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for mum, who gave me everything...

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"Leaves are falling all around
It's time I was on my way
Thanks to you I'm much obliged
For such a pleasant stay
But now it's time for me to go
The autumn moon lights my way
For now, I smell the rain
And with it pain
And it's headed my way

Ah, sometimes I grow so tired
But I know I've got one thing I got to do

Ramble on..."

(Led Zeppelin, 1969 Led Zeppelin II Ramble on)

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Preamble |

Nature constantly forces animals to make choices, which ultimately decide their fate. Such decisions might determine where, when or what to eat, with whom to bond or reproduce and when to fight or flee. Many of these choices can be based on predispositions, associative processes or expressions of current emotional states. However, especially in situations where animals are confronted with incomplete information, it would be adaptive to infer, based on known presumptions, which solution leads to a desirable outcome. Popper (1978) identified such an adaptive value of reasoning as the 'human step' in evolution, which allows to formulate hypothesis and proclaimed: "Let our conjectures, our theories die in our stead!".

Since Aristotle it has been assumed that the ability to reason is a uniquely human faculty, which sets us apart from other animals. But are our choices really purely based on logic and reason? And more crucially, is the divide between human and non-human animals based on the capacity to employ reason when making decisions?

Already Kant (1787) has been concerned with the conundrum that while natural sciences rely on logical inferences and reason to describe natural phenomena, we, as humans practicing these sciences, are limited in our thinking by our own perception. There are different ways in which such inferences may be formulated. Peirce (1878) has extended the until then commonly known concepts of deduction and induction by a third possibility, so that three types of logical inferences may be distinguished:

- Deductions, where a Rule (e.g.: 'All fledged kea have yellow cap feathers') is applied to a Case (e.g.: 'I have observed a kea with yellow cap feathers') and provide a Result (e.g.: 'The observed kea was a fledgling').

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- Inductions, which are based on a Case ('I have observed a kea with yellow crown feathers') and a Result ('The observed kea was a fledgling') from which a Rule ('All fledged kea have yellow crown feathers') may be formulated.

- Hypothesis or Abductions, which constitute incidents where Rules ('All fledged kea have yellow crown feathers') are postulated and given a Result ('The observed kea was a fledgling') may conclude Cases (e.g.: 'I have observed a kea with yellow crown feathers')[*].

In the study of comparative cognition, which largely relies on behavioural observations, it is difficult to assess if an abductive inference has been made by subjects, as these hypotheses require to be formulated. It is more feasible to test for inductive or deductive inferences by designing tasks that require a Rule to be apprehended (induction), which later can be applied to solve novel problems (deduction).

To overcome these limitations of testability on inferences, contemporary philosophers and scientists have adopted a more practical definition of inference, which describes it as the process of updating a mental representation with new information in order to achieve 'action goals' (Huber, 2009).

A recent comprehensive account of what constitutes rationality attempts to differentiate rationality and reasoning (Hurley & Nudds, 2006). In their introduction Hurley and Nudds consider reasoning as a process of producing behaviours which might involve higher cognitive abilities, such as reflection, consciousness, concepts and linguistic abilities (Hurley & Nudds, 2006, p. 5). Nevertheless, reasoning is not necessarily required for a behaviour to be considered rational (Kacelnik, 2006). There are different types of rationality depending on the perspective one takes and Kacelnik (2006) therefore differentiates three types of rationality:

(1) Economic or E-rationality - When behaviours are aimed at maximising profit or a gain.

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[*] Fledgling kea (*Nestor notabilis*) can be distinguished by bright yellow feathers on their heads, which darken after the first couple of months, whereas the cere and eye rings may remain yellow until the fourth year before taking the dark brown adult colouration (Diamond & Bond, 1999).

(2) Psychological/philosophical or PP-rationality - In instances where the process of generating behaviour is deriveld from reasoning based on thoughts and beliefs.

(3) Biological or B-rationality - which aimes at increasing fitness and is contrasted with the former two types of rationality.

Naturally, some aspects of E-rationality also apply when gaining fitness, for example considering optimal foraging. However, in instances where inclusive fitness is regarded, such as for example in parental investments, the 'currency' is shifted and maximising personal profit is suspended over investment in survival of a common genepool. The remaining question is: In what way PP-rationality may be adaptive to have evolved within a framework of B-rationality?

In order to investigate the latter question, we must return to a broad definition of reasoning as the process of reaching conclusions, which in turn guides our decisions and aids us in problem solving (Sternberg & Leighton, 2003). Reasoning therefore might employ logical processes, such as inferences, but is not limited to these. Hence, when empirically testing for inferential reasoning by behavioural observations, one has to carefully control for alternative mechanisms that might elicit the same responses, such as the formation of associations formed through classical conditioning (Pavlov, 1927) or stimulus generalisation (Pearce, 1987).

One of the first to suggest causal reasoning in non-human animals was Köhler (1925) by providing captive chimpanzees (*Pan troglodytes*) out-of-reach food rewards . He observed them to use sticks in an attempt to reach the rewards and later to stack wooden boxes in order to reach their goal. However, despite being one of the classic examples of causal reasoning, Köhler's conclusions were debated because chimpanzees perform many of the seemingly "insightful" actions also when there is no reward (e.g., Epstein, Kirshnit, Lanza, & Rubin, 1984; Seed & Byrne, 2010; Shettleworth, 2009). Köhler's studies and other early work on the mental capacities of animals has also been summarised and discussed in a comprehensive review by Tolman (1927), who highlighted the need for further investigations on the cognitive capacities of animals. Premack (1971) later reported higher order reasoning skills of a sign-language trained chimpanzee named Sarah who was able to express

abstract concepts, such as same and different, and therefore providing evidence for an understanding for the relation between objects in a non-human animal.

However, not only our closest evolutionary relatives have shown remarkable reasoning capacities: For example, considering a form of linguistic inference, which has been shown to play a crucial role in acquiring vocabulary in human language learning is termed 'fast mapping' (Wilkinson, Dube, & McIlvane, 1998). Dogs (*Canis lupus*) and sea lions (*Zalophus californianus*) have also exhibited this form of inference, when individuals were trained on referential cues (e.g. names) for a set of items (e.g. toys) and when provided with a novel cue (e.g. novel name) they immediately attributed it to a novel item (e.g. new or unknown toy; Kaminski, Call, & Fischer, 2004; Kastak & Schusterman, 2002). Also among avian species, African grey parrots (*Psittacus erithacus*), and especially a language trained individual named Alex, have exhibited most intriguing reasoning skills (e.g., Pepperberg & Shive, 2001; Pepperberg, 1987; Pepperberg & Brezinsky, 1991; Pepperberg, 2006). Alex was able to vocally express the relationship (same/different) between objects in absolute terms, as well as depending on different dimensions, such as size, material and colour (see Pepperberg, 2002 for a summary).

Nevertheless, all of the most convincing afore mentioned studies have involved 'language-trained' subjects, which has led some to attribute the fundamental divide between humans and non-human animals to be based on some linguistic competences (e.g., Penn, Holyoak, & Povinelli, 2008; Popper, 1978). However, over the last decades, research on animal cognition has produced many indications that also non-language trained animals might be capable of reasoning. Bonobos (*Pan paniscus*) and chimpanzees were suggested to be able to understand spatial relational similarities which was not possible for children younger than four years of age, gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*; Haun & Call, 2009). This study, as an example how to investigate relational in animals, implemented a setup with two sets of three cups each on a slanted platform. The cups were arranged to allow for inferring the location of a food reward by gravitational relations, proximity or spatial relations in the first pair and proximity or spatial relations in the second pair. The third pair could only be solved by assessing spatial relations, whereas employing a proximity rule

would lead to a wrong, unrewarded choice. In a first condition the corresponding cups were connected with tubes, so that causal relations could be followed but in the second and third crucial conditions, only lines or nothing (in the case of chimpanzees) connected the cups. Nevertheless, bonobos and chimpanzees chose the correct cups in these crucial conditions significantly above chance and at similar rates as human children older than four years.

Reasoning based on relations is considered as one of the most sophisticated forms of concept formation (Zentall, Wasserman, Lazareva, Thompson, & Rattermann, 2008). Not only great apes but also Guinea baboons (*Papio papio*) were able to match the relation of two stimuli to the relation of a sample set (Fagot & Thompson, 2011). Interestingly, recent studies also provide indications that orange winged amazons (*Amazona amazonica*; Obozova, Smirnova, Zorina, & Wasserman, 2015), as well as hooded crows (*Corvus corone*) might be able to solve such relational matching-to-sample tasks (Smirnova, Zorina, Obozova, & Wasserman, 2014). However, correct responses in a task where individuals must match the relation within sets of stimuli to the relation displayed by a sample set might be achieved by a simpler perceptual heuristic, as has been reported to be the case in pigeons (*Columba livia*; Cook & Wasserman, 2007; Young & Wasserman, 1997, 2001). In these studies, researchers have shown that subjects would visually assess and match stimulus entropy (as degrees of homogeneity or heterogeneity of icons within sets) as a source of information, without necessarily paying attention to the relation between sets. But even pigeons, which have relatively small brains, have exhibited impressive capabilities, such as the ability to perform transitive inferences (Daniels, Laude, & Zentall, 2014a, 2014b; see below for an explanation of what constitutes this inference process), or generalisation skills (e.g., Herrnstein, Loveland, & Cable, 1976; Watanabe, 2001; Watanabe, Sakamoto, & Wakita, 1995).

Conversely, humans have been shown to not always act purely rational, but are also prone to biases and suboptimal choices (e.g., Gigerenzer & Goldstein, 1996; Zentall, 2016), which has been referred to as 'ratiomorphic' reasoning (Riedl, Ackermann, & Huber, 1992; Riedl, Huber, & Ackermann, 1991). An even more cautious approach suggests that also humans employ a bound or ecological rationality, which postulates that all animals rely on simple heuristics adapted to their ecological setting (Simon, 1991; Todd & Gigerenzer, 2000; Todd & Gigerenzer, 2007). These

arguments further suggest that, despite ongoing debates about the fundamental differences in mental capacities between human and non-human animals (e.g., Penn et al., 2008; Premack, 2007, 2010), the divide might after all be "*one of degree and not of kind*" (Darwin, 1871).

The approach of an ecologically bound rationality sets the stage for studying which environmental factors have driven the evolution of reasoning capacities. In this sense two forms of deductive inferences seem to be especially ecologically relevant and adaptive, as they may be employed in the social as well as the physical context:

- Transitive inference: This sort of reasoning allows individuals to rank items in a specific order (such as 3 is larger than 2, and 2 is larger than 1) and to make deductions about the relationship between two items that previously have not been associated directly. For example, although no information about the relationship between 3 and 1 has been provided, given that 3>2 and 2>1, one might deduce that 3 is also larger than 1. Several studies have investigated and proposed different theories about the underlying cognitive mechanisms that may account for successful performance in such tasks (see Vasconcelos, 2008; Zentall, 2001 for a summary). In a natural setting this may be especially relevant to allow keeping track of dominance hierarchies in social groups. This is supported by the findings of several studies which have suggested the evolution of transitive inference capacities to be driven by an increase in social complexity (e.g. Bond, Wei, & Kamil, 2010; Cheney & Seyfarth, 1990; Gillan, 1981; Kitchen, Cheney, & Seyfarth, 2005; MacLean, Merritt, & Brannon, 2008; Paz-y-Miño C, Bond, Kamil, & Balda, 2004; Weiß, Kehmeier, & Schloegl, 2010).

- Inferences by exclusion: This form of reasoning has been considered as the process of logical exclusion of alternatives when faced with novel situations, for example to choose an unfamiliar option A over a known option B which certainly does not lead to a desirable outcome (Call, 2006). There are several accounts for exclusion performance in food storing species, which have led researchers to consider exclusion

as an adaption for food-storing behaviour (e.g., Mikolasch, Kotrschal, & Schloegl, 2012; Schloegl et al., 2009; Tornick & Gibson, 2013). However, other studies have shown this ability also in individuals of non food-storing species (e.g., Aust, Range, Steurer, & Huber, 2008; Call, 2004; Clement & Zentall, 2003; Nawroth, von Borell, & Langbein, 2014; Irene M Pepperberg, Koepke, Livingston, Girard, & Hartsfield, 2013), rendering foraging as the sole factor for the evolution of this kind of inference unlikely. Based on the distribution of exclusion skills across different species, other researchers have argued that it might be an indicator for general intelligence, available to many species but expressed in different contexts (Pepperberg et al., 2013).

This thesis addresses inferences drawn by exclusion through a bottom-up approach, which is achieved by parallel consideration of alternative mechanisms underlying choice behaviour in the spirit of ecological rationality and the recent emphasis on signature testing (Taylor, 2014; Todd & Gigerenzer, 2007). Taylor (2014) has proposed that studying the evolution of certain skills would benefit by not only looking at the presence or absence of a capacity in different species, but also by taking into account different types of errors that might be made and by investigating under which circumstances these occur. Such error profiles might yield 'signatures' for different species which ultimately may aid in establishing a coherent phylogenetic tree of cognitive abilities.

Therefore, I aimed to combine considerations of potential predispositions, influences of associative learning on exclusion skills (which might be of common descent) and higher reasoning skills required for such inferences. Further, applying this approach to selected species may unveil the socio-ecological conditions promoting cognitive abilities such as inference by exclusion. In this respect birds pose an interesting taxon as they occupy many different ecological niches and possess a large variety of social systems, exhibit cognitively advanced behaviours, and yet are phylogenetically very distantly related to humans. If reasoning skills are indeed found in some species of this taxa, but not in others, such a discovery would favour a convergent evolution, unless this ability can be traced back to a common ancestor, but has lost its function and thus diminished in some lineages

Besides ecological adaptations, another factor that has been proposed to positively correlate with advanced cognitive abilities is the availability of neuronal substrate, although its measurement is a topic of an ongoing debate (e.g., Roth & Dicke, 2005). While earlier studies have considered absolute brain size (Deaner, Isler, Burkart, & Van Schaik, 2007), others have argued that the relative brain size in relation to body size (Jerison, 1985; Martin, 1981; Williams, 2002), the relative size of certain parts of the brain in relation to total brain size (e.g., Iwaniuk, Dean, & Nelson, 2005) or, most recently, neuron counts to best represent or correlate with intelligence (Olkowicz et al., 2016; Roth & Dicke, 2005). Taking neuronal measures into account, corvids (*Corvidae*) and parrots (*Psittaciformes*) constitute prime candidates among birds for advanced cognitive capacities (Güntürkün & Bugnyar, 2016; Olkowicz et al., 2016).

The goal of this dissertation was to establish a method that would allow to discern different modes of decision making, focusing not only on inferential reasoning to guide choices, but also enable an integration of alternative lower-level mechanisms and would be applicable to different species. In the first chapter, I investigate the effects of predispositions, such as neophobia and exploration, on decision making in the presence of novel stimuli and over the course of learning a discrimination task. The results suggest coherent patterns of shifting exploratory behaviour depending on individual reactions to novelty and thus highlight the importance of considering neophobic and neophilic tendencies in cognitive testing.

Based on the findings in chapter one I developed a novel method investigating reasoning by exclusion abilities, which controls for neophilia and allows to distinguish several different response mechanisms. To validate and test the robustness of this method I presented it to two members of the *Psittaciformes*, Goffin's cockatoos (*Cacatua goffiniana*[†]) and the kea. In the second chapter, I report the performance of Goffin's cockatoos in this task. As they had already proven to be capable of causal inferences in an earlier study (Auersperg, Kacelnik, & von Bayern, 2013), we assumed that these

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[†] The scientific naming has changed from *Cacatua goffini* to *Cacatua goffiniana* in 2004 (Roselaar & Michels, 2004)

birds would be able to transfer their exclusion skills to an abstract setting, employing arbitrary stimuli on a touchscreen, hence validating our new approach.

The third chapter provides evidence that the exclusion paradigm may also be solved by the kea, who had earlier participated in an exclusion study with objects but failed (Schloegl et al., 2009). The results suggest that this capacity may be overshadowed by novelty preferences and therefore confirmed the robustness of the method towards overly neophilic individuals. Further this finding, complementing the study by Schloegl et al (2009), strengthens the argument for the need of a controlled design with respect to neophilia when testing for and comparing reasoning abilities in various species with differing levels of neophobia.

Finally, in the last (fourth) chapter, I summarise similarities found in Goffin's cockatoos and kea and briefly endorse the benefits of using the touchscreen as a method in cognitive testing. Furthermore, I suggest potential future avenues for investigations of the evolution of reasoning skills and discuss the contribution this dissertation may provide on efforts to unveil which species might possess exclusion skills and which mechanisms might underlie choice behaviour.

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Chapter 1 |

Does exploration depend on neotic style?

Does exploration depend on neotic style?

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Abstract

Exploration (interacting with objects to gain information) and neotic style (avoiding or seeking novelty) are considered independent traits shaped by the socio-ecology of a given species. However, in the literature it is often assumed that neophobia inhibits exploration. Here, we investigate how neotic style determines the time at which exploration is likely to occur across a number of species. We presented four corvid and five parrot species with a touchscreen discrimination task in which novel stimuli were occasionally interspersed within the familiar training stimuli. We investigated the likelihood that an animal would choose novelty at different stages of its training and found evidence for a shift in the pattern of exploration, depending on neotic style. The findings suggest that more neophilic individuals explored earlier, whilst neophobic animals showed similar amounts of exploration but did so later in training. Surprisingly, there was little effect of species, however age did influence the amount of exploration, with juveniles exploring more than adults. Thus neotic style involves a strong individual component, rather than being a purely species-specific trait. This suggests that variation in behavioural phenotypes within a species is likely to be adaptive.

Introduction

When animals are confronted with novel situations, their behavioural responses are usually determined by fundamental predispositions[1]. One such predisposition is the propensity for exploration, this is classed as any behaviour that serves to gain information but does not satisfy a current physiological need[2]. Responses where exploration is motivated by novelty may be associated with 'neophilia'[3] or a preference for novelty[4,5], whilst the opposing predisposition constitutes the avoidance of novel stimuli[6] and is commonly labelled 'neophobia'. Exploration is hard to quantify; a variety of approaches have been used, these include measuring the latency to approach a novel object[7], the manipulation of novel objects[8–15] and the number of different food items ingested[8,11]. Conventionally neophobia is measured as the latency to feed in the presence of a novel object[1,7,16,17], but may also include other measures (such as a bias towards familiar food or places[18]). It is generally assumed that neophobia is associated with a reduction in exploration[19] and the terms exploration and neophilia have been used interchangeably in the literature[18]. These ambiguities have led to

inconsistencies and confusion concerning the relationship between exploration, neophilia and neophobia, with the latter two also subsumed under the term 'neotic' responses in earlier literature[4,5,18,20]. To ensure clarity we heron use the term 'neotic style' to address the motivation to approach novel stimuli.

Recent research has suggested that exploration and neotic style are controlled by fundamentally different processes[1] and, as such, different predictions can be made regarding the environmental factors that promote different levels of exploration and neotic style in birds. A recent model[1], has suggested that feeding ecology and habitat complexity are key factors that determine exploration levels, whereas neotic style is impacted by riskiness of foraging and interspecific competition. Thus, behavioural predispositions are not shaped by ultimate pressures alone[14,18], individual experience can impact upon the functional expression of exploration and neotic styles, resulting in differences between individuals within a species[17,21–25]. Individual rank within dominance hierarchies has been shown to influence approaches to novelty, with higher ranking individuals exhibiting lower latencies to feed in close proximity to a novel object[17,26]. Developmental conditions have further been reported to effect neotic style, whereby individuals raised in more enriched environments showed lower levels of neophobia in later life[16,24,27,28].Even within an individual, levels of exploration may vary, this is most prominently observed during ontogeny[8,11,18,29]. It has been proposed that young individuals have sensitive periods in which they exhibit high levels of exploratory behaviour, supporting the hypothesis that exploratory behaviour yields the acquisition of information[8,18]. However, exploration and play during juvenile life can be difficult to tell apart and may often also be confused with each other[30].

Exploration and neotic style are generally thought to be important factors affecting problem solving capacities and complex behaviour such as tool use[5,9,13,15,18,30–40]. However, recent work has suggested that decreased neophobia had little influence over problem solving abilities[5]. Furthermore, evidence to support the idea that there will be increased innovation rates in neophilic animals due to the propensity to exploit novel resources is far from conclusive[5]. Rather, it may be a characteristic of widely distributed, generalist, families, such as corvids and parrots[5,36]. As they are predominantly

opportunistic feeders, that occur in different habitats[1] they represent ideal taxa to investigate the interdependence between neotic style and exploration.

We hypothesise that neotic style effects the point at which exploration is expressed and predict that the timing of exploration behaviour will shift, depending on the neotic style of the individual being tested (see Fig. 1). Thus, neophilic individuals should peak in their propensity to explore at the early stages of a task, whereas neophobic individuals would be more likely to select novelty once they have had substantial experience of the task. Further, we hypothesise that individual level selection (e.g. position in social structure) may play a pronounced role in the development of neotic style on top of selective forces acting at a species level (e.g. predation risk). Therefore, neotic style might be subject to pronounced individual variation, on top of ecologically grounded species-specific predispositions. If neotic style is based solely on species level propensities, one would expect to find consistent behavioural patterns within a species. Alternatively, if neotic style is expressed mainly on an individual level we expect to find large variation in responses within a species, and limited or no species specific differences. Finally, as exploration is important for the acquisition of information, one might expect more exploration in the early stages of life, where most learning occurs. Thus we predict that young individuals might exhibit generally more novelty responses than older individuals.

In order to test these hypotheses, we presented birds with a two-alternative forced choice procedure on a touchscreen. This apparatus was chosen as it allowed both the direct comparison across species and the opportunity to present an almost unlimited number of highly controlled novel stimuli. To assess changes in response to novelty during the task, we presented two trials within each session of 20 trials in which the unrewarded stimulus was replaced with a novel one. Thus, the novel stimulus was presented against a previously reinforced stimulus, making the choice of novelty an uncertain one.

To discern whether neotic styles are controlled by species- or individual-level traits, we compared the performance of nine different species from two taxa, corvids and parrots. These species were selected

to represent different taxa from specific ecological backgrounds which we predict would impact upon neotic style. Species endemic to islands are thought to face less predation pressure and therefore the costs for neophilia would decrease. Thus, increased neophilic tendencies could be expected in kea (*Nestor notabilis*), Goffin's cockatoos (*Cacatua goffiniana*), vasa parrots (*Coracopsis vasa*), eclectus parrots (*Eclectus roratus*) and New Caledonian crows (*Corvus moneduloides*) in contrast to carrion crows (Corvus corone), raven (Corvus corax), jackdaws (*Corvus monedula*) and African grey parrots (*Psittacus erithacus)*, which all are rather widely distributed, and have increased predation risk[1].

As a proxy for neophobia, we calculated delta latencies using the differences in response latency between the first trial of the final session and the first trial of the first session (after habituation and pre-training to touch the screen). Individuals were attributed to four types of neotic style (Very Neophilic, Neophilic, Neophobic and Very Neophobic) using quartiles of the total range of these latencies. Novelty responses were defined as choosing the novel stimulus over the rewarded one in the test trials. These responses were corrected for weak association with the rewarded stimulus by multiplying the number of novelty choices with the observed probability of choosing the rewarded stimulus in baseline trials of each session. The number of overall responses to the unrewarded stimulus throughout the task was used as an inverse measure of learning.

Results

Factors influencing Neotic style

General linear models revealed no effect of neotic style on the corrected novelty responses (GLM: $F_{1,33} < 0.01$, p = 0.96), the responses to unrewarded baseline stimuli (GLM: $F_{1,34} = 0.01$, p = 0. 93) or sex (GLM: $F_{1,35} = 0.41$, p = 0.53). Age had no significant effect (GLM: $F_{2,41} = 1.08$, p = 0.35) in a parallel model and was discarded in favour of species in the model structure, this showed a significant effect (GLM: $F_{8,36} = 2.65$, p = 0.021), indicating that eclectus parrots exhibited significantly lower delta latencies than African grey parrots ($\beta = -92.49$, SE = 1.15, p = 0.027), crows ($\beta = -85.75$, SE = 29.83, p = 0.029), Goffin's cockatoos ($\beta = -108.21$, SE = 28.84, p = 0.006), jackdaws ($\beta = -124.52$, SE

= 35.97, p = 0.01) and vasa parrots (β = -103.10, SE = 31.15, p = 0.011). However, no other significant species differences were observed (see Fig. 2).

Overall novelty responses

The total amount of corrected novelty responses was effected by species (GLM $F_{8,39}$ = 2.82, p = 0.014). However, this effect is driven by the large number of novelty responses exhibited by juvenile carrion crows who chose novel stimuli more often than five other species; no other species differences were observed (see Supplementary Fig. S1 and Table S1 for detailed contrast results). We therefore discarded species in favour of age as a fixed factor. Age yielded a significant effect (GLM: $F_{2,45}$ = 5.66, p = 0.006), with juveniles exploring significantly more than adults (β =0.50, SE = 0.15, p = 0.003), but not more than subadults (β = 0.34, SE = 0.24, p = 0.21). No difference was found between adults and subadults (β = 0.16, SE = 0.21, p = 0.46; see Fig. 3). In both parallel models, the amount of incorrect first choices had a significant effect on corrected novelty responses (GLM: $F_{1,45}$ = 7.32, p = 0.01) reflecting a positive relationship between exploration and choice of the unrewarded stimulus in baseline trials (β = 0.008, SE = 0.003, p = 0.013; see Fig. S2). No influence of sex (GLM: $F_{1,37}$ = 0.05, p = 0.83) or neotic style (GLM $F_{3,38}$ = 0.90, p= 0.45) was found.

Novelty responses over time

To investigate the time-dependent development of corrected novelty responses, data for all the sessions were pooled and then split into four blocks (each containing 25% of the data for that individual). Analysis of novelty responses over blocks revealed a significant interaction of species and block (GLMM: $\chi^2(8)$ = 18.56, p = 0.02). But as this effect rests mainly on carrion crows exhibiting a significantly different slope of novelty responses over time than jackdaws (GLMM: β = -1.21, SE = 0.40, p = 0.045), kea (GLMM: β = -1.37, SE = 0.41, p = 0.032) and a tendency to differ from vasa parrots (GLMM: β = -1.07, SE = 0.37, p = 0.05) and African Grey parrots (GLMM: β = -0.91, SE = 0.35, p = 0.09; see Supplementary Fig. S4 and Table S2 for additional information, as well as Fig. S5 for performance by session), we discarded species in favour of investigating the interaction between age and block as a fixed factor. While the model did not reveal a significant interaction between

choosing the unrewarded baseline stimuli and block (GLMM: $\chi^2(1) = 0.09$, p = 0.77), or an interaction of sex and block (GLMM: $\chi^2(1) = 0.20$, p = 0.66), a significant effect of block was found for the interaction with age (GLMM: $\chi^2(2) = 6.45$, p = 0.04), indicating that juveniles tend to show different temporal exploration patterns than adults (GLMM: $\beta = 0.49$, SE = 0.20, p = 0.058). However, no differences in slopes over blocks were found between subadults and juveniles (GLMM: $\beta = -0.12$, SE = 0.34, p = 0.72), nor adults and subadults (GLMM: $\beta = 0.37$, SE = 0.32, p = 0.35). Examination of the impact of neotic style on the block in which the corrected novelty responses were highest revealed a shift from the first block for very neophilic (individuals with low delta latencies), to the last block for very neophobic individuals (with high delta latencies; see Fig. 4). This is statistically supported by the significant interaction of neophobia by block affecting the slope of novelty responses throughout the task (GLMM: $\chi^2(3) = 11.28$, p < 0.01). Model contrasts revealed that slopes between very neophilic and very neophobic individuals (GLMM: $\beta = 0.55$, SE = 0.24, p = 0.058), as well as neophilic and neophobic individuals (GLMM: $\beta = 0.57$, SE = 0.26, p = 0.058) and between neophilic and very neophobic individuals (GLMM: $\beta = 0.81$, SE = 0.26, p = 0.015) differed significantly. Other comparisons were not significant (see Supplementary Table S3 for detailed contrasts).

Discussion

Our results reveal that neotic style does not impact upon the amount of exploration observed but rather effects the timing in which it takes place. Very neophilic individuals exhibited most novelty responses in the early trials of discrimination learning, but as individuals were increasingly neophobic, the peak in their exploration shifted towards the later stages of the task. This result suggests that neophobic individuals do not necessarily explore less, but rather do so once they have habituated to a situation. Further, we reveal that the neotic style of the individual played a much greater role in predicting the time of exploration than their species. This is in sharp contrast to the general findings of species level differences observed in the literature [1,7].

The results reveal little effect of species concerning exploration, with a clear difference only observed between the slopes of novelty responses over blocks in juvenile crows, suggesting that age rather than

species underlies this effect. While the finding that crows responded most strongly to novel stimuli is in line with ecological predictors, such as largest distribution patterns and omnivorous diet[1], this species effect is heavily confounded by age. A recent study with the same individuals, that has shown that explorative tendencies deteriorate as age increases[11]. Further, neotic style, did not differ consistently between species, except for eclectus parrots who generally exhibited relatively low delta latencies to approach the novel stimuli (see Fig. 2 and Fig. 5). This suggests that, rather than being driven at a species level, which the literature suggests, may be determined by potential risks connected with foraging[1,18], neotic style is more likely to result from an interaction between the social structure of the species, individual position in the social hierarchy and individual level experience [1,12,17]. These factors are likely to promote the large individual differences observed in this study.

It has recently been suggested that dominance hierarchies will influence neophobia [17,19], with higher ranking individuals expressing lower levels of neophobia, one might predict that inter-individual variation in neotic style would be less pronounced in solitary species. In contrast, gregarious species may have increased variation due to intraspecific competition, thus the largest range of variability in neotic style should be found in despotic social structures with strong competition and strict rank hierarchies. This interrelation might potentially also explain the differences that we observed regarding neotic style and age. Young individuals often are granted certain 'liberties' and social tolerance before being integrated into socially structured hierarchies[41,42], especially among kin[43]. If the social structure is related to the establishment of different neotic styles, one may expect a potential shift from neophilic to neophobic behaviour to depend on the formation of these rank hierarchies. Two studies on ravens might support such a correlation: Rank hierarchies have been reported to be established early in development[43] (in month 4-5 after fledging) and the shift in neotic style has been concluded to occur before the subadult stage[11] (18th month). However, further studies testing these assumptions directly may yield valuable insights into the interplay between neotic style, age and social structure of different species.

This study is the first to show the temporal effect that different neotic styles have on exploration, while neophilic individuals explore earlier, neophobic animals do not explore less, but rather express the behaviour later, after familiarisation with the situation. It is likely that these results represent a general phenomenon, however, corvids and parrots have been proposed as being amongst the most neophilic and explorative bird species[1,5], therefore future studies should investigate whether these patterns also apply to less explorative avian species. We hope that our findings will inspire discussions about the development of neotic styles and contribute to a more coherent understanding of the inter-relationship between neotic style and exploration. Being neophilic does not imply an individual never stops exploring and conversely, neophobia does not necessarily exclude exploration. This understanding will allow for more accurate interpretation of behaviour and the processes which control responses to changes in the environment.

Methods

Study subjects

Ravens (*Corvus corax*) and carrion crows (*Corvus corone*) were group-housed at the Haidlhof Research Station (University of Vienna and the University of Veterinary Medicine Vienna, Austria). Ravens and carrion crows were kept in adjacent aviaries (each 10m x 12m x 4m) and tested in neighbouring, visually isolated compartments (3m x 4m x 4m). Both groups were fed a diet of meat, pasta, curd cheese and bread twice per day with water for drinking provided ad libitum. Four male and two female ravens were tested, whereas two males and four female carrion crows participated in the study. All individuals were juveniles within their first summer after hatching.

Five New Caledonian crows (*Corvus moneduloides*) and three jackdaws (*Corvus monedula*) were tested at the Avian Cognition Research Station of the University of Oxford, U.K., hosted by and associated with the Max Planck Institute for Ornithology, Germany. The New Caledonian crows were kept in groups of three (a breeding pair and a subadult female) and two (a breeding pair) individuals within aviaries (3m x 5m x 2.5m) accompanied by heated indoor roosting places (1m x 3m x 2m) which also served as testing compartments. Diet consisted of meat, curd cheese, oats, cereal, fruit and cat food, as well as fresh water, which was provided once in the morning and available ad libitum.

Jackdaws (two adult males and one adult female) were housed in a large outdoor group aviary (15m x 9m x 2.8m) including testing compartments (2m x 3m x 2.8m). Diet was the same as for the New Caledonian crows.

Kea (*Nestor notabilis*) were housed at the Konrad Lorenz Institute for Comparative Ethology in Vienna, Austria, in a large (15m x 10m x 4m) enriched group aviary. They received a diet of fruit, vegetable, protein and seed twice a day as well as daily fresh water was provided ad libitum. Seven keas were tested, four males (two adult and two subadult) and three females (one adult and two subadult).

Five individuals of each, vasa *(Coracopsis vasa)*, eclectus *(Eclectus roratus)* and African Grey parrots *(Psittacus erithacus)* were tested at the Lincolnshire wildlife Park in collaboration with the University of Lincoln, U.K. Each species was housed in an aviary consisting of a heated indoor compartment (5m x 2m x 2m) including a testing chamber (1m x 1.5m x 2m) and enriched outdoor compartment (5m x 4m x 3m). The groups were provided a diet of vegetables, eggs, fruit and grain throughout day and water was provided in the outdoor compartment ad libitum. In the group of eclectus two individuals were females and three were males, whereas among African Grey parrots (two females, three males) and vasa parrots (one female, four males). Sex was assessed by morphological traits (size, colouration, behaviour). Exact ages are unknown, but all individuals had been kept at the Parrot Zoo for longer than two years and therefore were considered as adults.

Goffin's cockatoos (*Cacatua goffiniana*) were housed at the Goffin Lab in lower Austria (for detailed housing conditions see[48]). Seven individuals were tested, including one female and six males. One male subject was subadult and six subjects were adult.

Ethical Statement

All subjects that participated in reported experiments were housed in accordance with the Austrian Federal Act on the Protection of Animals (Animal Protection Act—TSchG, BGBl. I Nr.118/2004). Furthermore, as the present study was strictly non-invasive and based on behavioural observations, all experiments are classified as non-animal experiments in accordance with the Austrian Animal Experiments Act (§ 2, Federal Law Gazette No. 501/1989).

Apparatus

The study was conducted on a touchscreen computer which was an adapted mobile version of the operant conditioning system described by Steurer et al.[44]. The mobile version combined a CPU (based on a Schneider A4F® minicomputer (http://www.mappit.de) with Mini-ITX main board (VIA EPIA1 M10000, with 1-GHz CPU, 2 × USB, 1 × LAN 10/100 Mbit, sound, and VGA on board), 512 MB DDR RAM, a 40-GB 2.5-in. hard disc) and feeding system in one sealable cube (385mm x 500mm x 610mm) with touch sensitive screen and a reward tray (60mm x 60mm x 20mm) located in the front and flap on the back allowing access to a second screen, keyboard and mouse. The feeding wheel was attached behind the touch sensitive screen and would rotate one reservoir at a time, thus releasing a reward below the screen into the small tray, whenever a stimulus with positive contingency was touched. The screen was a 15-inch XGA colour TFTLCD Module (Model G150XG01 by AU Optronics Corp., Taiwan; http://www.auo.com), with a display area of 304mm × 228mm (381-mm diagonal) and a resolution of 1.024 × 768 pixels. A 15-inch IR "CarrollTouch" touchframe (Model D87587-001, 15 in., without a filter) by Elo (Menlo Park, CA; http://www.elotouch.com) was attached on top of the screen for detecting responses on the screen. The opening for delivering the reward was located centrally 80mm below the lower edge of the screen. The software program used for cognitive testing was CognitionLab (version 1.9; see[44] for detailed description).

Procedure

All individuals participating in this study were naïve to any touchscreen computer setup. Therefore, a habituation and a two choice discrimination pre-training phase preceded the actual task. Rewards consisted of 1/16th of Frolic™ for raven and carrion crows, one mealworm for jackdaws and New Caledonian crows, 1/4th of a peanut seed for kea, vasa, eclectus and African Grey parrots and 1/6th of a cashew nut for Goffin's cockatoos.

Discrimination task

After completion of the pre-training and discrimination training (see supplementary information for details of these procedures), each individual was presented with a randomly assigned novel baseline stimulus pair (S_1+ and S_1-), containing more visually complex (differing in colour and shape) stimuli (see Supplementary Fig. S6 for an exemplary stimulus set and information on how the stimuli were generated). As in discrimination training, each session consisted of 16 training trials but also included

two novelty trials. These occurred within the first half of each session (pseudo-randomly at trial 5, 6 or 7) and in the second half of each session (pseudo-randomly at trial 11, 12 or 13). These novelty trials were either *identical* novelty trials, in which the rewarded S_1+ remained the same and only S_1- was replaced by a new unrewarded stimulus (S_2-), or a *similar* novelty trials, in which S_1- was replaced by a novel stimulus (S_3-), as well as the positive stimulus S_1+ being replaced by a slightly different one (slight variation in colour and shape; S_n+). A new negative novel stimulus was displayed in every novelty trial throughout the task, while S_n+ differed from each other in the first eight sessions and the same set of S_n+ were then used respectively in the last eight sessions again. As in the discrimination training, pecking on an unrewarded stimulus resulted in a CT until S_1+ was pecked. Correct first choices (CFCs), CTs, pecks on screen (POS), response latencies, and stimulus positions for each trial were recorded.

Analysis

Pearson's product moment correlation was used to assess the relation of total number of novelty responses in similar and identical novelty trials. As the novelty responses in these trials were positively correlated (Pearson correlation: $t = 5.77$; n = 48, $p < 0.001$, $r = 0.677$; see Supplementary Fig. S7), responses to novel stimuli were pooled as a measure of total novelty responses. In order to correct for novelty responses solely based on a weak association with the S_1+, responses towards novel stimuli were multiplied by the observed probability to choose the rewarded stimulus in baseline trials of each session. Learning performance was assessed as the number of incorrect choices committed in baseline trials (see Supplementary Material for effects on learning performance). Individual neotic style was assessed by the latency to the first response in the discrimination task subtracted from the latency to approach the apparatus in the first trial of the last (non-consecutive) session. This measure is equivalent with conventional measures of neophobia where latencies to feed next to a novel item were recorded and corrected for general latency to approach food[5]. In this case individuals had associated the touchscreen with food rewards and novel items were represented by the two unknown stimuli (S_1+ and S_1-). Due to technical issues, latencies were not assessed for four keas and therefore latencies for these individuals were treated as missing variables. Linear models were used to investigate potential effects of species, exploration (as the amount of novel stimuli chosen in

novelty trials corrected by the error probability in baseline trials), incorrect first choices in baseline trials (as a measure of learning), age and sex on the delta latencies (time to respond to any stimulus in the first trial minus latency to respond in the first trial of the last non-consecutive session). The total range of these delta latencies were then divided into quartiles, determining four levels of neotic style, in which individuals would be grouped: 'Very Neophilic' < 5sec. < 'Neophilic' < 21.97sec. < 'Neophobic' < 66.87sec. < 'Very Neophobic'. (see Fig. 2 and Fig. 5 for distribution of different groups according to their response latencies in each species).

General linear models, assuming quasi Poisson distribution, were used to investigate the effect of exploration (as the amount of novel items chosen in novelty trials corrected by the error probability in baseline trials), neotic style, species, sex and age on the learning ability, as the amount of first incorrect choices in baseline trials. General linear models, with assumed quasi Poisson distribution, were employed to examine the effect of sex, age, species, learning ability and neotic style as fixed factors on exploration in the task.

To investigate the temporal effect of neophobia, age and species on exploration in this task the sixteen sessions were separated into "blocks", each containing four sessions. Linear mixed models were then employed to test interactions of block with neotic style, with age and with species. Individuals were introduced as random factor to account for repeated measures.

As age and species were confounded variables (as ravens and crows consisted solely of juveniles, but no other species included juveniles) we ran each model twice including either age or species as a fixed factor and report the results for the more sensible model structure. Normality of residuals was tested using Shapiro-Wilk test for normality and confirmed visually, while the assumption of homoscedasticity was tested for using the studentized Breusch-Pagan test, where appropriate. Best model fit was achieved by comparing Akaike Information Criterion (AIC) and fixed factor effects were calculated by stepwise reduction. Statistical analysis was carried out in R[45] version 3.2.3. Models were calculated using the lme4-package[46] and graphical representation of results was created using the package ggplot2[47]. Alpha levels were set to 0.05, factor level contrasts were set manually, p-values were adjusted for multiple testing employing the false discovery rate correction[48,49] at group level and all statistical tests were conducted two-sided.

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Author contribution statement

M.O., L.H., A.W. and G.G. conceived the experiment, M.O. and B.M. conducted the experiment, M.O., B.M. and G.G. analysed the results. L.H., A.A., A.B., A.W. and T.B. provided materials and testing facilities. All authors reviewed and contributed to the manuscript.

Additional information

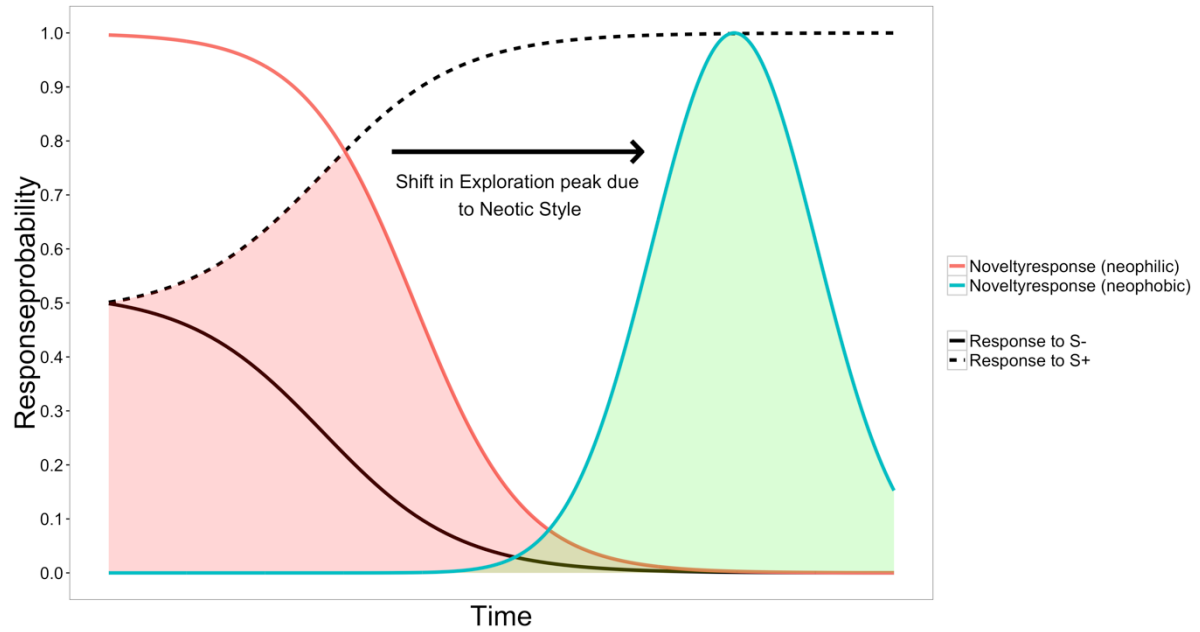**Competing financial interests:** The corresponding author declares, on behalf of all authors, that there is no competing financial interests.

Figure 1. Theoretical model illustrating the shift in exploration-probability dependent on neotic style; solid- and perforated black lines indicate assumed responses to baseline stimuli (S+ and S-) throughout the course of learning; coloured lines represent proposed total novelty response probability for neophilic and neophobic individuals over time, with assumed normal distribution, if novel stimuli are non-rewarded; shaded areas denote corrected total novelty responses; hence, we assume the total amount of corrected novelty responses (shaded area) as well as the height of the peak to be dependent on how explorative an individual is and its general learning capacity, whereas the location of the peak on the time axis to be defined by what neotic style an individual pursues.
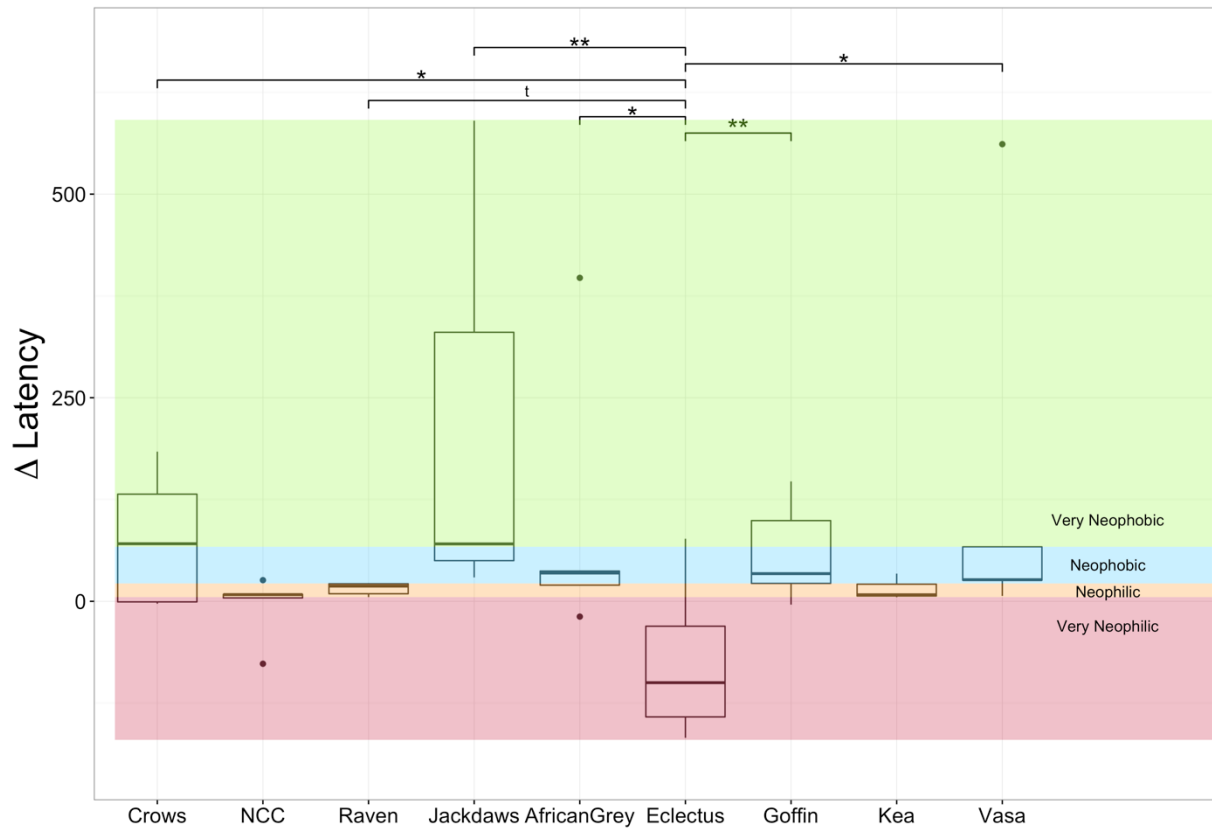
Figure 2. Delta latencies (approach latency in the last, non-consecutive session subtracted from the approach time in the first trial of session one) for all species; bold horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals; horizontal lines indicate species comparisons; Significance codes: '***' for $p < 0.001$, '**' for $p < 0.01$, '*' for $p < 0.05$, 't' for $p < 0.1$ (alpha adjusted for multiple comparisons).
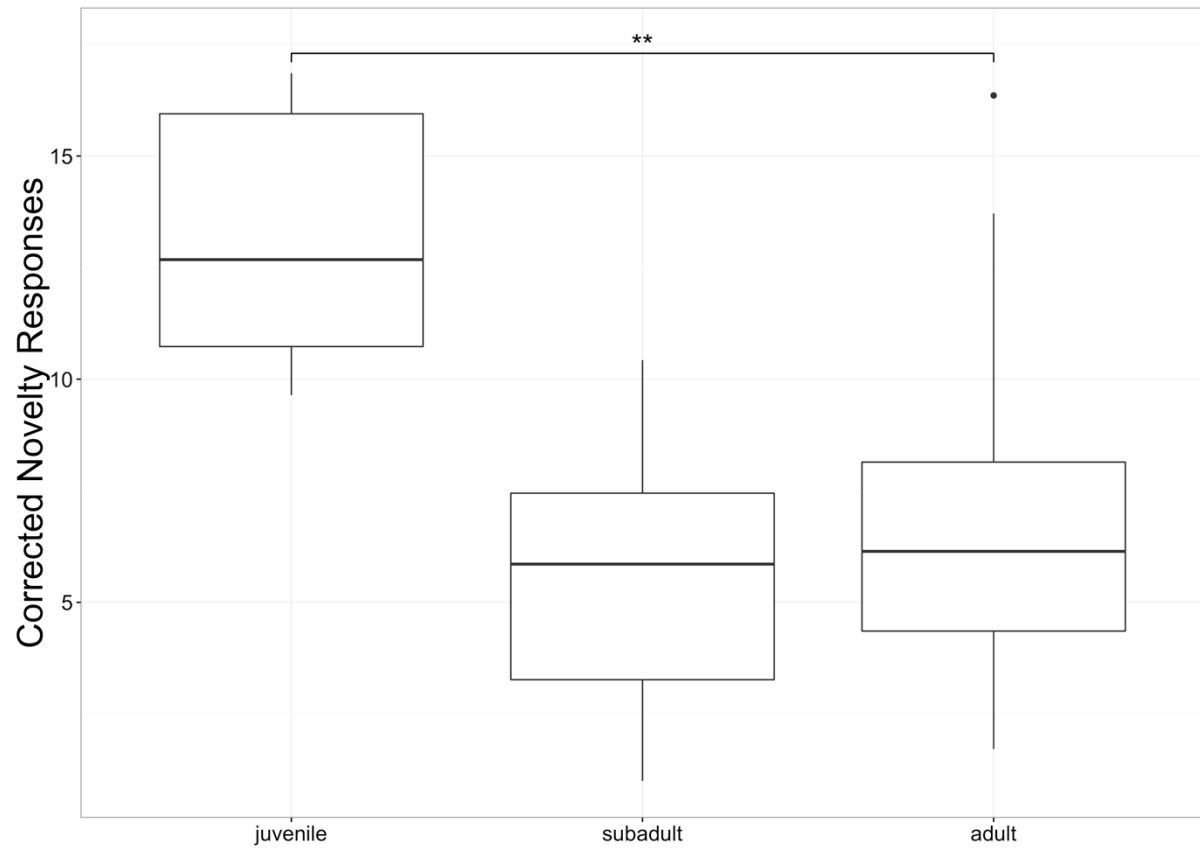
Figure 3. Age differences in corrected novelty responses; bold horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals; horizontal lines indicate species comparisons; Significance codes: '***' for $p < 0.001$, '**' for $p < 0.01$, '*' for $p < 0.05$, 't' for $p < 0.1$ (alpha adjusted for multiple comparisons).
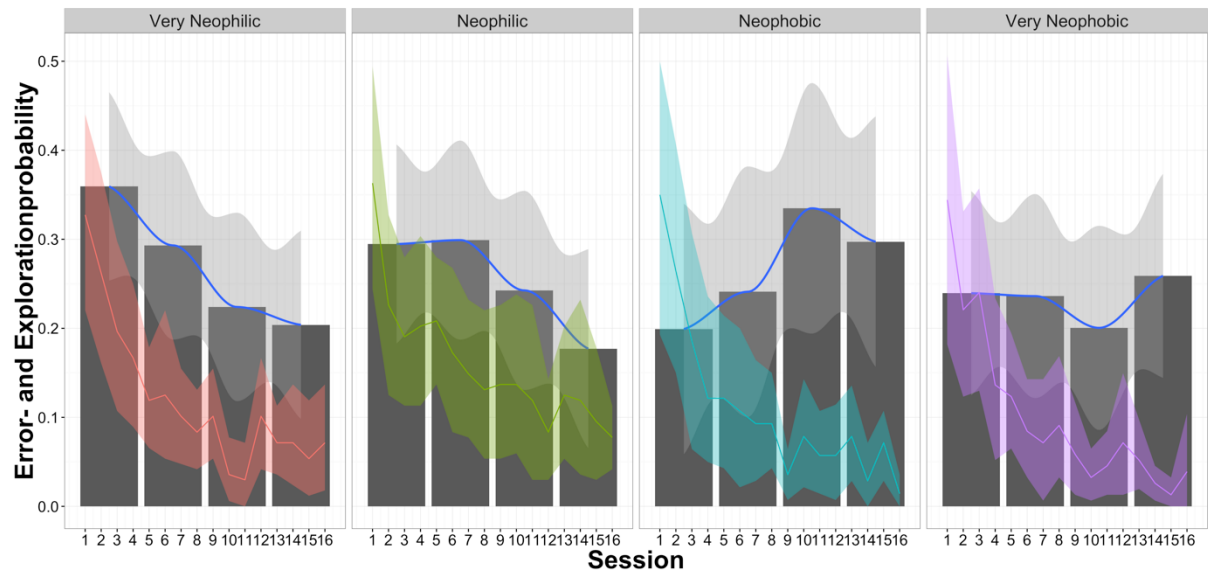
Figure 4. Bars show mean corrected probability to commit novelty responses, in each of the four task quarters for different groups of neotic responses; blue line indicates the smoothed slope by local polynomial regression fitting (locally weighted scatterplot smoothing-loess); the coloured lines indicate the probability to respond to the unrewarded baseline stimuli; shaded areas represent 95% confidence intervals.
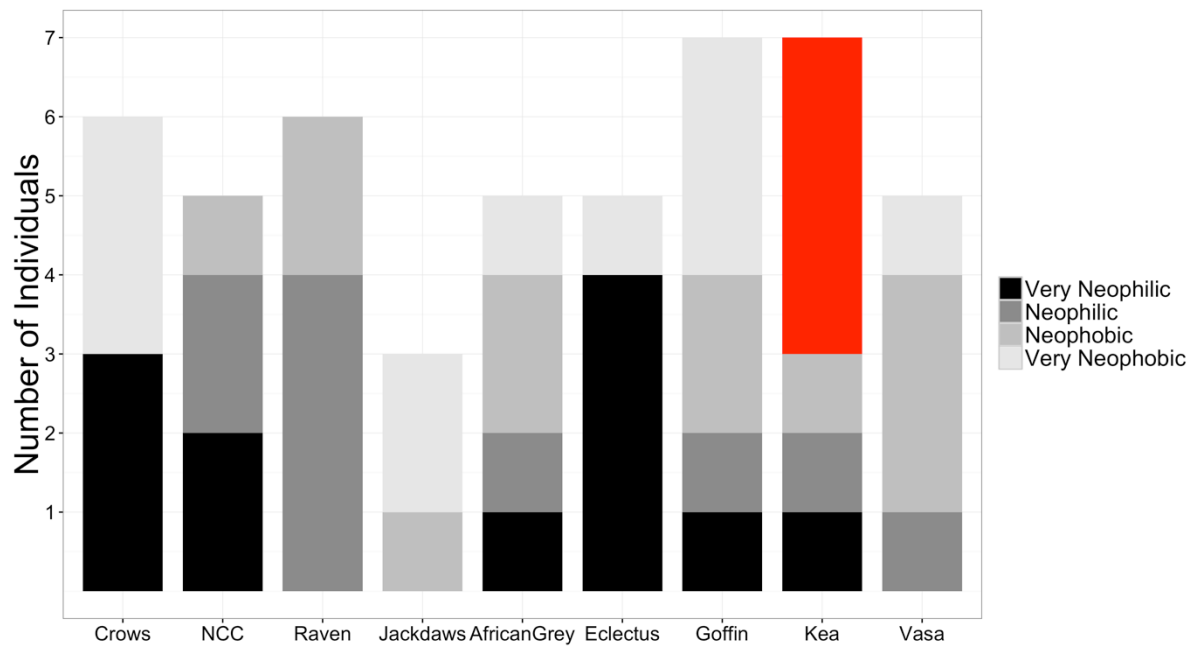
Figure 5. Number of individuals per species participating in the task. Shading indicates quartile latencies to respond to either stimulus in the first trial of the task after the touchscreen has been associated with a food reward: Black represents very neophilic individuals (responding below 5.00 seconds); dark grey indicates neophilic individuals (responses made between 5.00 and 21.97 seconds); neophobic individuals (responding within 21.97 and 66.87 seconds) were assigned medium grey; light grey shows very neophobic individuals (requiring more than 66.87 seconds to interact with the stimuli); the red bar indicates missing values of four individuals of kea for which no latencies are available.

SUPPLEMENTARY INFORMATION

Does exploration depend on neotic style?

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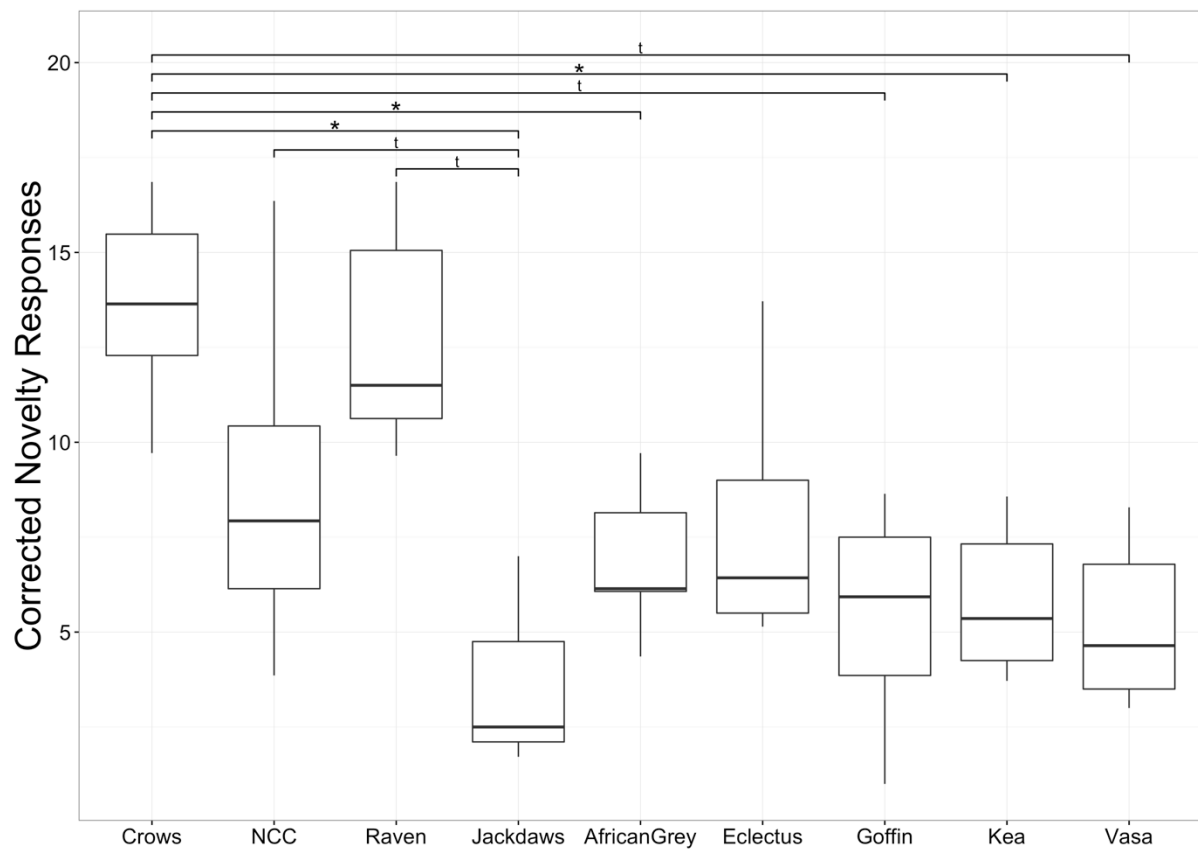* Corresponding author

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Figure S1. Boxplots of corrected novelty responses for all species; bold horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals; horizontal lines indicate age group comparisons; Significance codes: '***' for $p < 0.001$, '**' for $p < 0.01$, '*' for $p < 0.05$, 't' for $p < 0.1$ (alpha adjusted for multiple comparisons; see Table S1 for detailed test statistics).

Table S1. Multiple comparisons of means for novelty responses, corrected for association strength in each session, of all species. P values are adjusted for multiple comparisons.

Model: *Corrected Novelty Responses ~ Sum of errors + Species*

Significance codes: '***' for $p < 0.001$; '**' for $p < 0.01$; '*' for $p < 0.05$; '.' for $p < 0.1$

	Estimate	Std. Error	t value	P	Sig.
AfricanGrey vs Crows	0.628	0.206	3.049	0.028	*
AfricanGrey vs Eclectus	0.219	0.236	0.929	0.482	
AfricanGrey vs Goffin	0.004	0.254	0.015	0.988	
AfricanGrey vs Jackdaws	-0.482	0.350	-1.377	0.310	
AfricanGrey vs Kea	-0.059	0.237	-0.249	0.904	
AfricanGrey vs NCC	0.359	0.231	1.551	0.257	
AfricanGrey vs Raven	0.416	0.223	1.868	0.185	
AfricanGrey vs Vasa	-0.042	0.276	-0.153	0.930	
Crows vs Eclectus	-0.408	0.202	-2.022	0.155	
Crows vs Goffin	-0.624	0.229	-2.722	0.058	.
Crows vs Jackdaws	-1.109	0.329	-3.374	0.014	*
Crows vs Kea	-0.687	0.204	-3.364	0.014	*
Crows vs NCC	-0.269	0.197	-1.365	0.310	
Crows vs Raven	-0.212	0.171	-1.239	0.337	
Crows vs Vasa	-0.670	0.253	-2.643	0.059	.
Eclectus vs Goffin	-0.216	0.237	-0.912	0.482	
Eclectus vs Jackdaws	-0.701	0.341	-2.057	0.155	
Eclectus vs Kea	-0.278	0.225	-1.239	0.337	
Eclectus vs NCC	0.139	0.220	0.635	0.653	
Eclectus vs Raven	0.196	0.227	0.866	0.497	
Eclectus vs Vasa	-0.262	0.261	-1.005	0.454	
Goffin vs Jackdaws	-0.485	0.345	-1.408	0.310	
Goffin vs Kea	-0.063	0.232	-0.270	0.904	
Goffin vs NCC	0.355	0.229	1.553	0.257	
Goffin vs Raven	0.412	0.266	1.550	0.257	
Goffin vs Vasa	-0.046	0.255	-0.181	0.930	
Jackdaws vs Kea	0.423	0.339	1.245	0.337	
Jackdaws vs NCC	0.840	0.336	2.498	0.064	.
Jackdaws vs Raven	0.898	0.348	2.580	0.059	.
Jackdaws vs Vasa	0.439	0.362	1.215	0.337	
Kea vs NCC	0.418	0.218	1.916	0.181	
Kea vs Raven	0.475	0.232	2.046	0.155	
Kea vs Vasa	0.017	0.257	0.065	0.976	
NCC vs Raven	0.057	0.224	0.255	0.904	
NCC vs Vasa	-0.401	0.253	-1.583	0.257	
Raven vs Vasa	-0.458	0.287	-1.599	0.257	

Factors effecting learning

Responses to unrewarded baseline stimuli were significantly affected by the amount of corrected novelty responses (GLM: $F_{1,39}$ = 8.24, p = 0.007), indicating that individuals that responded more often to novel stimuli chose the unrewarded stimulus more often in baseline trials (β = 0.08, SE = 0.03, p = 0.039; see Fig. S2). Additionally, species had an effect on the amount of incorrect first choices in baseline trials (GLM: $F_{8,39}$ = 2.83, p = 0.014), with Goffin's cockatoos choosing the unrewarded stimulus significantly less often than African Grey parrots (β = -1.26, SE = 0.38, p = 0.032) and ravens (β = 1.27, SE = 0.40, p = 0.041). Also vasa parrots exhibited less incorrect first choices than African Grey parrots (β = -1.21, SE = 0.43, p = 0.048) and tended to perform better than ravens (β = -1.21, SE = 0.45, p = 0.056; see Fig. S3). Other factors, such as neotic style (GLM: $F_{3,31}$ = 0.11, p = 0.95) or sex (GLM: $F_{1,38}$ = 1.80, p = 0.19), did not affect learning performance. Age revealed no significant effect in a parallel model (GLM: $F_{2,45}$ = 1.05, p = 0.36) and was discarded in favour of a model structure including species as a fixed effect.

While neophobia did not seem to influence learning ability, we did find a positive correlation of the amount of novelty responses with the number of unrewarded choices in baseline trials. The fact that overall greater exploration indicated more responses to unrewarded stimuli may reflect general impaired associative skills, especially in young birds. As we controlled for associative strength of the rewarded stimulus in instances of novelty trials, and age did not affect learning ability, this explanation seems unlikely. Another possibility would be that more explorative individuals are less coherent in their choices and frequently 'revisit' the known unrewarded stimuli. Interestingly, this result stands in stark contrast to previous studies that found a positive effect of exploration on discrimination learning[‡].

[‡] Guillette, L. M., Hahn, A. H., Hoeschele, M., Przyslupski, A. M. & Sturdy, C. B. Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. *Anim. Cogn.* 165–178 (2014). doi:10.1007/s10071-014-0787-3
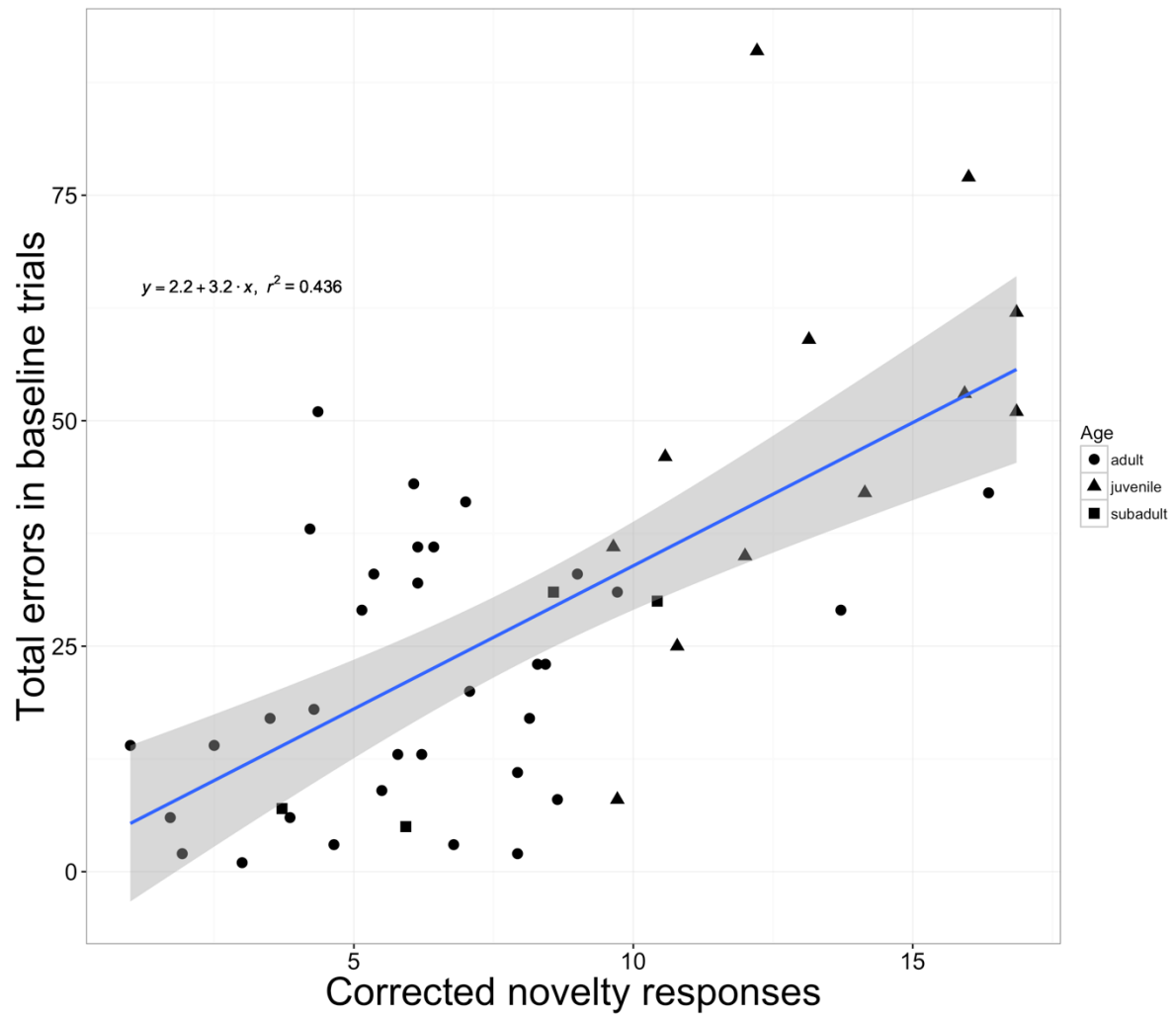
Figure S2. The relationship of learning performance, determined by the number of incorrect first choices in baseline trials, and total amount of corrected novelty responses in the task for individual birds; shape of points represents different age groups; blue line indicates assumed linear fit; grey area denotes 95% confidence interval.
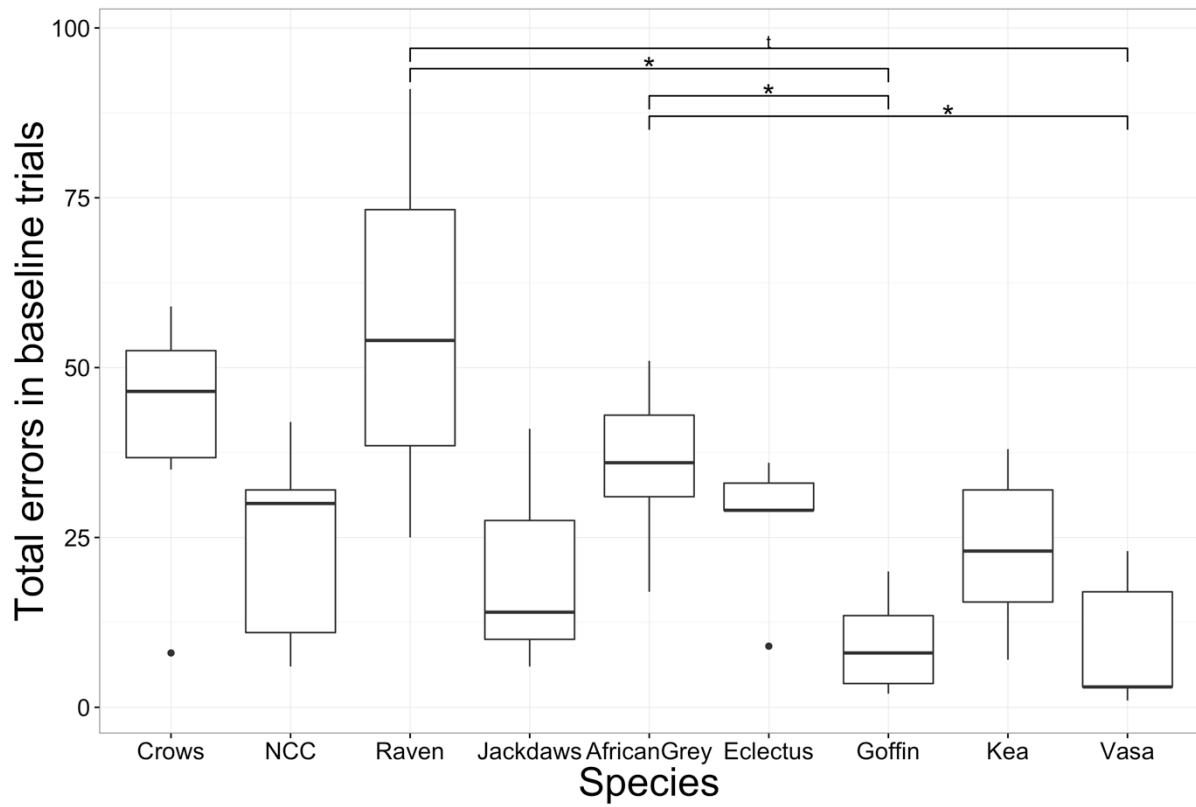
Figure S3. Boxplots of total amount of novelty responses, corrected for associative strength with the rewarded stimulus in each session, for all species; bold horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals; horizontal lines indicate species comparisons; Significance codes: '***' for $p < 0.001$, '**' for $p < 0.01$, '*' for $p < 0.05$, 't' for $p < 0.1$ (alpha adjusted for multiple comparisons).
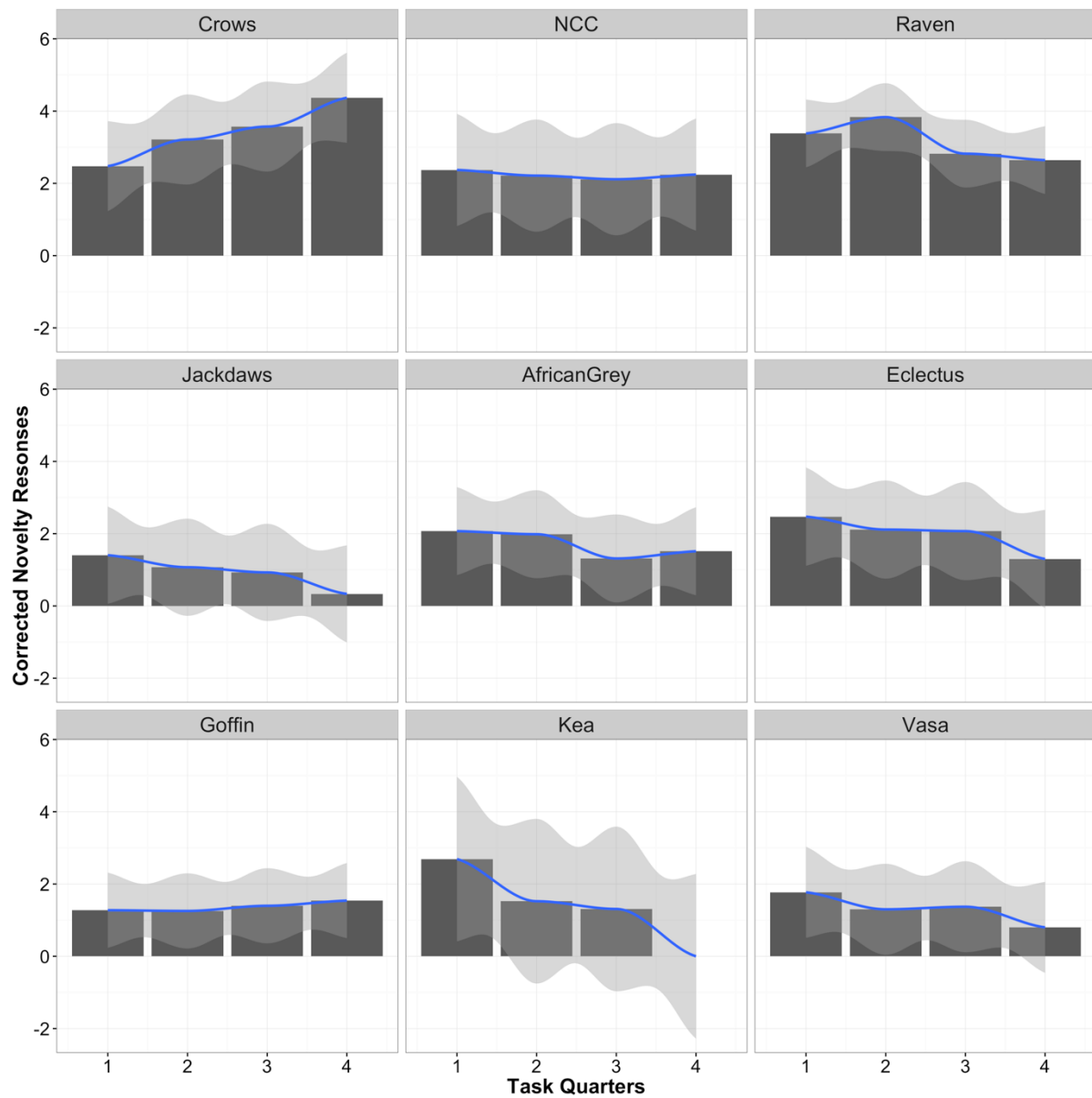
Figure S4. Bars show mean expressed exploration, as corrected novelty responses, in each of the four task quarters for different species; blue line indicates the smoothed slope by local polynomial regression fitting (locally weighted scatterplot smoothing-loess); shaded areas represent 95% confidence intervals.

Table S2. Multiple comparisons of slopes for the novelty responses, corrected for association strength in task quarters of all species. P values are adjusted for multiple comparisons. Significance codes: '***' for $p < 0.001$; '**' for $p < 0.01$; '*' for $p < 0.05$; '.' for $p < 0.1$

Model: *Corrected Novelty Responses in TaskQuarters ~ NeoticStyle*TaskQuarters +*

Species*TaskQuarters + (1 + TaskQuarter | Individual)

|	Estimate	Std. Error	t value	P	Sig.
AfricanGrey vs Crows	0.910	0.353	2.576	0.090	.
AfricanGrey vs Eclectus	0.117	0.376	0.310	0.801	
AfricanGrey vs Goffin	0.270	0.321	0.839	0.640	
AfricanGrey vs Jackdaws	-0.305	0.410	-0.745	0.640	
AfricanGrey vs Kea	-0.459	0.399	-1.149	0.531	
AfricanGrey vs NCC	0.389	0.351	1.108	0.533	
AfricanGrey vs Raven	0.017	0.348	0.049	0.961	
AfricanGrey vs Vasa	-0.160	0.347	-0.461	0.796	
Crows vs Eclectus	-0.793	0.337	-2.353	0.128	
Crows vs Goffin	-0.640	0.318	-2.012	0.199	
Crows vs Jackdaws	-1.215	0.402	-3.025	0.045	*
Crows vs Kea	-1.368	0.412	-3.322	0.032	*
Crows vs NCC	-0.521	0.359	-1.451	0.407	
Crows vs Raven	-0.892	0.388	-2.302	0.128	
Crows vs Vasa	-1.070	0.374	-2.863	0.050	.
Eclectus vs Goffin	0.153	0.351	0.436	0.796	
Eclectus vs Jackdaws	-0.422	0.437	-0.965	0.602	
Eclectus vs Kea	-0.575	0.424	-1.358	0.449	
Eclectus vs NCC	0.272	0.370	0.735	0.640	
Eclectus vs Raven	-0.099	0.408	-0.244	0.831	
Eclectus vs Vasa	-0.277	0.401	-0.690	0.654	
Goffin vs Jackdaws	-0.575	0.379	-1.518	0.389	
Goffin vs Kea	-0.728	0.387	-1.884	0.238	
Goffin vs NCC	0.119	0.336	0.355	0.801	
Goffin vs Raven	-0.252	0.337	-0.748	0.640	
Goffin vs Vasa	-0.430	0.328	-1.310	0.457	
Jackdaws vs Kea	-0.153	0.470	-0.327	0.801	
Jackdaws vs NCC	0.694	0.431	1.612	0.385	
Jackdaws vs Raven	0.323	0.432	0.747	0.640	
Jackdaws vs Vasa	0.145	0.412	0.352	0.801	
Kea vs NCC	0.847	0.397	2.135	0.168	
Kea vs Raven	0.476	0.396	1.203	0.515	
Kea vs Vasa	0.299	0.406	0.736	0.640	
NCC vs Raven	-0.371	0.345	-1.077	0.533	
NCC vs Vasa	-0.549	0.362	-1.515	0.389	
Raven vs Vasa	-0.177	0.346	-0.512	0.783	
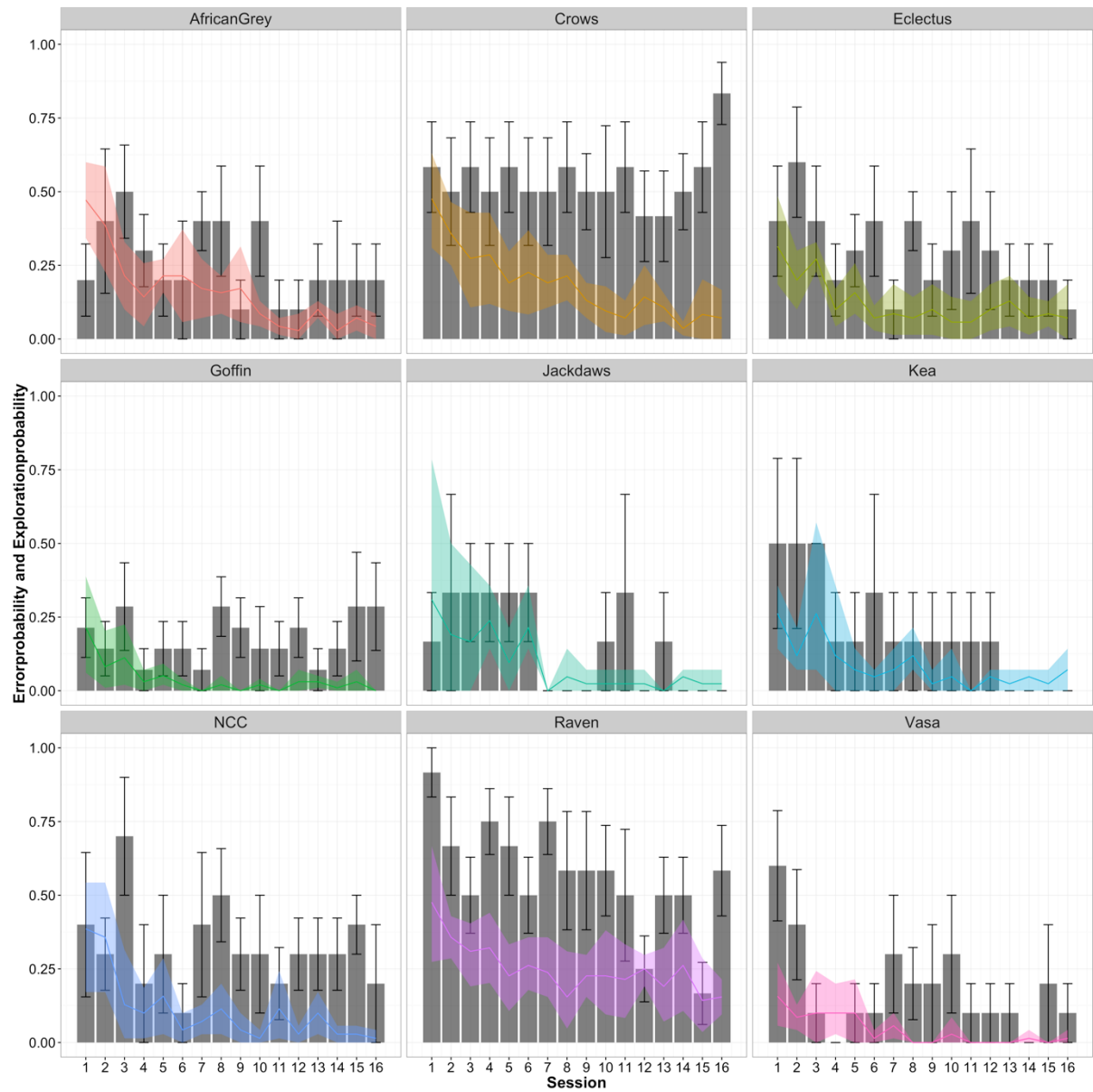
Figure S5. Bars show the mean observed corrected probability to respond to novel stimuli in each session, with whiskers representing SE; coloured lines indicate learning curves as mean probability of committing an error in baseline trials, with shaded areas representing 95% confidence intervals for different species.

Table S3. Multiple comparisons of slopes for the novelty responses, corrected for association strength in task quarters of all species. P values are adjusted for multiple comparisons. Significance codes: '***' for $p < 0.001$; '**' for $p < 0.01$; '*' for $p < 0.05$; '.' for $p < 0.1$

Model: *Corrected Novelty Responses in TaskQuarters ~ NeoticStyle*TaskQuarters +*

Age*TaskQuarters + (1 + TaskQuarter | Individual)

	Estimate	Std. Error	t value	P	Sig.
Very Neophilic vs Neophilic	-0.261	0.244	1.070	0.355	
Very Neophilic vs Neophobic	0.314	0.238	1.316	0.339	
Very Neophilic vs Very Neophobic	0.552	0.242	2.282	0.058	.
Neophilic vs Neophobic	0.575	0.258	2.233	0.058	.
Neophilic vs Very Neophobic	0.813	0.258	3.151	0.015	*
Neophobic vs Very Neophobic	0.238	0.237	1.004	0.355	
adult vs juvenile	0.489	0.200	2.446	0.058	.
subadult vs juvenile	-0.119	0.335	-0.356	0.722	
adult vs subadult	0.370	0.323	1.147	0.355	

Stimulus generation:

For this study a total of 48 stimuli were generated and divided into 12 simple habituation stimuli, 18 straight line stimuli, 18 curved stimuli (see Fig. S6 for examples). For the discrimination task each individual was randomly assigned a specific baseline pair of a positive (rewarded) and negative (non rewarded) stimulus. The baseline pairs contained one straight lined and one curved stimulus. Additionally, for each positive Stimulus 16 similar stimuli were created (differing slightly in colour and shape from the original positive stimulus). The colours of the stimuli were assigned randomly from a scale, differing in their RGB-scale by 20 steps from one colour to the next, but not in brightness. First the positive stimulus was randomly assigned to a colour, saving five colours above and below on the scale for the similar stimuli. Then the negative stimulus was assigned the most distant colour from the positive stimulus colour, excluding the six colours above and below the negative one. The remaining colours were then randomly assigned to the remaining stimuli.

Procedure

Pre-training

In order to pre-train the animals to use the touchscreen computer they were presented with a simple geometric figure (circle, triangle, square or star) that was centred on the screen. Individuals were shaped to reliably touched the stimulus and received the reward by moving the mouse cursor around the stimulus or in case of limited approach the screen was introduced in a group setting.

After this initial phase and once the stimulus was touched reliably by the animals, the stimulus was then presented in a random position. This phase consisted of two sessions with 35 trials each. Inter-trial-intervals (ITI) were set to one second, during this time the screen was blank.

Discrimination training

In this phase, each individual was given one additional stimulus, which was not rewarded when responded to. Additionally, a correction inter-trial-interval (CITI) of 1.3 seconds was introduced. The two stimuli were presented next to each other, with the rewarded stimulus (S_0+) displayed randomly on either the right or left side on a horizontal axis on the screen. The height of the stimuli was adapted for each species to ensure the stimuli would appear at head height. If the subjects pecked the

unrewarded stimulus (S_0-) the birds received a correction trial (CT), which was repeated until the S_0+ was selected. Pecking a stimulus resulted in differential acoustic feedback being played (depending on the stimulus that was being pecked).

Discrimination training consisted of two sessions with 16 trials each. The computer program recorded the retention latency (latency from onset of the trial until a peck occurred), correct first choices and number of correction trials, as well as pecks on the screen in other locations than where the stimuli were.
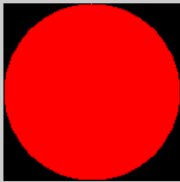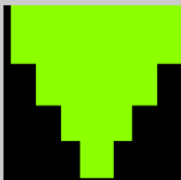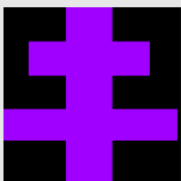
	S+	S-
Habituation		
Baseline pair		
Identical test		
Similar test		

Figure S6. Examples of generated stimuli used throughout the task; S+ indicates the rewarded stimuli, S- lists the unrewarded stimuli.
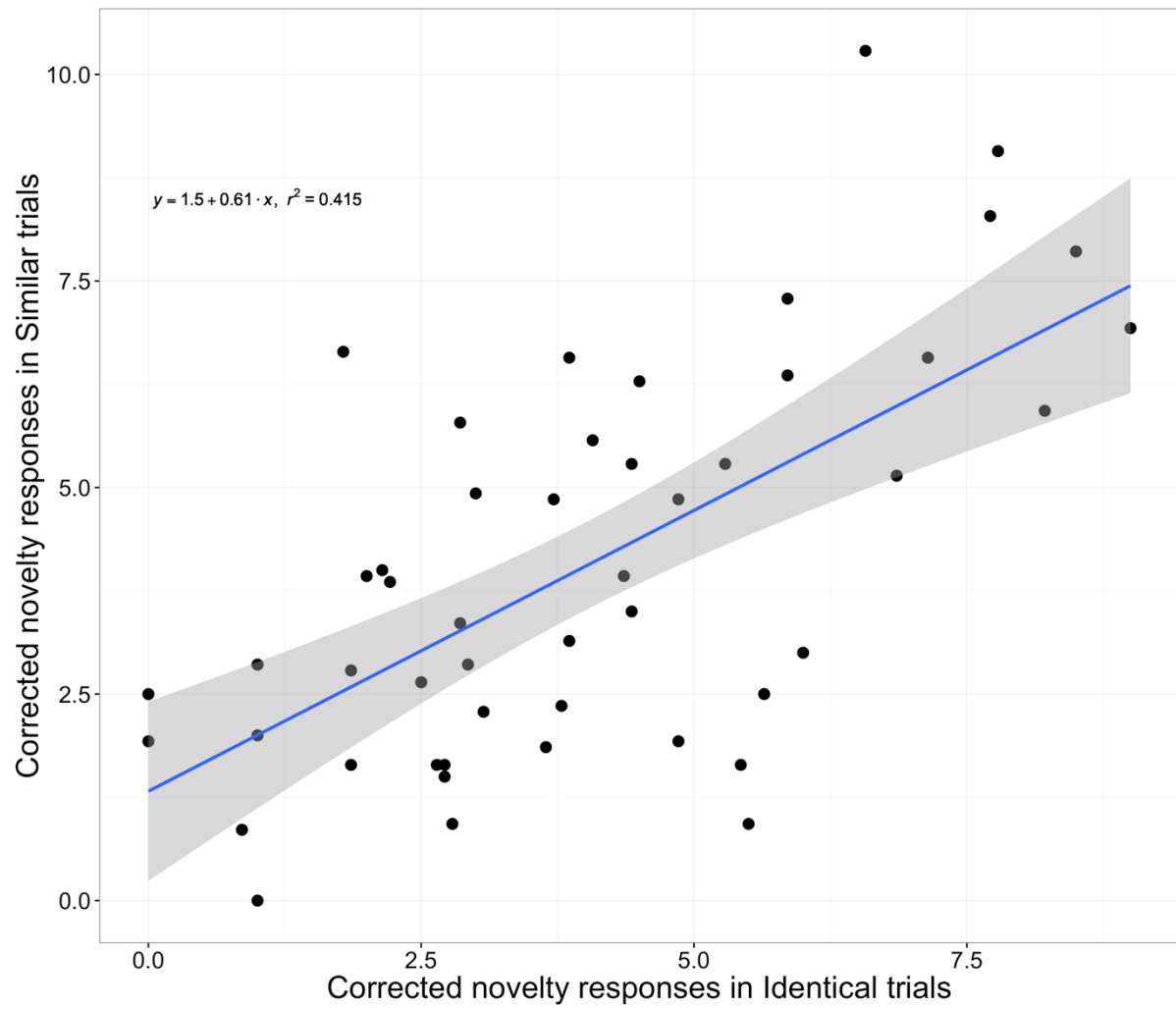
Figure S7. The relationship of novelty responses in 'Identical' and 'Similar' trials; blue line indicates

assumed linear fit; grey area denotes 95% confidence interval.

Chapter 2 |

Inference by Exclusion in Goffin Cockatoos (*Cacatua goffini*)

Inference by Exclusion in Goffin Cockatoos (*Cacatua goffini*)

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Abstract

Inference by exclusion, the ability to base choices on the systematic exclusion of alternatives, has been studied in many nonhuman species over the past decade. However, the majority of methodologies employed so far are hard to integrate into a comparative framework as they rarely use controls for the effect of neophilia. Here, we present an improved approach that takes neophilia into account, using an abstract two-choice task on a touch screen, which is equally feasible for a large variety of species. To test this approach we chose Goffin cockatoos (*Cacatua goffini*), a highly explorative Indonesian parrot species, which have recently been reported to have sophisticated cognitive skills in the technical domain. Our results indicate that Goffin cockatoos are able to solve such abstract two-choice tasks employing inference by exclusion but also highlight the importance of other response strategies.

Introduction

Animals frequently face situations in which only partial information about the problems at hand is immediately accessible. To cope with such situations individuals may employ different techniques involving various levels of cognition [1]. When faced with two or more alternatives, the simplest response strategy could be a random choice or, alternatively, generalisation from previously rewarding situations based on similarity, thereby using information from trial and error learning [2]. A cognitively more challenging strategy involves the analytical interpretation of the outcome of an unknown event using previous experience [3]. One way to reason in this manner is to infer by exclusion, i.e., choosing one option by logically excluding other alternatives [4].

Until recently it was believed that the ability to infer by exclusion might be associated with complex language learning and therefore a uniquely human trait [5,6]. However, in the past decade, extensive research on various different species has proved otherwise (primates [4,7–19], dogs (*Canis familiaris*) [7,20–22], dolphins (*Tursiops truncatus*) and sea lions (*Zalophus californianus*) [23–25], dwarf goats (*Capra aegagrus hircus*) and sheep (*Ovis orientalis aries*) [26], as well as corvids and parrots: [27–34]). In terms of ecological relevance, inference

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abilities have mainly been discussed in a foraging context (e.g. [15,26,30,31,33]). Nevertheless, other factors have also been considered as possible contributors to the emergence of this capacity, such as rejection of parasitic eggs [35], social complexity [16] or predator detection [27].

Studies on inference by exclusion have employed a wide range of different tasks in order to explore exclusion skills in various animal species. Perhaps the most common method, as originally devised by Call [8], required apes to locate hidden food items underneath two opaque cups. Test subjects were provided with partial information about these cups (either showing them the content of the cups, or shaking: both cups, only the baited cup, only the empty cup or neither cup). By giving individuals of the four great ape species—bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*)—information (visual, by showing the inside of the cups, or auditory, by shaking the cups) about the content of both cups or only the baited cup the authors controlled for the motivation to retrieve the reward and choice based purely on manipulation of the cups. A further control condition, in which neither of the cups was manipulated, was devised to investigate whether individuals used other cues (e.g. olfaction). The crucial condition though was providing the test subjects only with information about the non-baited cup, which required individuals to choose by inferring the location of the hidden food reward without direct information. Follow-up experiment that eliminated alternative mechanisms to locate the food (such as learning to respond correctly, or simply associating cues with the reward), provided further support for Call's [8] previous findings.

Nawroth et al. [26] have extended the investigation of inference by exclusion skills also to non-primate mammals by providing goats and sheep with the same task in the visual domain. In a critical experiment the authors showed that two goats but no sheep chose the correct cup significantly above chance levels. The authors discuss this possible species difference with regard to the species-specific feeding ecology, with sheep being dietary grazers, whereas goats forage more selectively.

A task by Call and Carpenter [9] that was adapted to the visual domain by using straight and bent tubes, was implemented by Schloegl and colleagues [30] to investigate exclusion performance in ravens (*Corvus corax*) and kea (*Nestor notabilis*). Here, subjects were able to see a reward if it was located in a straight tube with the openings oriented towards them, but not if the reward was placed in a bent tube or a straight tube that was rotated so that the openings were visually not directly accessible. Thus the individuals were required to look into the tubes in order to find the reward. By counting the looks into relevant and irrelevant tubes the authors were able to determine whether the birds were applying exclusion skills. In total the raven seemed to show significantly more exclusion-based choices, while kea were also significantly more likely to choose the correct tube, but only after visually inspecting both tubes. In fact the kea even looked into straight tubes from both sides in approximately 35% of all trials, a response that is really not suggestive of reasoning by exclusion capacities in this species. Schloegl et al. [30,33,36] proposed that different selection pressures might have been responsible for these differences: while food storing and competitiveness were discussed as the driving forces behind inference by exclusion in ravens, the kea's explorative nature may have hindered this trait from emerging [30,33,36]. However it is also possible that their explorative and neophilic tendencies might have only overshadowed the kea's propensity to reason by exclusion and that the task therefore was not fully suited for a direct comparison between ravens and kea because it did not control for neophilia. Schloegl et al. [32] later discussed the possibility of domain-specific advantages for different species and highlighted the importance of procedural differences in a study showing that African Grey parrots (*Psittacus erithacus*) are able to perform reasoning by exclusion with acoustic cues.

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Greenberg and Mettke-Hofmann [37] presented and tested an innovative theoretical model regarding exploration and neophobia, based on ecological factors. This two-factor model makes predictions when bird species will show i) more or less explorative tendencies and ii) neophilic or neophobic responses. The authors conclude that especially island species might exhibit the highest levels of exploration and neophilia as result of lower predation risk and exploitation of larger feeding niches. By that logic, island species such as the Goffin cockatoo should be a good model species to study the impact of neophilia and exploration on cognition and decision-making [38]. Neophilia, the attraction to objects or stimuli simply due to the fact that they are novel [39], has been discussed as a possible confounding factor in a variety of cognitive testing approaches in kea [40], another parrot species endemic to an island. However, implications of novelty seeking, with regards to cognitive testing in other species have so far, to our knowledge, been given little attention.

An abstract task using touch screens is a suitable approach to investigate species with different levels of neophobia and neophilia [41]. Aust et al. [7] devised an elaborate two-choice task on the touch screen in order to investigate inference by exclusion, while controlling for neophilic responses in humans, dogs and pigeons (*Columba livia*). They presented the individuals with a set of rewarded (S+) and unrewarded (S-) stimuli. Once the subjects reliably discriminated between the stimuli, they then introduced a novel stimulus (S') paired with the familiar S-, thus leaving two possible explanations for choosing the novel stimulus: either by excluding the former unrewarded S-, or choosing the novel stimulus due to a neophilic tendency. To be able to exclude the latter explanation the researchers controlled for neophilia by pairing the S' with yet another novel stimulus (S"). If subjects now shifted their responses to the S", then their responses would be guided by neophilic tendencies, whereas perseverative responses towards the S' would imply inference by exclusion. While most of the humans and half of the dogs in the study seemed to choose novel stimuli based on exclusion, only one pigeon chose the novel stimulus in the first test significantly above chance, but chose the second novel stimulus in the following test as well and thus was exhibiting neophilia. Despite the innovative rationale of this task, the procedure still had some serious shortcomings and limitations as discussed by Aust et al. [7]. Firstly and perhaps most importantly, test trials were not rewarded, which may have violated the expectations of individuals who initially performed according to the rationale of the task, but may have immediately abandoned this strategy following the absence of food rewards. Secondly, the experimental design of this task only allows mutually exclusively testing for either neophilic or exclusion strategies, but not both. If individuals fail in the second task, it may indicate that a correct response in the first test was guided by neophilic tendencies rather than exclusion skills. Finally, in contrast to the more traditional cup task of Call [8], which investigated this ability in a more ecologically valid setting, the study of Aust et al. [7] required the birds to first learn to associate certain stimuli with a reward. As this task involved training, and test stimuli were shown repeatedly, mere exposure might have influenced individuals' choices, whereas choices in a cup task may be more spontaneous. Still, an abstract task may be more suitable to investigate whether reasoning abilities can be applied in a more general way.

Here we present a modified procedure which partially adapts the basic idea of Aust and colleagues' [7] study, but at the same time controls for the first two of the above-mentioned shortcomings. We accomplished this by already introducing novelty trials during the training to habituate subjects to novel stimuli. However this training could result in a learned rule to avoid novel stimuli in general, despite the context in which the novel stimulus is presented. Violations of expectancies, promoted by not receiving a reward after selecting the logically "correct" stimulus might have accounted for weaker performance in later test sessions in the study of Aust et al. [7]. To overcome this effect, we decided to reward critical test trials differently. To discourage the birds from forming stimulus-reward associations we presented novel stimuli in

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every session. Furthermore, we introduced a new condition to additionally exclude the possibility of one-trial learning as originally introduced by Guthrie [42] (see Procedure). Preferences for or avoidance of particular stimuli could also determine choices between stimuli. With this protocol we wanted to test whether subjects exhibit exclusion skills, but also to what extent alternative strategies would be employed. We chose the Goffin cockatoo (*Cacatua goffini*) as a pilot subject species for several reasons: They are not only highly inquisitive and explorative in captivity [43,44], but also have exceptional skills in tool manufacture and use [45,46], can solve stage six Piagetian object-permanence [43] and have already shown some functional inferences in a sequential means-end task [47].

There are many ecologically relevant domains in which inference by exclusion may be adaptive for Goffin cockatoos, be it in a foraging context, dealing with social challenges, or in the technical domain when making inferences about the functionality of an action, as has been shown in the study of Auersperg et al. [47]. So far only little is known about these birds in the wild [48], so we can only speculate about the underlying ultimate mechanisms promoting such skills in this species. However, the question remains whether such exclusion abilities can be applied in a domain-general manner, thus being transferred from the original context, whatever it may be, and employed in an abstract task. We believe that in order to address the evolution of inferential reasoning abilities in a fair and sensible comparative framework across different strategies and species in the future, an abstract touch screen setup will be of great use, provided that differences in behavioural and ecological predispositions are appropriately controlled for.

Material and Methods

Ethical statement

The Animal Ethics and Experimentation Board of the Faculty of Life Sciences at the University of Vienna approved the study (Reference number: 2015–001). All subjects that participated in reported experiments were housed in accordance with the Austrian Federal Act on the Protection of Animals (Animal Protection Act—TSchG, BGBl. I Nr.118/2004). Furthermore, the animals' wings were not clipped and they rather than being inside a box during touch screen testing, were sitting on a perch inside the experimental room, free to fly off any time they chose to. If the birds were not motivated to participate they were released back into the group compartment. As the present study was strictly non-invasive and based purely on behavioural observations, all experiments are classified as non-animal experiments in accordance with the Austrian Animal Experiments Act (§ 2, Federal Law Gazette No. 501/1989).

Test subjects

Twelve individuals of Goffin cockatoos participated in this study (see Table 1). The whole group, consisting of 15 birds, was group-housed in a large, heated (20°C) indoor aviary (45 m^2, 3 m to 6 m high) with an adjacent outdoor aviary (150 m^2, 3 m to 4.5 m high), to which they had access all day at temperatures above 17°C and at least one and a half hours per day if temperatures rose above -2°C. The aviaries were enriched with branches, hiding places, bathing opportunities and wooden parrot toys. Individual birds were visually separated from the rest of the group in an indoor testing room (7.5 m^2, 3m high) adjacent to the group aviary. Five individuals were completely naive to the touch screen, seven had prior experience with the touch screen by participating in a two choice task investigating the effect of exploration and neophilia on discrimination learning (O'Hara et al., unpublished data).

All subjects were hand reared and obtained from European breeders in accordance with the CITES regulations. The daily diet consisted of basic food (Australian Parrot Loro Parque Mix

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Table 1. List of individuals participating.

Individual	Hatched	Sex	Touch screen experience
Doolittle	2011	♂	Yes
Figaro	2007	♂	Yes
Fini	2007	♀	No
Heidi	2010	♀	No
Kiwi	2010	♂	Yes
Konrad	2010	♂	Yes
Mayday	2011	♀	No
Moneypenny	2010	♀	Yes
Muki	2011	♂	No
Muppet	2010	♂	Yes
Olympia	2010	♀	No
Pipin	2008	♂	Yes

Names of individuals are listed in the first column, with year of hatching and sex in the following columns; the last column (Touch screen experience) refers to whether individuals have participated in prior discrimination tasks on the touch screen.

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supplemented with a selection of dried fruits) and fresh drinking water ad libitum and additional fresh fruit, soy yoghurt, eggs fried in red palm oil or cooked grains, noodles, vegetables in the mornings.

Apparatus

The touch screen setup was an adapted mobile version of the operant conditioning system described by Steurer et al. [41]. The mobile version combined touch screen, CPU (based on a Schneider A4F minicomputer (http://www.mappit.de) with Mini-ITX main board (VIA EPIA1 M10000, with 1-GHz CPU, 2 × USB, 1 × LAN 10/100 Mbit, sound, and VGA on board), 512 MB DDR RAM, a 40-GB 2.5-in. hard disc) and automatic feeding system in one sealable aluminium cube (385 mm x 500 mm x 610 mm) with touch sensitive screen and reward tray (60 mm x 60 mm x 20 mm) located in the front and a flap on the back allowing access to a second screen, keyboard and mouse. A feeding wheel was attached behind the touch sensitive screen. Whenever a stimulus with positive contingency was touched the wheel would rotate so that a reservoir released a reward into the reward tray below the screen. The screen, a 15-inch XGA color TFT LCD Modul (Model G150XG01 by AU Optronics Corp., Taiwan; http://www.auo.com), provided a display area of 304 mm × 22 8mm (381 mm diagonal) and a resolution of 1024 × 768 px. A 15-inch IR "CarrollTouch" touchframe (Model D87587-001, 15 in., without filter) by Elo (Menlo Park, CA; http://www.elotouch.com) was attached to the screen in order to detect responses. The opening for delivering the reward was centrally located, 80 mm below the lower edge of the screen.

The touch screen apparatus was placed on a table (1 m x 1 m) with a stone placed in front of it. This stone (approx. 40 cm x 20 cm x 30 cm) served as a perch for the birds. It was approximately the same height as the reward tray, so the birds could easily access the stimuli and the food reward (Fig 1).

The program used for cognitive testing was CognitionLab (version 1.9; see [41] for a detailed description).

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Fig 1. Experimental setup. Individual perching on the pedestal stone in front of the touch screen.
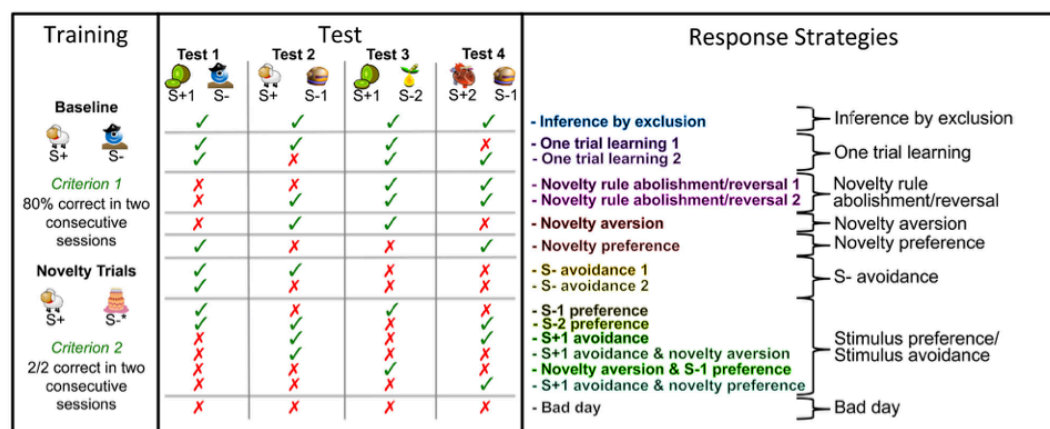
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Fig 2. Experimental Overview. Schematic representation of one of each baseline trials, novelty trials and test trials with example stimuli, as well as theoretical response predictions (see main text) colour-coded to match response patterns in Fig 4; + indicates stimuli with positive reward contingency,— indicates unrewarded stimuli; ✓ correct, ✗ incorrect choices. On the right we list the most parsimonious mechanisms (see main text).

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Stimuli

We downloaded a collection of license and restriction free clip arts from the Open Clip Art Library (http://www.openclipart.org/) as Scalable Vector Graphics (SVG). An arbitrarily chosen pool of 190 clip arts (see Fig 2 for an example) were resized to images on white background measuring 70 x 70 px, adapted for equal overall brightness and converted into Portable Network Graphic (png) files using Fiji (ImageJ 1.49e, http://imagej.nih.gov/ij; ImageJ 2.0.0-rc-9, http://developer.imagej.net/).

Two stimuli were presented simultaneously on the screen. They were positioned 484 px from the top and either 341 px (left) or 682 px (right) from the left side of the screen. In each trial, the program randomly placed the rewarded and unrewarded stimuli at either position. The background colour of the screen during the task was set to black (R = 0, G = 0, B = 0).

Procedure

General Procedure. To separate individuals, the birds were individually called into the testing compartment by name. After the birds entered the compartment, a sliding door separating the aviary and testing compartment was pulled shut. Any additional bird that had entered the compartment had to perch on the experimenter's hand and was then released back into the group aviary. Except for the habitutation phase (see below) each session consisted of 20 trials and usually one session per individual was conducted per day, except for weekends when the experimenter was present all day and occasionally up to four daily sessions were provided (depending on subject motivation).

Correct choices were rewarded with small pieces of cashew nuts, automatically dispensed by the feeding system implemented in the apparatus. During each session, the experimenter (MO) was present outside the view of individuals but remained motionless, wore mirrored sunglasses and did not pay attention to the responses, so as not to cue the test subject. The experimenter's presence during the task was kept consistent for all birds to minimize potential fear reactions

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towards the apparatus, since some individuals initially flew to the experimenter after first encountering the apparatus and would not perform when left alone in the testing compartment.

After each session the individuals had to step on the experimenter's hand and were then transferred back to the group. In the absence of the subjects the screen was wiped to remove stains and potential olfactory cues, and the apparatus was re-baited. The experiment was conducted four days a week between 5. March and 25. June 2014.

Habituation. Naive individuals were habituated to the touch screen and reward system by presenting a white square (70 x 70 px) centrally on the screen. Once individuals started to touch the square (with verbal and gestural encouragement from the experimenter (MO)) a reward (a twelfth to a sixteenth of a cashew nut) would be delivered into the reward tray. As soon as the stimulus was touched reliably in consecutive trials, the square was presented at random positions for 32 trials.

Training. For each individual, two stimuli (hereafter: the baseline pair) were randomly assigned a positive and a negative contingency, respectively. Responses directed at the positive stimulus (S+) resulted in the delivery of a reward, paired with a short sound (665 Hz, 200ms) and a time-out of one second during which the stimuli disappeared. Responses to the negative stimulus (S-) produced a shorter and lower pitched sound (405 Hz, 151ms) and led to a two second time-out during which the stimuli disappeared. Thereafter, the same trial was repeated as a correction trial until the individual touched the positive stimulus (S+).

Each session consisted of 20 trials in which two 'novelty trials' were semi- randomly interspersed (the first novelty trial randomly occurred in trials four to eight, the second randomly in trials thirteen to seventeen). In these novelty trials the S+ was presented together with a novel unrewarded stimulus (S-*), which was different for every novelty trial. Responses to the S-* had the same effect as responses to S- (low pitch sound, two second time out and correction trial). To ensure that the birds had learned the discrimination, the birds had to reach 80% correct first choices (15/18) in the baseline trials in two consecutive sessions (Criterion 1). Individuals were also required to completely inhibit responses to novel stimuli during all novelty trials (2/2) in two consecutive sessions (Criterion 2). The second criterion was introduced to ensure that responses to novel stimuli were not committed purely out of a neophilic tendency.

Testing. After reaching both criteria, the cockatoos were exposed to 25 test sessions, each in turn consisting of 20 trials. Four test trials were pseudo randomly distributed among 16 training trials (test trial 1 substituting trial 4 or 5, test trial 2 substituting trial 8 or 9, test trial 3 substituting trial 12 or 13 and test trial 4 substituting trial 16 or 17), but always occurred in the same sequence. For all test trials, stimuli with positive contingency were rewarded (as the S+), whereas responses in test trails to stimuli with negative contingency were immediately aborted (no sound) and followed by the next baseline trial.

In the first test trial the S+ was replaced with a novel positive stimulus (S+1), while the S- remained the same as in the baseline trials. In the second test trial a novel unrewarded stimulus (S-1) replaced the S- while the S+ remained the same, much like the novelty trials in training sessions. In the third test trial the novel positive stimulus of test one (S+1) was shown, now paired with a novel negative stimulus (S-2). In the fourth test trial the negative stimulus of test trial two (S-1) was presented together with a new positive stimulus (S+2; see Fig 2 for a schematic outline of a training and test session). For each test session a novel set of S+1, S-1, S+2 and S-2 was provided to avoid any learning effects other than one-trial learning. For each response pattern we tried to devise the most parsimonious explanation possible:

For answers to be classified as 'Inference by exclusion' individuals had to choose the novel positive stimulus (S+1) in the first test trial by inference or avoidance of the known S-, and continue to choose the S+1 in test trial three, by one trial learning or inference. Correct responses

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in test trials one and three therefore are indicative of inference by exclusion but alternative mechanisms are possible. However, correct responses in test trial two, either by choosing the stimulus with the greater associative strength, or possibly by inference, mean that individuals have gained no direct information about the contingency of the novel S-1 (as this stimulus was never encountered before and was not chosen). In such a case, individuals are faced with two stimuli (S-1 and S+2) with unknown contingencies in trial four. The only difference between these stimuli is that one (S-1) was previously presented with the S+ in test trial two. Individuals choosing the 'more' novel stimulus (S+2), counteracted what was rewarded for in the training, indicating an avoidance of the S-1 solely for contextual reasons, which can be considered an instance of reasoning by exclusion. Thus we employed a very strict criterion for a performance to be considered as representing 'Inference by exclusion': only if the correct stimuli (S+) were chosen in all four test trials.

We assumed that 'One trial learning' occurred whenever individuals did not directly infer the contingency of a stimulus without direct feedback (making a mistake solely in test trial four —'One trial learning 1'), or showed correct responses after one incorrect choice in test trial two ('One trial learning 2').

Other strategies may have been related to the relative novelty of the stimuli. Since the training included trials in which novel stimuli were not rewarded, it is possible that the subjects based their decisions on a general rule of novelty aversion: avoid the novel stimuli in the first and fourth test trial and choose the less novel stimulus in the third test trial. The reverse pattern would indicate instances of novelty preferences.

Furthermore, individuals may initially avoid the novel stimulus, but from then on choose the S+ ('Novelty rule abolishment/reversal 2'). Upon not receiving a reward in the first test trial, individuals may even reverse this aversion and choose the novel (but incorrect) stimulus in the second test trial, but respond 'correctly' in the last two test trials ('Novelty rule abolishment/reversal 1'). Therefore we labelled these two strategies 'Novelty rule abolishment/ reversal'.

We currently have no explanation for the case when subjects choose the incorrect stimuli in all test trials (which occurred only once), hence we labelled this as a 'Bad day'. Other response patterns we attributed to combinations of stimulus preferences or stimulus aversions (see Fig 2 for an overview of response patterns and corresponding strategies).

Data analysis

In order to assess performance on an individual level, we calculated the cumulative probability of each response pattern occurring by chance. Four test trials per session yield 16 possible different response patterns (see Fig 2). Therefore the cumulative probability for each pattern to occur by chance is $p = 0.0625$. This means that if individuals choose randomly, they should exhibit each pattern 1.5625 times over the course of the 25 test sessions. We employed a two-tailed binomial test to test whether the observed patterns were chosen more often than predicted by chance, which would imply preferences for certain strategies by producing consistently recurring patterns. Depending on how many response patterns a certain strategy predicts (see Fig 2), the probability for a strategy to occur by chance would increases by a factor of n (where n is the number of response patterns constituting a strategy). Strategies composed of only one response pattern (such as Inference by exclusion, Novelty aversion, Novelty preference and Bad days) therefore are statistically significant at $p = 0.018$ if the same pattern occurred in five of the 25 sessions. Strategies consisting of two patterns (such as One trial learning, Novelty rule abolishment/reversal, and S- avoidance) would need to be exhibited in seven out of 25 sessions to differ significantly from chance ($p = 0.03$). As Stimulus preferences/

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Stimulus avoidances account for six different patterns, this strategy requires to be displayed in 15 out of 25 sessions to reach significance (p = 0.023).

In order to investigate the effect of different factors on exclusion skills, incidents of Inference by exclusion were scored as successes, while all other strategies employed were considered failed attempts. We then applied a generalized linear mixed effects model with binomial error distribution and conditional log-log-link function to allow for asymmetry in the distributions. Including individuals as random factors this model allowed us to test for the influence of age (year of hatching), sex and prior touch screen experience by single term deletion from a full model and likelihood ratio testing. To investigate whether individuals had learned to infer by exclusion, rather than spontaneously applied their reasoning skills, we additionally included session as a fixed factor in our model. Furthermore, we included number of sessions required to reach Criterion 1 as well as Criterion 2 as a factor, to examine whether the time required to learn to inhibit responses to novel stimuli in the training influenced exclusion performance.

To investigate the effect of different response patterns on a group level we employed a generalised linear mixed model with assumed Poisson distribution. As in the binomial model we included sex, age, sessions to reach Criterion 1 in training (learning the baseline discrimination) and sessions to refrain from pecking on novel stimuli during training (Criterion 2). We performed Wilcoxon signed-rank tests for pairwise comparisons of all patterns with the pattern suggestive of Inference by exclusion.

Binomial exact tests were conducted in the statistical package R [49], models were fitted employing 'lme4' [50] and post-hoc adjustment for the Intercept using chance probability of 0.0625 was achieved by using the 'esticon' function of the package 'doBy' [51]. Visual representation of the data were created with the package 'ggplot 2' [52].

Results

Seven individuals learned the discrimination of the baseline stimuli (Criterion 1) before ceasing to respond to the novel stimuli (Criterion 2). Two individuals managed to inhibit their responses to novelty before reliably discriminating the baseline stimuli, and three subjects reached both criteria simultaneously. Overall, subjects required on average 7.92 sessions (+/- 1.22 SE) to complete the training phase. Individuals required on average 5.67 sessions (+/- 0.90 SE) to learn the discrimination of the baseline stimuli, whereas it took them on average 7.25 sessions (+/- 1.35 SE) to refrain from selecting the novel stimuli. All individuals chose a novel stimulus at least once (M = 6.25, +/- 1.33 SE; see Fig 3).

At the individual level, eight individuals exhibited the Inference by exclusion response pattern significantly more often than predicted by chance (see Fig 4a). The only other patterns that also occurred above chance level were One-trial learning, displayed by Figaro, Konrad Olympia and Pipin, as well as a preference for the second novel negative stimulus (S-2), which was shown by four individuals (Doolittle, Fini, Mayday and Muki). One individual (Konrad) seemed to have established an additional rule to avoid the unrewarded baseline stimulus (S-). It is important to note that these patterns are not mutually exclusive, as Figaro and Pipin also relied on inference by exclusion and one trial learning significantly, while Doolittle and Muki showed inference by exclusion and a preference for the S-2 significantly above chance. Konrad even simultaneously exhibited Inference by exclusion, One trial learning 1 and Avoidance of the unrewarded baseline stimulus at statistically significant levels.

Binomial modelling, with regard to sessions showing Inference by exclusion, revealed a significant intercept (GLMM: b = -1.52, SE = 0.13, $X^2(1)$ = 83.12, $p < 0.001$), but no significant effects of sex ($X^2(1)$ = 0.003, p = 0.956), age ($X^2(3)$ = 1.56, p = 0.670) or prior experience on the touch screen ($X^2(1)$ = 2.77, p = 0.096) on the occurrence of this response pattern. We found no

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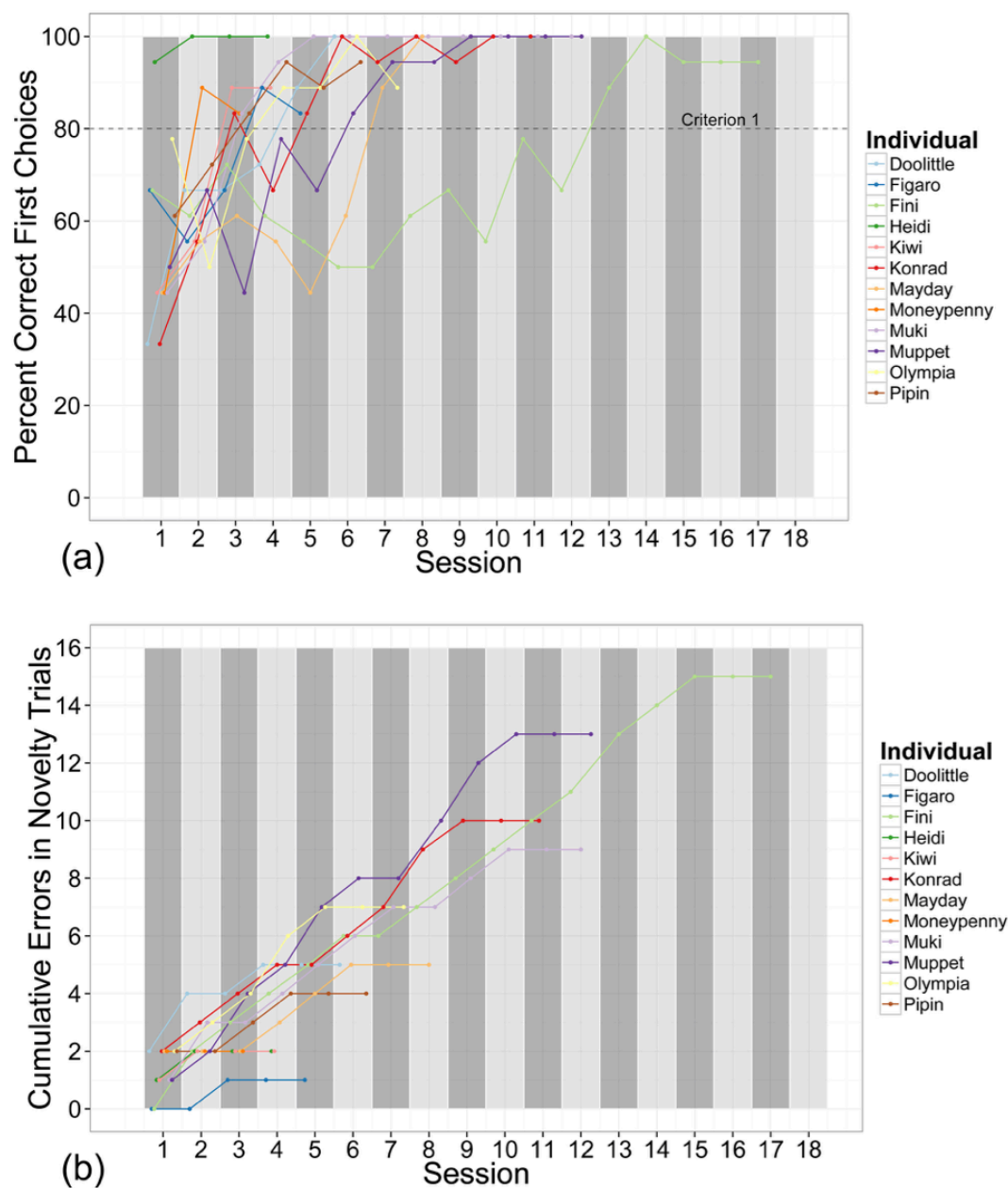
Fig 3. Performance in the training phase. a) Learning curves for all individuals over all training sessions, with the dotted line indicating the learning criterion of 80 per cent correct first choices (Criterion 1); b) Cumulative errors of novelty trials; a steep incline indicates novelty responses in both novelty trials, moderate incline indicates response to one novel stimulus per session and a straight horizontal line indicates no responses towards novel stimuli (Criterion 2); longer lines indicate individuals required more sessions to inhibit responses to novel stimuli.

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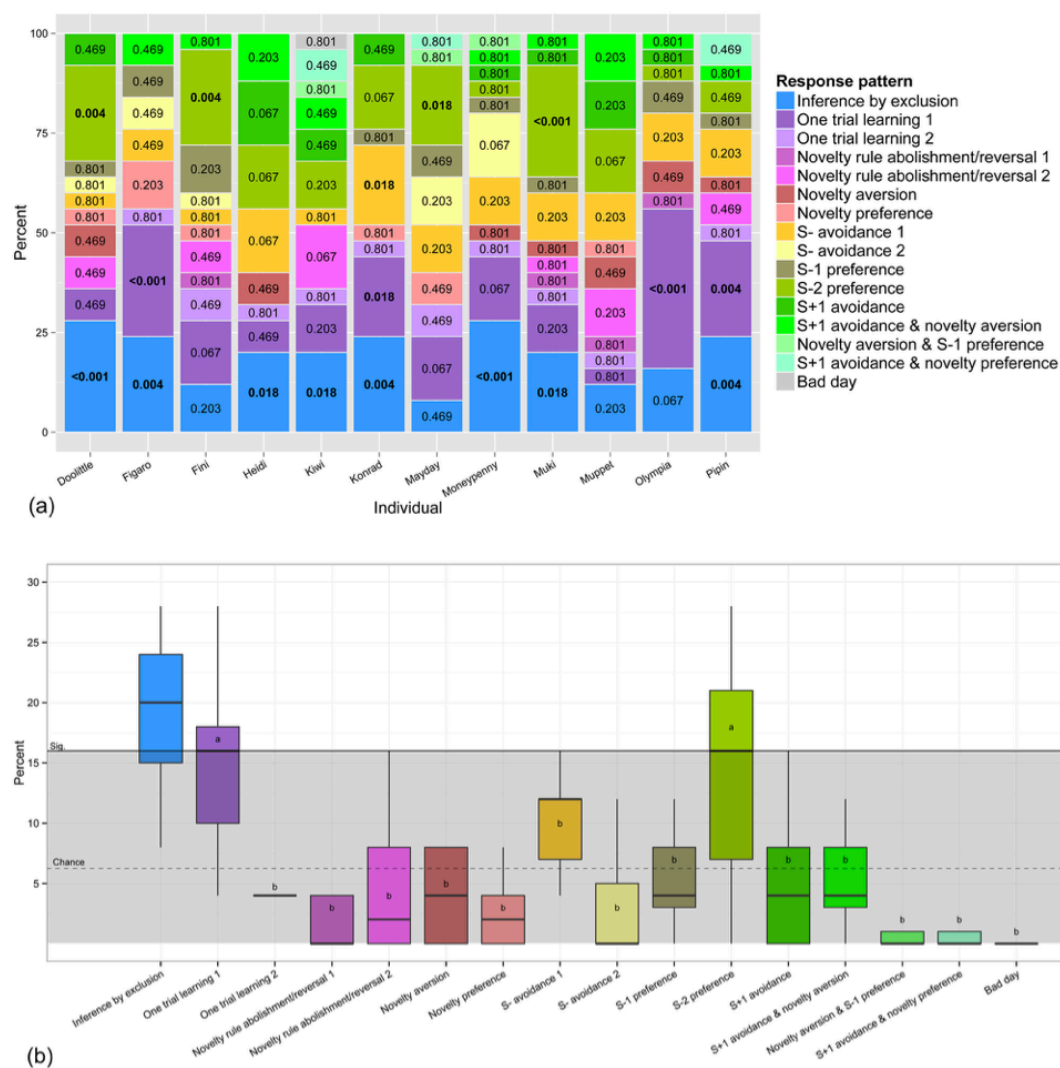**Fig 4. Percentages response pattern frequencies.** a) Detailed patterns exhibited by each individual in all 25 test sessions; values in the bar graphs correspond to the probability that the number of sessions with certain response patterns occurred by chance; significant values are printed bold; b) Frequency of patterns exhibited at group level; horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals. The dashed horizontal line represents chance levels; the grey area below the line denotes no significant divergence from chance. The letters in the boxplots refer to a Wilcoxon signed-rank test comparing patterns to 'Inference by exclusion'—a: no significance, b: significant, p< 0.05.

influence of session ($X^2(24) = 25.43$, $p = 0.383$) discrimination-learning performance in the training ($X^2(1) = 1.76$, $p = 0.185$), or inhibition of novelty responses during training ($X^2(1) = 0.03$, $p = 0.860$).

Generalised linear mixed models investigating how often each pattern occurred revealed only a significant effect of response patterns ($X^2(15) = 224.97$, $p < 0.001$). Post hoc tests revealed that Inference by exclusion occurred significantly more often than other response

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patterns, except for 'One trial learning 1' and preferences for the S-2 (see Fig 4b). Furthermore, when comparing frequencies of patterns for 'Inference by exclusion' and 'One-trial learning 1' only for those individuals that exhibited exclusion performance above chance, significantly more 'Inference by exclusion' ($M = 5.88$, +/- 0.24 SE) than 'One trial learning 1' ($M = 4.00$, +/- 0.53 SE) was employed on a group level (Wilcoxon signed-rank test: $p = 0.048$; $r = -0.51$).

When grouping the individual patterns to hypothesized response strategies (see Fig 2), combinations of stimulus avoidances and preferences, consisting of six possible response patterns, were exhibited on average in 32% of the test sessions ($SE = 2.83$). Furthermore, subjects seemed to rely on one-trial learning ($M = 21.00\%$, $SE = 2.79$), inference by exclusion ($M = 19.67\%$, $SE = 1.87$) and avoidance of the S- ($M = 14.33\%$, $SE = 2.00$).

Discussion

Two thirds of the subjects exhibited inference by exclusion by showing the corresponding response pattern in significantly more trials than predicted by chance. Since novel test stimuli were used in each test-session, experience cannot account for these results. However, an immediate association formed with the S+1 in the first test trial (by avoiding the known S-) could have underlain choices in test trial three, through one-trial learning. Such one trial learning, or rather 'One trial avoidance', cannot, however, account for correct responses in test trials two and four. Crucially, if individuals chose correctly in the second test trial, which was a prerequisite for being considered an instance of inference by exclusion, they received no direct feedback about the unrewarded (but not chosen) stimulus. Thus the contingency of the S-1 remained unknown to the individual, unless avoidance of this stimulus occured for contextual reasons (being presented in combination with a rewarded stimulus), which would be considered an exclusion performance.

An alternative explanation for patterns of 'Inference by exclusion' might consider correct choices in trials one through three, based on associative strength and avoidance of the S-, and a random choice in the fourth test trial. If so, there should be similar frequencies of patterns for 'Inference by exclusion' and 'One trial learning 1'. While this might have been the case for three individuals (Figaro, Konrad and Pipin; see Fig 4a), it is unlikely to apply to all individuals who exhibited successful exclusion performance. For those individuals who showed well above chance 'Inference by exclusion' patterns, we found a significantly higher frequency of 'Inference by exclusion' patterns than of 'One trial learning 1' at a group level. Therefore we conclude that at least those five individuals (Doolittle, Heidi, Kiwi, Moneypenny and Muki) chose the rewarded stimulus (S+2) of the fourth test trial by inferring that S-1 was unrewarded. In this crucial test, no other cues were available to evaluate the contingency of both stimuli.

These inferential responses did apparently not emerge as a consequence of incremental learning because session, as a factor, had no effect on the response patterns. Since the performance in the training (sessions required to reach Criterion 1 and Criterion 2) also did not affect inferential patterns during testing, we conclude that prior experience in the training, as well as experience during testing itself did not influence this ability. Thus, we suggest that at least five subjects were able to spontaneously solve the task in an inferential manner.

However, this does not mean that Goffin cockatoos respond entirely logically in categorization tasks like the present one. The individuals also exhibited other strategies with novel stimuli: One-trial learning, stimulus preferences and avoidances, as well as the avoidance of the S-, represent further strategies. From a different perspective, these strategies—one-trial learning and avoiding the unrewarded stimulus and stimulus preferences—can also be considered efficient. Learning to categorize novel items on the basis of a single encounter in this task requires high levels of cognitive plasticity, given that during training individuals were required

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to inhibit responses towards novel stimuli in order to proceed to testing. Preferences might emerge when test stimuli have a similar colour or shape as the S+. Ecologically, it would be adaptive to seek out items, which resemble other items that were previously rewarded and to avoid items similar to ones that were not. However, only one individual (Konrad) showed a significant avoidance pattern for the unrewarded baseline stimulus.

In humans, the prefrontal cortex and in particular the inferior parietal lobule play a major role in inference by exclusion tasks [6]. Since these brain areas have also been associated to language learning and tool use in primates [53], inferential reasoning has been suggested to be a uniquely human trait [5,6]. The present study as well as Aust et al. [7] provide cumulative evidence against this anthropocentric view. A very recent study by Nawroth and colleagues [26] further supports the argument of exclusion performance not being uniquely human by showing that goats (but not sheep) are able to successfully choose the position of a food reward by exclusion. The authors discussed the found species difference with respect to different feeding ecology, especially different foraging strategies, similarly as Schloegl et al. [30,31,36] did for different corvids and kea and Mikolasch et al. [33] suggested for carrion crows.

Goffin cockatoos are highly inquisitive and playful in captivity [43]. This may explain why most individuals kept responding towards the novel stimuli even though they had already reached the criterion in the initial discrimination task and had formed a positive association with the S+. Our data therefore challenge the hypothesis proposed by Schloegl et al. [30,36] that exclusion performance may be missing in highly explorative birds and may rather have evolved as an adaptive consequence of intraspecific competition during foraging in some species such as corvids. While this might be true for some corvids, a recent study showed that Eurasian jays (*Garrulus glandarius)*, a corvid species which habitually stores food items, failed this task [34], contradicting Schloegl et al.'s hypothesis. Mikolasch et al. [33] showed that contradicting social cues can overshadow exclusion performance in crows, which potentially also may have led to the Eurasian jay's failure [34]. However, considering the overall body of evidence, food-storing behavior cannot be the sole source of exclusion skills.

Given that the ability to infer by exclusion has been found in distantly related species with different ecological backgrounds, including humans [6,7,12], nonhuman primates [4,8–11,13–20], dogs [20–22], goats [26], ravens [30], carrion crows [33], New Caledonian crows [27], African grey parrots [28,29,32] and now Goffin cockatoos, we suggest that its repeated emergence is the result of convergent evolution. It is yet unclear why the ability seems to be missing in pigeons [7], sheep [26] jackdaws [31], and Eurasian jays [34], but some of the latter results may be influenced by methodological issues in past task setups.

In this study we showed that Goffin cockatoos are able to perform inferences not only in the technical domain [47], but also exhibit exclusion skills in very abstract tasks. Whether the Goffins' competence in physical cognition gave rise to the ability to infer by exclusion and also allowed them to apply this skill in different contexts, or whether this skill evolved due to other selective pressures and drove their advances in the physical domain remains speculative. The latter explanation would apply according to Pepperberg et al. [29], who suggested that exclusion might be a fundamental skill that developed in different species due to similar selection pressures and which ultimately makes the emergence of even more sophisticated cognitive skills possible.

However, precisely which environmental or social factors drove the emergence of the trait is difficult to say. The selection pressures that shaped the evolution of this ability in different species currently remain speculative and will have to be the subject of further comparative studies. We believe the testing paradigm introduced here has great potential to investigate inferential reasoning by allowing an evaluation in comparison to both, other species and alternative response strategies.

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Supporting Information

S1 Table. Complete dataset.
(XLSX)

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Author Contributions

Conceived and designed the experiments: MO AMIA TB LH. Performed the experiments: MO. Analyzed the data: MO AMIA TB LH. Contributed reagents/materials/analysis tools: AMIA LH. Wrote the paper: MO AMIA TB LH.

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Chapter 3 |

Reasoning by exclusion in the kea (*Nestor notabilis*)

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Reasoning by exclusion in the kea (*Nestor notabilis*)

Mark O'Hara[1,2] · Raoul Schwing[2] · Ira Federspiel[1] · Gyula K. Gajdon[2] ·
Ludwig Huber[2]

Abstract Reasoning by exclusion, i.e. the ability to understand that if there are only two possibilities and if it is not A, it must be B, has been a topic of great interest in recent comparative cognition research. Many studies have investigated this ability, employing different methods, but rarely exploring concurrent decision processes underlying choice behaviour of non-human animals encountering inconsistent or incomplete information. Here, we employed a novel training and test method in order to perform an in-depth analysis of the underlying processes. Importantly, to discourage the explorative behaviour of the kea, a highly neophilic species, the training included a large amount of novel, unrewarded stimuli. The subsequent test consisted of 30 sessions with different sequences of four test trials. In these test trials, we confronted the kea with novel stimuli that were paired with either the rewarded or unrewarded training stimuli or with the novel stimuli of previous test trials. Once habituated to novelty, eight out of fourteen kea tested responded to novel stimuli by inferring their contingency via logical exclusion of the alternative. One individual inferred predominantly in this way, while other response strategies, such as one trial learning, stimulus preferences and avoiding the negative stimulus also guided the responses of the remaining individuals. Interestingly, the difficulty of the task had no influence on the test performance. We discuss the implications of these findings for the current hypotheses about the emergence of inferential reasoning in some avian species, considering causal links to brain size, feeding ecology and social complexity.

Introduction

The field of cognition research attempts to unravel the mechanisms underlying the adaptive modification of behaviour through individual or social learning. A topic of great interest within comparative cognition is whether non-human animals are able to solve novel problems in a quick and beneficial way despite having incomplete information. One form of dealing with uncertainty when facing novel situations is to reason about known instances and logically exclude alternatives (Call 2006). The common approach to investigating such cognitive abilities is to devise tasks that, by systematically excluding alternative explanations, allow us to conclude if a certain ability is present or not (e.g. Call 2006; Aust et al. 2008; Schloegl et al. 2009a, b; Mikolasch et al. 2012; Shaw et al. 2013; Jelbert et al. 2015). However, behaviours other than the one of interest are rarely considered and often dismissed as not noteworthy, thus creating a very binary 'all or nothing' approach to the mental capacities of animals.

An earlier experimental design by Aust et al. (2008) already successfully investigated exclusion skills in pigeons (*Columba livia*), dogs (*Canis lupus familiaris*) and humans using a touch screen apparatus. The benefits of using such a touch screen to present abstract tasks include efficient data collection, reduction of biases through cues given by the experimenter and applicability to a large

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variety of different species (e.g. Steurer et al. 2012). However, while the experimental design of Aust et al. (2008) controlled for responses based on neophilia, it was not intended to test for inference by exclusion in neophilic species. A recent study of O'Hara et al. (2015a) adapted the design of Aust et al. (2008) to overcome previous limitations with respect to neophilia and shift the focus from an 'all or nothing' approach to a more holistic analysis of choice behaviour. This was achieved by implementing a test procedure, which considered all possible response patterns and attributed these to the simplest cognitive processes underlying choice behaviour (henceforth referred to as response strategies). Additional habituation to novelty during the training proved effective at controlling for neophilic responses of very investigative species such as the Goffin cockatoo (*Cacatua goffiniana*). Not only could the authors show, with this set-up, that Goffins were able to base choices on inference by exclusion, but also highlight the importance of other response strategies.

The kea (*Nestor notabilis*) is a parrot species endemic to the alpine and subalpine regions of the South Island of New Zealand. Sub-adult individuals form flocks of up to 20 individuals, whereas adults pair for life, forming family groups and joining larger groups occasionally at foraging sites (Clarke 1970; Diamond and Bond 1999). Thus, the kea's social structure may be best described as fission–fusion-like. Their climatically harsh environment and low predatory risk are believed to have caused the kea's explorative and curious nature (Diamond and Bond 1999; Huber and Gajdon 2006; Auersperg et al. 2011; O'Hara et al. 2015b). It is this neophilia we suspect to have overshadowed exclusion skills in a previous attempt to compare inferential abilities in ravens (*Corvus corax*) and kea (Schloegl et al. 2009b). Schloegl and colleagues used a foraging task, originally devised by Call and Carpenter (2001), in which either straight or bent tubes were baited with food items and presented simultaneously to the individuals. While ravens discarded empty, straight tubes that were oriented towards them and thus provided visual information of the presence or absence of food, kea investigated empty tubes from both sides in approximately a third of all trials before choosing the 'correct' tube. These results led Schloegl et al. (2009a, b) to conclude that competitiveness and food-storing behaviour may have promoted the raven's exclusion skills, while the feeding ecology of the kea, an extractive forager (Brejaart 1988; Diamond and Bond 1999), led to extensive search behaviour, which at a first glance seems inefficient sometimes (O'Hara et al. 2012, 2015b; Gajdon et al. 2013; Greer et al. 2015). However, extractive foraging has been suggested to also promote exclusion skills in primates (Bräuer et al. 2006; Paukner et al. 2009; Marsh et al. 2015), as it may require individuals to infer the location of hidden food,

whereas others (e.g. Petit et al. 2015) have argued that social complexity was the driving force for the ability to infer by exclusion.

Neophilia, as the predisposition to explore novel objects (Greenberg 2003), has been identified as an important factor accounting for biased test results especially in kea (O'Hara et al. 2012). Greenberg and Mettke-Hofmann (2001) have established a two-factor model that allows for predictions to be made based upon which ecological circumstances neophilia and exploration may be expected for different species. They conclude that a complex environment and low predation risk promote neophilic tendencies. Species inhabiting islands, such as the kea and Goffin cockatoos, seem more prone to investigate novel items, as on islands exploration may be very rewarding and at the same time not very costly (Greenberg and Mettke-Hofmann 2001). One way to overcome such tendencies in behavioural testing is to habituate individuals to novelty. Once individuals have sufficiently explored and habituated to a novel set-up they may exhibit cognitively more demanding abilities (Gajdon et al. 2013).

Kea have been shown to be exceptional problem solvers in the technical domain (Werdenich and Huber 2006; Huber and Gajdon 2006; Auersperg et al. 2009, 2011) and possess a large brain size compared to their body weight (brain weight/body weight = 0.015; see Iwaniuk et al. 2005), comparable to that of ravens (brain weight/body weight = 0.011; see Sol et al. 2010). Thus, corvids and parrots constitute prime candidates for advanced cognitive abilities among birds (Lefebvre et al. 2004; Iwaniuk et al. 2005; Roth and Dicke 2005). Therefore, we hypothesise that neophilia overruled the capacity to reason by exclusion rather than preclude such abilities in a previous study (Schloegl et al. 2009b).

Exclusion skills in non-human animals may have different origins. Several corvid researchers have proposed the emergence of exclusion skills in these birds as an adaption to their specialised feeding ecology (Schloegl et al. 2009b; Mikolasch et al. 2012), in support of the adaptive specialisation hypothesis (Krebs 1990; de Kort and Clayton 2006). Some primatologists, however, argued that in primates these skills have emerged as an adaptation to socially complex situations (Petit et al. 2015). Further, Pepperberg et al. (2013) have suggested that these skills are a fundamental cognitive ability and a marker of general intelligence.

If we accept relative brain size (defined as size of cortical or equivalent structures in relation to the overall brain size) as a reasonable indicator of cognitive abilities, and one marker of such to be the ability to reason based on exclusion, as suggested by Pepperberg et al. (2013), we would predict the kea to be capable of solving problems of this nature, if confounding behavioural predispositions

(e.g. neophilia) are controlled for. The alternative hypothesis that exclusion abilities constitute an adaption to a specialised feeding ecology of food-storing birds (Schloegl et al. 2009a, b; Schloegl 2011; Mikolasch et al. 2012) would predict this ability to be absent in the kea. Unless it has evolved independently (at least twice) in birds, under different evolutionary pressures, kea are not storing food and are only distantly related to corvids.

Studies on exclusion performance in animals have also discussed the effect of task difficulty on the ability to make inferences (Grether and Maslow 1937; Marsh et al. 2015). Therefore, in addition to the possible effects of neophilia we investigated the effect of cognitive load (Sweller 1988) on task performance. By modifying the original procedure (O'Hara et al. 2015a), we introduced a group that received the test trials in an alternative sequence, which should result in a decrease in test trial spacing, thus benefiting the working memory and could be considered computationally less demanding (Barrouillet et al. 2007).

Materials and methods

Ethical statement

The Animal Ethics and Experimentation Board of the Faculty of Life Sciences at the University of Vienna was informed and approved this study (Reference number: 2015-006).

Test subjects

Fourteen kea of different ages (one juvenile, 1 year of age; one sub-adult, 4 years of age; and twelve adults, mean age 9 ± 3 years) and sexes (nine males, five females) housed in a large group aviary (approx. 520 m^2) at the Haidlhof Research Station near Vienna, Austria, participated in this study (see Table 1). The group was fed three times per day with vegetables, fruits, protein and seeds, and water was available ad libitum. All individuals were familiar with the touch screen and had participated in prior touch screen tasks (O'Hara et al. 2015a).

Apparatus

We used an adapted version of the operant conditioning system described in detail by Steurer et al. (2012). The apparatus consisted of a touch-sensitive screen (304 mm × 228 mm display area, 381 mm diagonal, 1024 × 768 pixels), CPU and automatic rewarding system; rewards were delivered centrally, 90 mm below the lower edge of the screen. Individuals had easy access to the screen and reward tray by standing on a platform

Table 1 Overview of individuals participating in this study

Individual	Sex	Age group	Rearing	Experience	Group
Anu	♂	Adult	Hand	No	B
Coco	♀	Adult	Hand	No	B
Elvira	♀	Adult	Parent	No	A
Frowin	♂	Adult	Parent	Yes	B
John	♂	Adult	Parent	Yes	A
Kermit	♂	Adult	Hand	Yes	A
Lilly	♀	Adult	Hand	No	A
Linus	♂	Adult	Hand	Yes	B
Papu	♀	Juvenile	Hand	No	A
Paul	♂	Sub-adult	Parent	No	B
Pick	♂	Adult	Hand	Yes	B
Roku	♂	Adult	Parent	No	A
Sunny	♀	Adult	Hand	No	A
Willy	♀	Adult	Hand	No	B

Names of individuals participating in this experiment along with sex (♂ for males, ♀ for females) and respective age group; rearing indicates if individuals were hand raised or parent raised; experience denotes whether or not individuals had participated in the previous exclusion study by Schloegl et al. (2009a, b); group refers to experimental group which each individual was assigned to

(400 × 700 mm), which was installed directly below the reward tray. To avoid reflections of sunlight, wooden panels were attached above and behind this platform, nonetheless allowing the birds to retreat to the side at any time. The program used for testing was 'CognitionLab' (version 1.9; see Steurer et al. 2012, for a detailed description). An arbitrary collection of licence and restriction-free clip arts, downloaded from the Open Clip Art Library (http://www.openclipart.org/), was standardised to generate images on white background, measuring 70 by 70 pixels, adapted for equal overall brightness, and converted to Portable Network Graphic (png) files using Fiji (ImageJ 1.49e, http://imagej.nih.gov/ij; ImageJ 2.0.0-rc-9, http://developer.imagej.net/). Two stimuli were presented simultaneously within each trial, on the central horizontal axis of the screen, 341 and 682 pixels, respectively, away from the left side of the screen.

Procedure

The procedure followed the protocol of O'Hara et al. (2015a), with two exceptions: thirty test sessions were provided instead of 25, and testing was split into two groups, with one group exactly following the procedure of O'Hara et al. (2015a) and the second group only differing in the sequence of test trials. We give a short summary of the general procedure below and elaborate more on the differences between the groups.

Training

Each trial involved the simultaneous presentation of two stimuli, of which one was rewarded (S+) and one was unrewarded (S−). While touching the S+ led to the delivery of an eighth of a peanut seed, touching the S− led to a 2-s timeout during which the screen went blank. Each session consisted of 20 trials, 18 training (baseline) trials and two randomly intermixed 'novelty' trials. For each subject, we selected a different pair of images (S+ and S−) that would remain the same throughout all training trials. In the novelty trials, the negative training stimulus was replaced by a novel stimulus, being a different one in each novelty trial. The stimuli were chosen and assigned randomly to each individual from a pool of 190 possible icons. The novelty trials were intended to habituate the kea to novel stimuli and to reduce the neophilic tendencies to explore a novel stimulus. However, this procedure was not aimed at training inhibition towards novelty in general; therefore, training did not continue until the subjects would significantly choose the familiar stimulus over novel ones. For this reason, we continued training until individuals ceased to respond to both novel stimuli instead of choosing the S+ for two consecutive sessions (Criterion 1). To ensure that the birds had learned the basic discrimination, they were required to choose correctly in more than 80 % (15/18) of the training trials for two consecutive sessions (Criterion 2).

Testing

Once both criteria were met, 30 sessions of testing followed. Each session included four test trials intermixed within 16 training trials. In order to prevent a violation of expectancy in test trials, stimuli with positive contingency were rewarded (S+), whereas responses to stimuli with negative contingency (S−) were immediately aborted (no sound) and followed by the next training trial. Because this differential rewarding of test stimuli could lead to absolute stimulus learning, we used novel test stimuli for each test session.

Test trials were presented consistently in a sequential order. Test trial one consisted of a novel positive stimulus (S + 1), while the S− remained the same as in the training trials. In test trial two, the S− was replaced with a novel unrewarded stimulus (S − 1) and presented with the S+ of the training trials, while the test trial three offered a choice of the novel rewarded stimulus of the test trial one (S + 1) and a completely novel unrewarded stimulus (S − 2). In test trial four, the novel unrewarded stimulus of test trial two (S − 1) was presented with a completely novel rewarded stimulus (S + 2). To investigate an effect of cognitive load, the two groups A and B differed in the
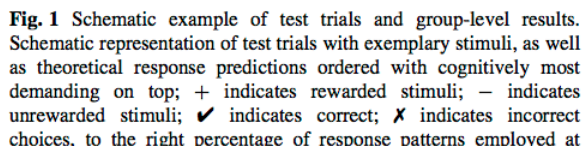
sequence in which test trials were presented. Group A received test trials one to four in an ordinal order resulting in a test trial sequence: 1–2–3–4. Group B was presented with test trial three before test trial two, resulting in a test trial sequence of: 1–3–2–4 (see Fig. 1 for a schematic outline of a test session and sequence for each group). This resulted in corresponding test trials (test trials one and three, respectively, two and four) to follow in consecutive instances rather than intermixed, thus decreasing temporal space between them along with the possibility to be addressed sequentially rather than in parallel. The exact position for each test trial within a session was determined pseudo-randomly (trials 4 or 5 for the first test; trials 8 or 9 for the second test trial; trials 12 or 13 for the third test trial; trials 16 or 17 for the fourth test trial), to ensure that at least three training trials would be presented before the first test trial and before the end of a session, as well as to provide at least two training trials between each of the test trials.

Data analysis

'Response strategies' were defined by attributing each possible response pattern the most parsimonious strategy (O'Hara et al. 2015a):

An instance of 'inference by exclusion' was only considered, if correct stimuli were chosen in all four test trials within a test session (see Fig. 1 for a graphic representation). These instances required individuals to either infer the contingency of the novel stimulus in the first test trial or simply avoid the S−. Further, in test trial three for group A (test trial two for group B) they had to avoid the novel stimulus (S − 2) and remain choosing the formerly rewarded S + 1. This is in principle the approach applied by Aust et al. (2008), controlling for correct responses in test trial one due to novelty preferences and simple avoidance of S−. However, individuals may have formed an association with the S + 1 as a result of being rewarded, which would qualify as one trial learning. Test trial two for group A (test trial three for group B) and test trial four are designed to control for such one trial learning. Here, the individuals should refrain from a novel unrewarded stimulus (S − 1) in test trial two for group A (test trial three for group B) and choose the known rewarded stimulus. This may be based on an avoidance of novelty, or simply a strong positive association with S+. However, in this case they have no direct information concerning the S − 1. Therefore, choosing the S + 2 in test trial four necessitates individuals to avoid S − 1 based on an inference, hence demonstrating the essence of inference by exclusion.

We assumed 'one trial learning' when individuals chose the unrewarded stimulus solely in the fourth test trial, as this indicates subjects fail to infer the contingency without direct feedback. We also considered it 'one trial learning'

Fig. 1 Schematic example of test trials and group-level results. Schematic representation of test trials with exemplary stimuli, as well as theoretical response predictions ordered with cognitively most demanding on top; + indicates rewarded stimuli; − indicates unrewarded stimuli; ✔ indicates correct; ✗ indicates incorrect choices, to the right percentage of response patterns employed at group level; *bold lines* indicate median values; *boxes* are spanning from the first to third quartiles; *whiskers* represent 95 % confidence intervals; outliers are not included; the *dotted line* and *grey area* indicate chance levels, while the *solid line* indicates significance as calculated by two-tailed binomial test

when the rewarded stimulus (S + 2) was chosen in the fourth test trial, after an initial response towards the novel stimulus (S − 1) in the second test trial.

A further possible strategy may have been guided by individuals transferring an acquired rule from the training that novel stimuli are always unrewarded. Therefore, they might avoid the novel S + 1 in the first test trial. However, if the subjects updated this rule and responded correctly in the following test trials or even reversed this rule, hence choosing the S − 1 instead of the original S+ in the second trial, we labelled this strategy 'novelty rule abolishment/reversal'.

'Novelty aversion' was considered as choosing the stimulus which was more familiar to the kea, therefore responding correctly in the first and fourth test trials, but incorrectly in the second and third. 'Novelty preferences' were assumed if birds exhibited a reversed response pattern in test trials, by responding correctly in the second and

third test trials, but incorrectly in the first and fourth test trials.

Multiple patterns that exhibited consistently avoiding rewarded stimuli or repeatedly choosing certain unrewarded stimuli—or combinations of such behaviours—were attributed to specific stimulus preferences or avoidances.

Finally, incorrect choices in all four test trials eluded any logical explanation on our part, which is why we inferred it must have been a 'bad day' for the individual.

We employed two-tailed binomial testing with a cumulative hypothesised probability (0.5 in test trial one × 0.5 in test trial two × 0.5 in test trial three × 0.5 in test trial four) of success of $p = 0.0625$. Generalised linear mixed effects models (GLMMs) with binomial error distribution and individual as a random factor were applied to investigate the effect of group, sex and session (in order to test whether certain strategies were acquired throughout the

task) on the occurrence of response patterns exhibited above chance on a group level. As our sample size for young individuals is very low, we did not include age as a factor in the analysis. Statistical analyses were conducted in the R statistical package (R Development Core Team 2008), and for fitting models 'lme4' (Bates et al. 2014) was used. Tests were two-tailed, and alpha was set to 0.05.

Results

Seven individuals learned the discrimination of the baseline stimuli (Criterion 1: $M = 3.7$ sessions, ± 0.43 SE) before ceasing to respond to the novel stimuli (Criterion 2: $M = 6.1$ sessions, ± 0.70 SE, see Fig. 2). Five individuals reached both criteria simultaneously ($M = 7.4$ sessions, ± 2.99 SE), and two kea quit responding to novel stimuli ($M = 2$ sessions, ± 0.0 SE) before reaching the learning criteria ($M = 3$ sessions, ± 0.0 SE), yielding a result bordering significance (Wilcoxon signed-rank test: $p = 0.053$, $r = -0.365$) for learning the discrimination faster ($M = 4.9$ sessions, ± 1.14 SE) than refraining from exploring novel stimuli ($M = 6$ sessions, ± 1.15 SE).

On an individual level, we found eight individuals exhibiting responses suggestive of reasoning by exclusion significantly more often than expected by chance. Figure 3 displays the relative frequency with which each pattern was employed for each individual and values within the bars indicate the probability of this frequency occurring by chance. However, patterns of reasoning by exclusion did not occur as the sole strategy in seven of these eight individuals, as also up to three other strategies occurred above chance levels. Other strategies employed by most animals were one trial learning, avoiding the unrewarded

baseline stimulus and stimulus preferences. Only one individual (John) seemed to rely solely on reasoning by exclusion. Individuals that did not exhibit reasoning by exclusion patterns above chance levels chose by avoiding novel stimuli, one trial learning and avoiding the S− in addition to stimulus preferences.

On a group level, the GLMM confirmed a significant intercept for occurrences of inferences based on exclusion (GLMM: $b = -1.686$, SE $= 0.12$, $X^2(1) = 73.89$, $p < 0.001$), but excluded any effects of group ($X^2(1) = 0.55$, $p = 0.46$), sex ($X^2(1) = 0.46$, $p = 0.497$) or session ($X^2(29) = 31.08$, $p = 0.36$). Similarly, one of the response patterns constituting one trial learning (GLMM: $b = -1.925$, SE $= 0.13$, $X^2(1) = 34.87$, $p < 0.001$), one pattern suggesting S− avoidance (GLMM: $b = -1.988$, SE $= 0.16$, $X^2(1) = 19.79$, $p < 0.001$) and preferences for S − 1 (GLMM: $b = -1.783$, SE $= 0.12$, $X^2(1) = 55.49$, $p < 0.001$) occurred more often than predicted by chance on a group level (see Fig. 1). However, none of the above-mentioned factors had a significant effect on either of these strategies. When grouping only individuals that successfully responded according to inferring by exclusion and testing for frequencies of patterns, we found that patterns for 'inference by exclusion' ($M = 6.33$, ± 0.57 SE) occurred significantly more often than patterns representing 'one trial learning 1' ($M = 4.00$, ± 0.26 SE; Wilcoxon signed-rank test: $p = 0.034$, $r = -0.53$).

Discussion

More than half of the subjects exhibited the ability to base their choices on inference by exclusion. They achieved this not only by considering direct feedback about a stimulus
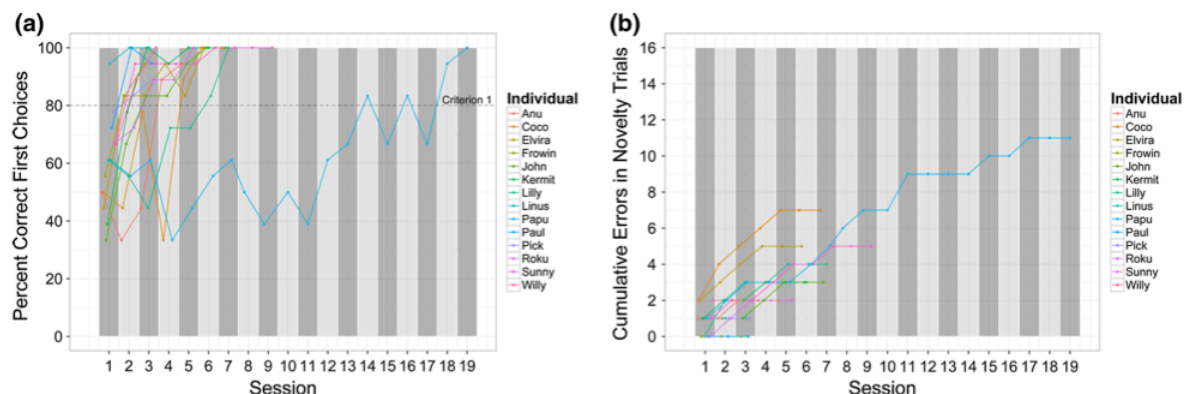

Fig. 2 Performance in the training phase. **a** Learning curves for all individuals over the sessions, with the *dotted line* indicating the learning criterion of 80 % correct first choices (Criterion 1); longer the *lines* indicate more sessions required to reach criterion; **b** cumulative errors of novelty trials; a *steep inclination of lines* represents novelty responses in both novelty trials moderate inclination response to one novel stimulus per session and a *straight horizontal line* indicating no responses towards novel the stimuli (Criterion 2)
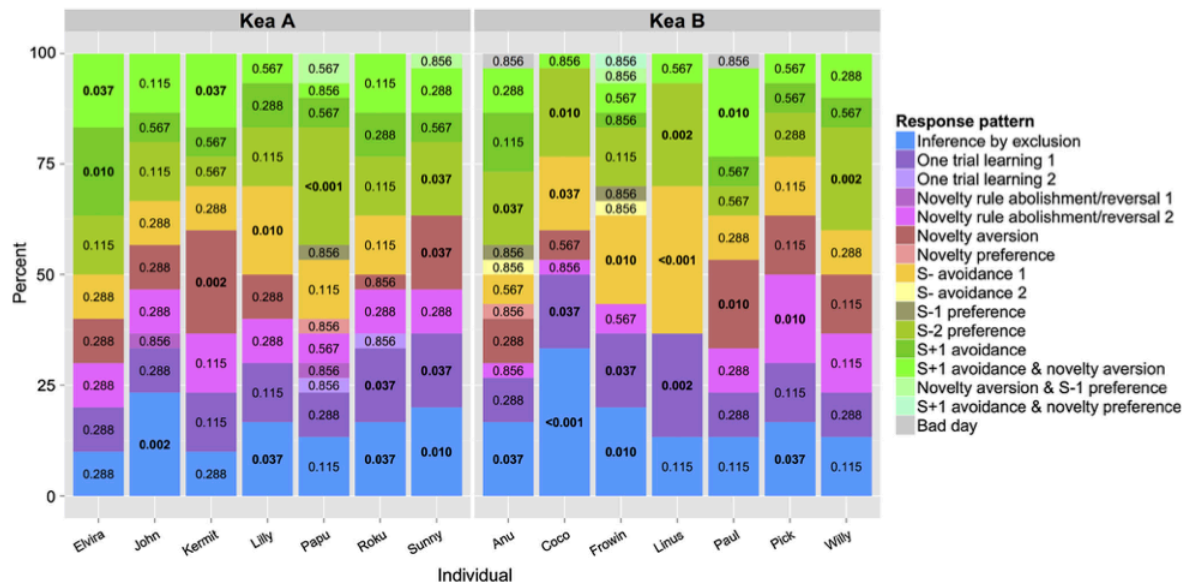
Fig. 3 Distribution of strategies employed. Categorical strategies relied on by individuals of each group in the test; values enclosed in the *bar graphs* correspond to the adjusted probability of the amount of sessions with certain response patterns to occur by chance; significant values are printed in *bold*

(from test trials one and three), but also by reasoning about the category of a stimulus based solely on the context in which it was presented and without any direct feedback (as in test trials two and four). This requires the individual to make an inference about the $S - 1$ in the absence of direct information about this stimulus. It is this lack of direct information that qualifies correct responses in the fourth task as exclusion based on an inference. One might argue that this pattern resulted from a combination of 'one trial learning 1' and random choice in the final test trial. However, considering that within individuals exhibiting significant exclusion performance, patterns for 'inference by exclusion' occurred significantly more often than the patterns for 'one trial learning 1', rendering this explanation unlikely. The fact that the number of sessions had no influence on the occurrence of this response pattern leads us to conclude that this strategy was not learned throughout the task (see Fig. 4). Thus, eight out of fourteen kea were able to spontaneously solve this abstract categorisation task by inferring the contingency of a novel stimulus through logical exclusion of the alternative.

It is interesting to note that the sequence in which the test trials were presented did not affect the performance of the individuals. Individuals of group A were required to store information about the $S + 1$ for longer and simultaneously pay attention to a novel stimulus with negative contingency $(S - 1)$ in order to respond correctly in all test trials. Subjects of group B could apply the information about these stimuli in a more direct sequential manner,

possibly implying a reduction in the cognitive load (Sweller 1988). Nevertheless, both groups performed equally well with respect to their exclusion skills. Therefore, it seems that an increase in cognitive load, in terms of working memory and parallel information storing, does not influence exclusion skills, at least not in this test design. An alternative explanation, as one reviewer pointed out, might be that the relatively subtle difference in procedure simply did sufficiently increase the cognitive load, and therefore, no effect was detectable. In this respect, future studies may address the effect of cognitive load more thoroughly by increasing the number of training trials between test trials to increase difficulty, or presenting corresponding test trials in direct succession, to decrease the load on the working memory.

However, the kea did not solely rely on inference skills in this task. On an individual level, we could show that novelty aversion, along with one trial learning, stimulus preferences and simply avoiding the S− also guided some individuals' choices. Avoiding the S−, by forming a negative association with the unrewarded stimulus, may represent an efficient, low-cost strategy. Ecologically it seems adaptive to decrease responses towards a stimulus that does not provide any benefits (such as nutrition or information) or might even be harmful. Several studies on exclusion performance have discussed this alternative as a potential confound (e.g. Aust et al. 2008; Shaw et al. 2013; Nawroth et al. 2014), but conclusive controls remain rare (Call 2006; O'Hara et al. 2015a).

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Fig. 4 Individual distribution of response patterns over sessions. *Each square* represents colour-coded response patterns expressed by individuals of each group for each of the thirty test sessions; individuals are ordered within their respective experimental group

Novelty aversion somewhat contradicts the kea's natural predisposition to explore novel objects (Diamond and Bond 1999; Kubat 1992). One explanation for this result may be that three individuals (Kermit, Paul and Sunny) established a rule to avoid novel stimuli during the training phase, as these were never rewarded during the discrimination training. One might argue that this rule could contribute to the performance with respect to the inference by exclusion patterns; however, only one individual (Sunny) simultaneously showed significantly more occurrences of novelty avoidance and inference by exclusion than would be predicted by chance.

One trial learning can be considered a cognitively demanding strategy as it requires individuals to flexibly respond to novel stimuli based on one single feedback event. In particular, considering that responses to novel stimuli were (to some degree) extinguished during training highlights this flexibility applied in test trials.

Stimulus preferences and avoidances seem to occur in most tested subjects and pose a further low-cost strategy. Such preferences may arise simply through shared features with known stimuli, which are utilised by the individuals to attribute a positive or negative valence to a test stimulus. Overall, the large variance in strategies employed by different individuals in this task is indicative that cognitively less demanding mechanisms may override more 'costly' ones, whenever the opportunity is provided. What exactly the features are that provide these opportunities and when a certain threshold for such more simplistic classifications is

passed remain subject to further research. Interestingly, however, none of the tested individuals seemed to have chosen purely randomly in the test trials, as would have been indicated by no preference for any particular response strategy.

As mentioned earlier, restriction in sample size of young subjects precluded an analysis of the effects of age on inference by exclusion. However, we would like to point out that both, juvenile and sub-adult, individuals (Papu and Paul) seem to have chosen based on perceptual cues, rather than employing inferences or one trial learning. In primates, it has been shown that exclusion abilities increase with age (Call 2006) suggesting that this ability may be subject to cognitive development. Although the small sample size of young individuals renders any conclusion from the current experiment highly speculative, this might open an interesting avenue for further studies, investigating if exclusion abilities in birds are developed with age as it appears to be the case in primates (Call 2006).

The holistic approach, allowing and considering multiple possible behavioural strategies underlying choice in the test trials, was essential to evaluate the effect of training to avoid novel stimuli in this study. Thus, we could show novelty aversion was not a strategy generally adopted, although some individuals did seem to have established this rule. Furthermore, the comparison of different strategies highlights the relative prevalence of inference by exclusion, as this appears to be the strategy that most often reached significance levels.

Taken together, the results indicate that kea are capable of inferring by exclusion, which contradicts earlier findings of Schloegl et al. (2009b). As has been hypothesised for other species (Mikolasch et al. 2012; Shaw et al. 2013), we assume that simpler cognitive mechanisms or predispositions (such as neophilia or stimulus enhancement) have masked previous attempts to reveal evidence for exclusion skills. In this respect, we would also expect the ravens, which showed reliable exclusion performance in the study by Schloegl et al. (2009b), to be guided by a range of different response strategies in this approach, similar to the kea. The fact that larger relative brain sizes are found in food-storing species has led some researchers to suggest that specialised feeding ecology is a driving force for brain evolution (Krebs 1990). However, by reversing the causality one might also assume that the evolution of large brains in relation to body size has allowed for cognitive abilities to emerge, which in turn provided some species with the cognitive framework to promote food-storing behaviour. There is growing evidence from psittacines and corvids, all with large relative brain sizes but differing in feeding ecology, to exhibit such inference by exclusion skills in different set-ups, such as African grey parrots (*Psittacus erithacus*, Mikolasch et al. 2011; Schloegl et al. 2012; Pepperberg et al. 2013), Clark's nutcrackers (*Nucifraga columbiana*, Tornick and Gibson 2013), Goffin cockatoos (O'Hara et al. 2015a), New Caledonian crows (*Corvus moneduloides*, Jelbert et al. 2015) and ravens (Schloegl et al. 2009b). However, only inconclusive data are available for other members of these families, e.g. carrion crows (*Corvus corone corone*, Mikolasch et al. 2012), Eurasian jays (*Garrulus glandarius*, Shaw et al. 2013) and jackdaws (*Corvus monedula*, Schloegl 2011), and no inference by exclusion skills could be observed so far in the greater anis (*Crotophaga major*), itself not a member of either psittacines or corvids, in respect to the rejection of parasitic eggs (Riehl et al. 2015). This yields the consideration of reasoning by exclusion being a more fundamental cognitive trait, possibly coinciding with the evolution of large brains (Pepperberg et al. 2013). The hypothesis that it is a convergent adaption to feeding ecology (Schloegl et al. 2009a, b; Schloegl 2011; Mikolasch et al. 2012) has only recently been challenged by Shaw et al. (2013). Another compelling factor that might have contributed to a species' capacity to infer by exclusion is the complexity of its social structure (Petit et al. 2015).

Here, we suggest a more holistic approach by considering multiple factors, such as social structure, migratory patterns, habitat complexity as well as specialised foraging strategies, as promoters of the evolution of advanced cognitive abilities (Tornick and Gibson 2013) in correlation with the evolution of larger brains (e.g. Harvey et al. 1980; Dunbar 1998; Reader and Laland 2002; Lefebvre et al. 2004; Connor 2007; Sol et al. 2010). In this sense, a mechanism would be adaptive that is capable of dealing with problems that require the same computation, but can be applied in different contexts. Hence, challenges in the physical and social domain may have selected for greater neuronal correlates that allowed establishing advanced cognitive capacities when confronted with similar problems in multiple domains.

The evidence of inference by exclusion in small-brained birds is far from compelling. There is some evidence for this ability in domestic chickens (*Gallus domesticus*, Hogue et al. 1996), graylag geese (*Anser anser*, Weiß et al. 2010), as well as pigeons (*Columba livia*, Wynne 1997). Pigeons could be 'encouraged' to select novel stimuli over defined ones, hence choosing by exclusion (Clement and Zentall 2003). However, this study could not show, given the applied set-up, whether pigeons would also be able to learn from this experience to infer unknown stimulus contingencies based on exclusion. The pigeon's sensitivity to the testing protocol was demonstrated in a study by Aust et al. (2008) that applied the same (touch screen) procedure to several species comparatively. While some dogs and nearly all human participants showed evidence for learning by exclusion, all pigeon subjects failed.

The need for standardised testing protocols involving rigorous controls for alternative strategies has also been demonstrated in mammals. Dwarf goats (*Capra aegagrus hircus*) but not sheep (*Ovis orientalis aries*) performed above chance levels (Nawroth et al. (2014). However, the researchers could not exclude that individuals had acquired the simple strategy of avoiding the empty cup. The method of testing multiple concurrent strategies as presented here has already been successfully employed with Goffin cockatoos (*Cacatua goffini*) showing surprisingly similar response strategies (O'Hara et al. 2015a). We therefore suggest that the abstract categorisation task, a modified training procedure to discourage explorative behaviour before the test, and the specific sequence of tailored tests provide a suitable paradigm for inter-species comparisons of inference by exclusion abilities and competing response strategies. In general, we suggest shifting the focus from binary-outcome-driven tasks towards investigating category decisions and choice behaviour in a more holistic manner.

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Discussion |

With this thesis I have aimed to establish a paradigm that would test for exclusion skills, incorporating different modes of decision making, and which may be suitable for many different species. In the first chapter I have highlighted the relation between neotic style, whether an individual is drawn to or refraining from novel stimuli, and explorative behaviour. Explorative behaviour may bias responses in critical test trials in which new configuration of a task setup or novel stimuli are provided in order to investigate generalisation, concept formation or other cognitive abilities (e.g., Aust, Range, Steurer, & Huber, 2008; O'Hara, Gajdon, & Huber, 2012; Zentall, 2001). It is therefore crucial to be aware of such effects and, whenever possible, to control for responses based on 'curiosity' rather than the focal mechanism under investigation.

Based on this notion, I have developed a task that allows to exhaust exploratory tendencies before providing individuals with critical test trials. Furthermore, traditional methods in comparative cognitive research have focused on investigating one particular ability, by applying additional control conditions to exclude alternative explanations for a given behaviour (e.g., Call, 2006; Seed, Call, Emery, & Clayton, 2009). However, these alternative, usually considered as lower level, mechanisms might constitute a large portion of cognition (Gigerenzer & Goldstein, 1996; Todd & Gigerenzer, 2000; Todd & Gigerenzer, 2007). A recent trend in comparative cognition research proposes to refrain from investigating the potential for sophisticated capacities in different species and shift towards an approach considering the naturally employed processes underlying behaviour (e.g., Huber, 2009; Mettke-Hofmann, 2014; Taylor, 2014; Todd & Gigerenzer, 2007). Previous studies investigating exclusion skills have provided mixed results as an effect of different testing paradigms and insufficient controls (e.g., Nawroth, von Borell, & Langbein, 2014; Schloegl, Dierks, et al., 2009;

Shaw, Plotnik, & Clayton, 2013). The here presented approach therefore attempts to incorporate the emphasis on a holistic way of assessing decision making by simultaneously allowing multiple 'strategies' to guide choices and aims at enabling a direct comparison between various species under similar experimental conditions.

Similarities Between Species

When comparing the results of both species, Goffin's cockatoos and kea, on a group level some intriguing similarities in the general response patterns arise. Several individuals of both species have exhibited choices based on inference by exclusion more often than predicted by chance. However, also other patterns have emerged with a large relative frequency in both species.

Firstly, patterns suggesting one-trial learning occurred in several instances which highlights their capacity to assess stimulus contingencies rapidly within one trial and act accordingly in following trials (Rock, 1957). Secondly, another heuristic employed by both species was to avoid the known unrewarded stimulus. This is a simple and effective measure to avoid an undesirable outcome but has often been discussed as a confound in previous studies investigating inferential reasoning by exclusion (e.g., Aust et al., 2008; Call, 2006; Marsh, Vining, Levendoski, & Judge, 2015; Nawroth, von Borell, & Langbein, 2014).

Finally, some incidents could be observed where stimulus preferences might influence the decision process. This is to be expected, especially in cases where test stimuli resemble the features of (known) training stimuli. Nevertheless, one case deserves special attention as it has been exhibited in both species more frequently than expected by chance. The pattern in question is what was initially referred to as S-2 preference. In these cases, individuals would only respond to the unrewarded icon, therefore opposing to the logical contingency, in test trials where the rewarded stimulus (S+1) of test trial 1 was presented with a novel unrewarded stimulus (S-2). If responses in these instances indeed represent stimulus preferences, this pattern should not have been elicited at such high frequencies as it is highly unlikely that so many S-2 stimuli would correspond to the known S+ by chance. An alternative explanation, proposed by Theresa Rößler who was testing this approach in hooded crows (Rößler, 2016), might be that subjects choose novelty except when presented with the known rewarded stimulus. One might argue against this hypothesis considering the rare occurrences of

patterns representative of 'pure' novelty responses and the habituation to novel stimuli during the training. However, during novelty trials in the training the original S+ was present and thus further associated with a reward. Therefore, individuals might have indeed followed a 'conditional novelty rule', namely choosing novelty only in the absence of the S+.

The inherent advantage of the design derives from the fact that the occurrence of any strategy does not necessarily exclude another. The focus of this approach is rather the degree to which a specific mechanism is relied on. This notion, together with the suggestion that neophilia has most likely overshadowed exclusion performance in the kea earlier (Schloegl, Dierks, et al., 2009), might be a first indication that inference by exclusion represents a 'not so simple' heuristic, which may be applied when other cues are insufficient to elicit less demanding decision-making mechanisms, such as preferences for a previously rewarded colour or shape.

Further Avenues

This thesis presents a novel paradigm that allows a truly comparative approach towards investigating choice behaviour in various species. I have pointed out how simpler mechanisms and predispositions might affect, or even overshadow, more advanced cognitive abilities in behavioural testing and what may cause these heuristics to be employed. Nevertheless, it is clear that further work is required to achieve a better understanding of what guides these decisions and how cognitive abilities that are considered 'demanding' could have evolved. To resolve these open questions I propose to follow a Tinbergian approach (Tinbergen, 1963), focusing on both proximate and ultimate mechanisms.

A first proximate question is if more parsimonious mechanisms, such as stimulus preferences (e.g., Klopfer, 1967) or generalisations (e.g. Pearce, 1987), really are employed whenever there is overlap in certain stimulus features (e.g. shape/colour)? To answer this question, further detailed analyses of the stimulus features as a function of the involved response pattern are required. The prediction would be that whenever stimulus properties overlap with the known stimuli, preferences, or respectively avoidances, should be exhibited. In instances where such points of reference are absent I would expect other mechanisms to be employed. This 'anatomy of choice' may reveal important

insights into the features individuals attend to and whether this is a general, species specific or individually based phenomenon.

The second of Tinbergen's (1963) proximate questions concerns the ontogeny of a behaviour. Following this approach, another valuable contribution to a more complete understanding of inferential capacities will be presented by the investigation of this ability at different developmental stages. A thorough examination of response patterns exhibited by juvenile, sub-adult and adult individuals would allow to discern the degree to which these skills are innate or acquired with experience. Piaget (1952) has provided a framework for cognitive development in children and Pepperberg and colleagues (1997) have shown similar patterns in African Grey parrots. Thus, I would predict the ability to exclude alternatives to occur gradually with experience, whereas the simpler decision-making mechanisms to be of importance in earlier stages. Alternatively, a recent study has shown the ability to imprint ducklings based on relational concepts (Martinho & Kacelnik, 2016), which opens the possibility that these capacities are already ingrained in early life stages and thus, not only reserved for cognitively highly developed species.

To address the ultimate question, concerning the evolution and function (adaptive value) of inference skills, it will be crucial to confront a number of different species with this task in a comparative manner. As a first step, we have chosen two large-brained species of *Psittaciformes*, where some positive indications for exclusion skills could be expected based on their previously exhibited cognitive capacities, such as object permanence, causal and functional inferences, tool use and other sophisticated forms of problem solving (e.g., Auersperg, Huber, & Gajdon, 2011; Auersperg, Kacelnik, & von Bayern, 2013; Auersperg, Szabo, von Bayern, & Bugnyar, 2014; Auersperg, Szabo, von Bayern, & Kacelnik, 2012; Auersperg, von Bayern, Gajdon, Huber, & Kacelnik, 2011; Huber & Gajdon, 2006). The positive findings in both of these species challenge the hypothesis of exclusion capacities necessarily being a faculty of food storing species (Mikolasch, Kotrschal, & Schloegl, 2012; Schloegl, Dierks, et al., 2009; Tornick & Gibson, 2013). While food storing might have promoted the evolution of such inferential skills in corvids, although even this notion has been debated recently (see Shaw, Plotnik, & Clayton, 2013 for a summary), it is highly unlikely to be a driving factor for parrots which do not store food. The next step would be to apply

this paradigm in smaller-brained species, such as pigeons. Pigeons were able to learn to choose by exclusion in a previous study (Clement & Zentall, 2003), from which one might conclude this ability to be within their capacities. However, evidence that inferences based on exclusion can be exhibited spontaneously in this species, rather than occurring as an effect of training, remains inconclusive (Aust et al., 2008; Schloegl, Bugnyar, & Aust, 2009).

One of the advantages of the approach used in this PhD project is its comparative potential. It is not restricted to avian species and for a comprehensive mapping of decision mechanisms it should be applied in a comparative manner across many animal taxa. First attempts to test dogs with this method have provided promising preliminary results (Schwarzl, O'Hara, Huber, & Wallis, 2016). Only a large scale species comparison, employing the same approach, will allow us to identify the factors responsible for a potential convergent evolution of inferential abilities and will inform which mechanisms are employed in its stead, in species where this ability has not evolved.

The Touchscreen as a Useful Tool

One key aspect of the presented approach, which was so far not emphasised, is the use of the touchscreen. The use of touchscreen technology may pose certain limitations, such as excluded haptic information about the stimuli available to the subjects, diminished stimulus qualities and generally subjects possessing less experience with two dimensional items (O'Hara, Huber, & Gajdon, 2015). However, when assessing abstract reasoning capacities the benefits of employing touchscreen paradigms certainly outweigh the disadvantages. Firstly, while the artificial element of this approach has little ecological validity, it poses an equally 'novel' environment to any species tested (except juvenile/sub-adult humans). Such an abstract task allows species to exhibit inferential abilities, irrespective of which context it has evolved in. Therefore, this approach constitutes a less biased comparison between species, rather than employing a food seeking paradigm, which might favour species that have evolved exclusion skills in this context, but penalises other domains in which such skills would be advantageous (e.g., Riehl, Strong, & Edwards, 2015). Furthermore, the touchscreen has been shown to be operable by a number of species, differing greatly in morphology (e.g., Steurer, Aust, & Huber, 2012) which is of particular importance for comparing different taxa. From a practical

standpoint, the use of an automated rewarding procedure avoids an experimenter bias. Finally, computerised methods allow the presentation of a large number of stimuli, which is crucial for a task that attempts to maintain novelty of test stimuli in each session in order to circumvent associative learning over test trials. To sum up, presenting such a task on a touchscreen computer allows coherent testing of various species by providing similar conditions with great efficiency.

Concluding Remarks

The initial aim of this doctoral project was to investigate how advanced forms of reasoning evolved in the causal, social and abstract domain in different bird species. I have come to understand that answering these questions is probably beyond the scope of a single doctoral thesis. Nevertheless, in the course of this project I was able to illuminate how basic predispositions can influence, and sometimes even overshadow, more complex decision-making processes. With this knowledge I developed a task that overcomes and attempts to disentangles these influences, allowing comparisons despite the predispositions an individual might exhibit. The here presented approach complements and benefits comparative cognitive research by providing a holistic experimental design which does not only focus on the presence or absence of a certain ability.

Applying this method in two members of parrot species I could demonstrate their capacity of inferential reasoning by exclusion. This is a small, but important first step into investigating which factors promote the evolution of such advanced forms of cognition in a comparative manner. Additionally, recent studies provided many reports of different (avian) species, with diverse ecological background, exhibiting reasoning capabilities (Jelbert, Taylor, Cheke, Clayton, & Gray, 2014; Jelbert et al., 2015; Martinho & Kacelnik, 2016; Obozova, Smirnova, Zorina, & Wasserman, 2015; Smirnova, Zorina, Obozova, & Wasserman, 2014), which further opens the gates for assumptions about what might contribute to the emergence of such abilities. Inferential abilities may indeed pose fundamental processes that are employed in different contexts (Irene M Pepperberg, Koepke, Livingston, Girard, & Hartsfield, 2013). This might indicate that they are adaptive in instances where animals are faced with challenges in different domains, but require similar mental processes. However, the answer to the question about how inferential abilities develop on an

ontogenetic and evolutionary scale still remains inconclusive and an interesting subject for further research.

Finally, I hope the herein presented methodology will continue to find resonance within the scientific community and will facilitate insights into the underpinnings of what constitutes forms of abstract reasoning, such as basing inferences on the logical exclusion of alternatives. Furthermore, following the Tinbergian approach will help to unravel the development, function and ultimately the evolution of reasoning skills.

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List of Publications

Published

O'Hara M, Gajdon GK, Huber L. (2012). Kea Logics- How These Birds Solve Difficult Problems and Outsmart Researchers. In: Watanabe S. (Ed.) *Logic and Sensibility.* Keio University Press.

O'Hara M, Huber L, Gajdon GK (2015). The advantage of objects over images in discrimination- and reversal learning by Kea (Nestor notabilis). Animal Behaviour. 101,51-60

O'Hara M, Auersperg AMI, Bugnyar T, Huber L. (2015) Inference by Exclusion in Goffin Cockatoos (*Cacatua goffini*). PLoS ONE. 10(8): e0134894.

O'Hara M, Schwing R, Federspiel I, Gajdon GK, Huber L. (2016). Reasoning by exclusion in the kea (*Nestor notabilis*). Animal Cognition. 19:5, 965-975.

Submitted

Huber L, O'Hara M. (in press). The Extractive Foraging Hypothesis (Parker & Gibson, 1977, 1979; Parker 2015). Brief entry in: Shackelford and Weekes-Shackelford (eds.) *Encyclopedia of Evolutionary Psychological Science*. Springer.

O'Hara M, Mioduszewska B, von Bayern A, Auersperg A, Bugnyar T, Wilkinson A, Huber L, Gajdon GK. (submitted). Does exploration depend on neotic style?

Griffin A, Federspiel I, Garland A, O'Hara M, Bugnyar T, Güntürkün O, & Healy S. (submitted). In transit or settled? A behavioural analysis of rural birds in an invasive avian urban exploiter.

In Preparation

Mioduszewska M & O'Hara M, Prawiradilaga D, Auersperg A, Huber L. (submitted). First insights into the ecology of wild Goffin's Cockatoo in the late dry season.

Auersperg A, Köck C, Plederman A, O'Hara M, Huber L. (in prep.). Safekeeping of Tools in Goffin's Cockatoos (*Cacatua goffiniana*).

Gajdon GK, Eigster M, Schwing R, O'Hara M. (in prep.). Improved awareness about spatial configuration in stick-tool using kea parrots.

Köck C, Schlumpp M, O'Hara M, Gajdon GK, Huber L. (in prep.). Size discrimination in kea.

Curriculum vitae

Mark Christopher Andrew O'Hara

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Born:
24th of November 1982 in Vienna, Austria
Nationality:
Austria

Education

04/2011 – 11/2016
> **PhD within the DK-Program: Cognition and Communication**
> PhD thesis: "Inferential reasoning in birds", with main focus on cognitive advanced reasoning abilities in corvids (Crows, Raven, Jackdaws & New Caledonian Crows) and parrots (African gray, Eclectus, Kea, Goffin Cockatoos & Vasa)
>> Academic skills acquired:
>> - Animal health supervision
>> - Study design
>> - Grant applications
>> - Scientific writing
>> - Statistic in R

10/2002 – 04/2011
> **Mag. rer. nat in Zoology at the University of Vienna**
> Master thesis: "Reversal learning in the Kea (Nestor notabilis): Comparing the touchscreen to a reality-approach"
>> - Study focus: Cognitive biology
>> - Additionally: Human ethology

02/1993 – 02/2001
> **Bundes Gymnasium & Bundes Real Gymnasium Wels,**
> **Realgymnasium mit naturwissenschaftlichem Schwerpunkt**
>> - High school with focus on natural sciences

Employment

06/2016 - 11/2016
> **University of Veterinary Medicine, Vienna,**
> **Messerli Research Institute/ Goffin Lab;**
> **Technical Assistant**
>> - Aviary construction and maintainance
>> - Construction of testing apparatuses

04/2011 - 05/2015
University of Vienna,
Department of Cognitive Biology;
Scientific Project Assistant

06/2010 - 11/2010
University of Vienna,
Department of Cognitive Biology;
Technical Assistant
- Construction work for the Haidlhof research station
- Construction work of metal aviary elements

10/2009 - 06/2010
University of Vienna,
Department of Cognitive Biology;
Scientific Assistants
- Assistant project management
- Data collection
- Animal care

10/2001 - 09/2002
Austrian Red Cross,
Upper Austria;
- Ambulance driver
- Paramedic

Skills

Languages:
German: native speaker
English: fluent
Spanish: basic

Scientific skills:
Observational protocols
Touchscreen/skinner box procedures
Programming for CogLab light$^{©}$
Field Experience: Research Project in French Guyana

IT-Skills:
excellent skills in MS Excel, MS PowerPoint and MS Word
SPSS and R

Driver license:
A, B, certified ambulance driver

Teaching

2013   Supervision of Master student:
Corinna Koeck ("Size discrimination in the Kea")

2014   Supervision of Master student:
Theresa Rössler ("Inference by exclusion in Crows and humans")

2014   Supervision of Master student:
Romana Gruber ("Matching and Non-Matching to Sample in Goffin Cockatoos")

Conference contributions/Presentations

August 2011	ASAB Summer meeting 2011, St. Andrews, UK, 18. - 19.08.2011. Poster: "Reversal Learning in the Kea (Nestor notabilis)"
May 2012	CompCog CRP Workshop 16. - 18.05. 2012 Vienna, Talk: "Aquisitional Neophilia, Retentional Blinders?"
April 2013	ASAB Easter Conference, Lincoln, UK, 03. – 05.04.2013 Talk: "Acquisitional Neophilia in the Kea"
July 2013	3RD TOK CONFERENCE OF COMPCOG Vienna, Austria, 03. - 05.07.2013 Talk: "Acquisitional Neophilia in Birds?"
August 2013	Comparative Cognition workshop, Edinburgh UK, 03.08.2013. Talk: "Screening neophobia and exploration in birds"
August 2013	IEC 2013 Newcastle UK, 04. - 08.08.2013. Poster: "Acquisitional Neophilia, Retentional Exploration"
December 2013	BeCog Conference - 1st int. Student Conference, Göttingen, Germany, 02. - 03.12.2013. Talk: "Exploration and Neophobia screened in birds"
August 2015	Behaviour 2015, Cairns, Australia 09.-14.08.2015 Talk: "Exclusion, what else? - Testing for inference skills using an abstract touch-screen approach"
December 2015	Talk at the Research Centre for Biology, LIPI, Bogor, Indonesia 4.12.2015: "Expedition Tanimbar: Investigating dietary composition of endemic free ranging Goffin cockatoos (*Cacatua Goffiniana*)"

Research Visits

Sep. - Dec. 2012	University of Lincoln, Faculty of Life Science, Dr. Anna Wilkinson, Lincoln, UK, parrot sanctuary; Data collection
Feb. 2013	CNRS Field Station, Nouragues, French Guyana, Camp Parare, Dr. Max Ringler & Prof. Walter Hödl; Data collection
Jan.- Mar. 2013	University of Oxford, Behavioral Ecology Research Group, Dr. Auguste von Bayern, Leutstetten, Germany; Data collection
Aug. - Nov. 2013	University of Oxford, Behavioral Ecology Research Group, Dr. Auguste von Bayern, Leutstetten, Germany; Data collection
Nov. 2014	Max Planck Institute for Ornithology, Comparative Cognition Research Group, Dr. Auguste von Bayern, Loro Parque, Puerto de la Cruz, Teneriffe, Spain; Lab visit
Feb. 2015	Max Planck Institute for Ornithology, Comparative Cognition Research Group, Dr. Auguste von Bayern, Loro Parque, Puerto de la Cruz, Teneriffe, Spain; establishment of research methodology & student supervision
Sept. – Dec. 2015	Indonesian Institute of Sciences, Research Center for Biology, Dr. Dewi M. Prawiradilaga, Bogor, Indonesia; Field expedition to Tanimbar, Indonseia "Dietary Composition of endemic Goffin cockatoos (*Cacatua goffiniana*)"

Publications

O'Hara M, Gajdon GK, Huber L. (2012). Kea Logics- How These Birds Solve Difficult Problems and Outsmart Researchers. In: Watanabe S. (Ed.) *Logic and Sensibility.* Keio University Press.

O'Hara M, Huber L, Gajdon GK (2015). The advantage of objects over images in discrimination- and reversal learning by Kea (Nestor notabilis). Animal Behaviour. 101,51-60

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O'Hara M, Mioduszewska B, von Bayern A, Auersperg A, Bugnyar T, Wilkinson A, Huber L, Gajdon GK. (submitted). Does exploration depend on neotic style?

Griffin A, Federspiel I, Garland A, O'Hara M, Bugnyar T, Güntürkün O, & Healy S. (submitted). In transit or settled? A behavioural analysis of rural birds in an invasive avian urban exploiter.

Grants

PhD-Grant within the Doctoral Program: "Cognition and Communication" (Reference number: W1234-G17). Project title: "Analogical Reasoning in birds"

ESF-Exchange Visit Grant (Reference number: 4207) ESF activity: Evolution of Social Cognition: Comparison and integration across a wide range of human and nonhuman animal species (Compcog) Project title: "Acquisitional Neophilia in Birds"

Abstract (English)

A core area of cognition is concerned with the process of decision making, with important implications for social and physical cognition alike. A heavily debated issue remains whether non-human animals are capable to reason. One ability that implies reasoning skills, poses the capacity to make inferences about novel stimuli, by logically excluding alternatives. To further our understanding of the convergent evolution of such abilities and hence, which socio-ecological conditions promote these, birds pose an interesting taxon, exhibiting cognitively advanced behaviours, yet being phylogenetically distantly related to humans.

With this thesis I attempt to identify and differentiate processes that may influence choice behaviour. In the first chapter I illustrate how fundamental predispositions, shaped by socio-ecological factors, affect responses to novel stimuli in several corvid and parrot species. The results provide evidence for a peak-shift in exploration depending on individual reactions to novelty and thus highlight the importance of considering neophobic and neophilic tendencies in cognitive testing.

Based on these insights I present a novel approach, using a touchscreen, to test for exclusion abilities in the second chapter. A stringent training procedure, intended to discourage neophilic responses, and the outcome in sequential test trials allow to distinguish different decision processes. This task is applied to the inquisitive Goffin's cockatoos (*Cacatua goffiniana*), which have been shown to be capable inferences in the technical domain, in order to validate the method.

The third chapter reports the findings of applying the same task to kea (*Nestor notabilis*), who previously had failed in a conventional inference by exclusion study. Similar to the cockatoos, more than half of the individuals show signs of exclusion performance, but also rely on alternative choice mechanisms. In the final section I discuss similarities between species, as well as potential further avenues to investigate what promotes the occurrence of different decision processes.

Zusammenfassung (German)

Ein zentrales Thema der Kognitionsforschung mit weitreichenden Implikationen für soziale und physikalische Kognition, befasst sich mit Entscheidungsprozessen. Eine heftig diskutierte Frage hierbei ist, ob Tiere die Eigenschaft besitzen rationale Schlüsse zu ziehen. Eine Fähigkeit die dies voraussetzt, ist die Möglichkeit nach dem Ausschlussprinzip zu wählen. Das Studium von Vögeln ist besonders geeignet um zu ergründen welche sozio-ökologischen Umstände Einfluss auf eine möglicherweise konvergente Evolution des logischen Denkens ausüben: Diese zeigen hochentwickelte Verhaltensweisen, sind aber genetisch mit Menschen nur entfernt verwandt.

Mit dieser Dissertation versuche ich verschiedene Prozesse zu unterscheiden, welche bei Entscheidungsverhalten eine Rolle spielen könnten. Im ersten Kapitel zeige ich auf wie grundlegende Prädispositionen, welche auf unterschiedlichen sozio-ökologischen Faktoren beruhen, die Reaktion von verschiedenen Corviden und Papageienarten auf neue Stimuli beeinflussen. Die Ergebnisse weisen eine zeitliche Verschiebung von explorativem Verhalten auf, abhängig von der individuellen Herangehensweise an neue Objekte. Dies unterstreicht die Bedeutung bei kognitiven Versuchen grundlegende Prädispositionen, wie Neophilie und Neophobie, zu berücksichtigen.

Basierend auf diesen Einsichten stelle ich im zweiten Kapitel eine neue Methode vor um mit Hilfe eines Touchscreens die Fähigkeit nach dem Ausschlussprinzip zu wählen, zu untersuchen. Ein striktes Training, welches dazu dient auf neophilie basierende Reaktionen zu unterdrücken und eine Reihe von aufeinanderfolgenden Tests ermöglichen hierbei verschiedene Wahlprozesse zu unterscheiden. Um diese Methode zu validieren wurde sie in einem ersten Schritt bei Goffinkakadus (*Cacatua goffiniana*) angewandt, welche als neugierige Art bekannt sind und schon in einer vorangegangenen Studie logisches Schlussfolgern aufwiesen.

Im dritten Kapitel beschreibe ich wie sich Keas (*Nestor notabilis*), welche in früheren Studien bezüglich des Ausschlussprinzips scheiterten, in diesem Versuch verhalten. Ähnlich wie Goffinkakadus zeigen etwa die Hälfte der Tiere Anzeichen für logisches Schlussfolgern, weisen aber gleichzeitig auch andere Wahlprozesse auf. Schlussendlich diskutiere ich Gemeinsamkeiten zwischen diesen beiden Arten sowie weitere Ansätze, um unterschiedliche Mechanismen, die den Wahlprozess bedingen könnten, zu untersuchen.