

**Inference by exclusion in the Red-tailed Black Cockatoo (*Calyptrorhynchus banksii*)**

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/1749-4877.12299](#).

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Running head: Exclusion reasoning in parrots

**Abstract:**

Inference by exclusion is the ability to select a given option by excluding the others. When designed appropriately, tests of this ability can reveal choices that cannot be explained by associative processes. Over the past decade, exclusion reasoning has been explored in several non-human taxonomic groups including birds, mainly in Corvids and Parrots. To increase our understanding of the taxonomic distribution of exclusion reasoning and therefore its evolution, we investigated exclusion performances in Red-tailed Black cockatoos (*Calyptrorhynchus banksii*), an Australian relative of the Goffin cockatoo (*Cacatua goffinia*), using a food-finding task. Cockatoos were required to find a food item hidden in one of the two experimenter's hands. Following training sessions in which they reliably selected the closed baited hand they had just been shown open, each individual was tested on four different conditions. Critical to demonstrating exclusion reasoning was the condition in which they were shown the empty hand and then offered a choice of both closed hands. The performance of all birds was above chance on all experimental conditions but not on an olfactory and/or cuing control condition. The results suggest that the birds might be able to infer by exclusion, although an explanation based on rule learning cannot be excluded. This first experiment in Red-tailed Black cockatoo highlights this species' potential as a model to study avian cognition and paves the pathway for future investigations.

**Keywords:** Cognition, Comparative cognition, Inferential reasoning, Parrot cognition, Psittaciforms

## INTRODUCTION

Whether the differences between human and non-human minds are one of degree or one of kind continues to be the subject of a lively debate (Cobley 2016; Shettleworth 2012; Penn *et al.* 2008). Over the decades, stimulated by these conversations, many different facets of human and non-human cognition have been explored. Although the debate is far from settled, this large body of empirical research has accumulated evidence for a broad diversity of cognitive abilities in non-humans that were originally thought to be uniquely human.

Mapping the taxonomic distribution of distinct cognitive abilities provides the only means by which the ecological factors that favour their evolution can be identified (Brown & Magat 2011). This approach is particularly suited to tests that are well defined from both a conceptual and a procedural point of view (e.g. Dean *et al.* 2007; Johnson & Deaner 2002; Shultz & Dunbar 2010). Unfortunately, for many decades, driven heavily by the motivation to study species whose brains appeared to be architecturally most similar to those of humans and a strong focus on dissecting mechanisms in a small number of model systems, comparative cognition was focused very heavily on primates (Permack & Permack 1983; Boesch & Boesch 1990; Povinelli *et al.* 1990; Tomasello & Call 1997; Call 2001; Hare *et al.* 2001). Now, however, the field encompasses a much welcomed broader taxonomic scope (Jaakkola *et al.* 2005; Carazo *et al.* 2009; Menzel & Fischer 2010; Fiset & Plourde 2012; Krueger *et al.* 2013). Birds have enjoyed particular interest because of the growing awareness that, despite its architectural dissimilarities, the avian brain is functionally much more akin to the mammalian brain than had been previously thought (Jarvis *et al.* 2005; Reiner *et al.* 2004; ten Cate & Healy 2017).

Inferential reasoning, whose investigation in non-human primates began in the 1970s (McGonigle & Chalmers 1977), is a rare example of a cognitive capacity that has been studied from both a proximate and ultimate perspective. The common thread of all inferential reasoning tests is that they require the subject to apply a logical rule to solve a novel problem (Burt 1911). One widely used inferential reasoning test is that of transitive inference (TI), in which individuals are required to infer an ordered relationship between items, which have not been previously compared, based on prior experience of the position of these items in other ordered relationships (McGonigle & Chalmers 1977; Gillan 1981; von Fersen et al. 1991; Benard & Giurfa 2004; Paz-y Mino et al. 2004; Grosenick et al. 2007). For example, if individual A is known to be dominant over individual B and individual B is known to be dominant over individual C, then an individual capable of TI will infer that individual A is dominant of C. For a long time, this form of deductive reasoning was upheld as the hallmark of logical-relational reasoning and lead to an intense effort to document this ability in a wide range of species. As a result, TI is one of best studied capacities from a taxonomical perspective, with studies in primates, birds, fish and even insects (Grosenick *et al.* 2007; Lazareva *et al.* 2004; Paz-Y-Miño *et al.* 2004). Like many abilities, however, once behavioral responses consistent with the capacity for transitive inference began accumulating in a taxonomically diverse range of species, alternative explanations based on differential reinforcement, rather than the existence of an integrated representation of ordered sequences, began to emerge, laying the foundations for more stringent tests (Allen 2006; Vasconcelos 2008; Guez & Stevenson 2011; Guez & Audley 2013).

An alternative inferential reasoning capacity that has received far less attention than TI, particularly from the point of view of its taxonomic distribution, is the ability to reason by exclusion. Reasoning by exclusion involves the ability to select the correct alternative by

logically excluding other potential choices (Call 2006). By doing so, it allows the solving of a problem based on incomplete information.

In order to explore exclusion skills, several methods have been employed. The oldest ones are those using matching-to-sample paradigms in which subjects are presented with a set of familiar items with which they learn to associate labels (visual or auditory, such as words, symbols or voices). To test for reasoning by exclusion, they are then presented with an unknown label and a choice between a familiar or a novel item. Chimpanzees (*Pan troglodytes*) and sea lions (*Zalophus californianus*) select the novel item when presented with an unknown label, suggesting they make the inference that the novel label refers to the novel unfamiliar item (Schusterman *et al.* 1993; Tomonaga 1993; Hashiya and Kojima 2001). More recent methodologies have involved developing computer-based tasks in which familiar stimuli are associated with a positive or negative value before being presented against an unknown stimulus. Domestic dogs (*Canis lupus familiaris*) spontaneously chose the novel over the negative stimulus, suggesting that they infer the novel stimulus was positive (Aust *et al.* 2008).

Because these procedures using computer-tasks or language-trained animals are often criticised for their artificiality (Boesch 2008), there has been a focus on developing more natural protocols, most often food-finding tasks. The most typical experimental design involves presenting individuals with several containers, under one of which, unbeknownst to the test subject, a desirable food item is placed. In a variety of conditions, the experimenter briefly lifts either the container that does, or the container that does not, contain the food item before covering the food once again, at which point the subject is asked to make a choice. The critical

test is whether the animal is able to choose the alternative cup when the cup without food has been revealed. Great Apes (Call 2006) pass this kind of test, as do domestic dogs (*Canis familiaris*) under some conditions (Erdőhegyi *et al.* 2007). In birds, evidence is patchy. Pigeons (Collumbiforms) fail tests of reasoning by exclusion (Aust *et al.* 2008). Some songbirds (Passeriform order, e.g. ravens (*Corvus corvax*), Schloegl *et al.* 2009; Clark's nutcrackers (*Nucifraga Columbiana*), Tornick & Gibson 2013) show reasoning by exclusion, but others do not (i.e. jackdaws (*Corvus monedula*) Schloegl 2011).

It has been suggested that the cups task as presented above is not enough on its own to prove that subjects exclude by inferring the correct location rather than by avoiding the incorrect option (Penn & Povinelli 2007; Schloegl *et al.* 2009). Despite its limitations, the task has the advantage that it taps a more relevant ecological context than other designs and is logistically much more simple to train than computer-based approaches. It is therefore likely to be more applicable to studying larger, more diverse collections of species.

In the parrots, exclusion reasoning has been found in the Cacatuinae subfamily (Goffin Cockatoo (*Cacatua goffinia*), O'Hara *et al.* 2015), the Psittacinea subfamily (Grey parrots (*Psittacus erithacus*), Mikolasch *et al.* 2011) and the Nestoridae family (New Zeland Kea (*Nestor notabilis*), O'Hara *et al.* 2016). When tested on a food-finding task requiring the birds to search for food in two tubes of different shape (one straight, one bent), keas, unlike ravens, failed to show any exclusion abilities and appeared to spend more time exploring the tubes (e.g. looking into both tubes through both ends even when it was not necessary) (Schloegl *et al.* 2009). Several explanations for the kea's unexpected performance have been put forward, including discussions of differing levels of intelligence and adaptive specialization hypotheses, which link the evolution of reasoning by exclusion to the evolution of food

caching in corvids (Schoelg *et al.* 2009; Schoegl 2011; Mikolasch *et al.* 2012). However, recent studies in parrots strongly suggest that the differences observed between corvids and parrots may be due to the application of methodologies ill-suited to testing neophilic parrots. O'Hara *et al.* (2015) have pointed out that the keas' excessive exploratory behaviours in the Schoegl *et al.* (2009) experiment might be the result of their neophilic tendencies. O'Hara *et al.* subsequently investigated exclusion reasoning using a modified procedure, first in Goffin cockatoos (O'Hara *et al.* 2015) and, more recently, in keas (O'Hara *et al.* 2016). Using a computer screen, these authors presented the birds with a large amount of novel, unrewarded stimuli in order to discourage their explorative behaviour, and under these conditions both Goffins and keas exhibited the ability to choose by exclusion.

These patterns of taxonomic distribution suggest that reasoning by exclusion might be a common trait to all Psittaciforms. Further investigation of the taxonomic distribution of this ability will contribute to developing large comparative data sets of cognitive performance which can be used to identify the ecological predictors of particular cognitive abilities and understand the evolution of cognition.

Within this context, Australian Red-tailed Black cockatoos (*Calyptorhynchus banksii*) make for a useful taxonomic comparison. Indeed, the taxonomy of parrots (Psittaciform order) was recently revised (Joseph *et al.* 2012) with Strigopoidea (Nestoridae, keas) splitting from the lineage leading to the Psittacoidea (containing Grey parrots) and the Cacatuoidea (containing Goffins cockatoos). Within the Cacatuoidea, the *Calyptorhynchus* genus containing the Red-tailed Black cockatoo split from the *Cacatua* genus containing Goffin cockatoos 21.6 million years ago (White *et al.* 2011) (Fig. 1). Given that reasoning by exclusion is present in Grey parrots (Psittacoidea), Goffin cockatoos (Cacatuoidea) and keas (Nestoridae), determining

whether this ability is present in a member of another genus within the Cacatuoidea (i.e. Red-tailed Black cockatoos) provides insight into whether the capacity has evolved due to the particular ecological conditions experienced by Goffin cockatoos, Grey parrots and keas or whether it is likely to be the result of shared ancestry of the Strigopoidea and the Cacatuoidea and common to all members of this taxonomic lineage. Hence, in this study, we undertook to test whether Red-tailed Black cockatoos show evidence of reasoning by exclusion.

The Red-tailed Black cockatoo is a Psittaciforme native of Australia, commonly seen in large flocks though it also occurs in pairs and trios. They mainly eat seeds but also fruits, berries, nectar, flowers and sometimes insects and larvae. They nest in tree cavity, generally *Eucalyptus*, where the female lays usually one egg at a time while the male feeds her. Their life span is around 20 years in the wild and can reach 50 years in captivity (Forshaw & Cooper 2002). We are aware of no previous studies regarding the cognitive abilities of this species. Thus, we chose to test them for the very first time on a food-finding task in order to quantify their ability to reason by exclusion.

## MATERIALS AND METHODS

### Subjects

The experiment was conducted at the Daintree Wild Zoo, Queensland Australia. We tested three adult Red-tailed Black cockatoos born in captivity: two males “Harley” and “Mephisto”, twenty and ten years old respectively and a five-year-old female “Root”. Although other birds were available to test, these birds were the only ones that were sufficiently food-driven and bold to interact closely with a human experimenter. The birds were housed in outside aviaries



(8 m length x 1.5 m width x 2.5 m height), containing perches and logs. Birds lived in social groups from two to five individuals, food and water were provided *ad libitum*. Birds were tested in their aviaries once a day between 2 pm and 5 pm and were free not to participate in the experiment. The zoo was not busy at the time of year when the study was undertaken, but in the rare instances when disturbance by visitors occurred, the experimenter interrupted the experiments. All subjects were completely naïve to cognitive testing when we began working with them a few month earlier and had no experience of the experimental procedure at the start of the study. The individuals we tested were not part of the same social group. Aviaries were half covered so that the tests took place out of sight of the other subjects, excluding any possibility for social learning. Because these birds can be neophobic, playful and destructive, the traditional use of cups to hide the reward when testing inference by exclusion had to be modified. We elected to hide the reward in the experimenter's hands, an approach with which the cockatoos quickly and willingly engaged. A fourth bird was trained to participate in the task (see below), but because he did not reach the training criterion of facing the human experimenter, he was excluded from the study.

## **General procedure**

### *Training*

All training and testing was conducted by the first author (L.S.). To train the birds to participate in the task, a rock was placed on a tray attached to the aviary's door in a position where the birds were routinely fed. The tray was located 114 cm above the ground and the rock was placed at the tray's edge, 48 cm from the aviary door. A small rectangular trapdoor in the aviary's door allowed the experimenter to move her hands into the aviary and present

them to the bird. Each bird was first trained to climb on the rock and face the experimenter by attracting and rewarding them with a half almond. Once they had learned to climb on the rock and to wait there facing the experimenter in expectation of a reward, the choice procedure began.

To initiate a trial, the subject had to be standing on the rock and facing the experimenter who was standing on the other side of the aviary door. The bird could see the experimenter through the aviary door but the experimenter prepared her hands (i.e placed the reward in one of them) outside the focal subject's line of sight. Each trial was then composed of a presentation phase followed by a choice phase. When the subject was ready (i.e on the rock, facing the experimenter), the experimenter opened the trapdoor and presented her two closed hands to the bird for 2 s at approximately 20 cm from the bird and a gap of 26 cm between the hands. The experimenter then opened both hands palms turned upwards. One of the hands was randomly baited, with the restriction that the reward was not on the same side consecutively more than twice (Fig. 2A). Once the experimenter made sure the subject had looked at the content of her hands (i.e. the birds rotated their head to inspect the content of the hands closely and then maintained their beak pointed towards the baited hand), hands were closed and placed at the two corners of the tray, fists down. In this position, the hands were approximately 48 cm apart and located 48 cm from the bird. The subject was then allowed to make a choice by leaving the rock and touching one of the experimenter's hands (Fig. 2B). If the bird selected the correct, baited hand, then the experimenter opened the selected, baited hand and proceeded to giving the reward (half almond) to the subject. If the subject selected the wrong, non-baited hand, the experimenter opened the selected, non-baited hand, but the subject received no reward. Importantly, the experimenter never showed the content of the non-selected hand after the bird had made its choice. In this way, the bird

never *saw* that the food was in the hand it had *not* chosen. A new trial was initiated as soon as the subject had finished eating the reward (if it had received one) and had returned to the rock.

Subjects were trained until they performed significantly above chance level on two consecutive sessions, where a session consisted of all the trials completed by a subject on a given training day. Given that this number fluctuated across days as a function of the bird's willingness to participate, this number varied from one session to another. Hence, we did not consider training days of fewer than 10 trials to assess whether or not subject had reached criterion. Although this differs from other more standardized procedures in which performance is calculated every set number of trials, we felt this approach better accounted for the fact that the bird's performance could vary quite substantially from one day to another just due to their motivation to participate. The approach therefore returned a more reliable training performance threshold where we could be quite certain the birds had learnt the task.

### *Testing*

Following the same procedure as for training, we tested the birds on four conditions. In all conditions, one hand was baited and one was not, but the conditions varied in how hands were presented during the presentation phase.

Birds received 12 inter-spaced trials of each condition. For each subject, condition order was randomized with the restriction that any one condition was not tested more than twice in a row. For each bird, the reward was presented an equal number of times in the left and the right hand for all trial types.

As during training, the experimenter opened only the selected hand, such that the bird received a reward only if it had selected the correct, baited hand. If it had not, the subject received no reward. Importantly, the bird never *saw* that the food was in the hand it had *not* chosen.

*Both hands open* (Fig. 2C). This procedure was identical to that used during the training procedure described above. We retained this condition during training to determine whether training performance dropped as a consequence of transfer testing, as well as to make sure the birds did not lose interest in participating. The experimenter opened both hands at the same time and presented their content to the subject. The experimenter then closed her hands and placed them onto the tray for the choice phase. This condition allowed us to maintain birds' motivation and check if the test conditions affected a subject's performances in this basic condition.

*No hands open* (Fig. 2D). The experimenter presented her two hands to the subject, but both were closed. The experimenter then placed her hands onto the tray ready for the focal bird to make its choice. This condition constituted an olfactory and cuing control.

*Baited hand open* (Fig. 2E). The experimenter presented her two hands to the subject but only the baited hand was open. The experimenter then closed her open baited hand and placed both her hands on the tray for the choice phase.

*Empty hand open* (Fig. 2F). The experimenter presented her two hands to the subject with only the empty one open. The experimenter then closed her open empty hand and moved both her hands onto the tray for the choice phase.

The last two conditions both involved presenting the bird for the first time with one closed fist during the presentation phase, a stimulus they had not experienced during the presentation phase of any previous training trial. The two conditions differed, however, in so far that in the *baited hand open* condition, the open hand was the one that contained food, as had been the case during training. In contrast, in the *empty hand open* condition, to succeed in finding the food, they needed to select for the very first time the hand that they had seen closed during presentation. These details are relevant to the discussion of the role of associative learning in solving the task.

### **Statistical Analysis**

We modeled the birds' performance using a Generalised Linear model with a binomial error and a probit link. The model included choice accuracy (correct/incorrect) as a binary outcome variable and condition, reinforced hand and individual as categorical predictor variables. The probit regression was performed using Wizard 1.8.27.

## **RESULTS**

It took on average 171 trials (+/- 53 trials) for the three birds to reach a criterion of performing significantly above chance for two consecutive sessions during the training phase. Performance across the first 30 trials is depicted in Figure S1.

Performances during the training phase are depicted in Figure 3. The probit regression model provided a good fit with an area under the ROC curve of 0.89 (Fig. 3A). Using the training condition as the reference (i.e. *Both hands open*), condition was found to be highly a significant predictor of the birds' performance accuracy ( $p < 0.001$ ; Fig. 3B). We found no evidence that performance differed across the conditions *Both hands open*, *Baited hand only* ( $\beta = 0.768$ , 95% CI [-1.75, 3.286]) and *Empty hand only* ( $\beta = -5.58e-16$ , 95% CI [-2.105, 2.105]) which were all above chance levels (Fig. 3B). Sequential correct choices were apparent from the very first test trials onwards (Fig. 4A, 4B, 4C). However, performance on the *No hand open* condition ( $\beta = -4.325$ , 95% CI [-6.462, -2.188]) was significantly lower than performance in all other conditions ( $p < 0.001$ ).

## DISCUSSION

Using a food-finding experimental design, we investigated whether Red-tailed Black cockatoos were capable of inference by exclusion. Patterns of choice accuracy were consistent with ability to infer the location of a bait based on partial information.

Our results show that birds performed at chance levels in the *No hand open* condition. Random performance demonstrates that accurate choice of the baited hand in the other conditions was not attributable to the use of olfactory cues. Nevertheless, we acknowledge that this control condition does not rule out completely the possibility that the experimenter inadvertently cued the birds to fail in the *No hand open* condition and succeed in the others conditions. As Grey parrots do not use human cues in choice experiments unless the cues are deliberate and obvious (Pepperberg 1990, 1999; Pepperberg *et al.* 2013), we can reasonably

infer that it may be the same in Red-tailed Black cockatoos. Nevertheless, future work should incorporate even more stringent cuing controls.

The ability of the cockatoos to chose correctly the baited hand on the very first test trial when only the empty hand had been presented is consistent with the capacity of these birds to reason by exclusion. It is also important to consider alternative explanations based upon differential reinforcement, however. In the present context, the essence of an associative account of performance would be that the birds learnt to respond to arbitrary cues (CS+) that reliably predicted a reward (US+). The vast majority of associative theories assume that these cues acquire associative strength as a consequence of reward expectations being violated, as occurs when a reward is received when it was not been expected, for example (Rescorla & Wagner 1972). An important part of putting forward associative explanations is identifying what these cues might be, and what part(s) of the experimental procedure, if any, allow them to be learnt.

During training, the birds were presented with a choice involving an open baited hand versus an open empty hand. Associative accounts indicate that with repetition birds could have learnt that the sight of the food (conditioned stimulus, CS+) predicted the food reward (unconditioned stimulus, US) and that the empty hand predicted no food reward (CS-). Hence, according to associative theory, the open hand would have acquired positive associative strength, while the open empty hand acquired either no or negative associative strength depending on initial expectations of food within the task, the details of which we leave aside here. Based upon such learning, the birds could have made a correct choice in *Baited hand open* condition as it involved presenting the CS+.

Drawing further upon this associative account, the birds encountered the CS- (empty hand open) during the *Empty hand open* condition. For the first time, however, the alternative hand was a closed fist. If the birds had learnt an association between the CS- and not receiving food, one must explain in associative terms why they correctly chose the closed fist the very first time they encountered this combination of cues. One possible associative explanation is that the closed fist had acquired a small amount of associative strength during the latter parts of training when the CS+ (open hand) was then closed and made available for choice. In the latter parts of training, this choice tended to be the correct one, turning the fist into a reliable predictor of reward.

This account requires some latent learning of a secondary cue that follows immediately a primary cue even though the secondary cue provides no additional predictive information. Although this is possible, we think the reliably high performance of the birds on the *Empty hand open* condition makes it unlikely. Indeed, during the olfactory control, the birds experienced two closed fists yet this cue was not reliably reinforced because the birds chose randomly. This experience should have reduced the associative strength of the closed fists, with for consequence that performance on the *Empty hand open* condition should have gradually declined. Although one bird's performance (Root) fluctuated slightly, that of two birds remained consistently highly accurate across all 12 trials in the critical *Empty hand open* condition. It is also essential to note that the assertion that birds solved the *Empty hand open* condition by applying a learnt "rule" to choose the other hand in response to the CS- (an empty hand) inherently relies upon the birds having learnt that food was always available in one of the two hands, even though they had never been shown the food in the non selected hand (see methods). Learning the rule that "if the food is not here, then it must be there" is reasoning by exclusion. Finally, it might be argued that birds learnt the CS+ or a CS- during



each presentation phase of each trial. This explanation would call upon an associative learning mechanism without the need for exclusion reasoning. Were this to have been the case, however, then the birds should have shown similar rapid accurate performance during the training phase of the study. Yet, it can be seen from Figure S1 that this was clearly not the case; it took Harley 179 trials to reach criterion (performing above chance on two consecutive sessions), 120 for Mephisto and 118 for Root. In sum, we conclude that when considering the overall performance of the birds, reasoning by exclusion is a more likely explanation than is an associative account.

In comparison with other studies, the number of training trials to reach criterion in the present study is unusually high. Previous studies involving keas (Schlogl *et al.* 2009) and Grey parrots (Mikolasch *et al.* 2011) reported 20 to 30 trials for the birds to reach the training criterion. Although slower acquisition might reflect differences in learning abilities between Red-tailed Black cockatoos on the one hand, and Grey parrots and keas on the other, it is important to bear in mind that the birds used here were naïve to any kind of cognitive testing when we began working with them some months prior to the present study. This is atypical of most avian cognitive research, which is generally conducted using long-standing captive colonies of highly tested individuals. Lack of training might have impaired the ability or the motivation of our birds to stay on task.

It is also important to bear in mind that direct comparisons of acquisition speed might be made difficult due to differences in how criterion performance is evaluated. Some researchers calculate performance across discrete blocks of set numbers of trials while we chose to measure performance using daily performance. For example, had our birds been considered to have reached criterion based on a minimum of 80% success across two consecutive blocks of 10 trials, the cockatoos would

have reached criterion in 180 trials, 120 trials, and 80 trials, respectively. Yet, despite being successful on two consecutive blocks of 10 trials, the cockatoos would not have performed at criterion levels the very next day. Defining what level of training guarantees equivalent levels of knowledge will be a challenge for future comparative research despite its attractiveness (Thornton & Lukas 2012).

In conclusion, both the Red-tailed Black cockatoo and the Goffins cockatoo belong to the Cacatuoidea but each one belongs to a different genus. Grey parrots belong to the Psittacoidea whereas New Zealand keas belong to the Strigopoidea which split from the lineage leading to the Psittacoidea and the Cacatuoidea. The finding that Red-tailed Black cockatoos appear to show reasoning by exclusion, as do Goffin cockatoos, Grey parrots and New Zealand keas suggests that this ability evolved prior the split of the Strigopoidea. The present study illustrates the potential for future cognitive work in this species and for the Psittaciforms to constitute a taxonomic group in which the faculty to infer by exclusion could be sampled more broadly to examine the environmental and social factors associated with this ability.

## REFERENCES

- Allen C (2006). Transitive inference in animals: reasoning or conditioned associations? In: *Rational Animals?* (Hurley S & Nudds M eds). Oxford University Press, Oxford, pp. 175–185.
- Aust U, Range F, Steurer M & Huber L (2008). Inferential reasoning by exclusion in pigeons, dogs and humans. *Animal Cognition* **11**, 587–597.

Benard J & Giurfa M (2004). A test of transitive inferences in free-flying honeybees: unsuccessful performance due to memory constraints. *Learning & Memory*. **11**, 328— 336.

Boesch C & Boesch H (1990). Tool Use and Tool Making in Wild Chimpanzees. *Folia Primatological* **54** (1-2), 86–99.

Boesch C (2008). Taking Development and Ecology Seriously When Comparing Cognition: Reply to Tomasello & Call (2008). *Journal of Comparative Psychology* **122**, 453–455.

Brown C, Magat M (2011). The evolution of lateralized foot use in parrots: a phylogenetic approach. *Behavioral Ecology* **22**, 1201–1208.

Burt C (1911). Experimental tests of higher mental processes and their relation to general intelligence. *Journal of Experimental Pedagogy* **1**, 93–112.

Call J. (2001). Object permanence in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and children (*Homo sapiens*). *Journal of Comparative Psychology* **115** (2): 159–171.

Call J (2006). Inferences by exclusion in the great apes: the effect of age and species. *Animal Cognition* **9**(4), 393–403..

Carazo P, Font E, Forteza-Behrendt E, Desfilis E. *et al.* (2009). Quantity discrimination in *Tenebrio molitor*: evidence of numerosity discrimination in an invertebrate?. *Animal Cognition* **12** (3): 463–470.

ten Cate C, Healy SD (2017). *Avian Cognition*. Cambridge University Press.

Cobley P (2016). Difference in Kind or Difference of Degree?. In: *Cultural Implications of Biosemiotics*. *Biosemiotics* vol 15. Springer, Dordrecht.

Deaner RO, Isler K, Burkart J & van Schaik C (2007). Overall brain size, and not

encephalization quotient, best predicts cognitive ability across non-human primates. *Brain. Behavior and Evolution* **70**, 115–24.

Erdőhegyi Á, Topál J, Virányi Z & Miklósi Á (2007). Dog-logic: inferential reasoning in a two-way choice task and its restricted use. *Animal Behaviour* **74**(4), 725–737.

von Fersen L, Wynne CDL, Delius JD & Straddo JER (1991). Transitive inference formation in pigeons. *Journal of Experimental Psychology. Animal Behavior Processes* **17**, 334—341.

Fiset S, Plourde V (2012). Object permanence in domestic dogs (*Canis lupus familiaris*) and gray wolves (*Canis lupus*). *Journal of Comparative Psychology* **127**: 2.

Forshaw JM & Cooper WT (2002). Australian Parrots (3rd ed.). *Robina: Alexander Editions*. ISBN 0-9581212-0-6.

Gillan D (1981). Reasoning in the chimpanzee: II. transitive inference. *Journal of Experimental Psychology. Animal Behavior Processes* **7**, 150—164.

Grosenick L, Clement TS & Fernald RD (2007). Fish can infer social rank by observation alone. *Nature* **445**(7126), 429–432.

Guez D & Audley C (2013). Transitive or not: A critical appraisal of transitive inference in animals. *Ethology* **119**, 703–726.

Guez D & Stevenson G (2011). Is reasoning in rats really unreasonable? Revisiting recent associative accounts. *Frontiers in Psychology* **2**, 277.

Hare B, Call J & Tomasello M. (2001). Do chimpanzees know what conspecifics know and do not know?. *Animal Behaviour* **61** (1), 139–151.

Hashiya K & Kojima S (2001). Hearing and auditory–visual intermodal recognition in the chimpanzee. In: Matsuzawa T (ed) *Primate origins of human cognition and behavior*. Springer, Berlin Heidelberg New York, pp 155–189.

- Jaakkola K, Fellner W, Erb L, Rodriguez M & Guarino E (2005). Understanding of the concept of numerically "less" by bottlenose dolphins (*Tursiops truncatus*). *Journal of Comparative Psychology* **119**: 296–303.
- Jarvis ED, Güntürkün O, Bruce L et al. (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience* **6**, 151–9.
- Johnson VE & Deaner RO (2002). Bayesian analysis of rank data with application to primate intelligence experiments. *Journal of American Chemical Society* **97**, 1–10.
- Joseph L, Toon A, Schirtzinger EE, Wright TF & Schodde R (2012). A revised nomenclature and classification for family-group taxa of parrots (*Psittaciformes*). *Zootaxa* **3205**, 26–40.
- Krueger K, Farmer K & Heinze J (2013). The effects of age, rank and neophobia on social learning in horses. *Animal Cognition* **17**: 645–655.
- Lazareva OF, Smirnova AA, Bagozkaja MS, Zorina ZA, Rayevsky VV & Wasserman EA (2004). Transitive responding in hooded crows requires linearly ordered stimuli. *Journal of the Experimental Analysis of Behavior* **82**(1), 1–19.
- McGonigle BO & Chalmers M (1977). Are monkeys logical? *Nature* **267**(5613), 694–696.
- Menzel R & Fischer J (2010). *Animal Thinking: Contemporary Issues in Comparative Cognition*. MIT press.
- Michael T & Call J (1997). *Primate cognition*. ISBN 978-0-19-510624-4.
- Mikolasch S, Kotrschal K & Schloegl C (2011). African grey parrots (*Psittacus erithacus*) use inference by exclusion to find hidden food. *Biology Letters* **7**(6), 875–877.
- O'Hara M, Auersperg AMI, Bugnyar T & Huber L (2015). Inference by Exclusion in Goffin Cockatoos (*Cacatua goffini*). *PloS One* **10**(8).

- Pacheco MA, Battistuzzi FU, Lentino M, Aguilar RF, Kumar S & Escalante AA (2011). Evolution of Modern Birds Revealed by Mitogenomics: Timing the Radiation and Origin of Major Orders. *Molecular Biology and Evolution* **28**(6), 1927–1942.
- Paz-Y-Miño CG, Bond AB, Kamil AC & Balda RP (2004). Pinyon jays use transitive inference to predict social dominance. *Nature* **430**(7001), 778–781.
- Penn DC, Holyoak KJ, Povinelli DJ (2008). Darwin’s mistake: explaining the discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences* **31**, 109–130. discussion 130–178.
- Penn DC, Povinelli DJ (2007). Causal cognition in human and nonhuman animals: a comparative, critical review. *Annual Review of Psychology* **58**, 97–118.
- Pepperberg IM (1990). Cognition in an African Grey parrot (*Psittacus erithacus*): Further evidence for comprehension of categories and labels. *Journal of Comparative Psychology* **104**, 41–52.
- Pepperberg IM (1999). The Alex studies. Cambridge, MA: Harvard.
- Pepperberg I, Koepke A, Livingston P, Girard M, Hartsfield AL (2013). Reasoning by Inference: Further Studies on Exclusion in Grey Parrots (*Psittacus erithacus*). *Journal of Comparative Psychology* **127**(3), 272–281.
- Povinelli DJ, Nelson KE & Boysen ST (1990). Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* **104** (3), 203–210.
- Premack D & AJ Premack (1983). The mind of an ape. *New York, London: W.W. Norton & Company*. Pg. 29.
- Reiner A, Perkel DJ, Bruce LL *et al.* (2004) Revised nomenclature for avian telencephalon and some related brainstem nuclei. *Journal of Comparative Neurology* **473**, 377–414.

Rescorla RA & Wagner AR (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In: Black AH & Prokasy (Eds), *Classical Conditioning II: Current Research and Theory*, 64–99. New York: Appleton-Century-Crofts.

Romanes GJ (1882). *Animal Intelligence*, First Vol. The International Scientific Series Vol XLI. London: Kegan Paul, Trench, & Co.

Schloegl C, Bugnyar T & Aust U (2009). Exclusion performances in nonhuman animals: from pigeons to chimpanzees and back again. In: Blaisdell AP, Huber L, Watanabe S, Young A & Yamazaki Y (Eds), *Rational animals, irrational humans*, 217–234. Tokyo, Japan: Keio University Press.

Schloegl C, Dierks A, Gajdon GK, Huber L, Kotrschal K & Bugnyar T (2009). What You See Is What You Get? Exclusion Performances in Ravens and Keas. *PloS One* 4(8), e6368.

Schloegl C (2011). What you see is what you get – Reloaded: Can Jackdaws (*Corvus monedula*) find hidden food through exclusion? *Journal of Comparative Psychology*. Vol. 125, No. 2, 162–174.

Schusterman RJ, Gisinier R, Grimm BK, Hanggi EB (1993). Behavior control by exclusion and attempts at establishing semanticity in marine mammals using match-to-sample paradigms. In: Roitblat HL, Herman LM & Nachtigall PE (Eds), *Language and communication: comparative perspectives*. Lawrence Earlbaum Associates, Hillsdale, NJ, 249–274.

Shettleworth SJ (2012). Modularity, comparative cognition and human uniqueness. *The Royal Society*, 367(1603):2794–2802.

Shultz S & Dunbar RIM (2010). Species differences in executive function correlate with

hippocampus volume and neocortex ratio across nonhuman primates. *Journal of Comparative Psychology* **124**:252–60.

Ströckens F, Güntürkün O & Ocklenburg S (2013). Limb preferences in non-human vertebrates. *Laterality: Asymmetries of Body, Brain and Cognition* **18**(5), 536–575.

Thornton A & Lukas D (2012). Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philosophical Transaction of the Royal Society B* **367**, 2773–83.

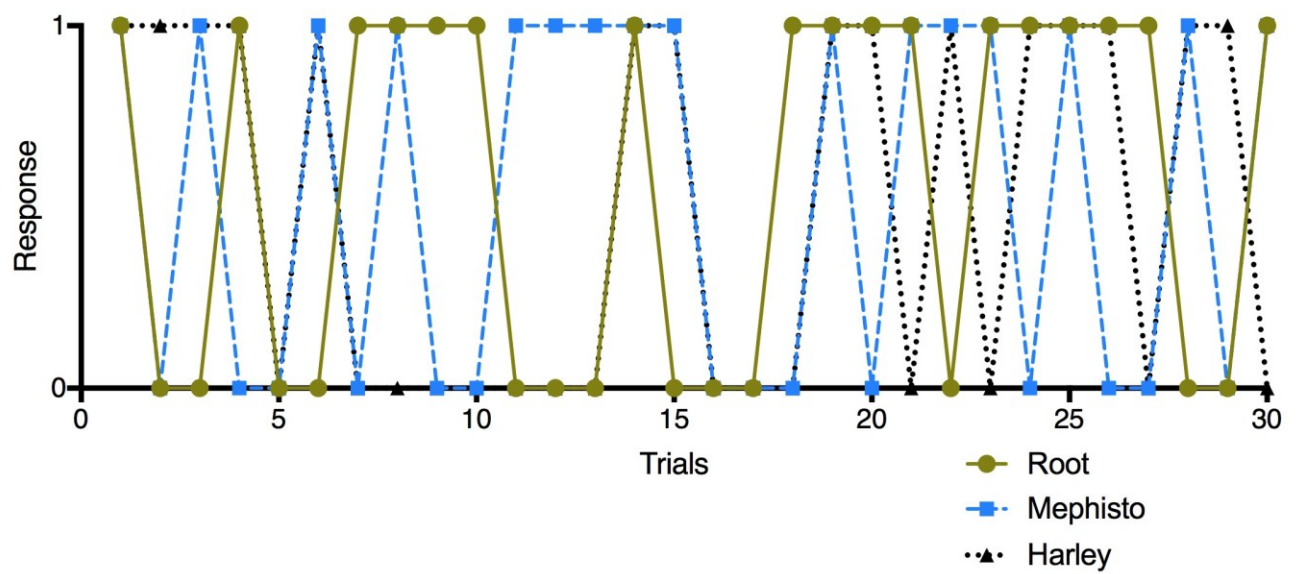
Tomonaga M (1993). Tests for control by exclusion and negative stimulus relations of arbitrary matching to sample in a “symmetryemergent” chimpanzee. *Journal of the Experimental Analysis of Behavior* **59**, 215–229.

Tornick JK & Gibson BM (2013). Tests of inferential reasoning by exclusion in Clark's nutcrackers (*Nucifraga columbiana*). *Animal Cognition* **16**(4), 583–597.

Vasconcelos M (2008). Transitive inference in non-human animals: an empirical and theoretical analysis. *Behavioural Processes*. **78**, 313–334.

White NE, Phillips MJ, Gilbert MTP, Alfaro-Núñez A, Willerslev E, Mawson PR et al. (2011). The evolutionary history of cockatoos (*Aves: Psittaciformes: Cacatuidae*). *Molecular Phylogenetics and Evolution* **59**(3), 615–622.



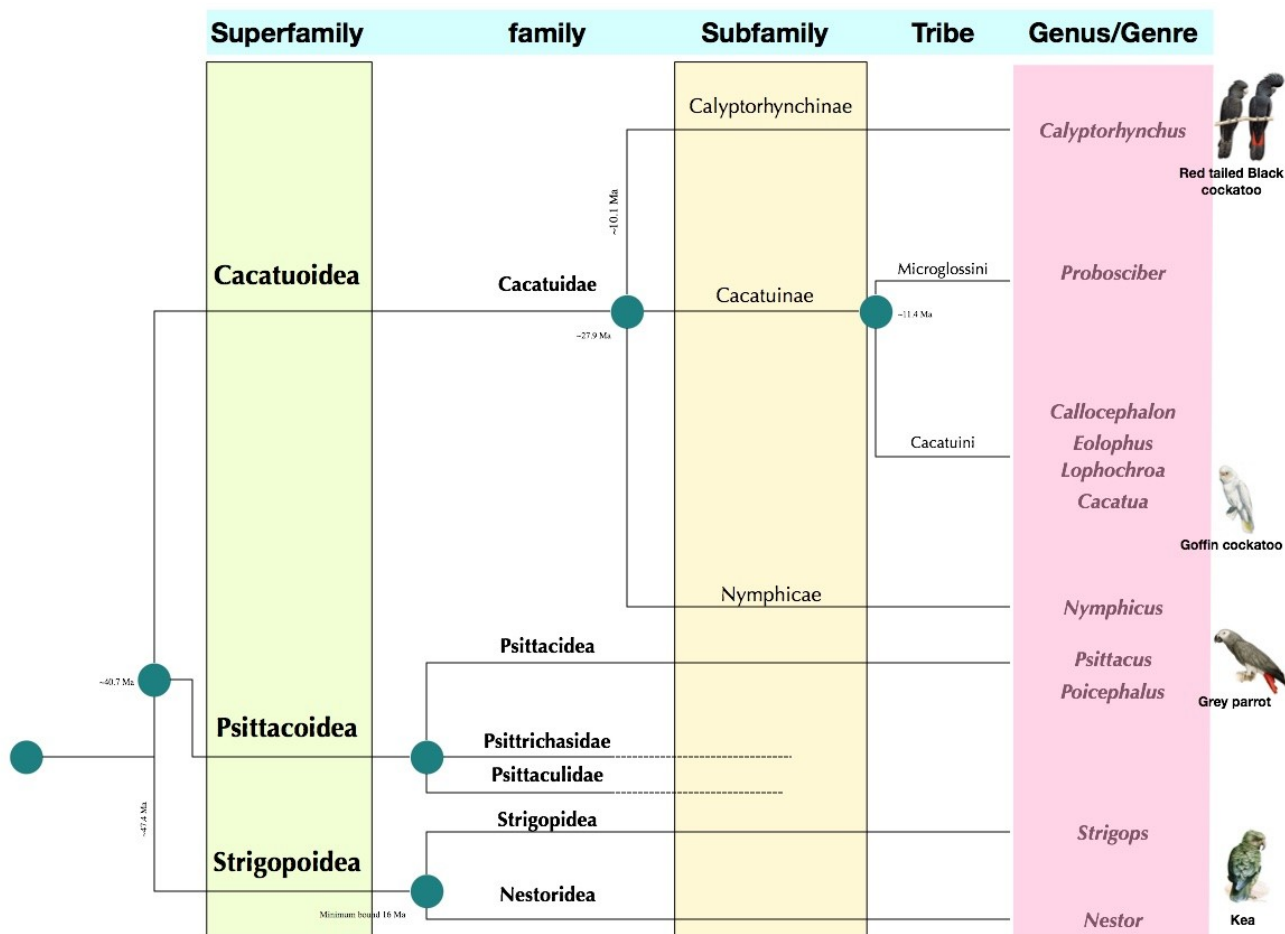


**Figure S1** Responses during the training phase for each individual during the first 30 trials. 1

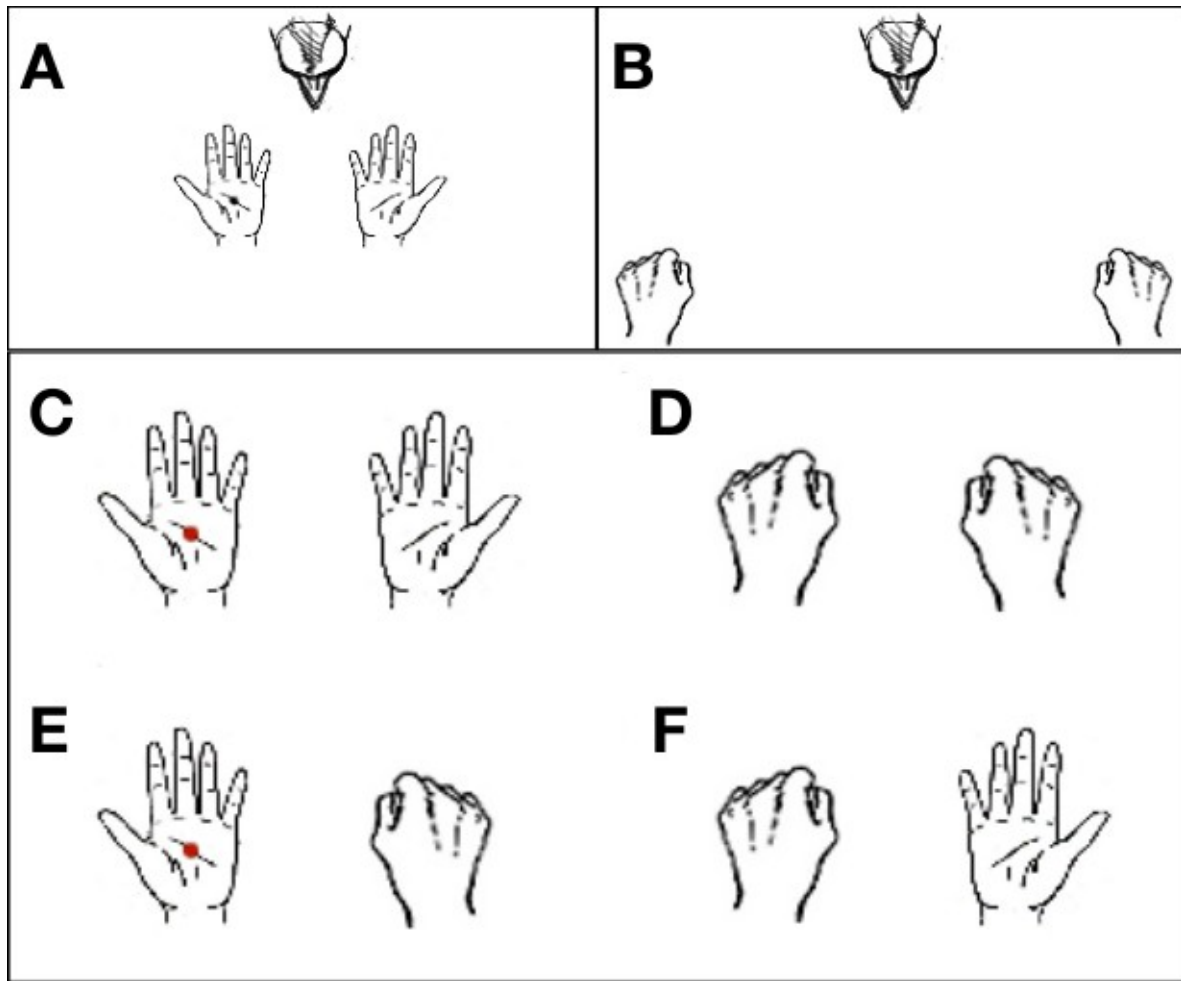
denotes success, 0 failure.

## SUPPLEMENTARY MATERIALS

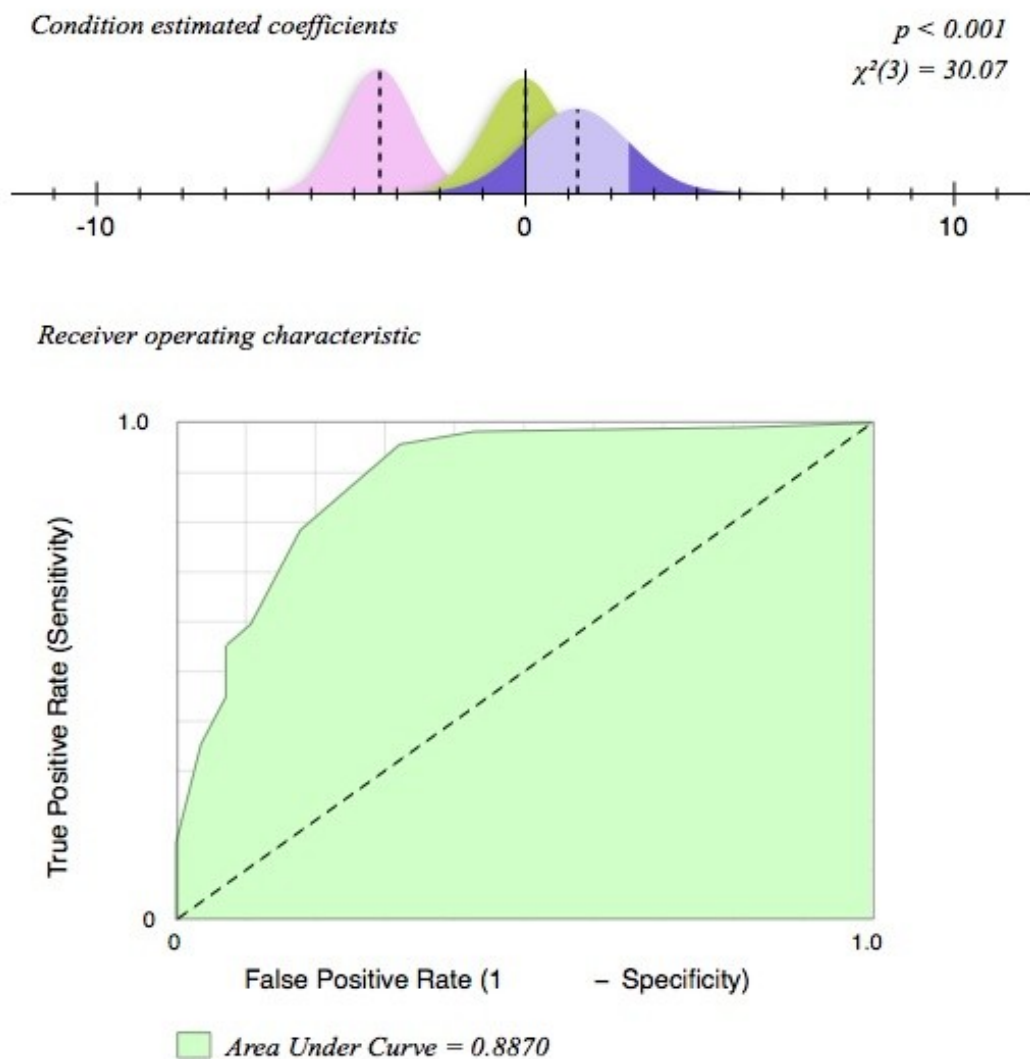
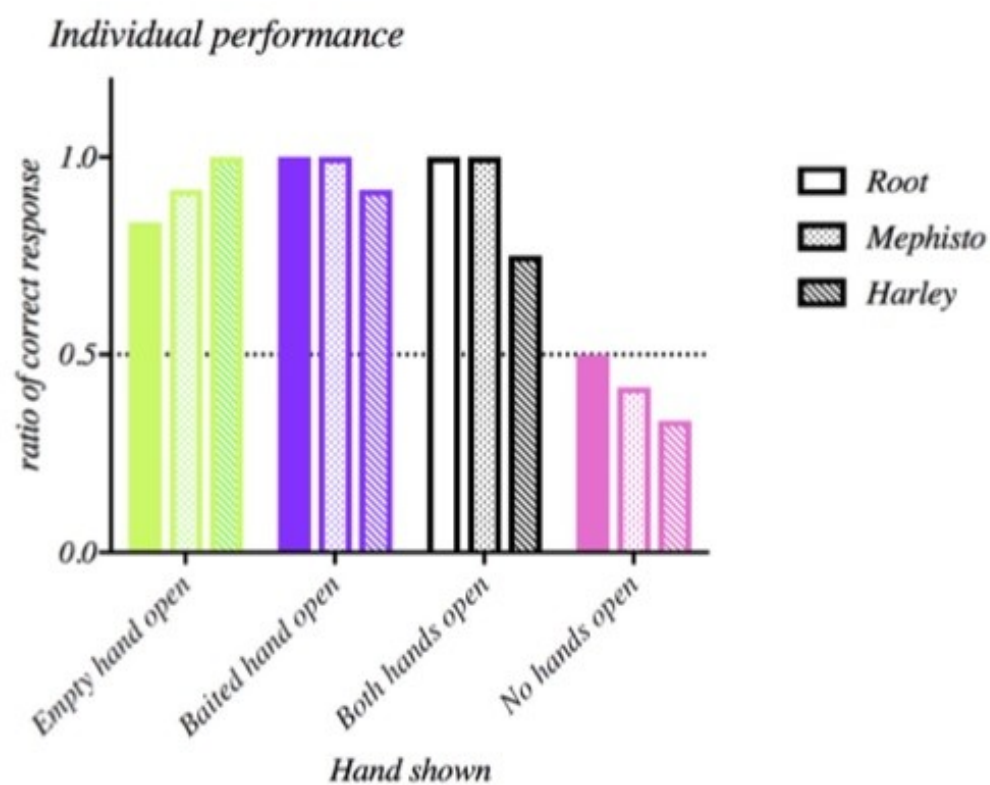
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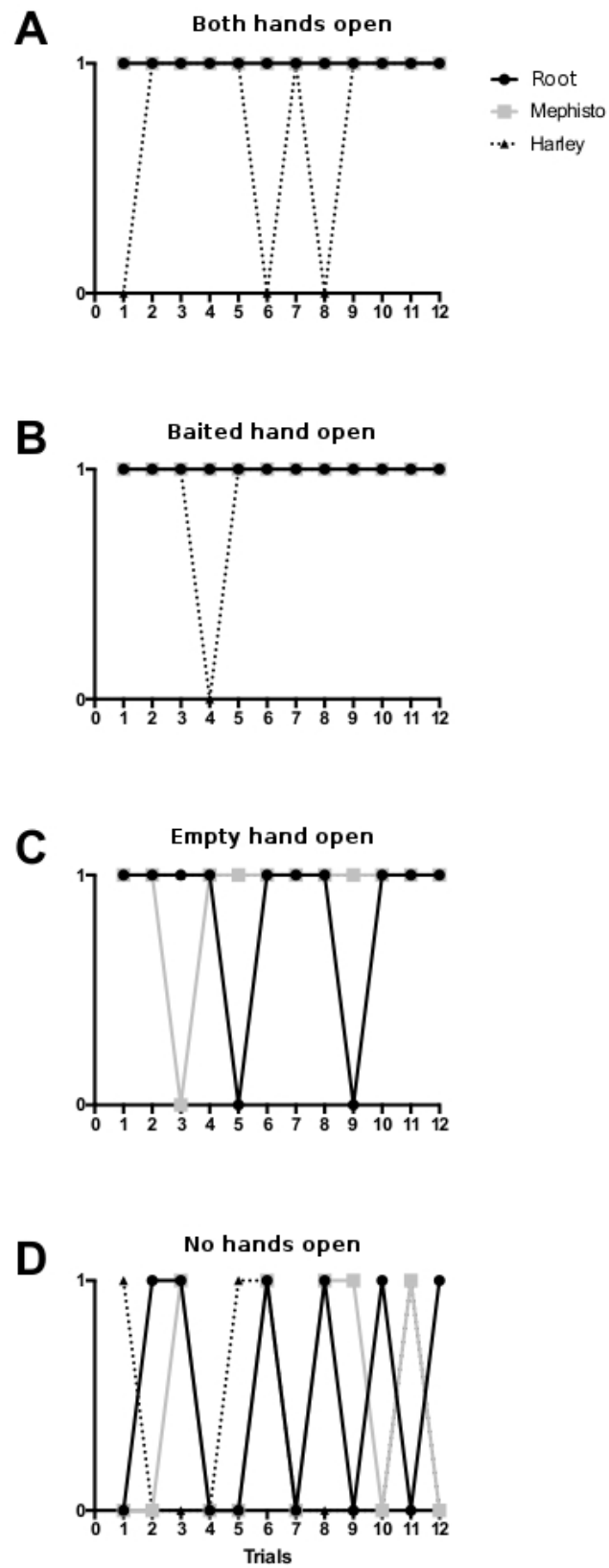
**Figure 1:** Tree diagram of the taxonomic distribution of Psittaciforms.



**Figure 2:** Training and testing conditions. **A-** Training condition: baited hand is randomly chosen and both hands are presented open for observation. **B-** Retrieval phase (for both training and test phases). **C-** Both hands open condition; **D-** No hands open condition; **E-** Baited hand open condition; **F-** Empty hand open condition.

**A****B**

**Figure 3:** Test results. **A- top:** comparison of the  $\beta$  coefficient for each conditions and confidence interval; 0 indicates the reference condition (both hands open); no hands open (pink); empty hand open (green); baited hand open (purple). **A- bottom:** ROC curve showing the quality of the probit model used. **B-** Individual performance for each condition.



**Figure 4:** Test result in order of presentation for each test condition. **A-** “Both hands open” (or reference condition). **B-** “Baited hand open”. **C-** “Empty hand open” **D-** “No hands open” condition. 1 denote success 0 failure.