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The ecology of spatial memory in four lemur species

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Abstract Evolutionary theories suggest that ecology is a major factor shaping cognition in primates. However, there have been few systematic tests of spatial memory abilities involving multiple primate species. Here, we examine spatial memory skills in four strepsirrhine primates that vary in level of frugivory: ruffed lemurs (*Varecia* sp.), ring-tailed lemurs (*Lemur catta*), mongoose lemurs (*Eulemur mongoz*), and Coquerel's sifakas (*Propithecus coquereli*). We compare these species across three studies targeting different aspects of spatial memory: recall after a long-delay, learning mechanisms supporting memory and recall of multiple locations in a complex environment. We find that ruffed lemurs, the most frugivorous species, consistently showed more robust spatial memory than the other species across tasks—especially in comparison with sifakas, the most folivorous species. We discuss these results in terms of the importance of considering both ecological and social factors as complementary explanations for the evolution of primate cognitive skills.

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Introduction

Many theories about the evolution of primate intelligence have emphasized the role of ecology in shaping cognitive abilities through natural selection. For example, complex spatiotemporal distribution of food, degree of environmental uncertainty, and use of extractive foraging techniques to acquire food have all been suggested as ecological conditions favoring the evolution of more complex cognitive abilities (Milton 1981; Gibson 1986; Byrne 1997; Parker and Gibson 1997; Deaner et al. 2003). Phylogenetic analyses of primate brain size have generally supported the importance of diet for primate intelligence. In particular, frugivorous primates—feeding on more patchily distributed fruit resources—have comparatively larger brains than folivorous primates feeding on relatively homogenously distributed leaves (Clutton-Brock and Harvey 1980; MacLean et al. 2009; Barton 2006). In terms of more direct measures of cognition, there is robust evidence that variation in spatial memory skills in birds is related to ecology—in particular the degree to which a given species is dependent on caching, or storing food, in the wild (see Healy et al. 2005 for a review). However, there have been few studies comparing memory skills of multiple primates that differ in their ecology.

There is increasing evidence that certain cognitive abilities may covary with ecological niche in primates. For example, common marmosets (*Callithrix jacchus*) are obligate gummivores that gouge holes in trees and wait for sap to exude. Marmosets are more willing to wait temporal delays compared with cotton-top tamarins (*Saguinus*

oedipus), a closely related species that consumes sap in an opportunistic fashion (Stevens et al. 2005a, b; Rosati et al. 2006). Similarly, Golden lion tamarins (*Leontopithecus rosalia*) and Wied's marmosets (*Callithrix kuhli*), which exhibit similar differences in dependence on gummivory, show patterns of memory across different spatial and visual memory tasks that accord with the spatial and temporal properties of their respective food resources (Platt et al. 1996). Evidence from apes also supports the importance of ecology in understanding differences in cognitive skills. Chimpanzees (*Pan troglodytes*)—who are thought to face a more complex environment with more variable, patchy resources—show a suite of differences in value-based decision making compared with bonobos (*P. paniscus*; Rosati and Hare 2012b, 2013; Rosati et al. 2007; Heilbronner et al. 2008; Haun et al. 2011). Moreover, chimpanzees exhibit more accurate spatial memory for multiple locations than bonobos when searching for food in a naturalistic context (Rosati and Hare 2012a). However, gummivory is a relatively specialized niche, so it is difficult to extend results from callitrichids to other taxonomic groups, and the ecological differences between chimpanzees and bonobos are relatively subtle (as both are frugivores). Consequently, comparisons of spatial memory in primate species with broader differences in diet specialization are also critical to address this issue.

Strepsirrhines (lemurs, lorises, and galagos) are a particularly interesting group for testing predictions about cognitive evolution in primates because they exhibit high levels of diversity in many evolutionarily relevant characteristics, including sociality, activity patterns, and diet (Richard and Dewar 1991; Fichtel and Kappeler 2010). Malagasy primates in particular are a closely related monophyletic group (Horvath et al. 2008; Yoder et al. 1996) with substantial variation in both social structure and feeding ecology—including both obligate folivores and frugivores. In the current set of studies, we examine different components of spatial memory in Malagasy lemurs that vary in level of frugivory. Both black-and-white ruffed lemurs (*Varecia variegata*) and red ruffed lemurs (*V. rubra*, classed as *V. variegata* subspecies until recently; Mittermeier et al. 2008) are among the most highly frugivorous lemur species: their diets can exceed 90 % fruit (Britt 2000; Vasey 2005). Mongoose lemurs (*Eulemur monogoz*) and ring-tailed lemurs (*Lemur catta*) both exhibit mixed diets including fruit, seeds, leaves, flowers, nectar, and insects; fruit can range from 30 to 60 % of their diet (Sauther et al. 1999; Curtis 2004). Finally, Coquerel's sifakas (*Propithecus coquereli*) are primarily folivorous (Richard 1977) with a specialized gut structure that serves as an adaptation for the microbial fermentation of fibrous foods (Campbell et al. 2000). The ecological differences in these species have shaped other morphological

characteristics as well, including differences in their dentition (Cuozzo and Yamashita 2006). Overall, these robust differences in feeding ecology make these species a strong test case for ecological hypotheses.

There is currently little known about memory abilities in lemurs, likely reflecting the general paucity of studies of lemur cognition compared with that of anthropoids. Indeed, most studies of lemur memory to date have focused on mouse lemurs (*Microcebus murinus*), likely due to their use as a biomedical model for human aging (Luehrs et al. 2009; Picq 2007; Picq 1993; Languillea et al. 2012). In terms of the species focused on here, the majority of comparative studies with multiple species have focused on testing hypotheses about social complexity. For example, ring-tailed lemurs—who live in relatively large groups with complex hierarchies—are adept at using social cues such as gaze direction when competing for food, whereas mongoose lemurs, ruffed lemurs, and sifakas—who live in smaller, less complex groups—do not use such information (Sandel et al. 2011; MacLean et al. 2013; Bray et al. 2013). Similarly, ring-tailed lemurs are more skilled than mongoose lemurs when making transitive inferences, which might be useful for understanding dominance hierarchies (MacLean et al. 2008). Other studies of cognition in various lemur species have focused on such skills as the understanding of numerical quantities (Jones et al. 2013; Lewis et al. 2005; Santos et al. 2005; Merritt et al. 2007), decision making (MacLean et al. 2012b; Stevens and Muhlhoff 2012), or social cognition (Ruiz et al. 2009; Shepherd and Platt 2008; Genty and Roeder 2006; Anderson and Mitchell 1999). However, the majority of these studies either focused on only one species or did not directly compare different species due to constraints on sample size.

In the current studies, we examined spatial memory in ruffed lemurs, ring-tailed lemurs, mongoose lemurs, and sifakas. We targeted three components of spatial competency thought to be dependent on the hippocampus (following Newcombe and Huttenlocher 2006). In the first study, we assessed whether these species can recall the location of food after a long delay, as the hippocampus supports long-term memory for items in spatial contexts (Bird and Burgess 2008; Sluzenski et al. 2004; Davachi 2006). As animals in the wild must locate resources that are dispersed in time and space, this type of long-term memory is also crucial in foraging contexts (Luehrs et al. 2009; Janson and Byrne 2007; Platt et al. 1996). In the second study, we examined the frame of reference that lemurs used to recall locations. In particular, we directly contrasted whether lemurs used an allocentric (spatial) frame versus an egocentric (motor- or habit-based) frame to encode the location of food. While neurobiological studies indicate that spatial encoding is dependent on the hippocampus,

egocentric encoding is dependent on other brain regions such as the basal ganglia (Burgess 2006; Newcombe et al. 1998; Packard and Goodman 2013; Hampton et al. 2004). Finally, in the third study, we assessed whether lemurs could recall multiple locations, as the ability to navigate through multiple locations in the environment also utilizes hippocampal-based place learning (Sluzenski et al. 2004; Maguire et al. 1998; Morris et al. 1982). This study also served as more naturalistic context that is meant to better reflect the type of foraging situations faced by wild primates (Rosati and Hare 2012a; Menzel 1973). If ecological factors influence these spatial memory skills, we predicted that the frugivorous ruffed lemurs should consistently show higher levels of performance due to their greater dependency on patchily distributed food compared with the other three species. This difference should be particularly pronounced in contrast to the most folivorous sifakas.

Study 1: Memory after a long delay

In Study 1, we examined the ability of lemurs to recall the location of food over a long delay. In this task, the lemurs first learned that one wing of a T-shaped platform always provided food in an introductory session. In a test session 1 week later, we examined whether lemurs would recall which location had previously been baited.

Methods

Subjects

We tested 44 lemurs at the Duke Lemur Center in Durham, NC: 11 mongoose lemurs, 9 ring-tailed lemurs, 12 sifakas, and 12 ruffed lemurs (see ESM Table S1 for all subject details). All lemurs were naïve to searching for hidden food on platforms or in landmarks prior to the start of these studies. Animal husbandry and research practices were complied with the policies of the Duke Lemur Center in Durham, NC, USA. Lemurs were housed in pairs or groups at the Duke Lemur Center. Lemurs had access to indoor and outdoor rooms with a variety of climbing structures, and many also had access to semi-free-ranging forest enclosures. Lemurs were tested individually in a familiar room. Lemurs had ad libitum access to water during the sessions, were not food-restricted, and were fed a species-appropriate daily diet of fruit, vegetables, leaves, and chow. Subjects completed no more than one test session per day, and all tests were voluntary: if the lemur stopped participating, the session was halted. All behavioral studies were noninvasive and had IACUC approval from Duke University (No. A264-08-09).

General setup and apparatus

We tested the lemurs' memory for locations on a blue T-shaped platform (136-cm-long entry wing; 122-cm cross-wing; 72 cm high; see Fig. 1a). A small opaque cup (approximately 6 cm deep) was affixed to each of the cross-wings and could be baited with food. The setup was held constant across sessions.

Sessions and trial procedure

Each lemur completed three sessions. In the *pretest session*, subjects first experienced a 5-min *habituation period* where they could investigate the apparatus; during this time, both food cups were baited with food. They then completed 12 *food preference* trials to select preferred, species-appropriate foods for use in the main study (see below).

In the *introductory session,* lemurs first completed 2 *exposure trials* to familiarize lemurs with the basic setup. Here, both cups were baited, and an additional visible food piece was placed outside both cups to attract the lemur to the food cups and give them experience with retrieving food from both locations. Lemurs then completed 12 *learning trials* in which only one cup was baited (no visible food; side counterbalanced across subjects). On each trial, Experimenter 1 (E1) stood at the head of the platform, and Experimenter 2 (E2) centered the lemur at the entry wing position using a small piece of food (see Fig. 1a). The lemur was therefore always facing away from the cups, so they could not see the baiting process. While the lemur was turned away, E1 baited the cups in counterbalanced order (baiting the correct location and fake-baiting the incorrect location). She touched both cups with her hand in the same way to prevent any auditory cues, and both cups were also rubbed with food prior to the test to prevent olfactory cues. Once baiting was complete, E2 said "start" and removed the centering food so that the lemur would turn around to approach the cups. Both experimenters looked down while the lemur chose to prevent any social cuing. In learning trials, all lemurs completed 12 learning trials. Following previous work examining memory in rodents (Packard 1996, 1999, 2009), lemurs that initially approached the incorrect location could self-correct. That is, the trial continued (with the experimenters holding their position) while the lemur continued searching on the apparatus until they located the food on the correct side. This allowed us to ensure that all lemurs had equivalent experience with receiving the reward in the initial session.

One week later, subjects completed a *test session* with 10 *choice trials* (see Video S1) to assess their long-term recall. These trials were identical to learning trials, except
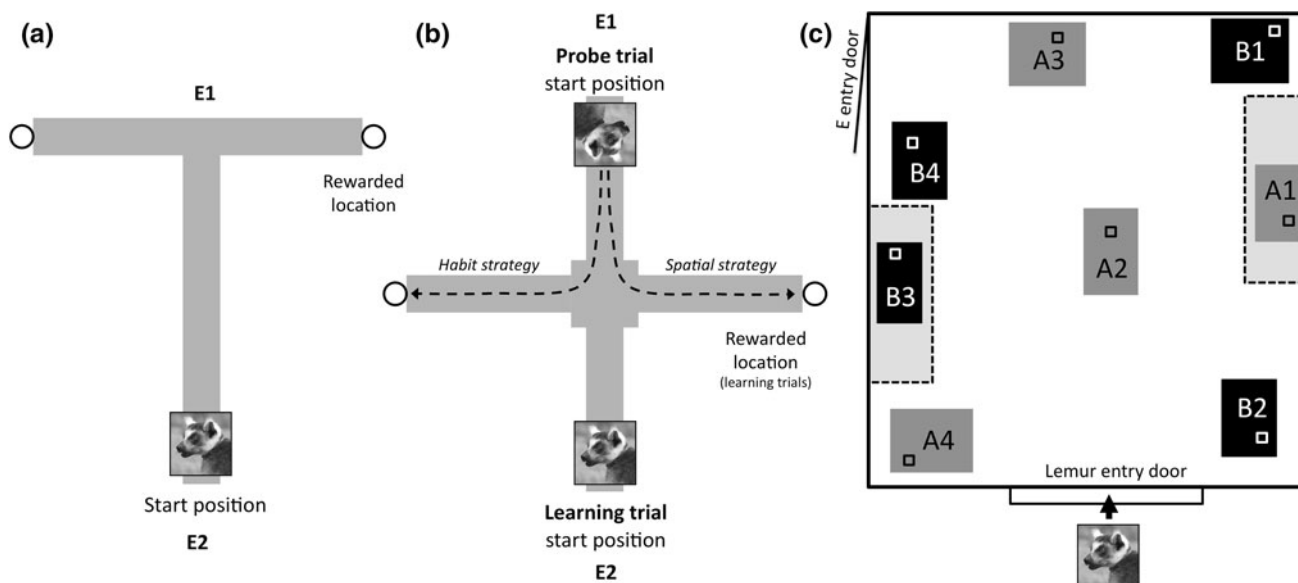
Fig. 1 Setup for studies. **a** In Study 1, lemurs first learned that a cup at the end of one wing on a T-shaped platform provided food. A week later, their memory for this location was tested. Experimenter 2 (E2) centered the lemur on each trial, and Experimenter 1 (E1) baited the locations. Small circles denote cups. **b** In Study 2, lemurs first learned that one wing of the cross-shaped platform provided food. In probe trials, they then approached from a flipped orientation to assess whether they had encoded the food's location (spatial strategy) or their own motor response (habit strategy). **c** In Study 3, lemurs were introduced to a room containing novel landmarks. Lemurs first experienced that one landmark set (A or B) contained visible food. After a delay, they were allowed to search, but now all locations were baited with hidden food. *Small squares* indicate the food boxes and *dotted lines* indicate raised platforms

that lemurs could not correct their choice. E1 therefore immediately removed the food from the correct cup if the lemur approached the incorrect cup initially.

Food preference pretest and reward manipulation

To assess whether lemurs exhibited improved memory in certain contexts, we also examined the effect of reward motivation, an important modulator of memory in both humans (Shohamy and Adcock 2010; Murty et al. 2011) and apes (Rosati and Hare 2012a). In particular, for the majority of trials in the introductory and test sessions, lemurs made choices about an intermediately preferred food type. The food type then changed on their last two introductory trials: here, they received either a more-preferred food (the positive condition) or a different intermediately preferred food (the neutral condition; condition assignment counterbalanced). Food assignments were based on an initial preference pretest conducted immediately after the habituation phase (see ESM). However, an initial set of analyses revealed no effect of this reward manipulation on either first test trial performance or overall performance across the test session (see ESM for all details). As this manipulation did not impact choices, and our main goal was to compare the species' abilities, we collapsed across reward condition in the main analyses.

Coding and data analysis

Lemurs had to approach a cup within 5 cm (lemurs typically moved directly toward one of the cups after reaching the center of the cross; see Video S1). Choices were coded live by the experimenters, and a coder blind to the correct side coded 20 % of sessions for reliability from video (agreement was 100 %).

We used two approaches in terms of analyzing the data. First, we examined first trial performance in the two sessions, as well as the lemurs' average performance across all trials, to assess whether their introductory session provided a memory benefit in the test session. Second, we used generalized linear mixed models (GLMM) to analyze test choices on a trial-by-trial basis while controlling for repeated measurements of the same subject (Bolker et al. 2008). We implemented models using the lme4 software package in the statistics program R (R Development Core Team 2011). These analyses also allowed us to assess the importance of different predictive factors and compare the fit of different models using likelihood ratio tests (LRT). Two lemurs (one ring-tailed lemur and one sifaka) stopped participating during the test session (but completed at least the first trial). Therefore, these individuals were not included in analyses that used mean performance over the test session.

Results and discussion

We first examined the lemurs' performance on their first trials in each session. We predicted that lemurs should exhibit chance performance in their first introductory trial (as they had not yet learned the baited location)—but should show a preference for the baited location in their first test trial if they recalled where they had located food 1 week previously. On their first *learning trial*, 24 of 44 lemurs chose correctly [binomial test: $p = 0.65$, n.s.], and no individual species differed from chance [$p > 0.18$ for all cases]. This indicates that in the absence of experience with the baited location, the lemurs could not detect the food's location using some other olfactory or auditory cue. However, on their first *test trial* 1 week later, 33 of 44 lemurs chose correctly, significantly above chance [binomial test: $p = 0.001$]. Breaking this down by species revealed that only ruffed lemurs were individually above chance on the first test trial [ruffed lemurs 12/12 chose correctly, $p < 0.001$; all other species: $p > 0.14$; see Fig. 2a]. A comparison of first trial performance in the most frugivorous ruffed lemurs relative to the other species (collapsing across the other species to reduce factors) further revealed that the ruffed lemurs were more likely to choose correctly on their first test trial compared the other lemurs [$\chi^2 = 5.50$, $df = 1$, $n = 44$, $p < 0.05$].

We next examined average performance across the two sessions (see Table 1 for means). These analyses accounted for two aspects of the lemurs' behavior: their learning within each session (across trials) and the impact of their initial experience in the introductory session on their performance in the test session 1 week later (memory after a long delay). In the introductory session, all four species selected the correct side above chance overall [one-sample t tests; ruffed: $t_{11} = 4.57$, $p = 0.001$; ring-tailed: $t_8 = 4.35$, $p < 0.005$; mongoose: $t_{10} = 3.75$, $p < 0.005$; sifakas: $t_{11} = 9.44$, $p < 0.001$], indicating that they were all capable of learning the correct location. However, there were differences in introductory session performance. A univariate GLM revealed a main effect of species [$F_{3, 40} = 5.44$, $p < 0.005$], and post hoc analyses indicated that sifakas outperformed both ruffed lemurs and mongoose lemurs [Tukey's tests: $p < 0.05$ for both cases].

Our main question, however, was whether their initial introductory session experience actually improved their later performance, indicating long-term memory. All species exhibited high levels of performance across all trials of the test session [ruffed: $t_{11} = 23.75$, $p < 0.001$; ring-tailed: $t_7 = 11.91$, $p < 0.001$; mongoose: $t_{10} = 4.30$, $p < 0.005$; sifakas: $t_{10} = 4.37$, $p = 0.001$; see Table 1 for means], and overall lemurs' performance was improved in the test session [paired t test: $t_{41} = 4.42$, $p < 0.001$]. Breaking this
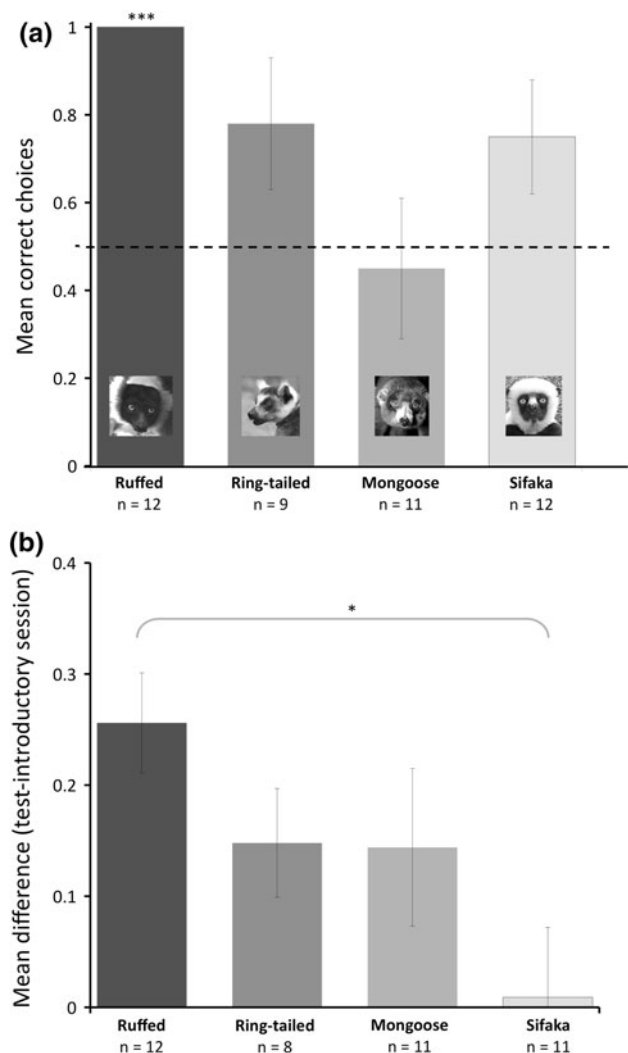

Fig. 2 Results from Study 1 (long delay). After completing an initial introductory session to learn about the location of food, lemurs completed a test session 1 week later to assess their memory for the baited location. **a** First test trial performance by species. **b** The benefit provided by memory: improvement between sessions by species. *Dashed line* indicates chance; *error bars* indicate standard error; *$p < 0.05$, ***$p < 0.001$

down by species, however, revealed that both ruffed lemurs [$t_{11} = 5.67$, $p < 0.001$] and ring-tailed lemurs [$t_7 = 2.99$, $p < 0.05$] significantly improved in the test session, mongoose lemurs showed a trend for improvement [$t_{10} = 2.02$, $p = 0.072$], but sifakas did not improve [$t_{10} = 0.14$, $p = 0.89$, n.s.]. To isolate the benefit provided by a lemur's initial learning experience to the test session performance, we calculated a difference score for each individual (percent correct in test session minus percent correct in introductory session). A univariate GLM revealed a main effect of species [$F_{3,38} = 3.16$, $p < 0.05$; see Fig. 2b], and post hoc tests revealed that ruffed lemurs showed more relative improvement than sifakas [Tukey's test, $p < 0.05$], but there were no other significant differences.

Table 1 Species' mean performance across the studies

Species	Study 1: long delay		Study 2: mechanisms		Study 3: multiple locations	
	Learning % correct	Test % correct	Learning % correct	Probe % spatial	Test locations	Control locations
Ruffed	70.1 ± 4.4	95.8 ± 1.9	94.9 ± 0.9	80.0 ± 4.4	2.50 ± 0.19	1.50 ± 0.19
Ring-tailed	79.6 ± 6.8	95.0 ± 3.8	87.5 ± 2.8	55.0 ± 8.2	2.33 ± 0.23	1.50 ± 0.26
Mongoose	62.9 ± 3.4	77.3 ± 6.3	87.1 ± 2.5	60.6 ± 9.3	2.27 ± 0.24	1.55 ± 0.21
Sifaka	86.8 ± 3.9	87.3 ± 8.5	96.2 ± 0.9	56.9 ± 9.4	1.67 ± 0.33	1.00 ± 0.27
Overall	74.8 ± 2.7	88.6 ± 3.1	92.0 ± 1.0	64.4 ± 4.1	2.19 ± 0.13	1.38 ± 0.12

Study 1 mean performance in learning and test trials. *Study 2* mean performance in learning trials, and spatial responses on probe trials. *Study 3* mean number of test and control pieces located in their first four approaches in the search phase

Finally, we used GLMM to model each individual test trial response as a binary outcome. Our first step was to fit a basic model including subject as a random factor, trial number (1–10) as a covariate, and proportion of correct learning trials as a covariate. Including trial number in the model allowed us to account for learning within the test session, and learning trial performance was included in the model to control for individual differences in the lemurs' within-session learning in the absence of long-term memory (note that all lemurs had equal experience with the correct location in the introductory session regardless of their initial choice, as they were allowed to self-correct following incorrect choices in the learning trials). Given our main hypotheses concerning differences between the species, we then added species as a factor (comparing ruffed lemurs with the others) in the second model. This full model revealed that trial number and introductory performance were both significant predictors of test trial success, but in addition revealed a strong trend for ruffed lemurs to make more correct test choices [estimate = 2.12, SE = 1.09, $p = 0.052$; see ESM Table S2 for all parameters from the full model]. Importantly, a comparison of the basic model to the full model revealed that including species as a factor significantly improved model fit [LRT: $\chi^2 = 4.26$, $df = 1$, $p < 0.05$], highlighting the importance of species as a predictor for the lemurs' success on test trials.

Overall, these results indicate that lemurs are capable of learning about the location of hidden food. In support of the ecological hypothesis, however, only ruffed lemurs chose correctly above chance on their first test trial after a one-week delay, and ruffed lemurs exhibited the greatest memory benefit in terms of relative improvement in the test session. Moreover, the GLMM analysis modeling test trial performance indicated that species was a significant predictor, even when accounting for an individual's introductory session performance as well as learning across trials. Importantly, this result does not mean the other species were unable to learn within a session—indeed, sifakas outperformed ruffed lemurs in the initial introductory session. However, comparisons across sessions revealed

that sifakas did not actually improve between the introductory and test session, suggesting their performance in the test session was driven by trial-and-error learning and not augmented by long-term recall.

These results highlight the fact that memory is actually composed of a set of interacting but distinct capacities (Sherry and Schacter 1987; Poldrack and Packard 2003). In particular, recalling the location of food on a trial-by-trial basis can be solved in two ways (Packard 2009; Packard and Goodman 2013; Burgess 2006). First, the lemurs could use a spatial strategy: recalling the specific location in space that the food is located (e.g., "the food is in that spot"). Alternatively, lemurs could use an egocentric or viewer-dependent strategy: remembering the set of motor movements needed to acquire the food (e.g., "turn left"). Indeed, studies indicate that these parallel memory systems are supported by different neurobiological substrates: whereas spatial strategies are dependent on the hippocampus, egocentric strategies are dependent on the basal ganglia, a region important for trial-and-error learning (Packard 1996, 1999; Poldrack and Packard 2003; Poldrack et al. 2001; Burgess 2008). One possibility is therefore that individual lemurs were encoding the food's location in the introductory session using different reference frames. This might account for the discrepancy between the sifakas' within- and between-session performance. For example, some lemurs might have been quite successful using a habit-based strategy to encode the food's location using trial-and-error learning within a session, but this strategy may have been less useful in terms of long-term memory over the delay. In contrast, the ruffed lemurs exhibited better long-term retention of spatial information. In Study 2, we therefore examined which type of memory system the different species of lemurs were relying on in this context.

Study 2: Memory mechanisms

In Study 2, we examined the memory mechanisms the lemurs were using to encode the location of food. Lemurs

first learned that one wing of a cross-shaped platform was consistently baited with food, similar to their experience in learning trials of Study 1. In the critical test, lemurs then searched on the platform starting from the opposite position (180°) relative to their original starting position. That is, we assessed their encoding strategy by flipping their orientation toward the potential food locations (following the basic procedure from Packard 1996). If lemurs encoded the place they found food via an allocentric strategy, they should search in the previously rewarded wing of the cross-platform—even though they must produce a new motor action to do so. If they encoded the food's location via an egocentric motor response, they should turn in the same direction—even though this now leads them to the opposite wing (a previously unrewarded location).

Methods

Subjects

We tested 48 lemurs from the same populations: 11 mongoose lemurs, 10 ring-tailed lemurs, 12 sifakas, and 15 ruffed lemurs (see ESM Table S1 for all subject details). Subjects who also completed Study 1 had a minimum break of one month between the studies and were tested with the new apparatus in a different room or new spatial arrangement in their home room to reduce any possible similarity between the two studies.

General setup and apparatus

We used the same general setup as in Study 1, except that the main apparatus was a red, cross-shaped platform (each wing was 74 cm in length, standing on legs 72 cm high).

Sessions

Lemurs completed six sessions, each with 13 trials. In the initial 12 *learning trials*, lemurs began from the starting position and learned that food was consistently located in one of the two cups on the side wings. At the end of each session, lemurs completed one *probe trial* where they had to locate the food starting from a flipped perspective, opposite their normal starting position (see Fig. 1b). Here, both locations were baited so as to not bias the lemur on subsequent probe trials. We used species-appropriate foods across all trials: ruffed lemurs, mongoose lemurs, and ring-tailed lemurs were tested with grape halves, and sifakas were tested with peanut halves. During the first two learning trials of the first session only, E1 placed an additional piece of visible food outside the baited cup to ensure that lemurs quickly learned the baited location, as our primarily interest was their probe trial performance.

Also, at the beginning of their first session only, subjects completed a 5-min habituation period (identical to that in Study 1) to familiarize them to the apparatus prior to the start of the test.

Trial procedure

We used a similar procedure as in Study 1. In the first 12 *learning trials*, E2 centered the lemur so that the lemur initially faced away from the cups as in Study 1. Here, E1 also held an occluder at the middle of the apparatus, while she fake-baited and baited the two cups. When E1 said "start," she moved the occluder to the center of the wing opposite the lemur to prevent the lemur from walking on that part of the apparatus (e.g., to ensure they would turn into one of the side wings rather than walk to the opposite wing). As in Study 1, if lemurs chose incorrectly on learning trials, they were always allowed to correct their choice two ruffed lemurs were tested with a slightly modified baiting procedure where E2 stood outside the testing room; additional analyses indicated that these individuals performed similar to the other ruffed lemurs and that removing these individuals reveal equivalent results (see ESM for details).

Subjects then completed one *probe trial* at the end of each session. These trials were identical to learning trials, except that subjects' starting position was flipped (see Video S2). Prior to the start of the probe trial, the experimenters switched positions (keeping the experimenter role constant), and then E2 attracted the lemur to the other side of the apparatus. Consequently, the lemur was then at a starting position directly opposite of the starting position in learning trials. As the apparatus itself was symmetrical and therefore looked identical from both positions (see Fig. 1b), only the lemur's orientation in the room was changed, as in previous work using this setup (Packard and Goodman 2013; Packard 1996, 1999, 2009). Here, E1 baited both locations with food and immediately removed the alternative piece of food once the lemur had made its choice.

Coding and data analysis

Choices were coded live by the experimenters following the same procedure for Study 1. A coder blind to the correct side coded 20 % of sessions from videotape for reliability; agreement was 100 %. We used the same basic approaches as in Study 2 to analyze the data. Four lemurs did not complete all six sessions because they either stopped participating or became ill (one completed five sessions and three completed four sessions). As we found no change in probe trial performance across sessions (see results), we averaged the data for those subjects when relevant.

Results and discussion

We first examined performance in learning trials. Overall, lemurs chose correctly on 92.0 ± 1.0 % of learning trials (see Table 1 for means). Each species was significantly above chance in choosing the correct side [ruffed: $t_{14} = 49.57$, $p < 0.001$; sifakas: $t_{12} = 51.03$, $p < 0.001$; ring-tailed: $t_9 = 13.35$, $p < 0.001$; mongoose: $t_{10} = 14.81$, $p < 0.001$], indicating that they all learned the correct location. A univariate GLM revealed a main effect of species [$F_{3,45} = 7.24$, $p < 0.001$]; post hoc tests indicated that while ruffed lemurs and sifakas did not differ in performance, both were correct significantly more often than mongoose lemurs and ring-tailed lemurs [Tukey's test: $p < 0.05$ for all significant cases]. In the second analysis, we compared performance across the study with session (one to six) as a within-subjects factor and species as a between-subjects factor (for subjects who completed all six sessions). As in the previous analysis, there was a main effect of species [$F_{3,41} = 6.51$, $p < 0.001$]; post hoc tests showed that ruffed lemurs and sifakas choose correctly significantly more often than mongoose lemurs and ring-tailed lemurs [Tukey's test, $p < 0.05$ for all significant cases]. In addition, there was a main effect of session [$F_{5,205} = 16.12$, $p < 0.001$]; planned linear contrasts revealed that the lemurs increased in performance across sessions, as would be expected with more experience [$F_{1,41} = 43.01$, $p < 0.001$]. Importantly, there was no interaction between species and session number [$p > 0.65$, n.s.], indicating similar levels of improvement across all four species. Overall, these results indicate that there were differences in learning trial performance, with ruffed lemurs and sifakas outperforming mongoose and ring-tailed lemurs. This is similar to the results from Study 1, where sifakas learned the location of the baited food more quickly than the other species. Importantly, however, all species showed high levels of correct choices in the task.

We next examined performance on probe trials. Across all species, lemurs made a spatial response on 64.4 ± 4.1 % of trials [$t_{48} = 3.54$, $p = 0.001$; see Table 1 for means]. Breaking this analysis down by species revealed that while ruffed lemurs chose the spatial option above chance [$t_{14} = 6.87$, $p < 0.001$], the other three species did not [$p > 0.28$, n.s. in all cases]. Indeed, this pattern was apparent even from the first probe trial (see Fig. 3a): only ruffed lemurs chose the spatial location above chance [binomial test: 13/15 choices for the spatial option, $p < 0.01$; $p > 0.55$, n.s., for all other species]. We then used average probe performance to classify the learning strategy of each individual lemur. Lemurs that made a spatial response more often than habit-based responses were classified as spatial learners, lemurs that made a habit-based response more often than spatial responses were classified as habit learners, and lemurs that made both types of responses equally were classified as having no preference. This revealed that ruffed lemurs were generally spatial learners (87 % of individuals showing a spatial preference), and none were habit learners. In contrast, only 56 % of the individuals in the other three species were spatial learners, and 29 % were actually habit learners (see Fig. 3b). We then examined the number of individuals using a spatial strategy, comparing the ruffed lemurs to the others (collapsing across species given their similar performance). This revealed that the ruffed lemurs were more likely to exhibit a spatial learning strategy than the other species [$\chi^2 = 4.35$, $df = 1$, $n = 49$, $p < 0.05$].

Finally, we used GLMM to model each individual probe trial response as a binary outcome. Our first step was to fit a basic model including subject as a random factor, session number (1–6) as a covariate, and proportion of correct learning trials in that session as a covariate. Session number allowed us to assess whether there were any shifts in probe trial performance over time, and learning trial performance was included in the model to control for the possibility that the lemurs' performance in the immediately proceeding session predicted their probe choices (note that all lemurs had equal experience with the correct location regardless of their initial choice, as they were allowed to self-correct following incorrect choices in the learning trials). This model revealed that none of these factors were significant predictors of the lemurs' choices. In the second model, we added species as a factor (comparing ruffed lemurs to the others) to assess whether this was a significant predictor. This revealed ruffed lemurs were significantly more likely to make spatial responses [estimate = 1.25, SE = 0.43, $p < 0.005$; see ESM Table S3 for all parameters from the full model]. Moreover, comparing the basic model to the full model revealed that including species as a factor improved model fit [$\chi^2 = 8.22$, $df = 1$, $p < 0.005$].

These results suggest that the different species' memory was supported by different mechanisms for encoding spatial frameworks. While all four species showed high levels of correct responses in learning trials, sifakas and ruffed lemurs outperformed mongoose and ring-tailed lemurs. Similar to the results in Study 1, this supports the idea that ecology is not necessarily a strong predictor of how successful the different species are at trial-by-trial learning within a session. However, the probe trials revealed differences in the specific type of learning mechanisms that the different species used in this context: whereas ruffed lemurs primarily used a spatial strategy, the other species showed a mixture of spatial and habit-based strategies. This difference in the type of reference frame that the different species used may account for the differences in long-term retention seen in Study 1.
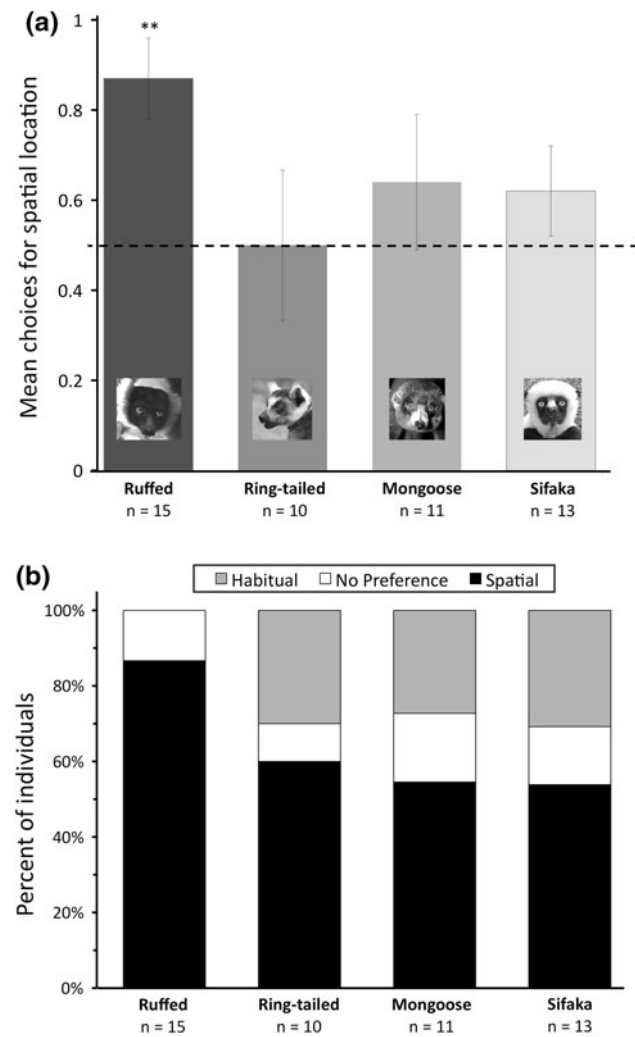
Fig. 3 Results from Study 2 (memory mechanisms). After completing initial learning trials, lemurs completed probe trials (from a flipped orientation) to assess their strategy. **a** First probe trial performance by species. **b** Individual strategies (spatial bias, no preference, or habit bias) across probe trials by species. *Dashed line* indicates chance; *error bars* indicate standard error; **p < 0.01
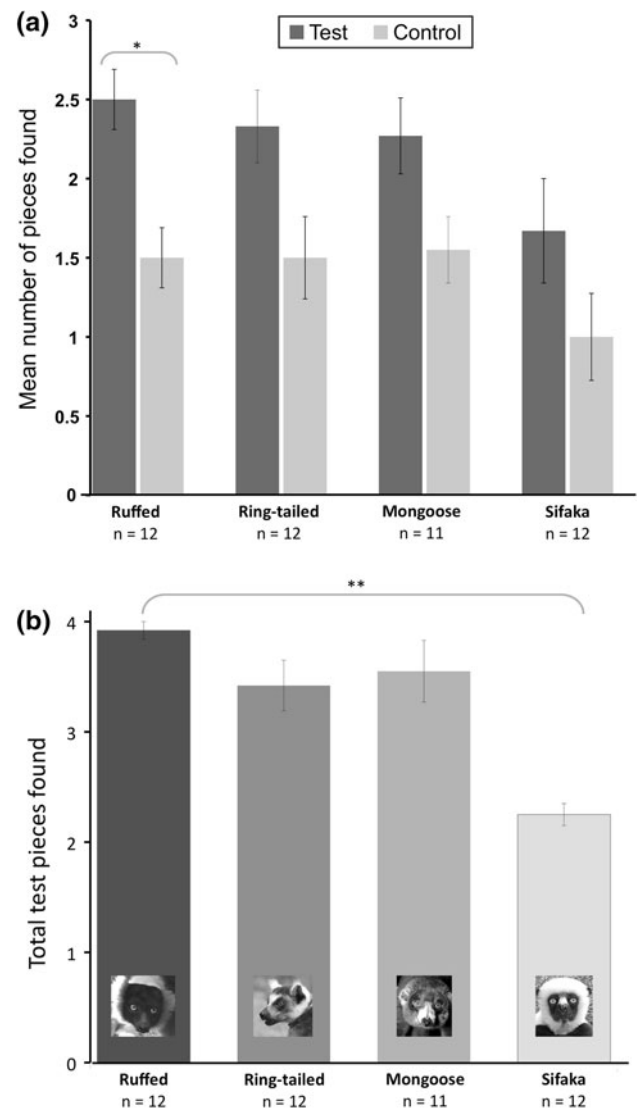

Fig. 4 Results from Study 3 (multiple locations). Lemurs were introduced to a room containing novel landmarks, some of which marked the location of food. After a delay, they could search for hidden food at the same locations. **a** Number of test versus control piece found in the first four searches. **b** Total number of test locations searched. *Error bars* indicate standard error; *p < 0.05, **p < 0.005

Study 3: Memory for multiple locations

In Study 3, we examined the lemurs' ability to recall multiple locations in space. Based on the results from Study 2, we predicted that the ruffed lemurs would be more skillful when faced with a more complex environment involving multiple locations, where a habit-based strategy would likely be less useful. In this study, we therefore adapted methods from a previous study with apes (Rosati and Hare 2012a) to examine the lemur's memory in a more complex environment. Each lemur completed one session where they searched for food in a room with eight novel landmarks. In the *introduction phase*, four *test landmarks* were baited with visible food; the *control landmarks* were empty. In the *search phase* 10 min later, both the test and

control landmarks were baited with hidden food. We examined whether lemurs preferentially searched at the test locations where they had previously found food. We were particularly interested in this ability to recall multiple locations in this more naturalistic context.

Methods

Subjects

We tested 47 lemurs from the same populations: 11 mongoose lemurs, 12 ring-tailed lemurs, 12 sifakas, and 12

ruffed lemurs (see ESM Table S1 for subject details). All lemurs were naïve to the landmarks used in the study.

General setup and apparatus

We placed eight novel landmarks in the test room (approximately 214 cm wide by 230 cm long). The landmarks were placed in the same approximate arrangement in the room relative to the entry door (see Fig. 1c). Each had a distinct form and color, and attached to each landmark was a small box that could be baited with visible food (with boxes approximately 5 cm^3), or covered with a removable lid so that the food was hidden (see ESM Figures S1 and S2 for photographs of all landmarks and the food boxes). Landmarks were divided into two sets (A and B) of similar distance to the lemurs' entry door, and set assignment as test or control was counterbalanced across subjects. The lemur's entry door to the room was approximately 3ft off the ground for the majority of subjects and could be opened by the experimenter outside the rooms by sliding a panel (see Video S3). As in Study 2, sifakas we tested with peanuts and the other species with fruit.

Session phases and procedure

Each lemur was tested in one session to assess their spontaneous memory. The test had three main phases, and lemurs waited in an adjacent room between phases.

Habituation phase: The lemurs entered the test room and could investigate the landmarks (here none were baited) in order to acclimate them to the novel objects. After 5 min, they returned to the waiting room.

Introduction phase: Once the lemur had returned to the waiting room, E entered the test room and baited the four test locations with visible food (e.g., with no lid). E also fake-baited the four control locations (rubbing them with the food to prevent olfactory cues) in a randomized order. Once the baiting was complete, E opened the door between rooms so the lemur could enter the test room, where they had 10 min to search for food. If the lemur did not locate all of the food during this time, then E entered the room and attracted their attention by visibly placing a very small piece of food next to the food box. This procedure ensured that all lemurs had experienced getting food at all four test locations. Lemurs then returned to the waiting room.

Search phase: Lemurs remained in the waiting room or a 10-min memory delay (timed with a stopwatch). At the beginning of this period, E entered the test room and baited all eight locations (order randomized), but here covered the food boxes with the lid so that the food was not directly visible. After the 10-min delay concluded, the lemur could enter the room again for the search phase. Lemurs again had 10 min to locate the food (see Video S3).

Coding and data analysis

The experimenter coded the order in which the lemur found the food in the introduction and test phases live. Searches were counted as taking the food from baited locations, or approaching a non-baited control landmark with the lemur's head oriented toward the food box within a 5-cm distance. The experimenter also confirmed the presence or absence of food at all of the locations at the end of each phase. A coder blind to the assignment of the landmarks coded 20 % of sessions from videotape for reliability, which was excellent for the number of locations searched [Cohen's kappa = 0.94] as well as the order of those searches [Spearman's rho = 0.99]. As there were few trials in this study, we first used nonparametric statistics to examine the lemur's performance. We then used the lm function in R to examine the lemurs' performance in the search phase using hierarchical multivariate regression and compared models using F-tests.

Results and discussion

We first examined the lemurs' approaches toward test versus control locations. We predicted that if lemurs did recall multiple locations, they should locate more test pieces of food than control pieces (after they had already experienced which locations were baited). To control for any potential differences in speed or motivation to search across individuals, we analyzed only the first four locations that lemurs approached. That is, an individual with perfect memory should first target the four test pieces, even if they then continue to search for any remaining time (following the approach used in Rosati and Hare 2012a). In the search phase, lemurs located an average of 2.19 ± 0.13 test pieces, but only 1.38 ± 0.12 control pieces [Wilcoxon signed-rank test, $n = 47$, $T+ = 21$, 23 ties, $Z = 3.45$, $p = 0.001$]. In contrast, in the initial introduction phase, they exhibited only a weak bias toward test locations [$n = 47$, $T+ = 16$, 22 ties, $Z = 1.67$, $p = 0.094$, n.s.] despite the fact that the food was actually *visible* during that phase (note that the lemurs' entry door was raised off the ground, which likely increased the food's visibility from afar). This suggests that lemurs recalled where they had found food in the introduction phase, and used this information to target test locations in the search phase. Breaking this down by species, no species individually targeted test pieces in the introduction phase [$p > 0.15$, n.s., in all cases]. In the search phase, ruffed lemurs individually targeted test pieces [ruffed lemurs: $n = 12$, $T+ = 5$, 7 ties, $Z = 2.12$, $p < 0.05$], whereas the others did not [$p > 0.096$ for each other species]. This suggests that ruffed lemurs were the most accurate at recalling the locations where they had originally found food (see Fig. 4a).

Next, we examined the first location that the lemurs approached, as a first approach toward a test location in the search phase would indicate that they recalled the baited location (even if subsequent searches were based on their proximity to the next nearest location). Overall, 32 of 44 individuals (who found at least one piece) first targeted a test location in the search phase [binomial test, $p < 0.005$]. This indicates that overall, lemurs were biased toward previously baited locations. Notably, the three individuals who found no food (of either type) in the test phase were all sifakas. Breaking down this analysis by species revealed that while individual ruffed lemurs targeted test locations above chance on their first search [10/12 searched in test locations; $p < 0.05$], no other species did [$p > 0.18$, n.s. for each other species]. That is, only ruffed lemurs individually first approached a test location in the search phase.

We then examined the total number of test pieces located. This analysis allowed us to examine any motivational differences across species in willingness to search the room or acquire food, as such motivation differences should also manifest in the initial introduction phase where the food was visible. On average, lemurs found 3.21 ± 0.16 test pieces on their own (e.g., without the additional assistance of the experimenter) in the *introduction phase*, with no difference across species in terms of the number of test pieces located [Kruskal–Wallis test: $\chi^2 = 5.51$, $df = 3$, $p > 0.13$, n.s.]. That is, the species all found comparable pieces of food in the introduction phase where food was visible, suggesting that the species were equally motivated to search and eat the food as long as they did not have to use memory to locate it. However, there was a significant effect of species on number of test pieces found in the *search phase* [Kruskal–Wallis test: $\chi^2 = 13.73$, $df = 3$, $p < 0.005$; see Fig. 4b]. In particular, ruffed lemurs located an average total of 3.92 ± 0.08 test pieces, mongoose lemurs located 3.55 ± 0.28, ring-tailed lemurs located 3.42 ± 0.23, and sifakas located 2.25 ± 0.45 total test pieces. Pairwise comparisons of the four species (with Bonferroni correction) revealed that ruffed lemurs found significantly more test pieces overall than sifakas [Mann–Whitney U: $z = -3.30$, $p < 0.005$]. That is, when the food was hidden such that lemurs had to use their recall to locate it, ruffed lemurs were more successful than sifakas.

Finally, we used multiple regression to examine the influence of species (ruffed lemurs versus the others) on the total number of test pieces that the lemurs found in the search phase. This approach allowed us to account for the number of test pieces lemurs located in the introductory phase (to control for any individual differences in motivation to search the room) as well as the landmark set assignment for a given individual (to control for any intrinsic biases for preferred locations in the testing room).

We first implemented a basic model with landmark set (A or B) and introductory performance as predictors. In the second model, we also added species as a predictor. This full model predicted lemurs' search phase performance [$F_{3,43} = 3.52$, $p < 0.05$]. While landmark set was not a significant predictor, there was a trend for the number of test pieces found in the search phase to increase with higher introductory performance [estimate $= 0.25 \pm 0.14$, $t_{43} = 1.80$, $p = 0.079$]. That is, although intrinsic location biases did not seem to influence the lemurs' performance, lemurs who found more test pieces on their own in the introduction also found more in the memory test. Finally, species also influenced search phase performance, as ruffed lemurs found more test pieces than the other species [estimate $= 0.74 \pm 0.36$, $t_{43} = 2.04$, $p < 0.05$]. Moreover, comparison of the basic and full models revealed that including species as a factor improved model fit [$F_{2,43} = 4.17$, $p < 0.05$]. That is, species influenced the lemurs' success at locating test pieces in the search phase, even when accounting for potential differences in introductory phase behavior.

General discussion

We conducted three studies targeting different components of primate spatial memory. Our results indicate that strepsirrhines possess many of the important spatial capacities seen in other primates—including memory after long delays, encoding items using a spatial framework, and remembering multiple locations in a complex environment. Our results also indicate that there are important differences in how different lemur species solve spatial problems. In Study 1, ruffed lemurs were the only species to individually recall the baited location on the first test trial after a long delay, and they tended to outperform the other species in the test session when controlling for introductory session performance. In Study 2, ruffed lemurs mostly used a spatial strategy to encode the food location, whereas the other three species exhibited a mixture of both spatial and habit-based strategies. Finally, in Study 3, only ruffed lemurs targeted test locations on their first search and found more test than control pieces. Ruffed lemurs also located more test pieces overall, even when controlling for motivational differences. These results support the predictions of the ecological hypothesis: the most frugivorous species have the most accurate spatial memory, particularly in comparison with the highly folivorous sifakas. Importantly, these studies involved individuals who were both naïve to the spatial memory tasks and had been reared in similar captive environment with food provisioning. Consequently, the memory differences seen here are unlikely to be due to the species having different experiences with foraging over

development (Tomasello and Call 2011), as might be the case with wild individuals who live in different ecological contexts. Overall, these results suggest that these lemur species may inherently differ in their memory capabilities even when living in similar environments.

Critically, these results do not indicate that the other species cannot learn and remember information. Indeed, in Study 1, sifakas exhibited the highest levels of trial-by-trial learning within sessions, and in Study 2, both ruffed lemurs and sifakas outperformed mongoose and ring-tailed lemurs in learning trials. However, this evidence *does* suggest a difference in the extent to which lemurs utilize the types of memory thought to be supported by the hippocampus (as evidenced especially by differences in the use of spatial encoding frameworks by the different species in Study 2). However, it is important to note that there may be important individual differences in the use of these strategies. For example, while ruffed lemurs favored spatial strategies in Study 2, the other species showed a mixture of spatial and habit-based strategies. Thus, larger sample sizes will be important in future studies disentangling cognitive differences in lemurs. Moreover, research with both humans and animals indicates that hippocampal-dependent spatial strategies and basal-ganglia-dependent habit strategies exist in parallel and can influence behavior depending on context (Newcombe and Huttenlocher 2006; Burgess 2008, 2006). For example, rodents that experience extended periods of training in a plus-maze task show a switch in their response to probe trials over time: initial responses tend to be allocentric, but egocentric responses increase with repetition (Packard 1996, 1999). Similarly, environments with an abundance of landmarks tend to favor the use of hippocampal-based spatial strategies, whereas more homogenous environments favor habit-based strategies (Packard and Goodman 2013). Thus, future research could systematically vary these contextual factors to examine whether these patterns of species differences hold across different situations. For example, our results from Study 3 cannot address the extent to which lemurs actually used landmarks (as lemurs could have simply used place memory without recalling specific landmarks). A comparison of these species' memory for multiple locations in the absence of distinct landmarks could therefore assess the landmarks' importance in the different species' memory abilities.

Comparative research on cognitive and brain evolution in primates has often focused on the importance of complex sociality (Jolly 1966; Dunbar 1998; de Waal 1982; Byrne and Whiten 1988). In terms of memory evolution, there are reasons to suspect that complex sociality might indeed be an important factor. For example, human neuroimaging studies have revealed broad overlap in the brain regions supporting both social cognition and hippocampal-based memory

abilities (Buckner and Carroll 2007). Cognitive studies in the domains of social cognition and memory in both corvids and apes also suggest some evolutionary coherence in these skills (Emery and Clayton 2004). Yet the ring-tailed lemurs—who live in large groups with anthropoid-like dominance hierarchies (Sauther et al. 1999)—did not consistently outperform the other species in the current studies. Indeed, their skills were generally similar to those seen in mongoose lemurs, a closely related species with similar diet but much smaller pair-bonded social groups (Curtis and Zaramody 1999). This contrasts with the social–cognitive abilities seen in these species, as ring-tailed lemurs are more skilled than mongoose lemurs at making transitive inferences that might be useful for understanding dominance hierarchies (MacLean et al. 2008) and are the most adept at social cues such as gaze direction when competing for food (Sandel et al. 2011; MacLean et al. 2013).

Together, this suggests that while social complexity may be an important predictor of skills used in social interactions, ecology may be a more important predictor of cognitive skills used predominantly in foraging contexts, such as spatial memory. However, future studies should take advantage of recently resolved evolutionary relationships among these species (Horvath et al. 2008) to examine spatial memory in a wider cross section of strepsirrhines using phylogenetic methods (MacLean et al. 2012a). While the current studies targeted species with large variation in their diet, sampling a broader range of species including other folivores and frugivores can assess the importance of evolutionary factors while also controlling for any effect of shared lineage. For example, a comparison of six species of lemurs on social and nonsocial tasks indicated that a strong relationship was found between group size and social cognition after controlling for phylogeny, but there was no such relationship between group size and nonsocial cognitive skills (MacLean et al. 2013). In the future, such phylogenetic approaches can therefore directly contrast the relative importance of sociality and ecology. More generally, these results suggest that social and ecological factors are complementary explanations for variation in cognitive abilities, not mutually exclusive hypotheses.

A final question for future research concerns the relationship between the memory abilities examined here and their neurobiological substrates. Neuroecology, or the study of the adaptive variation in cognition and the brain, assumes that cognitive and neurobiological traits are shaped by natural selection much like morphological traits (Sherry 2006; Shettleworth 2010; Krebs and Davies 1997). This approach has been largely successful in explaining the relationships between natural history, memory abilities, and hippocampal volume in birds (Balda and Kamil 1989; Bednekoff et al. 1997; Kamil et al. 1994; Garamszegi and Eens 2004; Krebs et al. 1989; Healy et al. 2005). It is important to note that the

current studies did not assess neurobiological measures, so it is currently unclear whether this type of neuroecological approach can also be used to understand spatial memory in primates. While there have been studies of overall brain size in lemurs (e.g. MacLean et al. 2009), to our knowledge, there have not been studies specifically comparing hippocampus size or medial temporal lobes in these strepsirrhine species. These types of investigations will be critical for understanding the neurobiological basis of lemur spatial memory. Given the ongoing debate concerning homology between the structure of avian and mammalian brains (Avian Brain Nomenclature Consortium 2005), these types of investigations linking cognition, brain substrates, and natural history in multiple taxa will also illuminate broader patterns of brain evolution. That is, such studies can illuminate how brain structures change to enable different cognitive functions across species.

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