The evolution of cognitive control in lemurs

Francesca De Petrillo[1,3]*, Parvathy Nair[1], Averill Cantwell[1], and Alexandra Rosati[1,2]

[1]Department of Psychology
[2]Department of Anthropology
University of Michigan
530 Church St
Ann Arbor, MI 48109 USA
*Francesca.De-Petrillo@newcastle.ac.uk

[3]School of Psychology
Newcastle University,
Newcastle upon Tyne, NE2 4DR, England, UK

Abstract

Cognitive control, or executive function, is a key feature of human cognition, allowing individuals to plan, acquire new information, or adopt new strategies when the circumstances change. Yet it is unclear which factors promote the evolution of more sophisticated executive function abilities like those possessed by humans. Examining cognitive control in non-human primates, our closest relatives, can help to identify these evolutionary processes. Here we developed a novel battery to experimentally measure multiple aspects of cognitive control in primates: temporal discounting, motor inhibition, short-term memory, reversal learning, novelty responses, and persistence. We tested lemur species with targeted, independent variation in both ecological and social features (ruffed lemurs, Coquerel's sifakas, ring-tailed lemurs and mongoose lemurs, N=39 lemurs), and found that ecological rather than social characteristics best predicted patterns of cognitive control across these species. This highlights the importance of integrating cognitive data with species' natural history to understand the origins of complex cognition.

Key words: executive function; comparative cognition; primates; cognitive evolution

Statement of Relevance

Cognitive control is a set of regulatory cognitive mechanisms that underpin flexible, intelligent behavior in humans and other animals. Capacities for cognitive control vary across species, but why these differences in cognitive abilities have evolved is unclear. Most comparative work to date has used brain size as a proxy for cognition, limiting our understanding of the evolution of specific cognitive skills. We therefore tested lemurs from four species on a novel battery of tasks tapping into multiple components of cognitive control, and then evaluated whether species' social system or their ecological characteristics predicted enhanced cognitive control. We found that ecological rather than social complexity best predicted cognitive control across multiple components of cognitive control. These results indicate that species' feeding ecology plays a crucial role in shaping cognitive evolution, in contrast to prevailing views that social complexity is the primary driver of intelligent behavior.

1. Introduction

Cognitive control (also known as executive function) is a set of top-down processes including inhibition, updating, and working memory (Diamond, 2013; Friedman & Miyake, 2017). These regulatory cognitive processes enable flexible, goal-directed behaviors and reflect a key distinction between more 'reflexive' responses, versus overcoming immediate reactions to modulate behavior in service of an overarching goal. These processes are thus benchmark components of intelligent behavior that allow individuals to adjust their actions, so they are appropriate in their current context. These cognitive abilities are further thought to be especially elaborated in humans, both because our species appears to show highly flexible behavior compared to other animals (Laland & Seed, 2021), and because cognitive control recruits brain regions like prefrontal cortex which are evolutionarily labile in primates and expanded in humans specifically (Bush & Allman, 2004; Schoenemann, 2006).

Why does robust cognitive control sometimes emerge across species, such as in humans? There are two major hypotheses for the emergence of intelligent behavior. The *social intelligence hypothesis* is the dominant view, and proposes that social complexity drives cognitive evolution (Byrne & Whiten, 1988; Dunbar, 1998; Moll & Tomasello, 2007; van Schaik & Burkart, 2011). Various social challenges such as maintaining multiple relationships in a large, complex group, out-competing others, and cooperating or learning from others have all been proposed to select for larger brains and enhanced cognition (Dunbar, 1998; Byrne & Whiten, 1988; Moll & Tomasello, 2007; van Schaik & Burkart, 2011). In contrast, the *ecological intelligence hypothesis* posits that ecological challenges spur cognitive evolution. For example, relying on foods that have a more heterogenous spatial or temporal distribution or experiencing environmental fluctuation may select for more sophisticated cognitive capacities to track resources in the environment (Milton, 1981; Van Woerden et al., 2010; DeCasien et al., 2017; Rosati, 2017b). While the social hypothesis has predominated for several decades, there is increasing support for the ecological hypothesis, as both larger brains as well as some cognitive features are best predicted by diet (Powell et al., 2017; DeCasien et al., 2017; Rosati, 2017a).

However, prior tests of the social and ecological hypotheses have been limited in several respects. First, a dominant approach has been to use brain size as a proxy for cognition rather than direct assessments of cognition (Dunbar, 1998; DeCasien et al., 2017), but broad neuroanatomical measures are only an approximate index for specific cognitive traits (Logan et al., 2018). Direct tests of cognition have heavily focused on individual species, or pairs of species, which limits evolutionary inferences (e.g., Rosati et al., 2007; Wobber et al., 2010; Rosati & Hare, 2012; Rosati, 2017b). Some studies have tested multiple species to understand the evolution of intelligence. For example, a study of 23 primates showed that species with greater dietary breadth, but not those living in larger groups, exhibited greater motor inhibitory control (MacLean et al., 2014), whereas another study tied inhibitory control to fission-fusion social systems (Amici et al., 2008). However, these studies focused primarily on motor inhibition, whereas research from cognitive science and neurobiology shows that cognitive control is a multidimensional set of processes that also includes flexible updating and planning (Diamond, 2013; Friedman & Miyake, 2017; Völter et al., 2018).

Here, we aim to bridge this gap by examining the evolution of cognitive control across primates varying in social and ecological complexity. We developed a battery of cognitive tasks measuring motor inhibition, delay of gratification, short-term memory, and shifting, which have been identified as the core, partially-dissociable components of executive function in studies of adult humans and children (Miyake et al., 2000; Wiebe et al., 2011; Diamond, 2013; Friedman & Miyake, 2017; Karr et al., 2018). We drew on the methods of recent work using a battery of tasks

to assess multiple aspects of cognition in tandem on animals (e.g., Herrmann et al., 2007; Schmitt et al., 2010; Joly et al., 2017; Fichtel et al., 2020) to implement tasks that have been also well-validated in prior studies of nonhuman primates (Deaner et al., 2006; Rosati et al., 2007; Amici et al., 2008, 2010; MacLean et al., 2014). We then used this battery to examine cognitive control in primates with clear variation in both social and ecological characteristics. Importantly, both the social and ecological hypotheses provide plausible pathways for the emergence of cognitive control: flexible adoption of new behavioral strategies could provide an advantage in ecological contexts, such as by allowing individuals to adjust to changing environmental circumstances (MacLean et al., 2014), but also in social contexts by allowing individuals to deal with a shifting social landscape due to others' unpredictable behaviors (Amici et al., 2018).

In a preregistered study, we examined cognitive control in four lemur species. Lemurs are an important taxonomic group for understanding cognitive evolution, as they exhibit high levels of evolutionary diversity in both social and ecological features, even in closely-related species (Richard & Dewar, 1991; Fichtel & Kappeler, 2010; Rosati, 2017a). We specifically selected lemur species that exhibit targeted, independent variation in both social and ecological characteristics to test alternative pathways for the emergence of cognitive control. Ruffed lemurs (*Varecia* spp.) are among the most highly frugivorous of lemurs, with diets that can exceed 90% fruit (MacLean et al., 2014; Vasey, 2005). In contrast, Coquerel's sifakas (*Propithecus coquereli*) are obligate folivores (leaf-eaters) with specialized dentition and gut structure for digestion of fibrous leaves (Campbell et al., 2000; Greene et al., 2018). Whereas fruits are a spatially- and temporally-variable resource, leaves are homogeneously-distributed and thus less cognitively demanding (Milton, 1981; Rosati, 2017). Yet both of these taxa live in medium-sized family groups (ruffed mean group size: 6.1; sifaka mean group size: 5.4; MacLean et al., 2009, 2013, 2014), thus showing similar social characteristics. Conversely, both mongoose lemurs (*Eulemur monogoz*) and ring-tailed lemurs (*Lemur catta*) exhibit intermediate diets with a mixture of fruit and leaves (Sauther et al., 1999; Ossi & Kamilar, 2006; MacLean et al., 2014), but differ in their social structure. Ring-tailed lemurs have some of the largest groups in lemurs (mean group size: 15.6; MacLean et al., 2013, 2014) with complex dominance hierarchies absent in other lemurs (Sauther et al., 1999). Mongoose lemurs, in contrast, live in small, pair-bonded groups (Ossi & Kamilar, 2006). Species who live in such larger, complex social groups experience greater social challenges related to tracking multiple individuals, assessing other's dominance, and competing or cooperating with others (Byrne & Whiten, 1988; Dunbar, 1998).

We used this data to evaluate the two main hypothesis for the evolution of intelligence. The social intelligence hypothesis predicts that ring-tailed lemurs, who live in larger groups with dominance hierarchies, will show enhanced cognitive control than other species, especially pair-bonded mongoose lemurs. The ecological hypothesis, in contrast, predicts that frugivorous ruffed lemurs, who feed on variable fruit resources, should consistently show higher cognitive control, particularly in contrast to the highly-folivorous sifakas. As the ecological and the social hypotheses are not mutually exclusive, an additive effect here would predict that both ruffed lemurs and ring-tailed lemurs exhibit higher cognitive control than the other species.

2. Methods

(a) Subjects

We tested 39 lemurs living at the Duke Lemur Center (see Figure 1a, and Table S1 for subject information). We assessed four taxonomic groups: ruffed lemurs (*Varecia* spp., n = 10; analyses collapsed across red-ruffed and black-and-white ruffed lemurs, given their

socioecological similarity and classification as subspecies until recently (Mittermeier et al., 2008)), Coquerel's sifakas (*Propithecus coquereli*, n = 10), ring-tailed lemurs (*Lemur catta*, n = 10), and mongoose lemurs (*Eulemur mongoz*, n = 9). This sample size includes all the individuals available for testing who completed the battery; 2 additional subjects (1 sifaka and 1 mongoose lemur) initiated the battery but failed to reach criterion in several tasks or stopped participating over several days. All tests were voluntary: lemurs were never food deprived, had *ad libitum* access to water, and could stop participating at any time. The lemurs had little or no prior experience in relevant cognitive tasks like those used here (see Table S1). All behavioral tests were approved by Duke University's Institutional Animal Care and Use Committee (Protocol #A268-16-12).

(b) General procedure

Lemurs completed a battery of six well-validated tasks that assessed multiple core aspects of cognitive control (see Figure 1b-g): a *temporal discounting task* assessed abilities to delay gratification (Rosati et al., 2007; Stevens, 2014); an *A-not-B task* assessed motor inhibition (Amici et a;, 2008; MacLean et al., 2014); a *short-term memory task* assessed abilities to hold information in mind (Amici et al., 2010; Rosati & Hare, 2012); a *reversal learning task* assessed abilities to shift responses when contingencies change (Deaner et al., 2006; Wobber et al., 2010); and finally the *novel object task* and *persistence task* both assessed individual variation in temperament (Herrmann et al., 2007; Wobber et al., 2014) that could influence cognitive performance.

In the basic procedure for the cognitive tasks, an experimenter sat across from the lemur at the sliding table and placed options containing hidden treats on the table, and then lemurs could indicate their choice by either touching or approaching one of the containers. All lemurs completed the tasks in the same order, typically completing one session per day, and at most two tasks with a break in between. In some tasks, subjects had to first meet criteria on a pre-test to demonstrate basic comprehension of the setup before proceeding to the main test, and could repeat sessions until they passed before proceeding. If the subject did not choose one of the options within 15s when responses involved making choices, the trial was stopped and repeated up to a maximum of 4 times. If the subject continued to not make a choice, the session was halted and repeated on a different day (see Supplemental materials for detailed testing procedures).

(c) Specific task procedures

Discounting task: The ability to delay gratification for future rewards is a key component of human executive functions (Diamond, 2013; Rosati, 2017b). To assess this, lemurs made decisions between a smaller option available immediately (1/16 of a grape or a peanut, depending on the species-typical diet) and a larger option (1/2 of a grape or peanut) available after either a 15s or 30s delay according to the conditions following prior work (Rosati et al., 2018). Subjects first completed a *number pretest* session where there was no delay attached to the larger reward, to ensure that they could discriminate these quantities and preferred the larger amount when there was no delay to receive it. Then they completed two *test sessions* that varied in the delay associated with the larger option (15s and 30s delay). In each test session, lemurs first completed 8 *exposure trials* (only one option available at a time) to introduce the rewards and delay contingencies. Then they completed 10 *test trials*, in which they made choices between the smaller and larger reward (see Figure 1b; Video S1). The side of the delayed option on the table was counterbalanced and quasi-randomized across trials (no more than 3 trials in a row on the same side), with a 30s inter-trial interval (ITI) between trials. We measured the lemurs' choices for the larger reward.

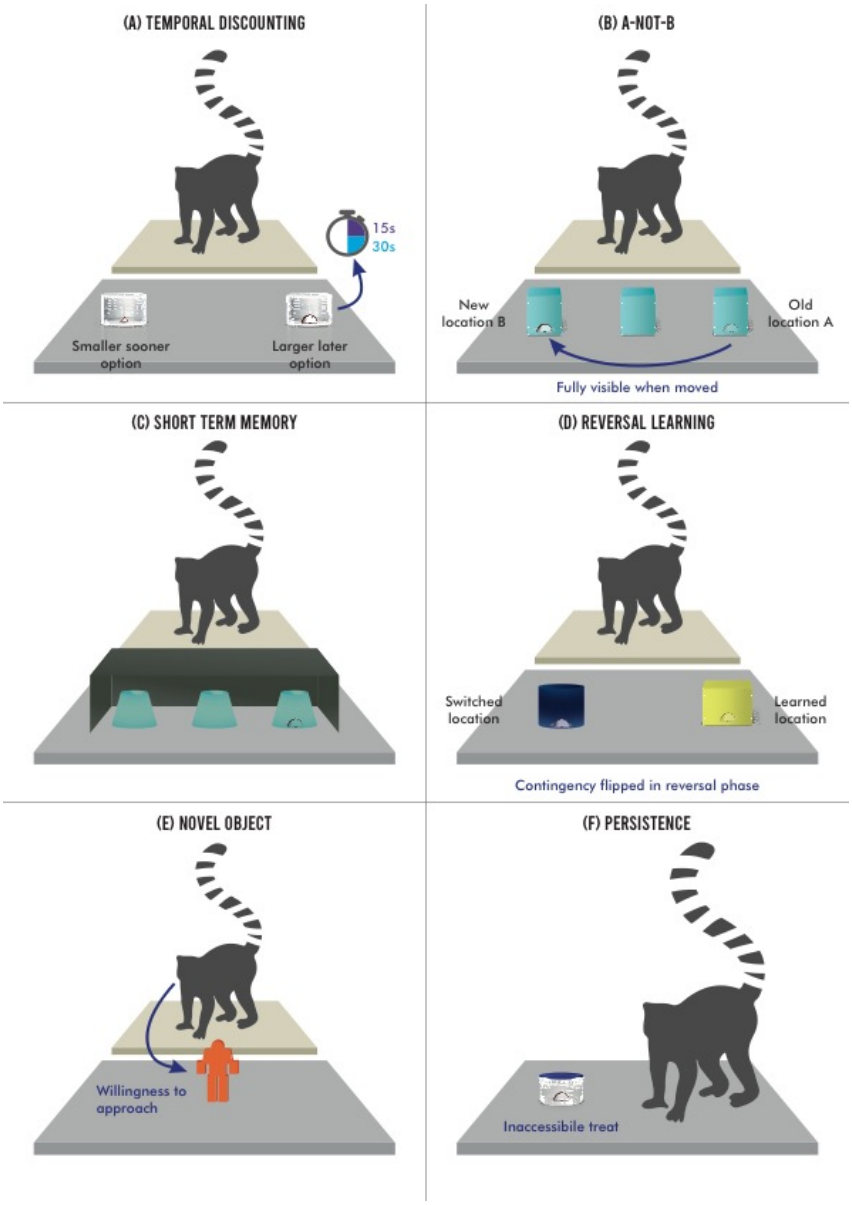

Figure 1: **Lemur cognitive control battery.** (a) In the *temporal discounting* task, lemurs choose between a smaller, immediate reward and a larger, delayed reward. (b) In the *A-not-B* task, lemurs had to inhibit a prepotent motor response to access a reward. (c) In the *short-term memory* task, lemurs had to recall the location of hidden food over a short delay. (d) In the *reversal learning* task, lemurs first learned that one location contained food, and then had to update contingencies. (e) In the *novel object* task, lemurs could approach and investigate novel stimuli. (f) In the *persistence* task, lemurs could attempt to access inaccessible food.

A-not-B-error task: The ability to inhibit ineffectual motor responses is another key component of executive functions (Diamond, 2013; Rosati, 2017b; Friedman & Miyake, 2017). To assess this, we used an A-not-B task where lemurs had to resist searching for food in a previous hiding location, when the food reward was then visibly moved to a new location following methods

from prior work (MacLean et al., 2014). Here, the experimenter put a food reward under one of three containers. Lemurs were allowed to retrieve the reward under that container three times, to develop the prepotent response. On the fourth test trial, lemurs watched as the reward was first hidden under the same container (container A), but then was moved to a different container on the other side of the table (container B; see Figure 1c; Video S2). The same procedure was repeated three more times with visually-distinct sets of containers and different hiding locations (different in color and shape, see Figure S2), for a total of 4 test trials. The order of presentation of the container sets was fixed across the subject, and the initially-baited container (left or right) was counterbalanced across trial blocks and subjects. We measured lemurs' choices for the correct container.

Short-term memory task: The ability to recall and manipulate information in mind is another key component of executive functions (Diamond, 2013; Friedman & Miyake, 2017). To test this, lemurs had to recall the location of hidden food over short time intervals. Lemurs were presented with three identical containers on a sliding table. The experimenter placed a piece of food under one container in full view of the subject, and the lemur could then choose one container either immediately (*no-delay trials*), or after a 5s delay in which the lemur' view was blocked by an occluder (*delay trials*; see Figure 1d; Video S3). Although this task does not require retaining information while performing a secondary task, as is the case for many measures of working memory used with humans (Engle et al., 1999), this kind of setup is commonly used with nonhuman primates (Amici et al., 2010; Rosati & Hare, 2012; ManyPrimates et al., 2019) and was designed to capture species variation in lemurs' cognition while avoiding floor effects in these species due to difficult task demands. In the task, lemurs first completed three familiarization trials where they could immediately retrieve the food reward from containers, and then completed three blocks of trials each consisting of three delay trials followed by one no-delay trial (for a total of twelve trials). The correct location was counterbalanced and quasi-randomized (no more than 2 trials in a row with same location) across trials. We measured lemurs' choices for the correct cup

Reversal learning task: The ability to flexibly update responses is another key component of executive functions (Diamond, 2013; Rosati, 2017b; Friedman & Miyake, 2017). To test this, we used a reversal learning task where lemurs had to switch their responses when reward contingencies changed. Lemurs were presented with two containers, differing in shape and color, on a sliding table. They initially learned that a food reward was hidden under one of the containers (unique in color and always appearing on the same side) whereas the other was always empty. Once lemurs consistently selected the baited container, the rule were switched, and the food reward was hidden under the container that was previously empty (see Figure 1e; Video S4). In the session, lemurs first completed two *exposure trials*, in which the experimenter put the food under the correct learning phase container in full view of the subjects. Then they completed at least 6 (out of a maximum of 10) *learning trials* in which that container was baited behind an occluder. Once lemurs consistently chose the baited container (choose the correct location in six consecutive trials), they completed 10 *test trials* in which the reward contingencies were switched. The assignment of the baited side and of the corresponding container for the learning phase was counterbalanced across subjects. We measured lemurs' choices for the correct container.

Novel object task: We also measured two aspects of temperament in the lemurs, as responses to novel or difficult situations may constrain cognitive control. For example, species might show poorer performance if they are more neophobic or less motivated to participate (Schubiger et al., 2020). To assess their responses to novelty, we showed lemurs a series of novel stimuli following prior work (Herrmann et al., 2011). On each trial, one experimenter centered the

lemur approximately 1.2 meters away from the table, and another experimenter placed the stimuli on the table (see Figure 1f; Video S5). Each lemur was presented with four stimuli in a fixed order: (1) baseline with table only, (2) baseline with a person sitting at the table, (3) novel stationary object, and (4) novel moving object (see Figure S5). On each trial, we measured how long they spent in close proximity to the stimuli.

Persistence task: In the second temperament task, lemurs were presented with an inaccessible food reward to measure their motivation to retrieve it. First, one experimenter positioned a clear box containing a piece of food on a table inside the lemur's room. For two consecutive *solvable trials*, the box's lid was left unsealed such that the box could be easily opened to retrieve the food. In the third unsolvable trial, the lid was closed such that it was impossible for the lemurs to open it (see Figure 1g; Video S6). We measured how long subjects manipulate the box in attempting to retrieve the food, out of a maximum of three minutes.

(d) Data coding and analysis

All tasks were videotaped, and a coder blind to the study's hypotheses coded at least 20% of tasks with high reliability (Cohen's kappa values over 0.97 for all choice tasks; Pearson's r = 0.99 for latency measures; see Supplemental materials for all coding details). The study design and statistical analysis approach were pre-registered (https://aspredicted.org/blind.php?x=r7k69z). We used generalized linear mixed models (GLMMs) to analyze trial-by-trial responses and compare species' performance for most tasks (see below and Supplemental materials for details). Models always included *subject* as a random factor to account for repeated trials when relevant, as well as *age*, *sex*, and *trial number*; we also accounted for pretest performance and the number of sessions to criterion for that individual (to account for each individual's learning experiences when relevant for that task). Then we added *species* as a factor to examine evolutionary variation. We compared model fit using likelihood ratio tests, and computed post-hoc pair-wise comparisons with a Tukey correction. In a final analysis, we compared species' integrative performance across tasks using a principal component analysis.

3. Results

An initial comparison of performance in the discounting task examining *delay duration* (0s, 15s, 30s) indicated a linear effect of delay: as expected, lemurs chose the larger reward less often as the delay increased [χ^2 =11.97, p = 0.002; p < 0.05 for significant comparison; and Table S3 for model parameters]. Furthermore, all species selected the larger reward significantly above chance in *number pretest*, where the larger reward entailed no delay [p < 0.05 for all comparisons]. This shows that lemurs accounted for the presence of delay costs in their choices. In the main analysis of the discounting tasks, all species except sifakas selected the larger delayed option above chance in both delay conditions [p < 0.05 for significant comparisons, see Supplemental materials for details]. To compare performance across species, a base model included *subject, age, sex*, *trial number,* and *discrimination score* (the proportion of correct choices in the number pretest, to account for any variation in numerical cognition). Adding *delay* (15s and 30s) in the second model did not improve model fit [χ^2 = 0.88, p = 0.347], indicating that lemurs responded similarly to delay conditions. Adding *species* however significantly improved model fit [χ^2 = 14.56, p = 0.006; see Figure 2a and Table S4 for parameters]; post-hoc comparisons showed that ring-tailed lemurs were more willing to wait for a larger reward than both mongoose lemurs and sifakas, and ruffed lemurs were more willing to wait than sifakas [p < 0.05 for significant comparisons, see Figure 3 and Supplemental materials for details]. These results support both the ecological and social

hypotheses, as the more socially complex ring-tailed lemurs outperformed mongoose lemurs, and the more ecologically-complex ruffed lemurs further outperformed sifakas.

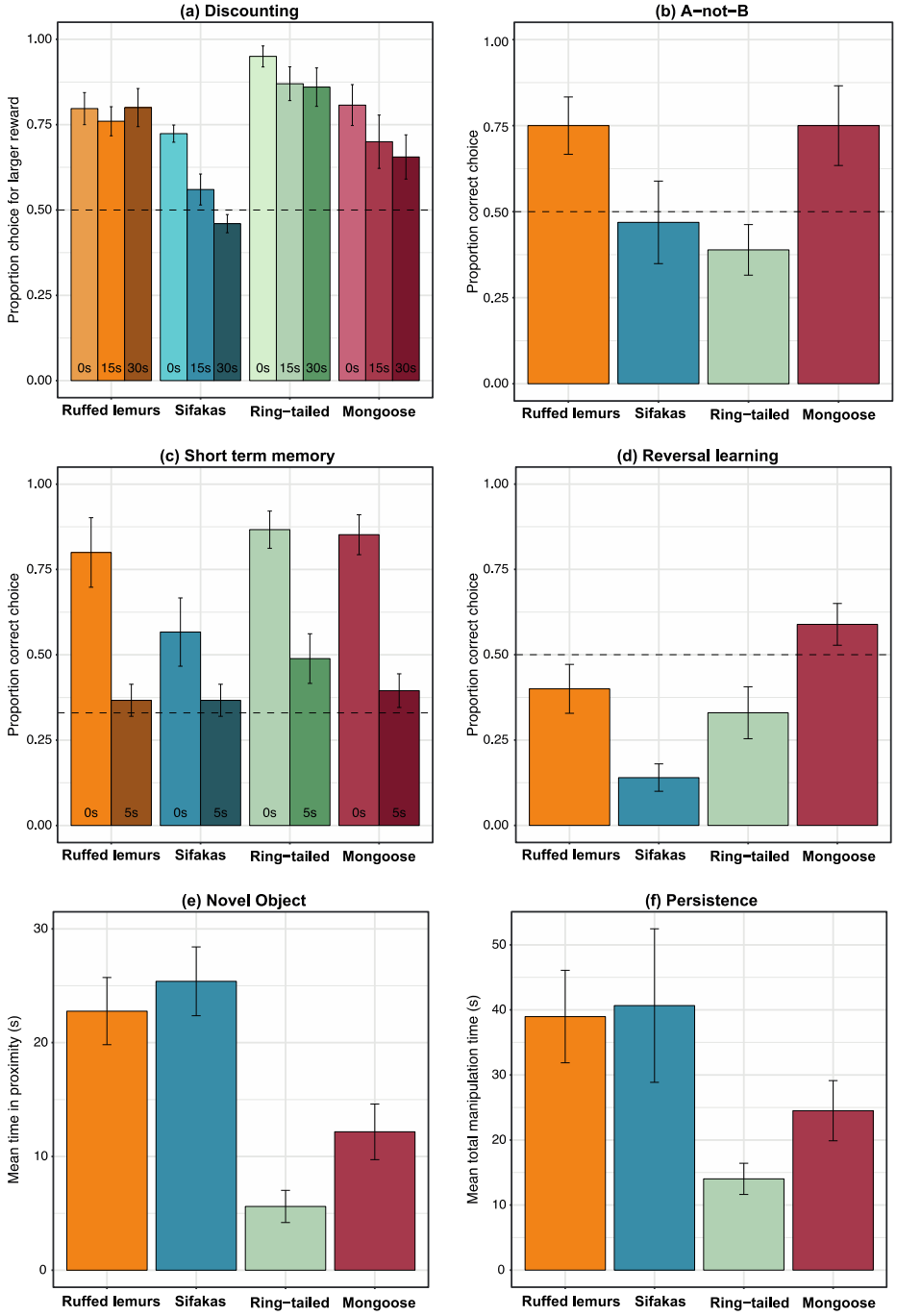

Figure 2. Lemur performance across tasks. (a) Proportion of choices for the larger option in the temporal discounting task, by delay. (b) Proportion of correct test choices in the A-not-B task. (c) Proportion of correct choices in the short-term memory task, by delay. (d) Proportion of correct test choices in the reversal learning task. (e) Mean time spent in proximity to all stimuli in the novel object task. (f) Mean time spent manipulating the box in the unsolvable trial of the persistence task. Error bars indicate standard error, and dashed lines indicate chance performance.

In the *A-not-B task*, only ruffed lemurs preferentially selected the correct container above chance on test trials [$p < 0.05$] and mongoose lemurs trended to do so [$p = 0.07$]; ring-tailed lemurs and sifakas did not differ from chance (see Figure 2b and Supplemental materials for details). To compare performance, in a base model we included *subject, age, sex*, *trial number,* and *number of sessions to criterion* (to account for any individual variation in performance on familiarization trials). Inclusion of *species* improved model fit [$\chi^2 = 11.52$, $p = 0.009$; see Figure 2b; Table S5 for parameters]. Post-hoc comparisons revealed a trend for mongoose lemurs and ruffed lemurs to outperform sifakas [$p = 0.09$], and for ruffed lemurs to outperform ring-tailed lemurs [$p = 0.06$; see Figure 3]. This pattern is most in line with predictions from the ecological hypothesis, as the ruffed lemurs tended to outperform the sifakas as well as the ring-tailed lemurs but does not support the predictions for the social hypothesis as the ring-tailed lemurs did not outperform the mongoose lemurs.

In the *short-term memory* task, all species selected the correct option above chance on no-delay trials [$p < 0.05$ for all comparisons], whereas in the delay trials only ring-tailed lemurs were marginally above chance [$p = 0.056$, see Supplemental materials for details]. In the comparison of species, a base model accounting for *subject, age, sex, trial number*, number of *sessions to criterion* (to account for experience in familiarization trials), and *condition* (immediate or delayed choice) confirmed that lemurs performed better when they could retrieve the food immediately. Adding *species* as a predictor in a second model trended to improve model fit [$\chi^2 = 6.35$, $p = 0.096$], as did the interaction between *species X condition* [$\chi^2 = 11.44$, $p = 0.076$; see Figure 2c; Table S6 for parameters]. We further explored this result by analyzing lemurs' performance only in the no-delay trials, given the lemurs' poor performance in delay trials. We found that adding species as predictor in a second model improved model fit [$\chi2 = 10.67$, $p = 0.014$]. Post-hoc comparisons in this analysis showed that ring-tailed lemurs outperformed sifakas [$p < 0.05$; see Figure 3], and that mongoose lemurs trended to outperform sifakas [$p = 0.072$]. No other differences among species were found. Overall, this suggests that lemurs have fairly poor short-term memory overall, but there was no evidence in support of the social hypothesis. Rather, the folivorous sifakas' relatively low performance was most in line with the ecological hypothesis.

In the *reversal learning task,* we focused on lemurs' ability to update their responses in the reversal phase. Overall, sifakas and ring-tailed lemurs remained below chance across reversal trials, whereas mongoose and ruffed lemurs were at chance [$p \leq 0.05$ for significant comparisons]; note that individuals are expected to start below chance and improve over reversal trials in this task as they learn the correct response after the contingency switches. Here, the base model accounted for *subject, age, sex, trial number,* and *learning trials to reach criterion* (to account for individual variation in initial learning experience), and showed that performance overall improved over reversal trials, as expected. Inclusion of *species* improved model fit [$\chi^2 = 19.08$, $p < 0.001$; see Figure 2d; Table S7 for parameters]. Post-hoc comparisons indicated that sifakas showed worse performance than all other species [$p < 0.05$ for all comparisons; see Figure 3]. No other differences among species were found. Overall, this supports the ecological hypothesis—given that the frugivorous ruffed lemurs as well as the intermediate mongoose and ring-tailed lemurs all outperformed the folivorous sifakas. However, there was again no support for the predictions of the social hypothesis, as the mongoose lemurs and the ring-tailed lemurs did not differ.

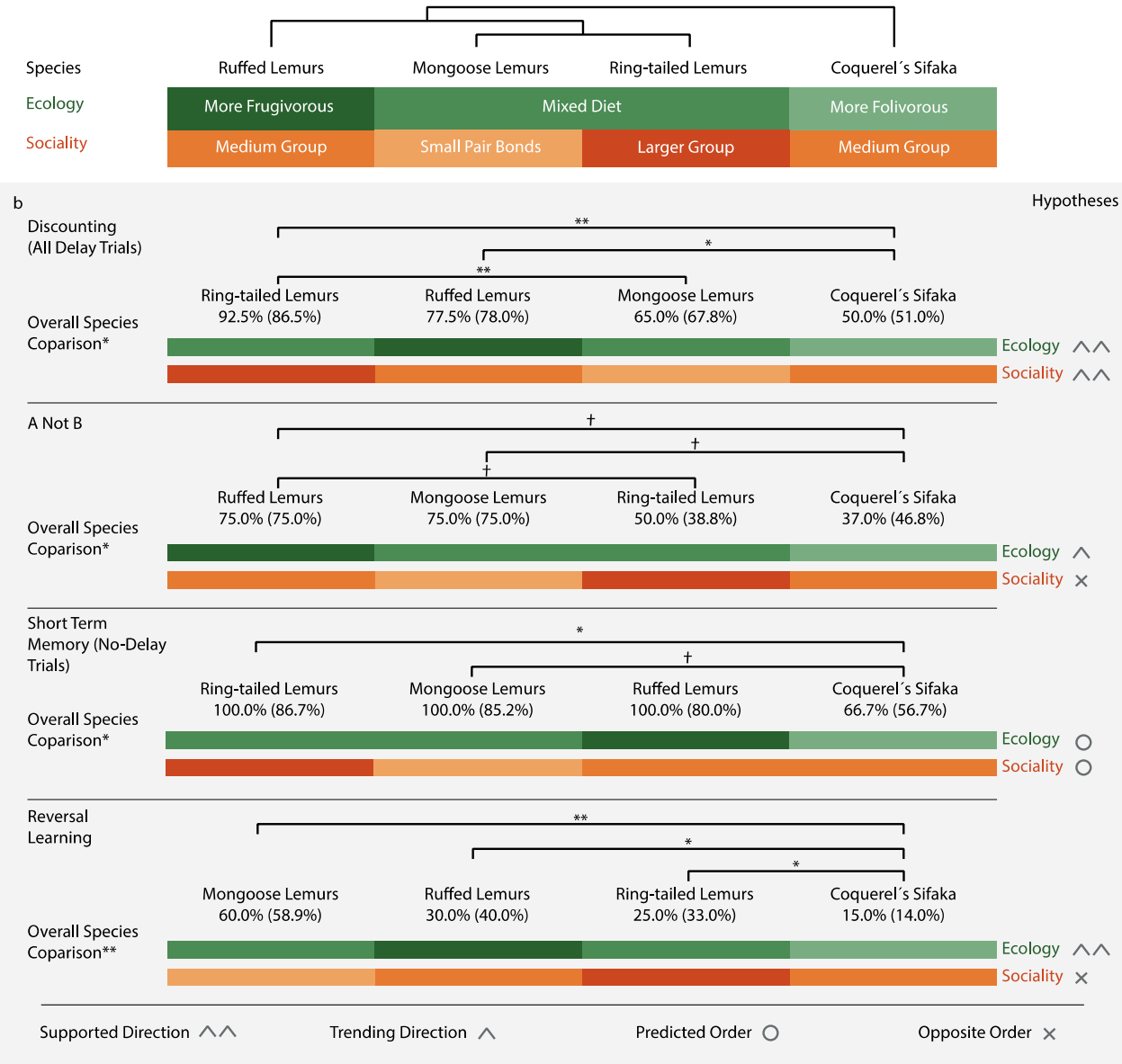

Figure 3. Lemur socioecology and cognitive performance. (a) The phylogeny and socioecological characteristics of each lemur species. (b) Species' cognitive performance order by their median performance in each task (means in parentheses), results of overall species comparisons, results of pairwise species comparisons, and concordance of results with socioecological predictions. We indicate support for the ecological hypothesis when ruffed lemurs outperform sifakas, while for the social hypothesis when ring-tailed outperform mongoose lemurs. Note that when differences across species went in the predicted direction but were not significant or only trended to be so, we use different symbols to indicate a trend or a direction in favor or against one hypothesis.

Some proposals suggest that temperament may constrain performance in cognitive tasks (Herrmann et al., 2007; Schubiger et al., 2020), so we next assessed if species-level variation in temperament could explain the pattern of results in the cognitive control measures. In the *novel*

object task, lemurs spent the longest overall amount of time in proximity to a novel stationary object (e.g., compared to a moving object or baseline trials, see Supplemental materials). Adding *species* to a base model including *subject, age, sex,* and *trial type* improved model fit [χ^2 =26.75, $p < 0.001$, see Figure 2e; Table S8 for parameters]; sifakas spent more time near the novel items than both ring-tailed and mongoose lemurs [$p < 0.05$ for both comparisons], and ruffed lemurs spent more time than ring-tailed lemurs [$p < 0.05$]. No other differences among species were found. Additional comparisons showed that these results were driven primarily by differences in responses to the stationary and moving objects (see Supplemental material). In the *persistence task*, the inclusion of *species* to a base model accounting for *sex* and *age* also improved model fit [χ^2 =14.65, $p = 0.002$, see Figure 2f; Table S9 for parameters]; sifakas and ruffed lemurs spent more time manipulating the box compared to ring-tailed lemurs [$p < 0.05$ for significant comparisons]. No other differences among species were found. Overall, these results indicate that sifakas, the species with the worst cognitive performance in general, were quite bold and willing to engage in tasks, and generally had similar temperament outcomes as the more cognitively-successful ruffed lemurs. Thus, neophobic responses or low levels of motivation did not seem to constrain performance across the cognitive control tasks.

As a final test of the social and ecological hypotheses, we implemented a principal component analysis (PCA) to extract summary scores of each species' responses across the four cognitive control tasks, and then compared variation in these extracted scores across the species to test for differences (see Supplemental material for details). The PCA yielded two principal unrotated components that best explained variation in lemurs' performance, based on an analysis that compared eigenvalues from actual data to randomly resampled and simulated correlation matrices (Budaev, 2010). The discounting, short-term memory, and reversal learning tasks positively loaded on the first component (explaining 38.5% of the variance), whereas the A-not-B task loaded on the second component (accounting for 29.7%; see Figure 4a; Table S11 for loadings of each task in the component). We then compared species' scores on these two dimensions, and found that the sifakas were significantly different from the other species in dimension 1, reflecting an overall lower performance in the cognitive control tasks [$p < 0.05$ for all comparisons; see Figure 4b; Table S12]. The ring-tailed lemurs also showed a pattern more like sifakas on dimension 2 primarily tracking A-not-B performance (see Table S13). Thus, results from the PCA complement the results seen in each individual task: we found that the least ecologically-complex species (sifakas) showed the worst performance across tasks on both dimensions. In contrast there was again limited or even negative support for the social intelligence hypothesis, given that the most socially complex species (ring-tailed lemurs) actually showed a decrement in performance on dimension 2.

4. Discussion

We examined the evolution of cognitive control in lemurs using a novel battery of cognitive tasks, and found that ecological complexity more consistently predicted cognition across species than did social complexity across contexts. In particular, the sifakas—the only obligate folivore—showed the worst performance across multiple measures, and specifically were often outperformed by the highly-frugivorous ruffed lemurs in the temporal discounting, motor inhibition, and reversal learning tasks. Crucially, these species exhibit similar social systems but differ in the complexity of their diets. In contrast, there was no consistent pattern of variation related to sociality. Ring-tailed lemurs, who live in large social groups with dominance hierarchies, were quite successful at delaying gratification and to a lesser extent in the short-term memory task, but otherwise did not

consistently outperform the pair-bonded mongoose lemurs or the other species in general; indeed, the mongoose lemurs showed stronger performance in both the motor inhibition and reversal task. The principal components analysis further indicated that the sifakas showed worse performance overall across both extracted dimensions, and that the ring-tailed lemurs also had worse performance in dimension 2. Crucially, the novel object and persistence measures indicate that these patterns of cognitive performance were not due to temperamental constraints. Thus, our study indicates that ecology rather than sociality plays a more fundamental role in shaping cognitive control in lemurs.

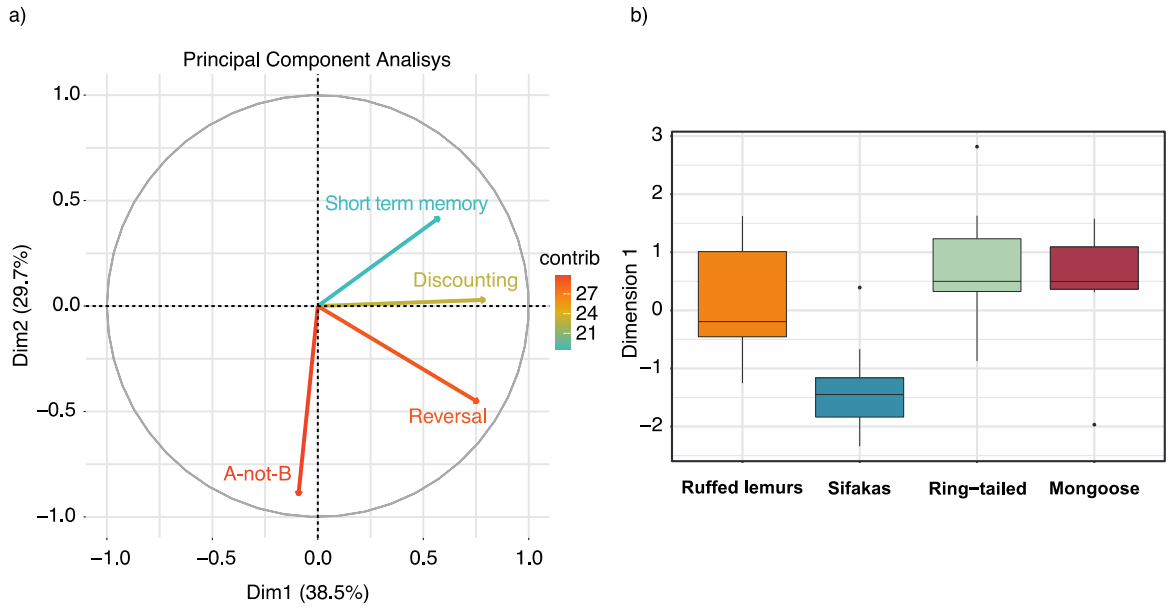

Figure 4. PCA of cognitive control tasks. (a) Contribution of each of the tasks to the two unrotated dimensions extracted from the analysis. (b) Boxplot of the average summary scores for dimension 1 for each species; sifaka summary scores indicated worse performance than the other species.

These results align with prior work showing that spatial memory and decision-making vary according to ecology in primates (e.g., Stevens, 2014; MacLean et al., 2014; Rosati et al., 2014; Rosati, 2017; De Petrillo & Rosati, 2020). Yet these findings also contrast with prior work showing that ring-tailed lemurs outperform mongoose lemurs in social cognition (MacLean et al., 2008, 2013). One possibility is that these different cognitive domains evolve independently: social capacities like perspective-taking may depend on social complexity, whereas abilities like spatial memory that are needed to locate food depend on ecological complexity (Rosati, 2017; Sandel et al., 2011). Importantly, cognitive control is often considered a domain-general process (Diamond, 2013; Friedman & Miyake, 2017), so our results indicate that some domain-general abilities may also be shaped primarily by ecological pressures. Yet an important consideration is that our battery, in adapting core measures of executive function from studies of humans (Miyake et al., 2000; Diamond, 2013; Friedman & Miyake, 2017; Karr et al., 2018), implemented tasks that in some ways resemble foraging tasks, as animals made decisions in nonsocial contexts to obtain a reward. Thus, an important question for future work concerns understanding the evolution of executive functions across different contexts. There has been some work implementing social versions of

cognitive control problems (e.g., social reversal learning: Wobber et al., 2010; social inhibitory control: Reddy et al., 2015), but there has been little attempt to assess if animals actually show different skill levels in social versus foraging contexts. In fact, some evidence suggests that several primate species show largely similar inhibitory control capacities across these contexts (Amici et al., 2008, 2018). Future comparisons of other components of executive function across both foraging and social contexts is therefore important to understand the evolution of cognitive control.

Another important question concerns the mechanistic basis of cognitive control in primates. In adult humans, different components of inhibition, working memory, and shifting represent distinct, dissociable components of executive control (Friedman & Miyake, 2017). Our principal components analysis suggests that some aspects of cognitive control (e.g., delay of gratification, short-term memory, and reversal learning) exhibit shared variation in lemurs. However, future work could build on this by implementing a battery with multiple measures capturing each component and using factor analysis to infer the latent structure of cognition (Herrmann et al., 2010; MacLean et al., 2017). Given that inter-relationships between cognitive skills can differ across species, this approach is also important to understand how cognition evolves (Völter et al., 2018; Herrmann et al., 2010; MacLean et al., 2017). A related question concerns the links between these skills and the brain regions that support them. In humans, core components of executive function are dissociable not just in behavioral measures but also in their neural basis. Prior work has linked inhibitory control in primates to absolute brain size (MacLean et al 2014), and a crucial next step is examining whether distinct components of cognitive control are linked to distinct brain regions as in humans.

A final point concerns the fundamental problem of how to best conceptualize ecological and social complexity across species. Here, we took the approach of comparing species that differed across broad, widely-accepted metrics of ecological and social complexity—degree of frugivory versus folivory, and the size and complexity of social groups. Yet there are alternative approaches to this problem. While frugivory is generally considered a more ecologically-complex diet than folivory in primates (Milton, 1981; Rosati, 2017; DeCasien et al., 2017), other metrics such as caching, niche specialization, or dietary breadth are sometimes used with other species (MacLean et al., 2014; Henke-von der Malsburg et al., 2020). Yet, it is worth noticing that obligate folivores like the sifakas are under-represented in comparative work, despite being critical for testing socioecological hypotheses (Tan et al., 2014). Similarly, while species with larger groups (Dunbar, 1998) or many differentiated social relationships (Bergman & Beehner, 2015), are generally considered to be more complex in primates, other features such as social tolerance, fission-fusion social groups, or pair bondedness may also be important (Amici et al., 2008; Dunbar and Shultz 2007; Joly et al., 2017). However, we note that the mongoose lemurs did not consistently outperform the other species, so we also did not find support for the pair-bond hypothesis here. Overall, this highlights the importance, but also the difficulty, of indexing social and ecological complexity in a manner that is generally useful but also appropriate for the species under consideration (Henke-von der Malsburg et al., 2020).

In conclusion, we examined cognitive control across lemurs, including measures of temporal discounting, motor inhibition, short-term memory, and reversal learning. Our results show that cognitive control capacities consistently varied according to these species' feeding ecology, but not according to their social complexity. Thus, our findings align with accumulating evidence that ecological complexity can be important driver of both cognitive and brain evolution in lemurs (Rosati et al., 2014; MacLean et al., 2009) and across primates in general (MacLean et al., 2014; Rosati, 2017; DeCasien et al., 2017). This also provides converging support for the

proposal that ecological processes were important in human cognitive evolution as well (e.g., González-Forero & Gardner, 2018). Making robust inferences about the evolution of cognition requires integrating both approaches from cognitive science concerning how to best capture the underlying cognitive mechanisms that influence behavior, as well as assessing cognitive abilities across diverse species.

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Contributions

F.D.P. and A.R. designed the study; F.D.P. and P.N. collected the data at the Duke Lemur Center; F.D.P., P.N. and A.C. coded the data; F.D.P. and A.R. analyzed the data; F.D.P. and A.R. wrote the manuscript with input from all authors.

Open Practices Statement

Preregistration documents are available at https://aspredicted.org/blind.php?x=r7k69z, and all data will be made available in Dryad Digital Repository upon publication.

Competing interests

The authors declare no competing interests

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