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Oriental pied hornbills (*Anthracoceros albirostris*) solve invisible displacement tasks in a test of Piagetian object permanence

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Object permanence, the ability to mentally represent objects even when they are not directly accessible to the senses, is of vital importance for the survival of both human and non-human animals. The Oriental pied hornbill (*Anthracoceros albirostris*) is an Asian species of hornbill displaying remarkable adaptability in various environments, yet little is known about their cognitive abilities. Their breeding behaviour is unique, as the female hornbill seals herself inside a cavity before laying eggs and the male feeds her and their offspring without visual contact, strongly suggesting the presence of object permanence to some degree. In this study, six Oriental pied hornbills underwent testing for object permanence, including a series of seven standard Piagetian tasks involving visible and invisible displacements. The subjects consistently demonstrated spontaneous object permanence in all stages leading up to the invisible displacement stage. Half of the subjects achieved full stage 6 double invisible displacement Piagetian object permanence, while the other half reached stage 5 double visible displacement. Breeding behaviour and the duration of developmental stages are proposed as potential factors influencing object permanence ability in this species of hornbill.

1. Introduction

We perceive objects as entities that persist through time and space. If our view of an object is obstructed, we know of its existence though we cannot see it. This is because we understand that an object still exists even when it is not accessible to our senses. Object permanence [1] is an essential developmental milestone in cognition because it is closely linked to the understanding of the concepts of space, time and causality [1–3]. Without object permanence, objects would keep disappearing and reappearing unexpectedly; we would attribute everything we experienced to our own actions; and the boundary between ourselves and the external world would be blurred. From an evolutionary perspective, the ability to represent other animals and objects when they are out of sight provides great adaptive advantages in activities such as foraging and avoiding predation. For example, prey hiding from the predator in a tree crevice will have a greater chance of surviving if the prey knows that the predator still exists outside of the crevice even though it is currently out of sight [4–6].

Piaget [1] defined six stages of object permanence (table 1 for an explanation of these stages), which are progressive in difficulty, that human infants would experience during the development in their first 2 years. Visible and invisible displacement are the two main types of tasks used to test for object permanence. Outside of human understanding of object permanence, the Piagetian framework has been widely adapted in comparative cognition to study how non-human animals fare under similar object permanence tasks, and how such understanding develops among different species (e.g. [7–11]). The

Table 1. Experimental tests.

test	description	
stage 1	Subjects do not respond to the object.	
stage 2	Subjects visually track the movement of the object.	
stage 3	In this test, the experimenter showed the subject a reward which was partially hidden under one of the cups, so that half of the reward was still visible to the subject.	
stage 4	This test was similar to stage 3, but now the reward was fully hidden under one of the cups.	
A not B test	This test was designed to assess 'A-not-B errors.' Initially, a reward was shown to the subject and completely hidden under one of the three cups (cup A). The hornbill was then allowed to peck at only one prong. If the hornbill picked the correct location (cup A) in two consecutive trials, the reward would then be hidden under a second cup (cup B). Successful completion of this test involved the bird selecting the prong corresponding to the cup where the reward was ultimately concealed (cup B) during the initial presentation. The bird searching under the first cup (cup A) would indicate an 'A-not-B error.'	
stage 5a	The reward was initially placed under one cup (as in stage 4), then visibly moved to another cup.	single visible displacement
stage 5b	This test was similar to the single visible displacement but with an additional cup involved in moving the reward. After the reward was visibly moved to second cup, it was visibly moved to a third cup.	double visible displacement
stage 6a	The reward was initially concealed beneath a smaller cup, which was then visibly displaced to one of the main locations and covered with the bigger experimental cup. At this juncture, the experimenter emptied the contents of the smaller cup into the experimental cup with one hand, while simultaneously obscuring the manoeuvre with the other. Finally, the experimenter revealed the now-empty interior of the smaller cup to the subject (see electronic supplementary material, video).	single invisible displacement
stage 6b	Similar to single invisible displacement but with the additional step of moving the smaller cup inside a second cup after the first move. The insides of the smaller cup would be emptied inside the second cup (see electronic supplementary material, video).	double invisible displacement

Note. Stages 1 and 2 were not tested in the current study.

comparison between species can reveal how the same cognitive ability has evolved in unrelated species and what species-specific characteristics have affected its development [12–14]. The similarities among species may contribute to our understanding of the cognitive ability of their common ancestor, while the differences may highlight selection pressures necessary for the development of cognitive ability [15].

Previous research on non-human primates suggests that most primates can solve visible displacement tasks, but only the great apes have been reported to solve invisible displacement tasks, the highest level of object permanence, with compelling evidence [7,8,16–23]. In avian species, most of the parrots and corvids tested have been able to pass invisible displacement tasks (e.g. [24–26]). However, outside of the Passeriformes and Psittaciforme order, no other avian species has been reported to reach such a level of understanding, with both ring doves (*Streptopelia risoria*) and tits (*Periparus ater* and *Parus major*) reaching stage 4, and some birds like horned puffins (*Fratercula corniculata*) having only reached stage 3 [27–29]. The observation that both parrots and corvids exhibit a superior level of object permanence compared to other bird species aligns with the prevailing consensus that these avian groups have evolved advanced cognitive abilities. These include delayed gratification, inference-making, and tool usage, which require high levels of object permanence, surpass the cognitive capacities of most other bird species studied so far, and seem comparable to the cognitive abilities of non-human apes [30–32]. For example, apes, parrots, and corvids can refrain from an immediate reward in exchange for a better

but delayed reward [33–35]. They have also demonstrated inference by exclusion in the visual domain in object-choice tasks [36–38]. Corvids have demonstrated episodic-like memory capability by remembering the *what*, *where*, and *when* qualities of an event [39]. Moreover, like apes, some cases of parrots and corvids manufacturing and using tools to retrieve food or water have been reported (e.g. [40–42]). Though parrots and corvids have very different brain structures than apes, they have developed similar cognitive abilities as a result of convergent evolution, likely because they must overcome analogous challenges in their respective environments [43]. Indeed Emery [43] concluded that the emergence of sophisticated cognitive abilities is associated with specific prerequisites including an omnivorous diet, social behaviour, large relative brain size, innovation, extended development, longevity, and habitat adaptability. Parrot and corvid species seem to have fulfilled most of these preconditions. For instance, the relative brain size of parrots and corvids is larger than most other birds and comparable to primates [44]. They have also demonstrated high frequencies of innovations in foraging by eating novel food or obtaining food with new strategies [45]. These preconditions have driven them to adapt to variable environments, and such adaptability is associated with the evolution of intelligence [30,43,46].

Similar to parrots and corvids, hornbills (family Bucerotidae, order Bucerotiformes) fulfil many preconditions described by Emery [43]. Primarily distributed in sub-Saharan Africa and southern Asia, hornbills exhibit an extended developmental period, encompassing 25–40 days of incubation and 45–86

Figure 1. Picture of the experimental set-up. This image is a demonstration of the types of cups and choicer used. Three cups were used in the actual experiment.

days as nestlings. In captivity, smaller hornbill species typically enjoy a lifespan of over 20 years, while larger species can live for up to 50 years [47]. Notably, their relative brain size surpasses that of some parrot species [44]. Many hornbill species display high levels of sociality, frequently engaging in social play, a behaviour associated with enhanced cognitive abilities [48–50]. To this day, our understanding of the cognitive capabilities of hornbills, with a specific focus on Asian hornbills, remains limited. Among the Asian hornbills, Oriental pied hornbills (*Anthracoceros albirostris*) have demonstrated incredible adaptability. All Asian hornbill species typically only inhabit forests; however, Oriental pied hornbills have been able to adapt to both semi-urban and rural areas [51,52], with reports of some individuals even nesting in clay jars instead of their usual tree crevice [53]. They have also adapted to a more diverse diet. While most hornbill species are frugivorous, Oriental pied hornbills are omnivorous and often also predate on nests of other birds [43,54,55]. Their ability to adapt to variable environments has enabled them to overcome challenges, such as habitat loss and degradation, and to thrive in the urban environment in Singapore [51,55]. Alongside this, Asian hornbills such as the Oriental pied hornbill are often known for their unusual breeding behaviour. Most of them are monogamous. The female will enter a tree cavity and seal the entrance with a mixture of droppings, mud, food remains and saliva, leaving only a narrow opening. The male is responsible for bringing food to the female and their offspring through the opening for a few months until the offspring fledge [47,56]. The male identifies the cavity either by vocalization or the fresh seeds from fruits consumed and droppings near the tree [56]. The female may leave the nest to assist the male in feeding the young, with fledglings subsequently resealing the nest cavity after the female's departure [47]. There may be intruding conspecifics attempting to take over the nest, and the male will need to defend it, mainly by sealing the nest with more mud. This unique breeding behaviour may have evolved due to the need to protect the nest from both conspecific and heterospecific invaders [57]. Drawing from this comportment, it seems that hornbills could gain an advantage from a certain degree of understanding that the female and offspring are situated within the cavity, even in the absence of direct visual confirmation. This conduct hints

at the potential existence of object permanence in this particular bird species. Consequently, the present study aims to expand the current understanding of object permanence in the avian taxa, by investigating how a seldom studied species of bird, the Oriental pied hornbill, performs in a battery of object permanence tasks.

2. Methods

(a) Subjects and housing

Six Oriental pied hornbills (*Anthracoceros albirostris*) (three females) participated in this study. The subjects belong to the Mandai Wildlife Reserve Collection and are housed either in pairs or individually for unpaired subjects in aviaries measuring (approximately $6 \times 4 \times 3$ m). The bird subjects in the study were either rescued from illegal trade or housed at the zoo because they were unable to survive in the wild, likely due to permanent physical injuries sustained before fledging. Although their exact ages are unknown, it is estimated that all subjects fell within the 5- to 10-year-old range. The hornbills were fed a maintenance diet of fresh fruit and always had ad libitum access to water.

(b) Procedures

The experiments were reviewed and approved by the National University of Singapore's Institutional Animal Care and Use Committee (IACUC protocol number R23-0737) and The Mandai Wildlife Reserve research panel.

(c) Pre-training

The hornbill subjects were previously trained to use a tool called the 'Choicer' (a 6-inch polylactic acid (PLA) bar with three prongs that can pass through the enclosure mesh) to indicate where they considered food was located among three possible locations (figure 1). Before the experiment, the subjects were already proficient in using the Choicer to find fully visible rewards, systematically scoring 12/12 correct trials in training batteries. However, they had not encountered situations where the reward was partially or fully hidden under an object. Before each testing session, the hornbills received a refresher involving five trials with visible rewards. If a hornbill failed more than one trial during the refresher, testing was postponed until the next day.

Table 2. Test results.

A) number of sessions required to reach the criterion of stage 3–6b						
	stage					
subjects (sex)	3	4	5a	5b	6a	6b
Chika (M)	2	1	3	1	1	1
Chiku (F)	1	2	5	2	5	1
Olivia (F)	2	2	1	5	N/A	N/A
Oscar (M)	4	1	1	4	N/A	N/A
Sam (M)	1	1	2	1	N/A	N/A
Yaz (F)	1	3	6	3	3	1
average	1.83	1.67	3	2.67	3	1
B) number of correct responses in the first session for stage 3–6b						
	stage					
subjects	3	4	5a	5b	6a	6b
Chika	9*	11*	9*	11*	10*	11*
Chiku	11*	9*	8*	9*	6	11*
Olivia	8*	9*	10*	8*	4	N/A
Oscar	9*	11*	10*	7	4	N/A
Sam	12*	11*	9*	12*	3	N/A
Yaz	12*	8*	6	9*	5	12*
p (Wilcoxon test)	0.035	0.034	0.035	0.036	0.201	N/A

Note. (a) Subjects needed to score 10/12 correct trials in order to progress into the next test. Olivia, Oscar and Sam were tested for 10 sessions of stage 6a tasks and did not reach the criterion, therefore they were not tested for stage 6b. (b) The underlined subjects had breeding experience. A binomial test was performed for each individual subject and the subject needed to score at least 8/12 correct trials in the first session for the test to be significant (indicated by *). On the group level, a Wilcoxon test was performed for each stage to compare the group performance to the chance level (0.33).

(d) Object permanence testing

The experiment consisted of seven Piagetian object permanence tests ranging from stages 3 to 6 (table 1 and electronic supplementary material, movie S1). Each test (except for the A not B test) had a minimum of one session with 12 trials. To progress to the next test, the hornbill needed to complete at least 10 correct trials in a single session. If this criterion was not met after 10 sessions, testing with that bird ended. The A-not-B test was conducted after the hornbill passed stage 4, as part of the progression from stages 3 to 6. The number of trials per session was not fixed but dependent on the performance of the hornbill. The passing criterion of the A-not-B test was three consecutive correct sessions within 10 sessions. For each test trial, the experimenter directed the hornbill to position itself at the Choicer's centre with the food reward, with the prongs outside its enclosure. The Choicer had cups behind its prongs, hiding rewards. The hornbill was allowed to watch the apparatus being set up. To mitigate the potential influence of hand tracking confounds, incorrect cups were frequently touched, before and after the display. After demonstrating, the Choicer was moved forward, making the prongs accessible. The hornbill was allowed to peck at only one prong, and success was based on choosing the prong with the reward. The reward was given to the hornbill when its bill touched the correct prong. No reward was given if it pecked at the wrong prong. During the trial, if the hornbill moved away from the set-up or lost attention, the experimenter would direct the hornbill back to the position with the food reward and restart the trial. The reward was either a food pellet or a small piece of fruit and its location was pseudo-randomized in each trial.

(e) Analysis

All analysis was conducted using RStudio [58]. We analysed subject performance during the initial sessions of each stage, which serves as an indicator of their spontaneous object permanence. For each stage, binomial tests and Wilcoxon's tests were used to evaluate the performance in comparison to expectation (0.33) on both the individual level and group level respectively. A generalized linear mixed model (GLMM) and *post-hoc* Tukey HSD tests were used to assess the effects of stages, trials, breeding experience (whether the subject has ever mated before, in the wild or in the captivity) and sex on performance of all sessions, with subject as a random effect (lme4 package [59] and emmeans package [60]).

3. Results and discussion

Among the six Oriental pied hornbills tested, three achieved full stage 6 double invisible displacement Piagetian object permanence, and the remaining three achieved stage 5 double visible displacement. To the best of our knowledge, Oriental pied hornbills are the first bird species outside of the corvid and parrot families to display object permanence levels comparable to apes.
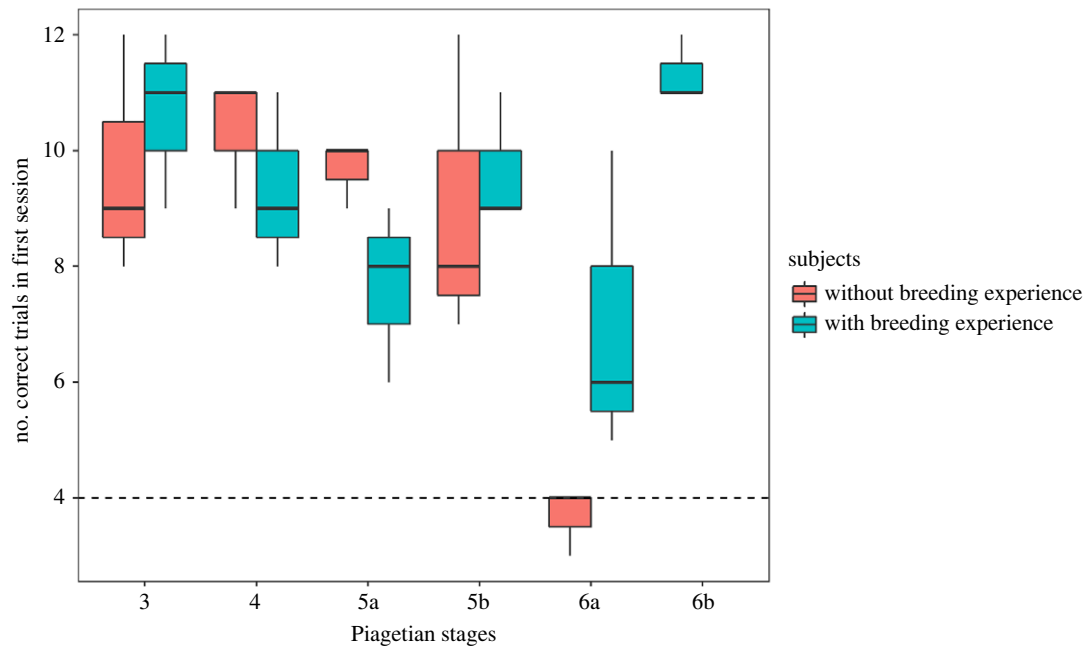
Figure 2. Number of correct choices in the first trials from stage 3 to 6a for subjects with and without breeding experience. Dashed line shows the number of correct choices expected by chance. *Group performance significantly above chance expectation.

The subjects' performance remained consistent across trials (GLMM, $p = 0.88$), indicating that their proficiency was not due to learning or practice during the study, but rather a genuine comprehension of object permanence. Among the subjects that completed a stage, they completed it in an average of 1–3 sessions (table 2), and they also exhibited spontaneous object permanence in all stages leading up to the invisible displacement stage (Wilcoxon's tests, $p < 0.05$; table 2). All subjects passed the A-not-B task within an average of 4.5 trials. The maximum number of trials required was 6. The presence of advanced object permanence capabilities in Oriental pied hornbills is not surprising, as it likely plays a crucial role in the breeding behaviour of both males and females. This could explain the evolutionary selection for a high degree of object representation and the absence of significant differences in performance between male and female subjects (GLMM, $p = 0.78$).

Before this study, full object permanence had been previously demonstrated in birds belonging to the Corvidae family and the Psittaciforme order. In comparison to eight Goffin cockatoos (*Tanimbar corella*) tested using a similar method, Oriental pied hornbills were more consistent in the average number of trials required to meet the criterion. The cockatoos varied in the number of sessions required to pass a stage, ranging from 1.57 to 8.86 sessions [4]. Compared to the Eurasian jays (*Garrulus glandarius*) tested using the Uzgiris & Hunt scale [61], which is still based on the Piagetian framework, the jays seemed to outperform the hornbills, as all jays successfully completed all the tasks, with most tasks mastered within three sessions. However, two jays took longer due to developing fear of the experimental apparatus [26]. Hornbills on the other hand seem to be less neophobic than crows [62]. Many studies on object permanence in avian species have primarily focused on development (e.g. [9,63,64]). Future ontogenetic studies on hornbills could offer valuable insights into the development of this cognitive ability, and how this development compares to that of other avian species.

One intriguing discovery in our study is that the three subjects who failed in the invisible displacement tasks lacked breeding experience, while those who passed had such experience. This raises the possibility that breeding experience might be a crucial factor in the development of object permanence in hornbills. Across all subjects, there were no significant performance differences between any two consecutive stages until stage 6a (Tukey HSD, $p < 0.001$). stage 6a appeared to pose more cognitive challenges for individuals without breeding experience (Tukey HSD, $p < 0.001$), but it did not significantly affect the performance of those with breeding experience (Tukey HSD, $p = 0.23$). Indeed, the performance of stage 6a was significantly lower than any of the previous stages for subjects without breeding experience, while it was only lower than stage 3 for subjects with breeding experience (figure 2; electronic supplementary material, tables S2 and table S3). This implies that breeding experience may be necessary for hornbills to understand invisible displacement but not visible displacement. When compared to visible displacement, understanding invisible displacement is more intricate, involving the integration of various cognitive skills, including memory, spatial reasoning and logical inference [65]. For hornbills, the experience of feeding a mate or chicks that cannot be seen or being fed by the male without visual contact may solidify their grasp of invisible displacement. It is also plausible that the development of object permanence is not solely a result of breeding experience. An alternative explanation for these results could be that they were influenced by the fact that the three specific subjects who failed the tasks were rescued birds that had fallen from the nest as fledglings. Oriental pied hornbills have an extended developmental period with parental care, staying in the nest for about two months before leaving when they are ready to fly [47,66]. Therefore, it is highly likely that these rescued subjects had not fully developed when they fell from the nest. If so, this suggests that the presence of fledglings in the nest with parental care may be critical for the full development of object permanence. However, it is essential to note that due to our small sample size of only six hornbills, the observed effect of breeding experience may have occurred purely by chance. Future more powered studies

should be conducted to fully investigate the impact of both breeding behaviour and developmental periods on object permanence capability.

Our study has demonstrated that Oriental pied hornbills can exhibit full object permanence, contributing to expanding our knowledge in not only Piagetian object permanence in avian taxa but also cognition of Oriental pied hornbills. Though object permanence in hornbills is comparable to that of great apes, parrots and corvids, it has been pointed out that the same cognitive ability of different species can arise from very different underlying mechanisms [25]. The southern ground hornbill (*Bucorvus leadbeateri*), which is a sister clade to and fairly far removed from the Oriental pied hornbill [67], has been reported to demonstrate complex cognitive abilities, such as means-end understanding [68], reasoning by exclusion [69], reversal-learning [70] and social learning [71]. With their excellent performance in object permanence tasks, hornbills appear to be another highly cognitive avian species. However, further research is needed to assess whether hornbills possess cognitive abilities at a level similar to that of parrots and corvids.

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