to the opening method (vertical movement) with the stopper being pulled out or pushed into the box (to estimate how long it took individuals to make a response); 3) the total response duration from landing on the test box to feeding, hence, completing the trial by retrieving the reward (to estimate how long it took

individuals to solve the task); as well as 4) the response type frequency of push vs. pull, black vs. white (to estimate how many individuals used the respective opening method). As the TG individuals were tested in the tunnel and the CG individuals were not, the distance to approach the test box was different for the two experimental groups. Therefore, the approach pace was calculated for each individual and each trial by dividing the approach time by the approach distance. The resulting pace made the individual traveling times comparable between groups irrespective of distance. One independent rater, who was blind to the study, scored 10% of all videos (assigned at random) to check for the interobserver reliability, with Kappa for the Categorical (push versus pull $k = 1.00$) and Intraclass Correlation Coefficient for the numerical data (approach duration ICC = 0.99, removal latency ICC = 0.99, response duration ICC = 0.94).

Statistical analysis

To analyse the behaviour of the Kea several generalized linear mixed models (GLMM) were fitted in R (version 4.2.0; R Core Team, 2021) using the function lmer of the package lme4 (version 1.1–27; Bates et al. 2015), using data from all completed trials. To answer our main research question–whether Kea matched the behaviour of the demonstrators–we used a binomial GLMM to test if the probability to push differed between experimental groups. To control for potential colour or side (bias) effects we ran a binomial GLMM to test whether there was a difference between the experimental groups concerning colour choice (white *versus* black) and side (left *versus* right). To assess whether the time it takes to complete the task differed between experimental groups we ran three linear mixed models. First, using the pace to approach the box as a response variable, we tested whether the observer birds were faster to approach the test box. With a second model, we investigate whether the total time to complete the task differed between experimental groups. Finally, we tested whether the latency to make a removal response differed between experimental groups, for details on the analysis see Online Resource 1. In all of the above models our key fixed effects were experimental group, session number, trial number, and all their interactions up to the third order. Additional fixed effects were age and sex. We also included random intercepts for the individual and sessionID (a factor combining session number and individual) nested within the individual. We included random slopes of session number and trial number and their interaction in individual as well as the random slope of trial number in sessionID. Full models were compared to their respective null models excluding the key fixed effects of interest (experimental group; session number; trial number) and all their interactions up to the third order, but otherwise similar with respect to the random effects structure to avoid cryptic multiple testing (Forstmeier and Schielzeth 2011). Cases in which an individual was carried in were excluded (on a trial basis) from approach pace and response duration (four individuals in six sessions and altogether nineteen trials) additionally we also excluded non- participation cases (three individuals did not participate in one session and one individual did not participate in four sessions). Our main models included data from all sessions (session 1–7) to make it comparable to Heyes and Saggerson. However, as kea are very fast learners, we predicted that potentially large differences between experimental groups would be most pronounced in the first session and may be gone by session two and onwards. A linear model may have little power to detect such a non-linear effect, therefore, session 1 was tested separately. To contrast our results from session 1 to the remaining sessions we also analysed sessions 2–7, see supporting material (Online Resource 1 and 2) for further information on model details, output and model diagnostics.

Results

Fourteen of the 18 individuals that participated in testing completed all seven test sessions with all ten trials. From the four individuals that did not complete all sessions and trials, two individuals completed six sessions (ID7 and ID18), one individual completed five sessions (ID 8) and the first three trials of session six and one individual completed three sessions (ID9), for details on IDs see Table 1. With regard to stopper colour choice, the full-null model comparison of the linear mixed effects model illustrated that there was an interaction between the experimental group, trial and session ($\chi^2 = 5.285$, df = 1, $P = 0.022$), revealing that while the control group was more constant in their selection behaviour the test group had a slightly higher probability to choose white, especially in later sessions and trials (see Online Resource 2). However, there was no significant difference between experimental groups concerning colour choice overall ($\chi^2 = 2.041$, df = 1, $P = 0.15$, see Online Resource 1 Fig. 6). In addition, all groups illustrated a strong side bias to the side that was closest to them (left side), however, this bias was the same across experimental groups ($\chi^2 = 0.13$, df = 1, $P = 0.72$, see Online Resource 1 Fig. 7).

Removal response

The predictors, experimental group, session number, trial number and/or their interaction, did not have an effect on the removal response (i.e., pushing or pulling stopper), as indicated by the full-null model comparison ($\chi^2 = 6.630$, df = 7,

P = 0.468). The main response for both groups was to pull (control group N = 593, test group N = 555). Push did occur on 16 separate occasions across experimental groups with no significant difference between the groups concerning the frequency (control group N = 10, test group N = 6), emphasising that their natural response is to pull. With respect to the response to push or pull there was no significant difference between experimental groups (chi-square test, χ^2 = 1.167, df = 1, P = 0.280). Observer birds did not align their removal response with the demonstrated direction/method.

Approach pace

Overall, the test predictors did not have an impact on the approach pace (full-null model comparison for all sessions (likelihood ratio test, χ^2 = 9.775, df = 7, P = 0.202)). Observer birds' average approach pace did not differ from the control group (observers: 2.82 (1.68) mean (SD); control: (3.68 (7.87)). The model revealed considerable variation among individuals as indicated by the estimated contribution of the random effect of individuals being in the same order of magnitude as the fixed effects. For instance, the estimated fixed effect of the experimental group was 0.216, while the random intercept of individuals contributed a standard deviation of 0.338, indicating interindividual variation was large compared to the difference between experimental groups. Individual full-null model comparisons for session 1 and session 2–7 did not reveal any effects of the test predictors on approach pace, see Online Resource 2.

Response duration

Concerning the time it took individuals to complete the entire task (response duration: from landing on the box to feeding) the full-null model comparison revealed that overall the test predictors had an impact (χ^2 = 24.448, df = 7, P = 0.0010) on the outcome variable. However, controlling for removal latency within response duration over all sessions illustrated that there was no more clear effect between the experimental group, trial, session or any of their interactions (χ^2 = 4.587, df = 7, P = 0.71), see Online Resource 1 Fig. 9.

Further analysis of session 1 (while controlling for removal latency) revealed a marginally significant effect of the test predictors as a whole on response duration (χ^2 = 6.808, df = 3, P = 0.078). Looking closer at this we found a significant interaction between the experimental group and trial number (χ^2 = 6.105, df = 1, P = 0.014). This means, while taking the effect of removal latency into account, the response duration of the control group slightly increased, whereas observer birds decreased in response duration over the trial number (see Online Resource 2). However, the influence of the test predictors was no longer detectable by session 2 (χ^2 = 6.641, df = 7, P = 0.47).

Removal latency

The latency to make a removal response was influenced by the test predictors ($\chi 2$ = 29.775, df = 7, P = 0.0001), but the three-way interaction between test predictors was

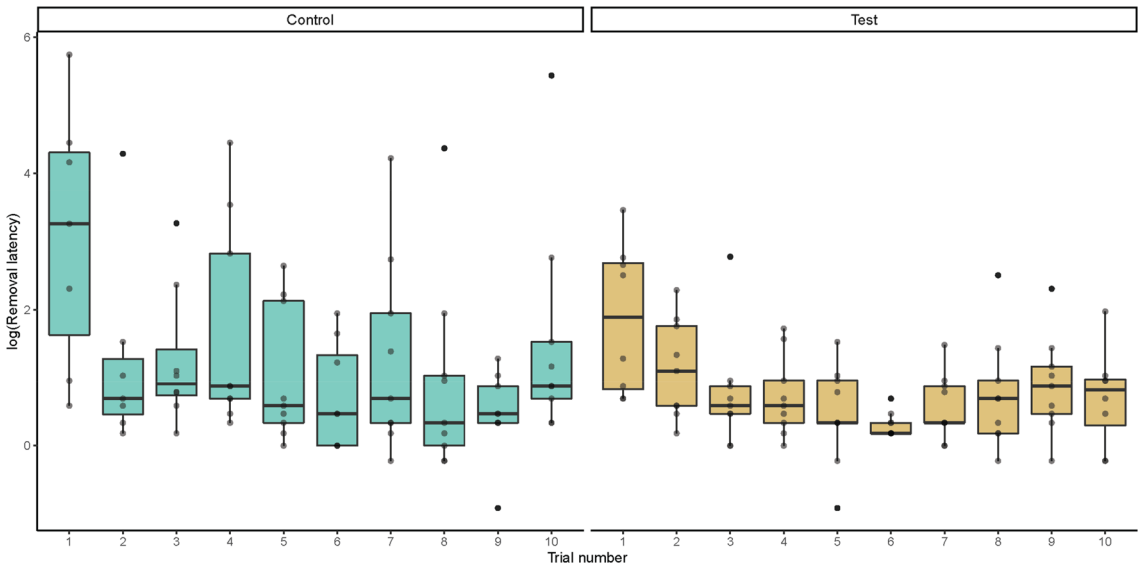

Fig. 4 Log of the removal latency session 1 for control (green) and test (yellow) birds across trials in the first session. Boxplots show the median (solid line), 25th–75th percentile (box) and the largest and smallest value (whiskers). Dots reflects outliers. Note that the figures show the raw data and does not represent the fitted model with log (removal latency) as a response. Full-null model comparison: $\chi.^2$ = 21.579, df = 3, P = 0.000079

non-significant. After removing this and other non-significant interaction terms we found effects of the interaction between session and trial. The removal duration showed a strong decrease over successive trials in session 1 (see Fig. 4), but did not change much in the later sessions, see Online Resource 1 Fig. 10. On average the observer birds took a similar amount of time to remove one of the two stoppers than control group birds did.

As the main effect was expected in the first session with individual learning occurring in all groups once the task was acquired we ran a separate analysis for session 1 and session 2–7, respectively. And indeed, after subsetting the data to only contain session 1, the full-null model comparison revealed an effect of the test predictors (χ^2 = 21.579, df = 3, P = 0.000079), but revealed no significant interaction between the experimental group and trial. After removing the interaction, the effects of the experimental group (χ^2 = 7.167, df = 1, P = 0.0074), trial (χ^2 = 12.217, df = 1, P = 0.00047) and age (χ^2 = 5.923, df = 1, P = 0.015) all appeared significant, see Online Resource 2. The observer birds (test group) on average took 0.745 log seconds less to make a removal response in session one and older birds were faster than younger birds.

There was an effect of trial which did not differ between experimental groups as well as an average decrease of latency across all groups to remove a stopper. Birds were on average 0.328 log seconds faster per trial to remove stoppers. The full-null comparison for the subset including sessions two to seven did not reveal any effect of the test predictors (χ^2 = 11.108, df = 7, P = 0.134).

Sex differences

Each of the above models also included sex as a control predictor; the analysis of the individual models revealed that there was a significant difference between the sexes in approach pace, response duration and removal latency across all trials and sessions. Males on average were significantly faster in approaching the test box (males versus females: 1.99 (1.89) versus 4.72 (7.99) seconds, (χ^2 = 12.198, df = 1, P = 0.0005); males had a shorter response duration to complete the task (males versus females: 2.0372 (1.64) versus 3.04 (3.56) seconds; (χ^2 = 6.321, df = 1, P = 0.0119)); and males were faster to make a removal response (males versus females: 1.69 (2.06) versus 5.27 (19.1) seconds; χ^2 = 7.049, df = 1, P = 0.0079)), see Fig. 5.

Discussion

Kea that observed a trained demonstrator (1) took less time from hopping on the box to feeding (response duration) in session one, and (2) were faster in making a vertical removal response on the stopper once they hopped on the box (removal latency) in session one than non-observing control group individuals. Despite the clear social effects on

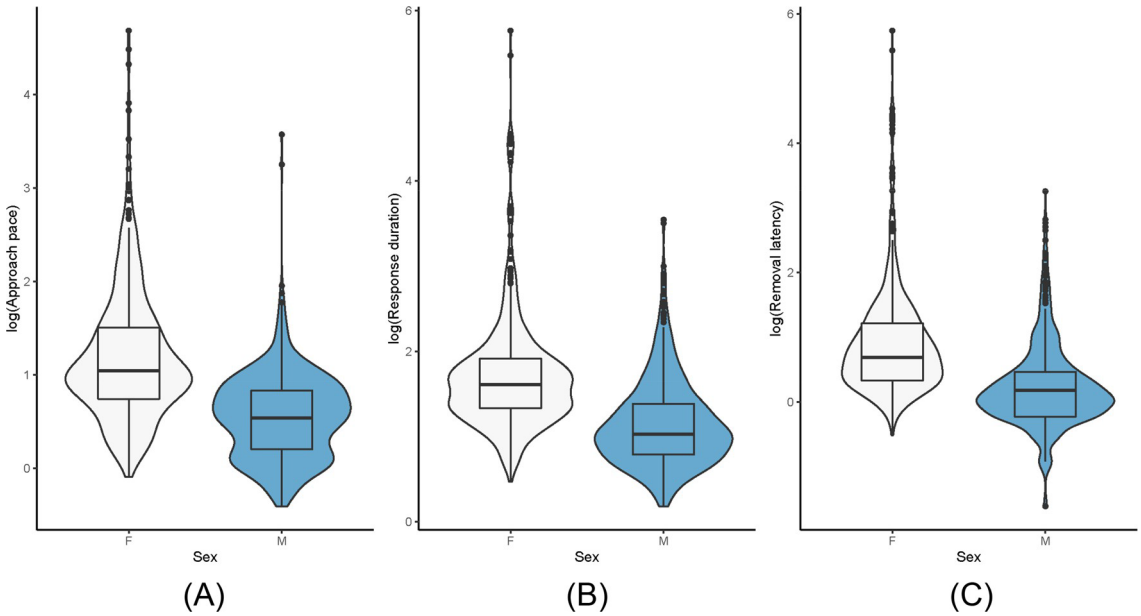

Fig. 5 Logs of the approach pace, response duration and removal latency for females and males across all trials and sessions. Sex differences in **A** approach pace between females (F) and males (M), P = 0.0005; **B** in response duration between females (F) and males (M), P = 0.0119 and **C** removal latency between females (F) and males (M), P = 0.0079. Violin plots with boxplots showing the median (solid line), 25th–75th percentile (box) and the largest and smallest value (whiskers). Dots reflects outliers. Note that the figures show the raw data and not the corresponding models

observers' initial behaviours, there was no matching of the demonstrated stopper colour or action. Hence, in contrast to budgerigars' (Heyes and Saggerson 2002), the present study could not find evidence of motor imitation in kea.

The highly significant effect of the experimental group, in regards to removal latency in session one, suggests that observers extracted some information from the demonstration. On the motivational level (Zentall 2006), the mere presence of a conspecific could have amplified the motivation to participate in the task (social facilitation, Zajonc and Sales 1966). Hence, the demonstration might have incentivised observers to engage with the set-up and led observer birds to be quicker to respond than the non-observing control. On a perceptual level, the demonstration could have also amplified the spatial location of the stimuli test box and stoppers via the process of local enhancement (Thorpe 1963). Observer birds, therefore, had the benefit of knowing the relevant locations of the test set-up and could exploit this advantage in their first attempts at solving the task.

The response duration decreased across trials in session one for observer birds while it increased slightly for the control group, pointing towards a demonstration effect. Conversely, control group individuals illustrated a steep decline in response duration in session two, allowing them to catch-up by the third trial of the second session and redressing any differences between the groups. The demonstration had no more effect once an individual had gained experience at solving the task, erasing any differences between the groups by session two. In contrast, the budgerigars increased their response matching in a linear fashion across the seven test sessions indicating persistent demonstration effects (Heyes and Saggerson 2002). For kea, the individual experience seemed to trump any advantage an individual could gain through a demonstration, eliminating any significant difference between the groups. This is in line with previous findings from Huber and colleagues (2001) who illustrated that for kea individual experience with a task takes precedence over close copying of a conspecific demonstrator. It is likely that kea abandon paying any attention to a demonstration once they have acquired the necessary information to solve the task on their own. However, the activities of the demonstrator did enhance the performance of the observers significantly in the first session, with the observer birds being faster to remove the stoppers in their first attempts. This points towards kea possibly having learned something about the relationship between a given stimulus and the reinforcement which amplified their motivation. In other words, the observed connection between manipulandum and reinforcement for the demonstrator could form a "Pavlovian association" (Whiten and Ham 1992) for the observer. This association between stimulus and reinforcement would indicate observational conditioning (Zentall 2006). These results are in line with previous studies on kea illustrating that motivation, manipulation propensity and efficiency are amplified by a demonstration (Huber et al., 2001), albeit without including imitation effects.

Arguably, the combination of social facilitation, local enhancement and observational conditioning is an efficient way of dealing with foraging problems. These mechanisms mitigate the risk of trial-and-error learning that is solely reliant on spatial or environmental cues. By responding to conspecifics with increased motivation (social facilitation), focusing the attention on the box (local enhancement), with the anticipation of a reward (observational conditioning) individuals will likely succeed in solving a task. If we assume that kea gather as much information as possible (about place, object and potential reward) from observing a knowledgeable demonstrator, the question remains why they favour individual strategies of solving the task over imitation, especially in the first trial/session. In the first instance, a demonstration shows the direct pathway from manipulation to reward, it would, therefore, seem beneficial for any observer to follow said pathway to obtain the reward. Our results, however, illustrated that even though all birds successfully solved the task, none of the observers applied the demonstrated opening method to achieve this goal. Even with a propensity for individual manipulation, in the first instance, imitation would constitute the most promising strategy. It, therefore, seems that an additional level of kea behaviour has to be considered when discussing a lack of imitation.

All kea were likely to engage with the task due to their highly neophilic and exploratory nature. Their exploratory characteristic corresponds with their natural feeding strategies, as extractive and opportunistic group foragers (Diamond and Bond 1999) and has likely promoted social learning. Indeed, kea fulfil many criteria that may promote social learning, such as long lifespan, several reproductive cycles, extended juvenile periods and care, group foraging, curiosity and resourcefulness (Lefebvre 2000; Richardson and Boyd 2000 in Gajdon et al. 2004, 2006). Accordingly, experimental evidence for social learning in kea has been provided by Huber and colleagues (2001). Furthermore, field observations have shown that kea pay close attention to what conspecifics are feeding on and interacting with (Diamond and Bond 1999). However, we know from juvenile kea that they are not prone to directly reproducing specific foraging techniques, in terms of action patterns or topographies, but rather focus on obtaining information about the appearance and location of any potential food resources (Diamond and Bond 1999). Within the process they learn to "recognize and locate food, the social structure [however] reduces the incentive and opportunity for them to practice individual foraging" (Diamond and Bond 1999: 98). It is therefore very probable that even as adults kea pay attention to the information provided by others concerning the location and quality

of resources while at the same time depending on individual strategies to manipulate and extract said resources.

In general, island species, as kea are, have been shown to exhibit more exploratory behaviour, hence spending more time acquiring information on individual resources than mainland species. For instance, in 2002 Mettke-Hofmann and colleagues tested 76 species of captive parrots (*Psittaciformes*) on their exploratory behaviour and found that there was a significant difference in exploration time between island and mainland species with the former spending more time on exploratory behaviour. They argue that "the value of information is high on islands and exploration helps island species to acquire information" (Mettke-Hofmann et al. 2002: 267) which is particularly valuable in areas with fluctuating food availability. Similarly, while the number of food sources kea can take advantage of is high, with "as many as a hundred species of plants and animals" (Diamond and Bond 1999:17), there is a relative scarcity of any one resource across their highly diverse habitat. Therefore, the depletion rate of any resource is very high and the likelihood to find that resource at the exact same location is very low. After all, imitation "may also be disadvantageous, if copied information is outdated or mismatched to the observing individual" (Aplin et al. 2017:7837). Thus, for kea it might be advantageous not to waste time on a potentially depleted resource and to gather as much information as possible on how to access that resource at another place.

Together with the propensity toward exploration this may explain low copying fidelity, seeing as kea are likely to be very interested in the potential affordances of objects (Diamond and Bond 1999; Huber et al., 2001) and hence in applying trial and error-based strategies. This predisposition arguably is opposed to any tendency to reproduce demonstrated actions even in the first instance and instead would suggest a stronger likelihood that kea devise their own behavioural strategies from the get go, i.e. engage in emulation learning (Tomasello 1998). Previous studies indicate exactly this propensity and, given the aforementioned profile, provide a very probable interpretation of kea behaviour and social learning mechanisms. Hence, kea may have a predisposition towards emulation over imitation in their response to any given demonstration, based on their natural feeding ecology. Alternatively, kea may be flexible in applying any one social learning mechanism depending on the task. This would mean that the composition and complexity of the task guides the strategy applied. For instance, dogs have illustrated to apply inferential selective imitation in a rod-pulling task (Range et al. 2007) and in 2014 Kuczaj and Eskelinen could show that dolphins not only differentiated what to imitate from whom (i.e. individuals and context-dependent) but also that calves selectively only copied behaviours that were either novel or more complex than their own. This would mean that indiscriminate imitation might not be the sole strategy in social learning species but rather that some species may apply imitation selectively dependent on the "behavioral context, novelty of the behaviour, (and) significance of the model" (Kuczaj and Eskelinen 2014: 232).

One limitation of the study at hand may be a potential selection bias that was introduced through the test setup, as individuals were selected for the test groups that were tolerant towards the observation tunnel (see *Subjects* section). This might have inadvertently introduced a STRANGE-related bias (Webster & Rutz, 2020). Hence, a selection bias towards those individuals that were bolder and more exploratory and, therefore, could easily be trained to stay inside the observation tunnel. Subsequently, those individuals that were faster, in general, may have been selected for the test groups, hence, explaining any differences we see in the experimental treatment. The significant difference between the sexes in all scores, with the males performing more quickly than the females can potentially also be explained as an artefact of the test set-up (replication study) with four high-ranking males as demonstrators and an unbalanced male–female ratio across experimental groups (the test group had more males and the control group more females). To that effect, the selection bias may have amplified a known aspect of the social structure of kea. Diamond and Bond suggested that male kea are bolder and show more exploratory behaviour than females (Diamond and Bond 1991, 1999). Past experience has shown that male kea are faster to respond in test settings, while females seem to be more tolerant towards waiting, i.e. more patient. For instance, tested in a triadic cooperation task, male kea were faster to approach partners to initiate cooperation, however, females were better at waiting for the second partner to collectively solve the task (Schwing et al. 2020). An additional constraint on female participation may have been the breeding season, which leaves females less motivated to participate in testing. The combination of a selection bias (resulting in uneven sex ratio within the experimental groups), sex difference in general motivation to participate, paired with the seasonal unavailability of females could explain the present results and should be closely monitored in future studies.

In conclusion, our results illustrated that exploration rates were high in those groups that received a demonstration, indicating motivational and attentional shifts and hence pointing toward social learning effects in observer birds during initial exposure to the task. The study offers a valuable contribution to the ever-growing literature on social learning, which is marked by a distinct lack of truly comparative studies, as noted by Galef and Whiten (2017). In fact, although there seems to be undisputed agreement on the value of replication studies the pressure to publish novel, positive (significant) results limit the availability of such

studies, for a comprehensive review on the topic see Farrar et al. (2021).

In line with previous studies, our results suggest that kea have a tendency toward applying individual techniques to solving a task which opens the question of whether kea engage in motor imitation at all or if in contrast they favour emulation over motor imitation. Alternatively, the task may have been too simple, or the two actions (push and pull) too similar and hence not suitable to test for imitative behaviour. Corresponding with social learning behaviour, the low difficulty level of the task may not have been adequate to induce imitative behaviour as a response (Garcia-Nisa et al. 2023). Kea may apply imitation selectively (Kuczaj et al. 2012, 2014) depending on the complexity, context and novelty of the task which would require a test set-up conducive to this propensity. Future studies will have to focus on devising a task that will tip the balance in favour of the application of imitative behaviour. This could be achieved by increasing the overall complexity of the task, and therefore, making it less likely that kea depend on individual learning to solve the task. Alternatively, rewarding could be manipulated by introducing asymmetry in the pay-offs, in line with Aplin and colleagues (2017), to incentivise observers to apply imitative behaviour.

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Data availability The r script and workspace (containing all data) is available at the Science Data Bank repository https://doi.org/10.57760/sciencedb.07974.

Declarations

Conflict of interest There is not conflict of interest to declare.

Ethical approval The study is in accordance with the Good Scientific Practice guidelines and national legislation (ETK-10/11/2016) and has been approved by the institutional ethics and animal welfare committee at the University of Veterinary Medicine Vienna.

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MANUSCRIPT TWO: Kea, bird of versatility. Kea parrots (*Nestor notabilis*) show high behavioural flexibility in solving a demonstrated sequence task

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ORIGINAL ARTICLE



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Abstract

Social learning is an important aspect of dealing with the complexity of life. The transmission of information via the observation of other individuals is a cost-effective way of acquiring information. It is widespread within the animal kingdom but may differ strongly in the social learning mechanisms applied by the divergent species. Here we tested eighteen Kea (*Nestor notabilis*) parrots on their propensity to socially learn, and imitate, a demonstrated sequence of steps necessary to open an apparatus containing food. The demonstration by a conspecific led to more successful openings by observer birds, than control birds without a demonstration. However, all successful individuals showed great variation in their response topography and abandoned faithfully copying the task in favour of exploration. While the results provide little evidence for motor imitation they do provide further evidence for kea's propensity towards exploration and rapidly shifting solving strategies, indicative of behavioural flexibility.

Keywords Kea (*Nestor notabilis*) · Behavioural flexibility · Sequence-task · Problem-solving

Zusammenfassung

Keas, Vögel der Vielseitigkeit. Kea-Papageien (*Nestor notabilis*) zeigen eine hohe Verhaltensflexibilität bei der Lösung einer demonstrierten Sequenzaufgabe.

Soziales Lernen ist ein wichtiger Aspekt im Umgang mit der Komplexität des Lebens. Das Erlangen von Informationen durch die Beobachtung Anderer ist eine effiziente Möglichkeit der Informationsbeschaffung. Diese Art des Lernens ist im Tierreich weit verbreitet, kann sich jedoch hinsichtlich der unterschiedlichen sozialen Lernmechanismen, welcher sich die verschiedenen Arten bedienen, stark unterscheiden. Achtzehn Kea-Papageien (*Nestor notabilis*) wurden auf soziales Lernen, im Speziellen auf imitatives Lernen einer demonstrierten Abfolge von Schritten zum Öffnen eines mit Futter gefüllten Apparats, getestet. Die Resultate ergaben, dass eine Demonstration durch einen Artgenossen bei Beobachtervögeln zu erfolgreicheren Lösungsansätzen führten als bei Kontrollvögeln welche keine Demonstration erhielten. Allerdings zeigten alle erfolgreichen Individuen große Unterschiede in der Topographie ihrer Reaktion, der genauen Abfolge an Bewegungen. Ebenfalls gaben sie das getreue Kopieren der Aufgabe zugunsten von Erkundungs- und/oder individuellen Lösungsstrategien auf. Insgesamt zeigten unsere Ergebnisse, dass Keas starke Verhaltensvariabilität und Flexibilität zeigen, wenn sie eine komplexe motorische Aufgabe lösen. Damit stellen sie ein großartiges Modellsystem zur Untersuchung der Verhaltensflexibilität dar.

This article is a contribution to the Topical Collection '50 years anniversary of the Nobel Prize in Physiology or Medicine to Karl von Frisch, Konrad Lorenz and Niko Tinbergen in 1973'.

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Introduction

Social learning can be defined "as a change in behavior that follows the observation of another (typically a conspecific) perform a similar behavior, the products of the behavior, or even the products alone" (Zentall 2012: 114). Which type of information is acquired through observation may differ strongly and is reflected in so-called social learning mechanisms. Motivational factors such as social facilitation (Zajonc 1965) promote the acquisition of information or change in behaviour by the observer via the mere presence of a demonstrator (Zentall 2001). Perceptual factors such as local (Roberts 1941) or stimulus enhancement (Galef 1988) can facilitate information acquisition by drawing the attention of the observer to either the location or stimulus of importance (Zentall 2001). In emulation (Tomasello 1998) the results of a demonstrated behaviour affect the observer who may strive to generate the same effect on the environment/objects as the demonstration did, without necessarily understanding the actions or reproducing the behaviour. Imitation is a specific learning mechanism, defined by a high degree of copying fidelity/response matching (Whiten and Ham 1992; Whiten et al. 2009), and cannot be explained by motivational, perceptual, or attentional factors alone (Zentall 2012), for a comprehensive overview of social learning mechanisms see Hoppitt and Laland (2013). Social learning is taxonomically widespread, ranging from insects to birds and mammals, possibly because it is a cost-effective way of acquiring information. Yet, social learning is not always advantageous (Giraldeau et al. 2002; Garcia-Nisa et al. 2023) and different social learning mechanisms may have different thresholds in this respect.

Great apes, for instance, seem to be less prone to show imitation than other forms of social learning like emulation (Horner and Whiten 2005; Tennie et al. 2006; Clay and Tennie 2018). On the other hand, Marmosets (*Callithrix jacchus*) (Bugnyar and Huber 1997; Voelkl and Huber 2000, 2007) and dogs (*Canis familiaris*) (Huber et al. 2009, 2018, 2020) show high-fidelity imitation despite not being closely related to humans (*Homo imitans* as proposed by Meltzoff 1988). This suggests that high-fidelity imitation may be driven by natural ecology and social structure rather than phylogenetic relatedness. In fact, experimental evidence has illustrated that various avian species, namely budgerigars (*Melopsittacus undulates*) (Dawson and Foss 1965; Heyes and Saggerson 2002), European starlings (*Sturnus vulgaris*) (Fawcett et al. 2002), Japanese Quail (*Coturnix japonica*) (Akins and Zentall 1998; Akins et al. 2002), Common Ravens (*Corvus corax*) (Loretto et al. 2020) and Pigeons (*Columba livia*) (Nguyen et al. 2005) show (simple forms) of motor imitation.

Parrots are renowned for their technical intelligence, vocal mimicry and social learning capacities (Pepperberg and Funk 1990; Huber et al. 2001; Funk 2002; Huber and Gajdon 2006; Werdenich and Huber 2006; Auersperg et al. 2009, 2011, 2012, 2014; Miyata et al. 2011; Goodman et al. 2018; Klump et al. 2021; Smith et al. 2022). Yet surprisingly few parrot species have been tested on their motor imitation skills (budgerigars: Dawson and Foss 1965; Galef et al. 1986; Heyes and Saggerson 2002; grey parrots (*Psittacus erithacus*): Moore 1992; kea (*Nestor notabilis*): Huber et al. 2001; Suwandschieff et al. 2023; Goffin cockatoos (*Cacatua goffiniana*): Auersperg et al. 2012), revealing mixed results. Whereas most studies find evidence for motor imitation, the studies on kea remained inconclusive.

Kea (*Nestor notabilis*) possess well-developed technical skills (Huber and Gajdon 2006), have long lifespans with multiple reproductive cycles, extended juvenile periods accompanied by considerable in-group tolerance, are highly neophilic and exploratory (Diamond and Bond 1999). They also have a very large number of documented food sources (Brejaart 1988; Clarke 1971; O'Donnell and Dilks 1994) many of which need to be extracted, which strongly suggest transfer of knowledge between individuals. All these characteristics facilitate the development of social learning (Gajdon et al. 2004), yet experimental evidence for imitation in this species is still missing. Therefore, we tested kea, for their social learning skills in a demonstrated sequence task. Specifically, we aimed at exploring kea's imitative social learning capacities. We hypothesised that when confronted with a relatively complex two-step task, kea would pay attention to, and copy the behaviour of, a skilled conspecific. We thus predicted that observers would preferentially use the demonstrated opening side, sequence and colour whereas non-observing control individuals would apply trial-and-error learning to solve the task.

Method

Subjects

Eighteen kea from the Haidlhof Research Station (Bad Vöslau) participated in this study. All individuals were group-housed in an outdoor aviary equipped with perches, nesting areas, ponds, and various enrichment. All birds were fed three times a day, had access to water ad libitum and were not food deprived for testing. All individuals had prior experience with experimental testing and participated on a voluntary basis in the task. The testing compartment at the Haidlhof Research Station can be visually separated from the rest of the aviary and can be further divided into two

different areas. The individuals were assigned to test groups of three and five individuals and two control groups of five individuals each. The distribution was sex and age balanced, for details see Table 1 of the supplementary material.

Apparatus

A rectangular box (44 × 18 × 18 cm) with two aluminium sliding lids, two pins, two strings and two rings served as the test box, see Fig. 1. The test box was designed to provide a sequence function, requiring the subjects to pull a pin on top of the box, to then be able to open the opposite sliding lid by pulling a ring attached at the side of the box. The adjacent sliding lid remained locked. Hence, the only solving sequences for the test box were left pin–right ring or right pin–left ring. Electronics were added inside the box to provide the sequence function. If no pin or both pins were pulled the mechanism locked both lids and no rewards could be retrieved. Manual locking keys were added to provide a full and partial locking function for demonstrator training and demonstration sessions. The box was divided into equally sized reward sections underneath the sliding lids and a GoPro fixture was attached at the base.

The pins were coloured in red and yellow, which is on the preferred spectrum for kea, and the strings and rings in green and blue (less preferred spectrum) respectively (Weser and Ross 2013). Each side and sequence had one preferred and one less preferred colour pairing, minimising the potential for a side bias based on colour preference alone. To increase salience, only those parts that needed direct manipulation were coloured, i.e., the pins, strings, and rings.

Procedure

To minimize the effects of individual learning over social learning, all test sessions consisted of one trial only. Each session/trial was terminated either after successful reward retrieval or a maximum of two minutes of exploration—i.e. pulling and touching different ring-pin combinations without opening success. A stopwatch was used to track the two minutes and all sessions were terminated by removing the individuals from the test compartment once either criterion (removal response or time-out) was met. Subjects from test groups received two experimental phases, whereas subjects from control groups received three phases (see below). In all phases, both sides of the box were baited and each sequence was rewarded. However, removing a pin and pulling on the wrong ring, pulling both pins or pulling on the rings without having removed the respective pin did not lead to any reward (as the doors were locked). Altogether four sessions (of one trial each) were tested on three consecutive days. On the first day, phase one (consisting of only one session) was tested in the morning and the first session of phase two (consisting of three sessions) in the afternoon. On the second and third day, each individual only received a morning test session of session two and three of phase two respectively.

The experimenter wore mirrored sunglasses (as has been applied before by Bastos and Taylor 2020; Suwandschieff et al. 2023) and remained silent during testing (excluding direct commands such as “enter”, “exit” etc.) to avoid unintentional cueing.

Phase 1: Forced failure task to all birds Pins were removed on this occasion and the test box could not be opened. All individuals (of all experimental groups) received access to the test box and were allowed to try and open it for two minutes. As the pins were missing all individuals were forced to fail this task. After two minutes passed the individual exited the testing compartment and the session was completed. This phase was introduced to prime individuals on the non-functioning of the task, focusing the attention towards the essential pins and increasing the motivation to follow a demonstration.

Phase 2: Non-demonstrated task Control Group (CG) Control group individuals were allowed to try and solve the task by trial-and-error for three sessions (on three consecutive days).

Phase 2: Demonstrated task Test Groups (TG) Test group individuals received three demonstration sessions of three trials each followed by three test sessions of one trial each (test following demonstration session in direct succession) on three consecutive days. Side/sequence and demonstrator assignment were counterbalanced across the two groups (see Table 1 of the supplementary material).

Phase 3: Demonstrated task Control Test (CGTest) In the third phase, former control group birds (minus the two demonstrator birds) were randomly assigned to the two demonstrators and were tested again, this time as observer individuals. The test setup was identical to the phase two demonstrated task of the test group.

Data scoring and analysis

All experiments were videotaped from two sides, behind the observation compartment and directly above the test box (GoPro) within the test compartment, for the exact setup see Fig. 1 of the supplementary material. All GoPro videos of the test sessions were scored/coded with Solomon Coder (version beta 19.08.02) and one independent rater (blind to the study) scored 10% of all videos. Interobserver reliability was tested with Cohen’s Kappa for the categorical ($k = 0.93$) and Intraclass Correlation Coefficient for the numerical data (ICC = 0.711, approach duration; ICC = 0.999, response duration; ICC = 1, solving latency), for more information see the supplementary material.

A total of 74 sessions were analysed. Two individuals did not participate in two sessions and one session respectively,



Fig. 1 Test box **a** front view of two pins **b** side view of green and blue ring respectively

all other individuals completed all three of their test sessions. A binomial test was applied to compare the success rate of the test versus the control group, using the proportion of successful control birds as the baseline chance level of solving the setup spontaneously without demonstration. All other analyses were strictly descriptive.

Results

After all subjects had experienced a non-functional apparatus (phase 1), they were allowed to engage in the task with or without prior demonstration of a skilled conspecific (phase 2). In sum, four individuals from the test group (out of a total of 8) successfully solved the task and two individuals from the control group (out of a total of 10). The exact binomial test resulted in a nearly significant trend between the test and control group ($x = 4$, $n = 8$, $p = 2/10$; *p-value* = 0.056).

The control group individuals participated in an additional round of testing (phase 3), in which they received a demonstration prior to getting access to the task again. Four individuals who had failed to solve the task without receiving a demonstration successfully solved the task after receiving a demonstration. In contrast, one of the individuals from the control test group, who had solved the task without receiving a demonstration (in the control group round), did not solve the task after receiving a demonstration (in the control test group round). Assessing the birds' performance after receiving a demonstration (test group plus control test group) *versus* without a demonstration (control group), the exact binomial test revealed a significant difference between the groups with the test groups performing much better on average than the control group ($x = 8$, $n = 16$, $p = 2/10$; *p-value* = 0.007). When comparing the within-subject design of the control group *versus* the control test group (repeated measure) twice as many individuals successfully solved the task after having seen a demonstration ($x = 4$, $n = 8$, $p = 2/10$; *p-value* = 0.056). Half of the successful individuals (4/8) that saw a demonstration solved the task via the opposite (non-demonstrated) sequence and later reversed to the demonstrated sequence in subsequent sessions, see Table 1.

Discussion

We show that kea were able to solve a rather difficult two-step sequence task and that receiving a demonstration of a skilled conspecific had a positive effect on solving success. However, successful birds showed a high variation in their response topography and often abandoned faithfully copying the task in favour of exploration. This is particularly interesting in the case of John, who followed the demonstrated sequence twice and then generalised in the other direction.

The effect of demonstration becomes particularly clear when combining the results from phase two and three. Eight out of 10 subjects that came to solve the task did so after a demonstration. That kea can profit from social learning is in line with previous studies (Huber et al. 2001; Huber 2002; Suwandschieff et al. 2023). However, the current study provides little evidence for motor imitation, despite various methodological differences from the other studies. For instance, previous experiments illustrated that the motivation to follow a demonstration was low. It was theorized that the complexity of the demonstrated actions could have contributed, as they likely were too simple to require a demonstration to solve the task (Suwandschieff et al. 2023), or too complex to follow the demonstration from afar (Huber et al. 2001) and reproduce with high fidelity. Therefore, the task was made more difficult than the basic two-choice task, while avoiding the complexity of the multi-lock box, and the forced failure in phase one was introduced to prime individuals on the task difficulty and to increase their motivation to

Table 1 Individuals that successfully solved the task per experimental group

Name	Sex	Age	Raised	Group	No of successful sessions (out of 3)	Demonstrator	Applied demonstrated sequence	Applied non demonstrated sequence	Stayed consistent for no of sessions	Switched in session no
Frowin	Male	17	Parent	Control	3	NA	NA	NA	3/3	NA
Papu	Female	8	Hand	Control	1	NA	NA	NA	1/1	NA
John*	Male	22	Parent	Test	3	Frowin	in Session 1 and 2	in Session 3	2/3	3
Tai*	Female	3	Parent	Test	2	Frowin	in Session 1 and 3	Never	2/2	NA
Coco	Female	14	Hand	Test	2	Paul	in Session 2	In Session 1	1/2	2
Pick	Male	17	Hand	Test	2	Paul	Never	In Session 1 and 2	2/2	NA
Sunny	Female	14	Hand	Control Test	1	Paul	Never	In Session 1	1/1	NA
Skipper	Male	4	Hand	Control Test	2	Paul	in Session 2 and 3	Never	2/2	NA
Fay	Female	5	Parent	Control Test	1	Frowin	in Session 1	Never	1/1	NA
Plume	Female	14	Hand	Control Test	2	Frowin	in Session 3	In Session 1	1/2	3

Table indicates name, sex, age, rearing, and experimental group. Number of successful sessions out of three test sessions, assigned demonstrator, application of demonstrated sequence and according session information, application of non-demonstrated sequence and according session information, count of consistent opening sequence out of three test sessions, and number of switches in opening sequence out of three test sessions

*Received two additional trials

follow a demonstration. Yet, these measures did not result in a higher copying fidelity than the other studies. On the one hand, half of the solvers used the opposite sequence to the demonstrators. On the other hand, solving success appeared not to reference solving consistency, as successful birds continued to explore the solving potential by applying different opening methods (see supplementary material for details). This variation in solving behaviour unfortunately made a statistical comparison not possible in terms of actual mechanisms, or quantifiable behavioural differences with previous studies.

As all individuals, regardless of the experimental group, participated in the forced failure task, it is improbable that our results can be solely explained by social facilitation or local enhancement. Although we cannot rule out the possibility that the mere presence of a demonstrator motivated individuals to engage in the task, we have established that all individuals will do so even in the absence of a conspecific. Therefore, the presence of another individual does not appear to be the primary factor explaining our results. Additionally, since the location of the test box remained constant throughout the different phases, no additional information could have been gained from the demonstration. Consequently, this does not explain the discrepancy between the experimental groups. While the success rate of observer birds and the varied response patterns exhibited by successful individuals indicate emulation, we cannot dismiss the potential influence of stimulus enhancement. A test setup that clearly distinguishes these two mechanisms would have to be devised, i.e., one including a ghost control (Whiten and Ham 1992). Consistent with previous findings kea show high behavioural flexibility (Werdenich and Huber 2006; Auersperg et al. 2011; Laschober et al. 2021) and preferentially engage in exploratory behaviour, being more interested in potential affordances than feeding success (Diamond and Bond 1999; Huber et al. 2001; Smith et al. 2022; Suwandschieff et al. 2023). These results are in accordance with kea's natural feeding strategies, as opportunistic group foragers, with kea paying close attention to what others feed on while engaging in individual manipulation strategies to obtain the resources (Diamond and Bond 1999). In addition, it corresponds with the characteristics of island-dwelling parrots, as described by Mettke-Hofmann and colleagues (2002) who found that island species spend significantly more time on exploratory behaviour especially in areas of seasonally fluctuating food availability.

In conclusion, we find strong evidence that observing a conspecific opening an apparatus via two steps affected the solving success of observer kea. They thus profit from social learning, which aligns well with other studies on parrots and songbirds showing social information transmission and the spread of novel foraging techniques within captive groups

and wild populations (e.g. Slagsvold and Wiebe 2011; Auersperg et al. 2014; Aplin et al. 2015; Klump et al. 2021). However, in our study, the response topography of solvers was variable and the copying fidelity was at a very low level, providing no indication of motor imitation over emulation or stimulus enhancement in kea. Therefore, our findings corroborate that kea display strong behavioural variability when attempting to solve a complex motor task. They also keep on exploring options after a successful solution and may rapidly shift solving strategies. Taken together, this makes kea a great model system to study behavioural flexibility but not so much for imitation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-023-02127-y.

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Author contributions ES: design, data collection, data curation and analysis, manuscript original draft, revisions, final manuscript; LH: conceptualisation, design, supervision, manuscript review; TB: conceptualisation, design, supervision, manuscript review; RS: conceptualisation, funding acquisition, design, supervision, manuscript review and editing. All authors read and approved the final manuscript.

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Data availability All data generated or analysed during this study are included in this published article [supplementary material file: raw data].

Declarations

Conflict of interest All authors have read the submitted version of this manuscript and declare no conflicts of interest. The authors have no relevant non-financial interests to disclose.

Ethical approval The study is in accordance with the Good Scientific Practice guidelines and national legislation (ETK-10/11/2016) and has been approved by the institutional ethics and animal welfare committee at the University of Veterinary Medicine, Vienna.

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MANUSCRIPT THREE (SUBMITTED):
Stimulus enhancement in kea (*Nestor notabilis*) in an object choice task

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Stimulus enhancement in kea (*Nestor notabilis*) in an object choice task

ABSTRACT

Previous studies illustrated that kea (*Nestor notabilis*) can apply socially acquired information to solve both simple and complex tasks. However, evidence of the exact information kea utilised in social learning is still vague. In this study, we therefore, investigated the role of stimulus *versus* local enhancement as mechanisms of social learning in an object choice task. We presented twelve kea individuals with objects of four different shapes and nine different colours and tested whether kea would acquire information based on the object (stimulus enhancement) or the location of the apparatus (local enhancement). Our results illustrate that, while social facilitation may have been at play, kea utilized the information provided by the stimulus and paid no attention to the location. Hence our findings support stimulus enhancement as the prime social learning mechanism adapted by kea when solving a simple object choice task. The results help explain ambiguous results from past experiments and support distinguishing the different processes at play in social learning of kea.

INTRODUCTION

Social learning is the acquisition of information from an individual through observation (Heyes, 1994). Learning from conspecifics has 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. In copying a conspecifics' behaviour, an individual can find new food or water resources, learn about predators and/or how to move through their habitat safely, without having to explore the whole habitat itself (Laland, 2004). 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)

Local and stimulus enhancement are processes which can play a role in different types of social learning, such as imitation, emulation or observational conditioning (Heyes, 1994; W. J. E. Hoppitt & Laland, 2008; Laland, 2004). Both local and stimulus enhancement can occur simultaneously and are not always distinguishable from one another. Local enhancement (term coined by Roberts, 1941) occurs when the observer's attention is drawn to a specific location because of the demonstrator's behaviour in that location (Zentall, 2006). Stimulus enhancement (Galef, 1988) occurs when the observer's attention is drawn to a stimulus, or features thereof, because of a demonstrator interacting with it. However, stimulus 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" (Spence, 1937; Giraldeau, 1997; in Fritz et al., 2000, p. 1120). 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 (W. Hoppitt & Laland, 2013 in; Wild & Hoppitt, 2022, p. 6519), hence it is locally bound.

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 remain ambiguous. For instance, kea parrots (*Nestor notabilis*) were tested on their imitative and non-imitative social learning capacities in several experiments (Huber et al., 2001; Suwandschieff, Huber, et al., 2023; Suwandschieff, Wein, et al., 2023). The 2001 study by Huber and colleagues illustrated that, although kea utilized information obtained from a demonstration, the very high complexity of the task seemed to impede copying fidelity. Observers had greater success opening the locks than control birds, yet none solved the task, and the type and sequence of actions differed from the demonstrations. The following experiment (Suwandschieff, Wein, et al., 2023) therefore reduced task complexity significantly (replicating Heyes & Saggerson, 2002) which also led to a complete lack of copying fidelity, likely due to the task simplicity. Motor imitation was utterly missing in this study, as none of the kea, in contrast to the budgies in the original study, matched the opening action demonstrated. Furthermore, there was no significant matching of the demonstrated colour or side. As all subjects solved the task, independent of a demonstration, in the first trial, it was theorized that

the simplicity of the task allowed the highly explorative kea to solve it spontaneously. The final relevant study aimed again to investigate motor imitation (Suwandschieff, Huber, et al., 2023), and increased task complexity to such a degree that it was unlikely for individuals to solve it from the get-go. Here, one of two pegs needed to be removed, before pulling a ring on the opposite side of the apparatus to gain access to a reward; both pulling on the ring adjacent to the pulled peg, or pulling both pegs, did not open a reward compartment. The results suggested that kea solved the task via emulation, as, within three test trials, subjects varied in solving the task in the same manner as demonstrated as well as the opposite. This novel setup would have been conducive to stimulus enhancement (but not local enhancement), however, the variation in solving the task did not show it to be necessary to solve the task. While all three studies could find clear 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, i.e. to be able to focus on effects of the demonstration, all options presented, and all actions that led to these, were rewarded. Therefore, basic knowledge about these mechanism of social learning in kea is still missing, which may explain the inconsistent results. 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 which support social learning (Gajdon et al., 2004), making them good candidates for behavioural experiments. Low predation rates during their evolution along with the uncertainties of their natural habitat, that is marked by seasonally and local fluctuations in food availability, has rendered kea highly exploratory birds that show strong behavioural flexibility and curiosity (Diamond &

Bond, 1999; Huber et al., 2001; Smith et al., 2022; Suwandschieff, Huber, et al., 2023). While kea clearly apply social learning, their behavioural flexibility and curiosity seems to constrain direct imitation in studies to date (Suwandschieff, Huber, et al., 2023). Hence, experiments that aimed at finding motor imitation in kea could not provide evidence for imitation. However, the experimental setups did not conclusively prove other forms of social learning (i.e., stimulus or local enhancement) as these were not directly tested.

The study at hand, therefore, specifically tested for stimulus and 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). 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 to test cognitive abilities in an experimental setting (Bastos & Taylor, 2020; O'Hara et al., 2015). By adding an object selection to the demonstrator-observer setup we aimed at narrowing down on and separating the effects of local *versus* stimulus enhancement. In addition, it 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 were limited as each demonstrator only performed a single action or sequence of actions. Here we presented a demonstrator with a choice of different objects to insert into a box. By rewarding any demonstrator choice, while changing the objects and offering different box positions, we were able to address effects of stimulus and local enhancement in the observers' choice. Our experiment, consisted of four conditions, two demonstrators and ten observers (test

subjects). Our main research question was, can kea learn to select the same stimulus as a conspecific demonstrator in an object choice task? We hypothesised that observing a conspecific solving an object choice task would affect the stimulus choice of an observer bird. Furthermore, we predicted that the location of the demonstrator's stimulus choice would influences the observer's stimulus choice.

METHODS

Subjects, housing, and experimental compartment

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 (52x10x4 m, LxWxH, Figure 1), which is equipped with hanging branches, shelters for resting and protection against the weather, ponds, feeding tables, and environmental enrichment which is renewed regularly. The aviary contains two breeding compartments, which are closed during the breeding season, two experimental compartments (10x6x4 m) on opposite ends of the aviary, and a large central area which served as the main living quarters. Outside of testing times the experimental compartments are left open, as serve as additional living space. The experimental compartments can be divided into two equally-sized sub-compartments with a sliding, see-through wire-mesh door. All testing took place in the experimental compartments.

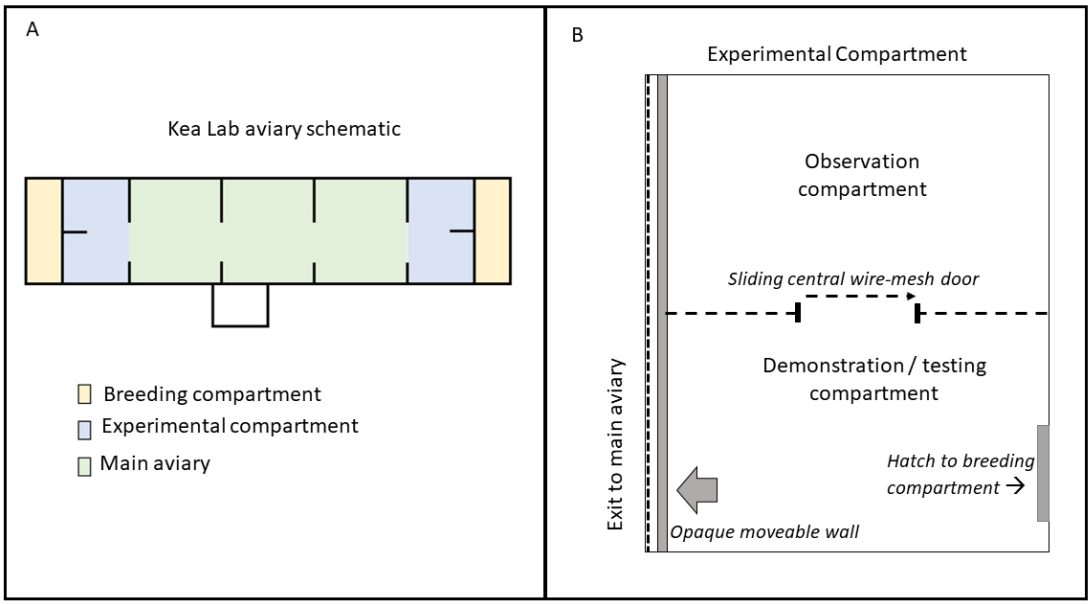

Figure 1 Schematic of the whole kea aviary (A), as well as detailed view of the experimental compartments where all testing took place. Outside of testing times the experimental compartments were left open as part of the main living space for the kea. (B) Observers stayed in the observation compartment, 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.

The kea are fed three times daily with a mixture of fruit, vegetables, seeds, and a protein (cooked meat or eggs) once daily. 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 which 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, laying 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.

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. In order to prevent disruption during breeding season (which affects females significantly) and to modulate the effect of rank (van de Waal et al., 2013) two high-ranking males served as demonstrators and the ten remaining individuals participated as observers.

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

Subject	Age	Sex	Role	Conditions			
				1	2	3	4
Di	6	F	observer	y	y	y	y
Kr	8	F	observer	y	y	x	x
Ly	16	F	observer	y	y	x	x
Ma	9	F	observer	y	y	x	x
Pl	16	F	observer	y	y	x	x
Je	8	M	observer	y	y	y	y
Jo	23	M	observer	y	y	y	y
Od	8	M	observer	y	y	y	y
Pn	6	M	observer	y	y	y	y
Sk	6	M	observer	y	y	y	y
Fr	19	M	demonstrator	y	y	x	x
Ke	19	M	demonstrator	y	y	y	y

Test apparati

Two identical wooden boxes were custom-built for this experiment (27x16x27 cm). Each box had a square opening on the top (8x8 cm) for the subject to drop in an object (object descriptions below), see Figure 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 PVC tube protruded from the top of the box and reached through the box to the reward tray (10x8 cm). To reward the subjects, the experimenter dropped ¼ of a peanut seed into the tube, which fell through and landed in the reward tray for the subjects to access.

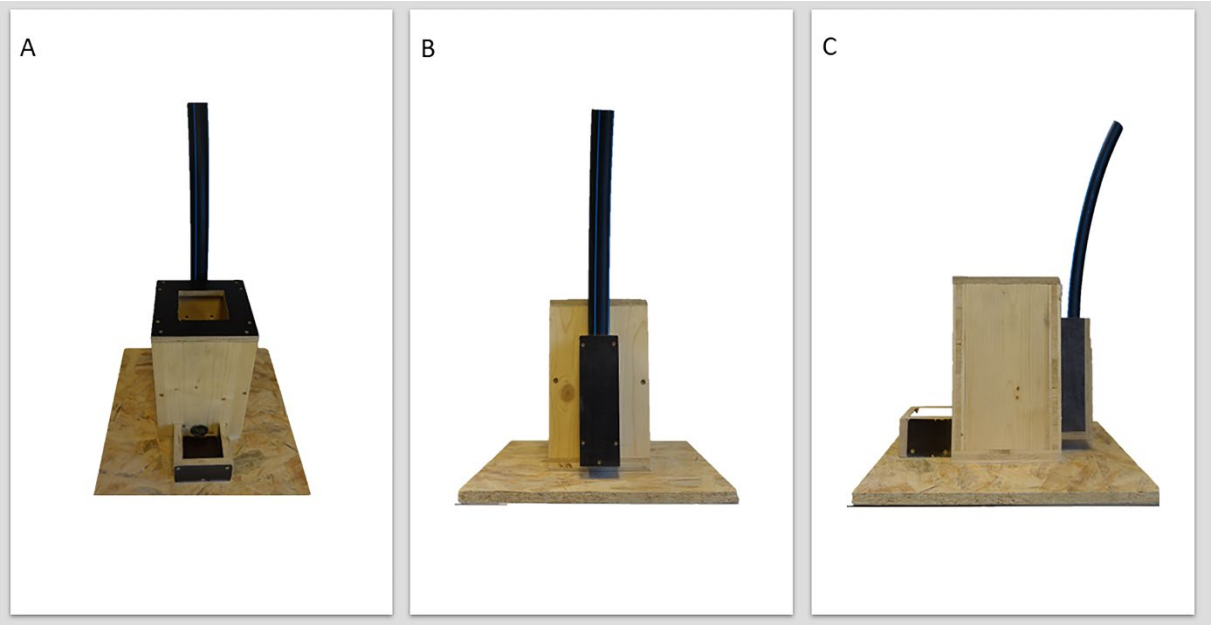

Figure 2 Test apparatus: Example of one of the two identical test-boxes: (A) front view of reward tube, square opening for the object, and feeding tray, (B) back view with reward tube and, (C) side view both feeding tray and reward tube.

Stimuli

The objects consisted of four shapes (cylinder, cube, sphere, pyramid), each handmade from 28.5g modelling clay (FIMO, Staedtler). They were made in the following nine colours: brown, green, orange, violet, white, blue, red, yellow and black (Figure 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.

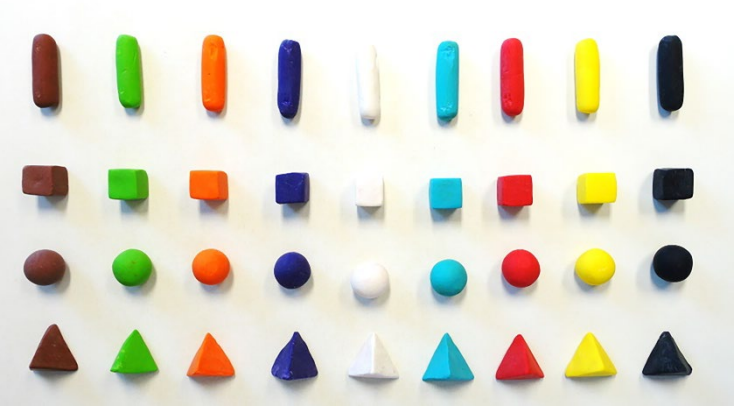

Figure 3 Stimuli: were small objects made from exactly 28.5 g of modelling clay. The objects were hand-made in four shapes (cylinder, cube, sphere, pyramid) and nine colours (brown, green, orange, violet, white, blue, red, yellow and black).

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, in accordance with good scientific practice guidelines and national legislation. The housing conditions comply with the Austrian Federal ActN on the Protection of Animals (Animal Protection Act -§ 24 Abs.1 Z 1 and 2: § 25 Abs. 3 – TSchG, BGBI. I Nr. 118/2004 Art. 2). As the study was strictly non-invasive, according to the Austrian Animal Experiments Act (TVG 2012), it was not classified as an animal experiment.

Procedure

Training

Each training session consisted of ten trials, and all subjects received one training session per day. In training step one, all twelve 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. Criteria for completing training step one was 10/10 in a single session.

Once an individual reached the criterion in training step one, they moved on to training step two, where they learned the choice 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. Criteria for completing training step two was 10/10 correct choices in a single session.

Once training was completed, two subjects (Fr, Ke) received additional demonstrator training. This consisted of three sessions each and was focused on

entering/leaving the compartment through either the exit to the main aviary or the hatch to the breeding compartment, see Figure 1. In all conditions, each demonstrator choice was rewarded regardless of object colour or shape. This novel approach was applied to reduce training rotations for the demonstrator individuals, while ensuring that observers could not solve the tasks based on previous trial experience. As demonstrators chose at random there was no pattern to be detected.

Testing

The general procedure was identical for all four test conditions. Each observer received ten test sessions per condition. Each session consisted of five trials, and took around 15 minutes. Observers were tested once per day. A trial comprised of one demonstration followed by the test. Each trial ended after an object was placed into the box, or after one minute had passed with no interaction with the objects. Object colour, shape and side assignment were randomized across trials.

Each trial began with the observer separated in the observation sub-compartment of the experimental compartment, and the demonstrator outside the testing compartment, see Figure 1. The experimenter set up the apparatus and stimuli in the demonstration/test compartment and once the apparatus and stimuli were in place, the experimenter gave the demonstrator access. After the demonstration the experimenter, the demonstrator left the compartment and the stimuli and apparatus were re-setup, and the sliding 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. For a detailed overview of the setup per condition see supplementary materials section *experimental setup*.

The conditions were as follows:

a) Condition 1 pre-test for stimulus enhancement. Two objects were placed in front of one box for both demonstrator and observers. Observers were rewarded only for the demonstrated object.
b) Condition 2 tested for stimulus enhancement. Four objects were placed in front of one box for both demonstrator and observer. Observers were rewarded for choosing the same object as was demonstrated.
c) Condition 3 tested 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.
d) Condition 4 tested for local enhancement. The demonstrator received one object and one box while the observers received one object and two boxes (old box in old location and new box in new location). Observers were rewarded for choosing the same box/location as was demonstrated.

The different experimental setups resulted in different probabilities to make a correct choice for the observers. 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 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 condition 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 object was offered in front of two boxes again, resulting in a 50 % probability level of making a correct choice by chance.

The objects were semi-randomly assigned and differed in colour and shape over all trials to reduce biases. For a detailed depiction of all conditions and setups see supplementary materials section *experimental setup*.

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 condition, it was additionally noted in which box the object was put. Furthermore, the number, colour and shape of objects offered, object chosen by demonstrator and observer and whether an object was put into the box at all was 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. In each of these models, we used “correct_choice” as the response variable (binary with no/yes) in an intercept only model including subject as random effect. The intercept in each of the models represents the sample mean estimated by the models. The corresponding p-value indicates whether the intercept deviates significantly from 0, which in a logistic model represents a probability at chance level (as revealed by inverse logit-transformation (exp(0)/1+exp(0) = 0.5)). A probability of 0.5 was the null hypothesis for the responses for condition one and four, however for the responses for condition two and three the chance level was 0.25. For the latter

responses we therefor tested for a significant deviation from chance level by subtracting the logit-transformed chance-value of 0.25 from the model estimate and calculated the corresponding z-value and p-value of these adjusted estimates. Thus, by testing the significance of the intercept of these models we tested if individuals differed from chance level. Across all data sets we removed data where individuals did not make a choice.

Moreover, factors which might influence the results were analysed. We investigated whether there was a colour or shape preference on the part of the demonstrators. Since only one box was presented during demonstrations, it was not necessary to test for a demonstrator side bias with respect to box position. However, as observer individuals received two boxes in both condition three and four, a potential side bias was tested in those two conditions. For more information on the results of these factors see the supplementary materials section *additional data analysis.*

During the first and second condition, all twelve kea completed the full test – ten observers and two demonstrators. In the third and fourth condition, four observers and one demonstrator kea were excluded from the study. Two of the individuals entered breeding during the study, while one was injured during a conflict 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. In most cases, individuals selected the object directly as soon as they reached it. Only once, an observer kea did not select an object within the time frame of one minute. 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

There were individual difference 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 % (22/50 correct choices) of the time, see Figure 4. Overall, observers chose the same object as the demonstrator significantly more than expected by chance (57.7 ± 2.9 % correct, $z = 2.65$, $p = 0.008$).

Second condition: four objects and one box

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 14 % (7/50 correct choices), and on average 39,4 %. Overall, observers chose the same object as the demonstrator significantly more than expected by chance (39.4 ± 3.5 % correct, $z = 4.48$, $p<0.001$).

Third condition: four objects and two boxes

The highest score choosing the same object as the demonstrator over all 50 trials was 50 % (25/50 correct choices), the lowest 20 % (10/50 correct choices), and on average 32.7 %. Overall, observers chose the same object as the demonstrator significantly more than expected by chance (32.1 ± 3.7 % correct, $z = 2.06$, $p =0.04$). However, observers did not have a preference for old *versus* new box/location (47.7 ± 2.9 % old, $z = -0.81$, $p = 0.419$). In 157 out of 300 trials the observers selected the new

(non-demonstrated) box/location to place their object. In 87/157 cases the object choice was correct. In those 87 cases, they placed the correct object in the new (non-demonstrated) location/box and in 11 cases they placed the correct object in the (demonstrated) old box/location.

Fourth condition: single objects and two boxes

Six observers chose the same box as demonstrated in 142 trials and in 152 trials the other non-demonstrated box. Overall, the observers choice of box did not differ significantly from expected random chance level (48.1 ± 2.9 % correct, z = -0.58, p = 0.559). However, there seemed to be a slight preference for the left box with 177/294 left choices. Only one object was offered per trial, hence no further analysis of object choice and/or preference was conducted.

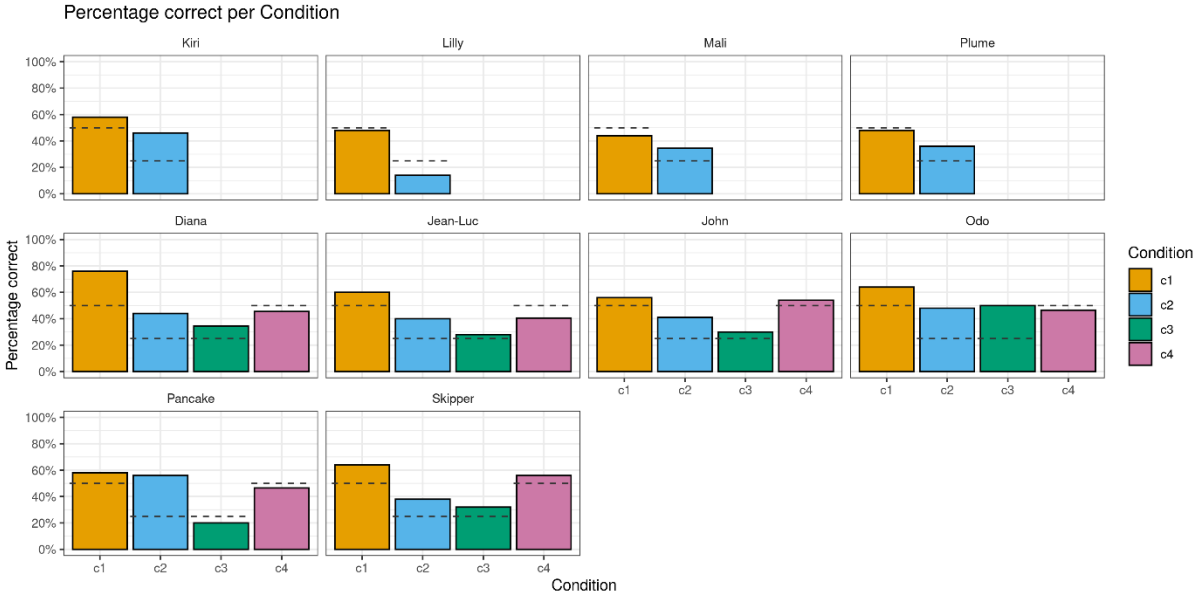

Figure 4 Percentage correct per condition: shown is the percentage of demonstrated object choices in condition1-3 and the percentage of demonstrated box choice in condition 4 for each kea. The dash lines indicate the chance level for the different condition to choose the same object or box as demonstrated.

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, however, no major shape or colour preference could be identified across individuals and/or conditions. The object choice task, which was used within demonstrator-observer experiment, was a novel approach that has not been employed with kea before and constitutes a promising method for the future.

While our analysis showed significant object choice matching in all three conditions where stimulus enhancement was a factor (condition 1-3), no indication for location matching could be illustrated in those conditions (condition 3-4) where local enhancement was a 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 influences 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).

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. The behavioural flexibility demonstrated by kea in those past task does still suggest that emulation remains relevant as a social learning mechanism. However, when solving more complex tasks kea could benefit from stimulus enhancement, especially in the first trials. 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 setup, allowed demonstrators to choose any object. Subsequently this object became the rewarded stimulus for observers. This setup 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 to be a promising technique to reducing training rotations while at the same time eliminating potential learning effects.

Some aspects of the study should be considered when interpreting the results. First the experimental setup did not test for social facilitation (Zajonc & Sales, 1966) and it is possible that this mechanism was at play. The presence of a conspecific could have increased the motivation of the observes to engage with the task (Zentall, 2012). As kea are group foragers, it is likely that “the mere observation of foraging conspecifics encourages foraging” (Zajonc, 1965, p. 1122) in the observers and hence that they are prone to social facilitation. As our experimental setup did not specifically test for this factor it is difficult to exclude with certainty. Second, the experimental setup may have primed kea on stimulus enhancement, therefore potentially inhibiting local enhancement. Specifically condition three, which targeted contrasting stimulus and local enhancement, might have been affected a) by the previous two conditions which primed the subjects on the stimulus and b) stimulus remained the rewarded factor within the condition. The final condition (four) 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 test 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.

In conclusion, while some aspects remain indistinct, the study provides clear evidence that kea show stimulus enhancement as the main effect in this social learning task. The observer’s attention was drawn to an object because a demonstrator kea 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 clearly tested for and excluded when investigating social learning in this species.

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FIGURE AND TABLE LEGEND

Figure 1 Schematic of the whole kea aviary (A), as well as 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. 40

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. 42

Figure 3 Stimuli: were small objects made from exactly 28.5 g of modelling clay. The objects were hand-made in four shapes (cylinder, cube, sphere, pyramid) and nine colours (brown, green, orange, violet, white, blue, red, yellow and black). 42

Figure 4 Percentage correct per condition: shown is the percentage of demonstrated object choices in condition1-3 and the percentage of demonstrated box choice in condition 4 for each kea. The dash lines indicate the chance level for the different condition to choose the same object or box as demonstrated. 49

Table 1 List of subjects, age, sex, role in experiment, condition participated. 7

DISCUSSION & CONCLUSION

This thesis aimed to investigate if imitation can be found in kea parrots and further explored socially facilitated matching-to-sample in order to help explain the lack of imitative behaviour found in this species so far. The main questions addressed in the empirical work were; Do kea show imitative behaviour in a two-action task, where budgerigars succeeded in response-matching? Do kea show imitation in a sequence task, designed too complex to solve via individual trial and error learning? Do kea utilize local or stimulus enhancement, when required to do so to solve a simple object-choice task?

Manuscript one investigated whether imitative behaviour could be induced in a simple experimental setup. The basis for this starting point was the study by Huber and colleagues (2001) that could not find evidence for imitation in a very complex two-action, two-sequence artificial fruit task [67]. They hypothesised that the task complexity may have required too much information to be taken in by the observers, making it difficult for them to follow the exact response topography over the sequence and thus inhibiting imitation. Therefore, in a first step a simple two-action task, utilising the methodology provided by Heyes and Saggerson [15], was replicated. With this experimental design Heyes and Saggerson successfully induced response matching in budgerigars. The testing protocol of the original study was followed closely, with minor adaptations to account for the size and testing facility differences in kea.

The results of the first experiment indicated clear social learning effects, with observers being faster in their initial solving response, both in terms of response duration and removal latency. Additionally, exploration rates were high for observers pointing towards attentional and motivational shifts. However, in contrast to the budgerigars no evidence for matching demonstrated colour or action and, therefore, no imitative behaviour could be illustrated. Kea were engaged in individual learning very early on and this was hypothesised to be due to the simplicity of the task, which offered the opportunity for individual learning. Task complexity is important for copying behaviour [74], as simple tasks do not require the additional information that could be gained via observation. While the simplified design was successful in inducing response matching in budgerigars, this did not seem to be adequate in the case of kea. Therefore, the attempt to reduce complexity from the original 2001 study [67] may have overshot the mark.

With this caveat in mind, a second experiment that was far more complex was designed to reduce the potential for solving the task through individual learning while at the same time encouraging information acquisition by observers (manuscript two). As a result, a sequence task was introduced that required two individual steps to be completed in a discrete order on a diagonal. First a pin had to be pulled at the top of the box (either left or right side of the box) after which a ring could be pulled to open a sliding door at the opposite side of the box. The diagonal sequence was counterbalanced across observer groups, i.e., one group observing a left-to-right and the other a right-to-left sequence, and non-observing control groups receiving no demonstration. All other solving variations were blocked by automated locking devices, necessitating response matching to successfully complete the task. The saliency of the solution was increased in two ways, a) through colour contrasts at the individual steps of the sequence, and b) through a spatial separation of the individual steps to the opposite sides of the apparatus (the diagonal). Additionally, testing rotation was reduced significantly to decrease the effects of individual learning across sessions and trials.

The second experiment was indeed sufficient in inducing social and reducing individual learning and clearly indicated an effect of demonstration. Twice as many observers successfully solved the task compared to the non-observing control. This suggested that the sequence was successful in coercing response matching. However, response topography matching fidelity was low. Individuals of all groups preferentially engaged in exploratory behaviour, frequently changing solving strategies and solving sequences even after successful attempts; this was hypothesised, to be indicative of emulation rather than imitation. Kea that solved the task demonstrated that some individuals copied the observed action sequence more precisely than others, however, none of the individuals followed the exact response topography.

The results of the second experiment clearly indicated that kea show a vigorous propensity toward exploration and behavioural flexibility, finding their own strategies to successfully solve the task. These findings correspond with previous studies demonstrating that kea are interested in object manipulation and affordance learning and therefore likely engage in emulation rather than imitation [67,81,90–93]. The sequence of the task required response matching in terms of the task only being solvable by following the diagonal on either side. However, due to the locking mechanism of the apparatus matching of perceptual factors was not required to solve the task. Within the limits of the apparatus properties (full-locking mechanism) an individual could perform any number of intermediary steps and still

successfully solve the task. This was hypothesised to have caused the lack of topography matching which requires both response and stimulus matching to achieve the degree of precision contained in high-fidelity response topography matching. Thus, while response matching was present stimulus matching was missing. A third experiment was, therefore, devised to test if kea could at all be motivated to pay attention to this level of detail concerning the perceptual factors. Concurrently, the final experiment intended to tease apart local and stimulus enhancement as potential factors underlying kea's behavioural response.

In the absence of high-fidelity response topography matching, the third experiment was devised to examine the specific perceptual factors necessary for exact topographic matching but seemingly irrelevant to kea in the previous experiment (manuscript three). An object choice task with 36 objects (four different shape and nine different colour combinations) and varying locations was introduced in the third experiment. The setup was designed to first test for stimulus matching and then to differentiate between stimulus and local enhancement as potential factors influencing observers' behaviour. The results illustrated that observer individuals showed clear evidence of stimulus matching while disregarding the information provided by location. This suggests that stimulus enhancement can play a major role in social learning in kea. However, the setup could have primed observers to attend primarily to stimulus rather than location, so local enhancement cannot be discounted conclusively as a possible factor. The final experiment clearly illustrated that, given the right conditions, kea can be motivated to pay attention to perceptual factors. This was a promising result concerning the potential for kea to show high-fidelity response topography matching and, therefore, imitation.

All three experiments showed clear evidence of social learning, suggesting that it is well developed in this species. Their distinct exploratory behaviour and strong behavioural flexibility confirm their propensity towards emulative learning. Additionally, stimulus enhancement could be illustrated as a relevant perceptual factor. Finally, the potential for attending to both response and stimulus matching could be demonstrated, albeit not simultaneously. A brief look at the social structure and natural environment of kea may help explain the described results.

Kea live in dynamic fission-fusion flocks, with non-linear hierarchies and high in-group tolerance [81,94]. They have extended juvenile periods in which they experience extensive group tolerance and free access to resources [95]. The long process of maturation (up to four years) leaves this group with plenty of time to continuously explore and manipulate objects, which they spend most of their time on [90]. Kea's natural habitat can be considered

challenging, marked by fluctuating and seasonal food availability and relative food scarcity. Consequently, kea feed from a large number of food sources [81,96–98]. While they are predominantly herbivorous, feeding on fruits, leaves, seeds and roots, they also take advantage of other resources such as carcasses [99–101]. Subsequently, “the considerable breadth of the kea’s diet and the often harsh nature of the alpine environment require kea to retain a great deal of information” [100 p. 256]. Thus, a lot of information must be learned and a diverse skillset regarding the manipulation and extraction of food must be developed. Their evolutionary history, characterised by minimal predation and opportunistic feeding strategies, has rendered them highly neophilic and exploratory. Kea spend significant amounts of time engaging in group foraging, accounting for more than half of their time budget in the wild [90,102]. Juveniles, subadults and adults all “show distinctive patterns of foraging behavior, patterns that are shaped by social abilities and status, as well as by foraging expertise” [90 p. 10]. Older birds are more proficient foragers than juveniles [100], and young individuals learn from others about the specifics of their diet (what to eat, when and where) [81,90]. It is, therefore, not surprising that social learning is well developed in this species and could be illustrated in the experiments described above.

Kea’s interest in object affordances is likely associated with their pronounced neophilia as well as their extended juvenile periods during which they spend the majority of their time exploring and manipulating objects. This propensity may well carry-over into adulthood and seems to be inherently rewarding. Additionally, food availability can be scarce, and, at least locally, resources are depleted easily in kea’s natural environment. While information is acquired by discovering and observing successful feeding of conspecifics, the likelihood of also finding food at that exact location is low as it can be expected to be depleted. Therefore, searching at the exact location of a demonstrated feeding could be disadvantageous, as there may be nothing left when an observer individual gets there. This requires individuals to apply information flexibly, encouraging them to devise their own behavioural strategies with the information they have acquired via observation. Thus, it is not surprising that kea show well-developed behavioural flexibility. This is also in line with the experimental evidence presented above. Exploration and individual solving strategies were very pronounced, indicating emulative learning and behavioural flexibility, which matches what has been illustrated in the past [67,84,90,103,104]. The value of information in general is high for island species [105], and locality may provide outdated information [106] due to depletion rates. Stimulus may be the most reliable source of information that can be applied across different terrains and

situations. This would explain why kea are prone to pay specific attention to the information a stimulus provides (i.e. stimulus enhancement).

In general, environmental instability is considered an important factor in selecting for cognitive and behavioural flexibility, as individuals are required to adapt to fluctuating and sometimes unpredictable conditions [107]. It is, therefore, unsurprising that kea portray well-developed physical cognition and technical intelligence [67,84–86,108,109] along with strong behavioural flexibility [67,72,84]. Given the aforementioned profile, emulation and behavioural flexibility would allow kea to quickly adapt to the fluctuating and unpredictable conditions of their natural environment. Additionally, their propensity towards extensive exploration and interest in affordances may explain why they are very interested in engaging with their environment as this seems to be inherently rewarding. Therefore, to date, the most parsimonious explanation of the results of the experimental work at hand may be that emulation and the ability to flexibly adapt to their changing environment is more relevant for kea than imitative behaviour.

To summarise, the presented experimental setups did not succeed in finding imitative behaviour in kea. However, sufficient task complexity was achieved to decrease individual learning and encourage social learning, which ultimately led to more response matching in observing individuals compared to non-observing controls. Additionally, a focus on perceptual factors could be induced, illustrating that stimulus matching can be attained if required. This suggests that, given the right circumstances (i.e. experimental design) it may be possible to coax kea to simultaneously attend to response and stimulus, potentially leading to high-fidelity response topography matching, and therefore imitation.

In conclusion, although to date the capacity for imitation remains unverified in kea an explicit proficiency in social learning could be demonstrated. Additionally, clear signs of emulative learning and an ability to attend to perceptual aspects of a demonstrated behaviour could be illustrated. Currently, the most parsimonious explanation for a lack of imitative behaviour may be that imitation is not very relevant to kea in their natural environment and hence this competence has not been developed. Alternatively, the lack of evidence for imitative behaviour may be an artifact of the testing methodology. Therefore, the present thesis provides some key elements that may be necessary for future experimental designs to prompt imitative behaviour in this species.

Future directions

Imitative behaviour might be very difficult to find in this highly skilled and exploratory species and it remains questionable if it is ecologically relevant to them. Past experiments have illustrated that kea are highly motivated to engage in object exploration to the point of technical innovation [92,108]. And the presented experiments suggest that this motivation, along with their behavioural flexibility, need to be addressed in order to pave the way for imitative behaviour. If one would like to continue testing for imitation in kea, future experimental designs may depend on the development of tasks that suffice in complexity to warrant the extended attention of observers for task acquisition while at the same time reducing individual exploration and learning. Furthermore, to prompt high-fidelity response topography matching, both response and stimulus matching would need to be induced simultaneously. Other components, such as, for instance, ecology and social structure may provide additional information and could prove beneficial in enticing kea to engage in imitation.

Take, for instance, group foraging which provides the grounds for a certain degree of resource competition. While in-group tolerance is very high in kea, feeding competition does occur, and resource theft is common [90]. Such resource competition could reduce free exploration in situations that require focused attention. The lack of competition in artificial settings (i.e. dyadic demonstrator observer setups) may influence the likelihood of kea paying close attention. Under the missing pressure of competition kea may potentially show much exploration and affordance learning. However, this could also be taken advantage of as Miyata and colleagues pointed out, “[kea’s] exploratory behavior might decrease when there is competition” [87 p. 56]. This would be advantageous for tasks that require close observation and replication of conspecific responses, and could potentially draw their attention to response topographies.

Additionally, demonstrator characteristics have been found to have a significant effect on social learning in other species [110]. Some individuals provide more reliable information due to their age and experience, and status plays an additional important role in the likelihood of being copied. The fluidity of the non-linear hierarchy kea portray, however, make it very difficult to determine the status of an individual across time and can be a confounding factor in experimental designs reliant on consistent observer-demonstrator dyads. While captive populations show a more stable hierarchy than has been observed in the wild, it may be beneficial to consider that fluctuations may and do occur. A group setup with changing demonstrators might be advantageous in solving this dilemma in two ways. First, it could

motivate kea to pay attention to a demonstration by simulating competition, and second, it could account for the fluidity of their hierarchies. Hence, fluid non-dyadic observer-demonstrator experimental designs may help generate imitative behaviour in kea.

Alternatively, a focus could be placed on behavioural flexibility, curiosity, and affordance learning, which seem to be pillars of their typical behavioural responses and, by virtue of consistently being found, must have an ecologically relevant basis. While the work presented in this thesis and previous studies underline that social transmission of information is undisputed in this species [67,72,90,111], studies directing their attention towards behavioural flexibility in task acquisition and skill learning may contribute to understanding the relationship between ontogeny and social factors, problem-solving abilities, and even play.

In general, a momentous task lies ahead in the study of imitation in kea. But designing an adequate experiment to find imitative behaviour in kea is an exciting prospect, challenging the real barrier of any animal cognition study – namely us, the study designers. After all, more often than not it turns out that our methods are inadequate for testing what we are really looking for, and that human imagination and innovation are the true limitations to being able to show what animals can do.

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