

# Object permanence in lemurs

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**Abstract** Object permanence, the ability to mentally represent objects that have disappeared from view, should be advantageous to animals in their interaction with the natural world. The objective of this study was to examine whether lemurs possess object permanence. Thirteen adult subjects representing four species of diurnal lemur (*Eulemur fulvus rufus*, *Eulemur mongoz*, *Lemur catta* and *Hapalemur griseus*) were presented with seven standard Piagetian visible and invisible object displacement tests, plus one single visible test where the subject had to wait predetermined times before allowed to search, and two invisible tests where each hiding place was made visually unique. In all visible tests lemurs were able to find an object that had been in clear view before being hidden. However, when lemurs were not allowed to search for up to 25-s, performance declined with increasing time-delay. Subjects did not outperform chance on any invisible displacements regardless of whether hiding places were visually uniform or unique, therefore the upper limit of object permanence observed was Stage 5b. Lemur species in this study eat stationary foods and are not subject

to stalking predators, thus Stage 5 object permanence is probably sufficient to solve most problems encountered in the wild.

**Keywords** Cognition · Choice task · Memory · Cognitive ecology · Prosimii

## Introduction

For animals to locate food, interact with conspecifics and avoid predators, the ability to comprehend that objects continue to exist even when no longer in view should be advantageous, and is termed object permanence. Piaget (1937/1954) pioneered object permanence research using human subjects and divided its gradual development into six major stages. By 1 year of age, children reach Stage 4 where they are able to mentally represent and retrieve an object that has been hidden in a single hiding place but often continue to search the initial location when the object is visibly placed into a new hiding place. The apparent difficulty in adjusting to a new hiding place is referred to as the perseverance error (Diamond 1991) or A-not-B error (Piaget 1937/1954) and may be due to either an inability to separate the object from a previously reinforced location, or to incomplete information processing (Bjork and Cummings 1981; Gratch et al. 1974; Harris 1973). Between the ages of 12–18 months (Piaget 1937/1954; Siegler 1986), object permanence is usually fully functional and a child is able to find an object that has been hidden successively in multiple locations (Stage 5). However, at this level it is still important that the child has direct visible contact with the object before it enters a final hiding place; therefore, these types of manipulations are referred to as visible displacements. By the age of 24 months most children are able to infer an object's location and no longer

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require direct perception of the object (Stage 6; Piaget 1937/1954; Siegler 1986). In a typical test, an object is placed in clear view into an opaque container which is then moved into one (Stage 6a) or successively into several (Stage 6b) hiding places. After the object has been left in a final location, the empty container is presented to the subject who must deduce that the object can only be hidden in a location along the container's trajectory. Such manipulations are referred to as invisible displacements.

Standardized tests based on Piaget's theory of object permanence have also been used to compare object representation among animals, which are faced with disappearing, reappearing and moving objects such as predators, prey or conspecifics. Numerous studies have demonstrated the ability to solve visible object displacements (Stages 4 and 5) in various taxa including birds (Etienne 1973; Funk 1996; Pepperberg and Kozak 1986; Pepperberg et al. 1997), cats (Dore 1986; Dumas 1992; Fiset and Dore 2006; Gruber and Girgus 1971; Triana and Pasnak 1981), dogs (Collier-Baker et al. 2004; Fiset and LeBlanc 2007; Gagnon and Dore 1992; Triana and Pasnak 1981), New World monkeys (de Blois et al. 1998; Mathieu et al. 1976; Mendes and Huber 2004; Natale 1989; Neiworth et al. 2003; Schino et al. 1990; Vaughter et al. 1972), Old World monkeys (Natale 1989; Natale et al. 1986; Schino et al. 1990) and great apes (Call 2001; de Blois et al. 1998; Mathieu et al. 1976; Natale et al. 1986; Redshaw 1978; Wood et al. 1980). In contrast, few species have demonstrated Stage 6 object permanence. The ecological relevance of invisible displacements is harder to imagine, but an example would involve a predator disappearing behind a rock and moving on through high grass, providing only swaying grass as an indirect visual cue indicating its location. The ability to locate an invisible moving object has consistently been reported only in psittacine birds (Funk 1996; Pepperberg and Funk 1990; Pepperberg and Kozak 1986), great apes (Collier-Baker et al. 2006; de Blois et al. 1998; Natale et al. 1986) and humans (e.g. Call 2001). Findings regarding other taxa are mixed. For example, even though Triana and Pasnak (1981) concluded their cat subjects demonstrated Stage 6 object permanence, other studies did not confirm this finding (Dore 1986; Dumas 1992; Gruber and Girgus 1971). Recent testing suggests that dogs may depend on (inadvertent) visual cues provided by the experimenter or the position of the displacement device to solve invisible displacements (Collier-Baker et al. 2004; Fiset and LeBlanc 2007) putting into question earlier reports of Stage 6 object permanence in dogs (Gagnon and Dore 1992; Triana and Pasnak 1981). Findings in monkeys are also controversial because some studies found Stage 5 to be the upper limit (de Blois et al. 1998; Natale 1989; Vaughter et al. 1972) whereas others reported Stage 6 abilities (Hauser 2001; Mathieu et al. 1976; Mendes and Huber

2004; Schino et al. 1990; Wise et al. 1974). However, some of the latter studies (Mathieu et al. 1976; Schino et al. 1990; Wise et al. 1974) have been criticized based on methodological grounds, such as the presentation of a high number of trials which may favor associative learning (Dore and Dumas 1987; Pepperberg 2002). In addition, macaques (Natale et al. 1986) have been shown to employ search rules and, like dogs, to rely on external cues (Collier-Baker et al. 2004). It may be, however, that some monkey species possess Stage 6 abilities whereas others do not. In light of the mixed findings in primates it is surprising that a large group of primates, the strepsirhines (lemurids, lorises and galagids) have never been involved in standardized object permanence tests. Being in many morphological and behavioral aspects the most primitive primates (Fleagle 1999), the strepsirhines are an important taxonomic group for understanding primate cognition in an evolutionary context. Relatively little is known about the cognitive abilities of this group (for a review see Tomasello and Call 1997). Many early studies investigating learning and object discrimination in strepsirhines, most notably lemurs, found performances inferior to those of monkeys (Ehrlich et al. 1976; Glickman et al. 1965; Jolly 1964; Maslow and Harlow 1932) but later studies showed that some lemur species had learning abilities matching those of monkeys (Cooper 1978; Hosey 1997; Voessing 1987). Lemurs have also demonstrated a general understanding about objects and their properties because they are able to use simple tools to obtain rewards (Santos et al. 2005a) and to represent quantities (Lewis et al. 2005; Santos et al. 2005b).

The objective of this study was to examine whether lemurs are able to mentally represent objects that have disappeared from view. We administered a total of ten Piagetian object permanence tasks testing Stages 4–6 object permanence. In addition to seven traditional visible and invisible tests, we presented single visible displacements where the subject was not allowed to search immediately but had to wait a predetermined time-delay to examine how long lemurs were able to represent an object in their minds. We also presented two modified invisible displacement tests where hiding places were not visually uniform in order to determine whether markings enhance memory (de Blois et al. 1998).

## Methods

### Subjects

Thirteen adult subjects representing four species of lemur were tested (Table 1), including *Eulemur fulvus rufus* (red-fronted brown lemur), *Eulemur mongoz* (mongoose lemur), *Lemur catta* (ring-tailed lemur), and *Hapalemur g. griseus* × *H. g.*

**Table 1** Subjects involved in this study

Species	Name	Sex	Age (years)
<i>Eulemur fulvus rufus</i> (n = 5)	Redlake	Female	18
	Strawberry	Female	7
	Redwood	Female	7
	Akako	Male	7
	Redwing	Male	5
<i>Eulemur mongoz</i> (n = 2)	Christina	Female	5
	Gustavo	Male	14
<i>Lemur catta</i> (n = 3)	Adea	Female	6
	Alexandra	Female	7
	Valgius	Male	6
<i>Hapalemur griseus</i> (n = 3)	Beyoung	Female	11
	Bewhiskered	Male	7
	Beriddled	Male	7

Age was at the time of testing. All subjects were adults

*alaotrensis* (gentle bamboo lemur). All species are diurnal, native to Madagascar, and except for *H. griseus*, have a fruit-based diet. *Eulemur f. rufus* and *L. catta* live in social groups of between 7 and 15 individuals (Jolly 2003; Overdorff and Johnson 2003), and *E. mongoz* live in family groups of 3–7 individuals (Grassi 2006; Overdorff and Johnson 2003). All subjects were captive born and raised at the Duke Lemur Center in Durham, North Carolina, except for the female *E. mongoz* (Christina), which was born and raised at the Philadelphia Zoo. At the time of testing (2001), the animals were housed at the Lemur Conservation Foundation (LCF), in Myakka City, Florida, to which all subjects had been transferred between 1 and 2 years before this study. At the LCF, each species was housed in a 5.6 × 5.8 m enclosure that was divided into an indoor area and outdoor wire mesh cage. Lemurs were also often allowed to semi-free range in 5 ha of slash pine forest. Animals were fed once daily with commercial monkey chow, fresh vegetables and fruit. On days of testing, feeding was delayed until after testing sessions were completed to ensure motivation. All subjects were well habituated to humans and acquainted with the experimenter. None of the subjects had previously been involved in cognitive studies.

#### Apparatus

The testing apparatus was comparable to ones used in other studies (de Blois et al. 1998; Neiworth et al. 2003; Pepperberg et al. 1997) and consisted of three round glass dishes (locations A, B, C) each with a diameter of 10 cm and a rim-height of 1.5 cm. Dishes were aligned 24 cm apart measured from the center of each dish and fixed onto a

wooden board (61 cm × 14 cm), and could be individually covered with soft yellow cloths (13 × 13 cm). The apparatus was placed on a 70-cm high rectangular table (45 cm × 80 cm) just outside the cage wire mesh. The experimenter sat at the table facing the enclosure and could slide the board in and out of reach of a subject on the other side of the wire mesh. Raisins, highly desirable to all subjects, served as the object.

#### Procedure

The day before testing began the unbaited apparatus was placed into the lemurs' cages for 30 min so that the subjects could habituate to it but lemurs ignored the apparatus and seemed afraid to approach it in the subsequent testing situation. Therefore, each subject received up to three pre-trials where the object was hidden in an arbitrarily-selected dish and then partially exposed by the experimenter (similar to Stage 3 object permanence hiding) to encourage touching of the cloth. Pre-trials were set-up like subsequent testing trials: a subject was isolated into the outdoor cage, separating it from the experimenter and its social group. The apparatus was placed on the table just out of reach. Once the subject was shown a raisin, it approached and clung to the mesh in front of the experimenter and apparatus from where it watched the raisin being hidden. The apparatus was then pushed towards the subject, which could now easily reach the cloth through the wire mesh. During pre-trials, the experimenter partially exposed the hidden raisin by pulling the cloth until the subject reached for the raisin. During subsequent test trials, the experimenter did not touch the cloth after the hiding was completed.

At the beginning of each trial, the experimenter held the raisin in clear view between her fingers and lured the subject in front of the middle dish (B). At this point the empty dishes were covered with cloths. Next the hiding manipulation was performed. During the visible displacements, the raisin was hidden by lifting the cloth completely off the target dish, placing the raisin in clear view into the dish, and then re-covering the dish completely with the cloth, so that the dish was no longer visible. During invisible trials, the raisin was placed in clear view into the experimenter's palm who then concealed the raisin by making a fist (de Blois and Novak 1994). The fist was moved underneath the cloth where the raisin was dropped, invisibly to the subject, in the target dish. The experimenter then presented both empty palms to the subject and pushed the apparatus into reach of the subject.

Great care was taken to control for possible cues provided by the experimenter or the raisin. Even though previous studies suggest that odor cues are irrelevant in object permanence tests (Gagnon and Dore 1992; Triana and Pasnak 1981), we nevertheless smeared all dishes with

raisins to eliminate possible odor cues. Dogs were shown to be highly sensitive to visual cues inadvertently provided by the experimenter (Collier-Baker et al. 2004; Fiset and LeBlanc 2007) but dogs are domesticated animals selectively bred for sensitivity toward human signals (Hare et al. 2002). To minimize possible cueing, the experimenter rested her hands underneath the table and directed her gaze down at the end of each manipulation.

### Testing

Lemurs each received five visible tests (Tests 1–5), four invisible tests (Tests 6–9), and one single visible test where the lemurs had to wait a predetermined time-delay before being allowed to search (Test 10; Table 2). All visible tests except Test 10 consisted of six trials each. Test 5, a triple visible displacement task, was subdivided into three trials where the raisin was hidden in the target dish, followed by three trials where the raisin was left in the second dish but the experimenter continued to move her hand into the third dish to control for the search strategy “always choose the last dish touched”. Of the four invisible displacement tests, two had “marked screens” where each cloth was made distinct by coloring one with black stripes, one with black dots, and one which was left plain, thus creating unique light/dark contrasts on two of the cloth screens. Failure on the more difficult invisible displacements may be due to difficulties in encoding or recalling the hiding places, so giving each location a unique appearance may enhance memory and thus performance (de Blois et al. 1998). The single visible hiding where the subject had to wait a pre-determined time delay before being allowed access to the apparatus consisted of three trials in each of six different time delay tests ranging from 0 to 25 s. Procedural details of all tests are outlined in Table 2.

All subjects received the tests in the same ascending order beginning with Test 1 (Collier-Baker et al. 2004; Funk 1996; Neiworth et al. 2003). Time-delay tests were presented in order from shortest to longest delay. Testing took place in the morning and ceased after a subject had completed four tests or lost motivation (subject moved away). For each subject, no more than 2 days elapsed between sessions. Attention was closely monitored and if a subject looked elsewhere (e.g., distracted by a bird) or moved away during the hiding manipulation the trial was scored as a mistrial and repeated. A trial was scored as correct when the subject retrieved the raisin on the first search attempt, or in double or triple displacements, searched for it along the raisin’s trajectory. A trial was scored as incorrect when the subject removed the wrong cloth or no cloth. A trial was terminated once the subject made a search response, or after 45 s.

### Data analyses

Because results were expressed on an ordinal scale (0–6 possible correct responses per lemur per test) and were not distributed normally, we used a Kolmogorov–Smirnov one-sample test (hereafter “K–S test”) to determine, for each displacement test, whether the distribution of the number of correct responses differed from random expectations. To minimize the increased likelihood of Type 1 error associated with performing multiple tests, we defined alpha as 0.01. Because of low sample sizes for individual species, all lemurs were combined into a single group to determine whether lemurs understand visible and invisible displacement problems. To determine if there was a location bias for certain dishes, we used a  $\chi^2$  goodness-of fit test to compare the total number of times each dish was selected against expected frequencies based on chance.

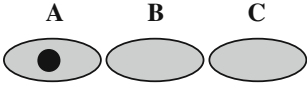










For time delay tests, we used a Spearman rank correlation to determine if the mean number of correct responses per lemur decreased with increasing time delay. To determine whether lemurs outperformed chance in each time delay test we used K–S tests. As above, all lemurs were pooled for analysis.

### Results

There was considerable variation in participation among the subjects. Four subjects, including two *L. catta* (Adea and Alexandra) and two *H. griseus* (Bewhiskered and Beriddled), were removed from analyses because they often searched on the ground below the apparatus or reached for or looked at the experimenter, examining a dish in only 9 of 216 total trials. The nine remaining subjects were highly motivated and only two trials had to be repeated due to inattentiveness of the subject.

Lemurs outperformed random expectations in all visible displacement trials (K–S tests,  $P < 0.01$  in all tests; Fig. 1), including Test 5c which controlled for the “always choose the last dish touched” search strategy. Collectively, subjects responded correctly in 91.7% of all searches, and all lemurs got at least two-thirds of the trials correct in every test, with the exception of the *H. griseus* female (Beyoung) which responded correctly in only 4 of the 24 trials administered in Tests 1–4, but in 5 of the 6 trials administered in Test 5. We found no evidence of A-not-B error, as no errors were committed in Test 2 when the hiding location changed from A to C. However, all subjects made between one and two mistakes on the double visible displacements, indicating a shift in task difficulty. Similarly, during the triple visible displacements four subjects made one error each, three of which occurred during the control trials that tested whether lemurs employed the strategy “always pick the last location touched”.

**Table 2** Description of tests and procedures for visible (Tests 1–5 and 10) and invisible (Tests 6–9) displacements

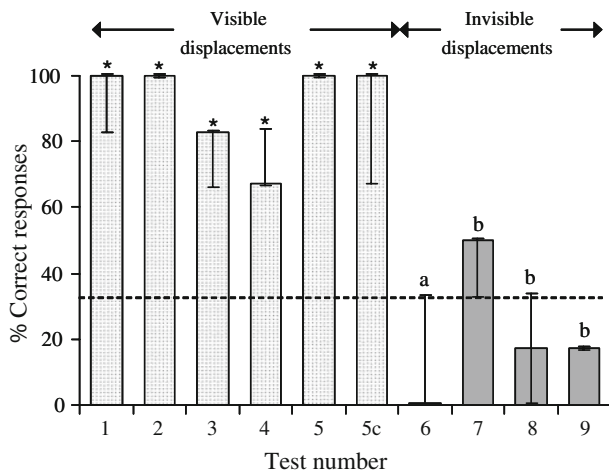
Test	Procedure	Graphic representation
Visible displacements		
1. Single visible (Stage 4a)	Raisin always hidden in location A	
2. Single visible (Stage 4b)	Raisin always hidden in location C (A-not-B test)	
3. Alternate single visible (Stage 5a)	Raisin hidden twice in each location, order random	
4. Double visible (Stage 5b)	Raisin hidden twice in each initial and final location, order and trajectory random	
5. Triple visible (Stage 5b)	Raisin hidden once in each initial, intermediate, and final location, order and trajectory random	
5c. Control trials	Raisin hidden once in each initial and final location, order and trajectory random	
Invisible displacements		
6. Single invisible (Stage 6a)	Raisin travels concealed to location A	
7. Alternate invisible (marked screens)	Raisin travels concealed to each location twice, order random	
8. Double invisible (Stage 6b)	Raisin travels concealed to each initial and final location twice, order and trajectory random	
9. Double invisible (marked screens)	Raisin travels concealed to each initial and final location twice, order and trajectory random	
Time delay test		
10. Time delay Single visible	Raisin hidden once in each location during each time delay trial: 0, 5, 10, 15, 20, and 25 s	

Object permanence levels are indicated in parentheses. Number of trials per test was either three (Tests 5, 5c, 10) or six (the rest)

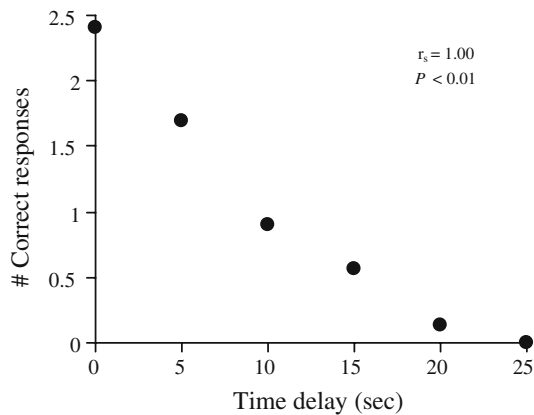
Errors increased dramatically during invisible tests where lemurs responded correctly in only 28.4% of all search responses, and did not outperform chance in any tests (K–S tests,  $P > 0.01$  for test 6,  $P > 0.20$  for Tests 7–9; Fig. 1). During invisible tests 79.2% of all errors were made at the B location, showing a strong location preference ( $X^2 = 107.39$ ,  $P < 0.001$ ,  $df = 2$ ,  $n = 208$ ).

Only the seven *Eulemur* subjects were involved in the time-delay tasks because only they had been consistently responsive. The mean number of correct responses per lemur decreased as time delay increased ( $r_s = 1.00$ ,

$P < 0.01$ ; Fig. 2). All lemurs responded correctly in at least two of three trials after no time delay, but none achieved this level of success following a 20-s or greater delay. Lemurs subjected to no time delay significantly outperformed chance expectations (K–S test,  $P < 0.01$ ,  $n = 7$ ), whereas subjects experiencing a 5- or 10-s delay did not (K–S tests,  $P > 0.2$ ,  $n = 7$  in each case). It was not possible to compare the responses from the 15-, 20-, and 25-s delays to random expectations because most ( $\geq 71.4\%$ ) of the subjects did not exhibit any search behavior during these tests.



**Fig. 1** Median number ( $\pm$ interquartile range) of correct responses for nine lemurs in object permanence tests, expressed as a percentage of the number of trials administered. Number of trials per test was either three (Tests 5, 5c) or six (the rest). The dashed line indicates the expected mean number of correct responses due to chance alone. Lemurs significantly out-performed chance in all visible displacement tests, but in no invisible displacement tests. Significant outcomes are indicated by \* ( $P < 0.01$ ), and insignificant outcomes by a ( $P > 0.01$ ), or b ( $P > 0.2$ )



**Fig. 2** Mean number of correct responses per lemur during time delay tests. Each lemur was administered three trials per test.  $n = 7$  lemurs examined per test

## Discussion

The objective of this study was to examine whether lemurs are able to represent objects that have been removed from view. Overall, lemurs demonstrated an upper limit of Stage 5b object permanence as they were consistently able to perform all visible, but no invisible displacement tasks. This is comparable to what has been found in many monkeys (de Blois et al. 1998; Natale 1989; Vaughter et al. 1972), cats (Dore 1986; Dumas 1992; Fiset and Dore 2006; Gruber and Girus 1971) and dogs (Collier-Baker et al. 2004; Fiset and LeBlanc 2007). Our findings suggest that lemurs were

representing tasks rather than using associative strategies. We did not observe the A-not-B error on Test 2, ruling out a “win/stay” search rule (Mac Donald et al. 1994) and performance did not increase across trials, indicating that learning was not taking place across time (Gagnon and Dore 1992). Even though more errors occurred on the double and triple visible displacements, mistakes did not increase in control trials (Test 5), suggesting that lemurs were not employing a search rule such as “always pick the last location touched”. The possibility that lemurs learned to solve visible displacement problems during pre-trials by associating a reward with a dish or cloth manipulated by the experimenter is also unlikely given that lemurs solved double and triple visible displacements as well as controls, and because during invisible displacements lemurs showed no tendency to choose dishes that had been manipulated. Furthermore, several lemurs appeared to be able to solve visible displacements without pre-trial experience as indicated by grabbing the correct dish during the first pre-trial even before the cloth was contacted to expose the raisin. Taken together, our findings suggest that the lemurs tested were capable of understanding and mentally representing visible displacements.

Despite their high accuracy on visible displacements, lemurs appeared to have a very short-term memory of the raisin following displacement tests. By a wait time of 15 s, most subjects had moved away from the apparatus and did not return when given the opportunity to search. Subjects did, however, quickly approach when a raisin was presented in clear view after the trial had ended. This readiness to retrieve a visible raisin, in combination with the lack of any search activity in dishes or near the apparatus after longer time-delays, suggests that they had forgotten about the raisin rather than its precise hiding location.

During invisible displacements, in contrast, lemurs remained motivated but could not correctly locate the object. The strong location bias observed, also found in other studies (de Blois et al. 1998; Call 2001; Hood et al. 1999; Mendes and Huber 2004), is indicative of a search strategy such as “always pick the middle dish”, or it may simply reflect a preference for the dish most directly in front of the subject. We conclude that lemurs did not comprehend the invisible displacements and either do not possess Stage 6 object permanence or did not express it in the context presented.

Motivation varied considerably among subjects and though sample sizes were too small to draw strong conclusions, may have been related to both inter- and intra-specific variation in understanding the tests themselves. This is supported by the fact that whereas all seven *Eulemur* individuals solved all visible displacements consistently across tests, most of the six *Lemur* and *Hapalemur* subjects often did not attempt searches at all, though when they did, they

were usually successful. Interspecific variation in motivation was not strictly related to diet or group size as both *Eulemur* and *Lemur* have a preference for fruit whereas *Haplemur* is a folivore, and both *E. f. rufus* and *L. catta* live in larger groups than do *E. mongoz* and *H. griseus* (Grassi 2006; Jolly 2003; Overdorff and Johnson 2003).

The degree to which a trait like object permanence is present or expressed in an organism depends, at least in part, on its ecological relevance. Two of the most important challenges that animals face in the natural world are the avoidance of predators and the location of food. It is in such contexts that object permanence would be most commonly expressed. Lemurs are faced with numerous predators with varying hunting techniques including raptors, snakes and viverrids (Goodman 2003; Karpanty and Wright 2006). Raptors fly overhead and may come in and out of view when observed through foliage whereas snakes are mostly sit-and-wait hunters. The most dangerous viverrid, the fosa *Cryptoprocta ferox*, usually attacks lemurs while they are sleeping (Goodman 2003). Thus lemurs are not generally confronted with predators that would present a Stage 6 object permanence scenario where an object is initially seen and then continues moving unseen. Consequently, Stage 5 capabilities seem sufficient to effectively deal with lemur predators. In contrast, animals that are preyed upon by terrestrial stalking predators like felines may benefit from the ability to track a concealed object.

The location of food poses another challenge and animals such as lemurs that eat stationary foods like fruit and leaves face different problems than those that eat live prey. For example, a fruit or leaf, when approached, may come in and out of view because vegetation enters the animal's line of vision, but unlike live prey that may hide, fruits and leaves do not move. Therefore, Stage 5 object permanence is sufficient for effective foraging in lemurs. In addition, fruits and leaves are often clustered and/or abundant, therefore lemurs may not benefit from maintaining a mental image of a particular food item for long, which may help explain why our subjects appeared to be forgetting about the hidden raisin so quickly. In contrast, animals that hunt live prey should benefit from the ability to hold a mental image longer because their food may hide. Indeed, cats and dogs have been found to perform better on time-delay tasks than lemurs, outperforming chance on time-delays of up to 60 and 240 s, respectively (Fiset and Dore 2006; Fiset et al. 2003).

In conclusion, our findings suggest that Stage 5 object permanence is within the capacity of lemurs. The ability to solve visible displacements is ecologically relevant to diurnal lemurs in the context of finding food and avoiding predators. Lemurs did not demonstrate the ability to solve invisible displacements, possibly because the capability to

track concealed objects and infer movements may not be applicable in the natural environment of these animals.

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