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# Capuchins, space, time and memory: an experimental test of what-where-when memory in wild monkeys

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There is considerable controversy about the existence, extent and adaptive value of integrated multimodal memory in non-human animals. Building on prior results showing that wild capuchin monkeys in Argentina appear to recall both the location and amount of food at patches they had previously visited, I tested whether they also track and use elapsed time as a basis for decisions about which feeding patches to visit. I presented them with an experimental array of eight feeding sites, at each of which food rewards increased with increasing elapsed time since the previous visit, similar to the pattern of ripe fruit accumulation in natural feeding trees. Over the course of 68 days, comprising two distinct renewal rate treatments, one group repeatedly visited sites in the feeding array, generating 212 valid choices between sites. Comparison of observations against simulated movements and multinomial statistical models shows that the monkeys' choices were most consistent with dynamic memory for elapsed time specific to each of the eight sites. Thus, it appears that capuchin monkeys possess and use integrated memories of prior food patch use, including where the patch is relative to their current location, how productive the patch is and how long it has been since they last visited the patch. Natural selection to use such integrated memories in foraging tasks may provide an ecologically relevant basis for the evolution of complex intelligence in primates.

## 1. Introduction

A critical underpinning of human intelligence is the ability to recall specific events in the past with a wealth of context-specific details (what happened, when it happened, where it happened and who was involved). Such an ability, called episodic memory, has been postulated to be uniquely human [1]. However, a variety of animals in captivity have been shown to behave as though they have integrated memories of past events, including at least what happened, where and when (WWW; reviews: [2,3]). Whether these integrated WWW memories of non-human animals are analogues or precursors of human episodic memory is controversial [4,5], but they are evidence for considerable cognitive sophistication.

It is not yet clear what selection pressures favour integrative intelligence in wild animals. Evidence for integrative memory in animals, including primates, derives mostly from controlled studies in captivity (e.g. Allen & Fortin [6] cite 13 studies on eight animal species from various birds to rats to chimpanzees, but none are in the wild). Evidence in 15 wild animals for WWW memory is descriptive and generally sparse [7]. While there is abundant evidence that wild animals remember the locations and qualities (such as reward amount or species) of specific locations [8–10], there is relatively little evidence that wild animals incorporate any temporal dimension into their decisions [11] (but see [12–15]). An ability to integrate subjective (or elapsed) time with who-what memory would be particularly useful for animals feeding on limited but renewing resources such as fruiting trees [16], as such integrated memories could allow animals to anticipate the amount of food to be expected at each of
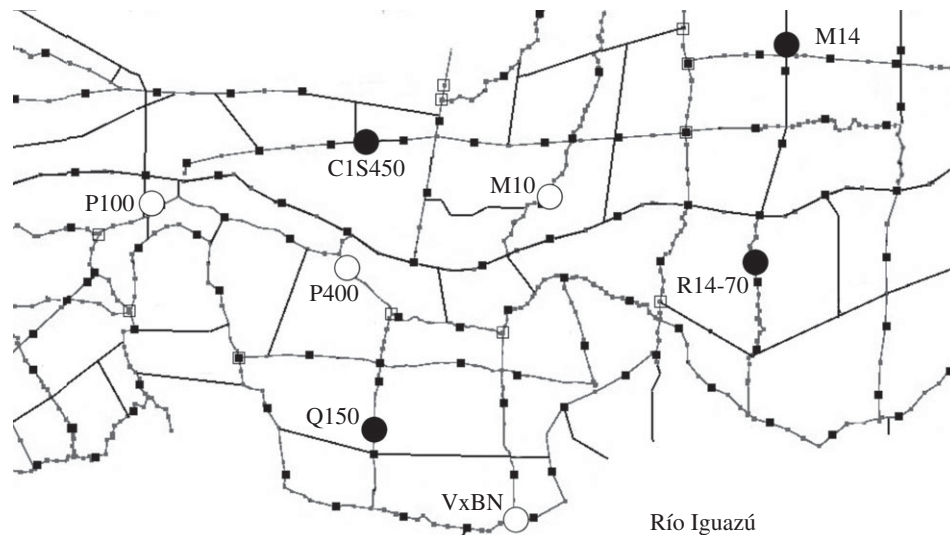
**Figure 1.** Map of the experimental array of feeding sites (circles), each of which consisted of three platforms about 10 m apart, suspended from tree branches at 5–15 m above the ground. The trail network shown was marked every 100 m (black squares). Food was provided at each site when the group arrived within 50 m of it. The amount of food was determined by the time interval since the group had last visited the site, at two rates: high (black circles) and low (white circles). After 46 days, the renewal rate treatments were reversed across sites.

several possible feeding trees, similar to renewing nectar in flower patches [13]. This report is the first experiment in a wild primate, the black-horned capuchin (*Sapajus* (*Cebus*) *nigiritus*), designed to test memory for elapsed time in realistic foraging decisions that depend on WWW characteristics of individual feeding sites. Specifically, the amount of food at individual feeding sites increased through time so that the reward at a given site at any moment was a function of how long the group had spent away from it.

It is not easy to obtain evidence in the wild for memory of the elapsed time since specific events in the past [2,15]. Because sequences of animal movements are nearly always autocorrelated in space and time [17], it does not make sense to test whether the effects of space and time on movement choices are significantly different from zero; it would in fact be paradoxical if they were zero [18]. To generate a meaningful null hypothesis, the movements of the animals need to be modelled in the absence of the effects I wish to test, in this case temporal memory. In this study, I use a varied set of movement simulations to test whether the observed destination choices are consistent with 'null' movement models that either do not or do include memory for elapsed time associated with specific destinations.

Assuming that observed patterns of destination choices of the study animals differ from null movement models, it is still not clear which cognitive variables are required to fit the data. To assess whether a particular cognitive variable had a significant effect on the observed movement choices in this study, I tested a small sequence of progressively more complex cognitive models of destination profitability. Each successively more complex model incorporates one more kind of information (elapsed time) or level of spatial integration (summing rewards and costs over combinations of two or more sites) [19,20]. If a more complex cognitive model predicted the capuchins' behaviours significantly better than did a less complex model, I tentatively conclude that they must be capable of sensing and using the added kind of information. Previous work in the same study site has shown that the group movements of wild capuchins are consistent with the ability to remember where feeding sites

are located relative to their current location [10], and to incorporate information on different amounts of constant rewards across two sites [20]. In this experiment, their movement decisions seemed to include the time elapsed since their last visit to each destination, a variable that required updating at every decision point. This use of WWW information appears to be both integrated and flexible, and thus supports the notion that ecological challenges could select for complex cognition in primates [16].

## 2. Material and methods

### (a) Field site

The field site is in northeastern Argentina at Iguazú Falls National Park. It is the locus of a long-term study of black-horned capuchin ecology, behaviour and demography (review: [21]). Black-horned capuchins weigh 2.5–3.5 kg (adult females and males, respectively), are generalized omnivores that prefer fruit and insects, and live in social groups of 3–45 animals. Each group has a well-defined social hierarchy primarily enforced by dyadic agonistic interactions [22]. The habitat is subtropical moist forest near the banks of the Iguazú River. Productivity of fruit and insects is highly seasonal [23] with minima during the austral winter when I conducted the experiments in this study. Typical canopy trees are 30–35 m tall, with occasional emergents up to 50 m. The canopy is often discontinuous, so capuchins typically travel at 10–20 m above the forest floor.

This experiment built on previous work [24] using a set of fixed feeding sites, each site consisting of three 1 × 1 m feeding platforms spaced about 10 m apart, suspended from tree branches. In 2008, eight sites were located a minimum of 160 m apart (figure 1), both to avoid potential visual or olfactory cues to the presence of alternative feeding sites [25] and to prevent the group from splitting up to visit more than one site at a time. Although several social groups have been used in other experiments on ecological cognition at this site [20,24], this study focused on only the well-studied Macuco group [21]. To avoid providing food-related cues that might attract the monkeys to a feeding site, observers placed food on the platforms only once the group had arrived near it (less than 50 m away). Previous studies had kept the amount of reward at a given site

constant and imposed a restriction that a group would receive food at a site only once per day. Under these conditions, groups consistently chose closer over more distant sites, and they chose sites with larger rewards over those with smaller ones [10,26]. Later experiments [20] showed that the movement decisions of these capuchin groups were accounted for by a simple profitability measure of food reward divided by distance to the feeding site(s), when rewards and distances were summed over paths that visited two sites.

## (b) Experimental design

In the current experiment, the expected reward at a site was a function of the time elapsed since the group's previous visit to that site, increasing linearly with time until 48 h, after which it was held constant at the site's maximum reward value. The eight sites were assigned one of two reward treatments: high (one piece of banana per hour of elapsed time since the prior visit; 48 pieces maximum reward) and low (one piece of banana per 2 h of elapsed time; 24 pieces maximum reward). For instance, if the previous visit to a site had been 22 h earlier, a high site would receive 22 pieces of banana. Each banana piece was roughly 2.5 cm in length.

The original assignment of reward rates was maintained for 46 days (24 June–8 August), at which time each site was switched to the other reward rate until 30 August (22 days). Data from the first 16 days (24 June through 9 July) are not used here as the group was still learning the locations of the sites and the reward regime; likewise the first 8 days following the change in treatments is excluded from this analysis, to allow the group to adjust to the change in reward structure (electronic supplementary material: homogeneity of process). Switching the treatments in mid-season allowed each site to serve as its own control for the effect of treatment. Because data on choices accumulated slowly (average of only one choice per site per day), there was not enough time in the winter field season to change the position of the feeding sites while also allowing the group to find and learn the parameters of the new design and collect a statistically adequate sample of choices.

## (c) Statistical analysis of movement choices

Analysis of the movement decisions used the 'Choice' platform in JMP (v. 11.0.0; SAS Software Corp.), which implements a multinomial logistic regression of the observed choices as a function of the characteristics of the options provided at each trial [27]. The output of the model provides parameters that index the relative utility for each option in a given choice situation. To allow for the possibility that the monkeys might have site-specific preferences due to factors that are not part of the experimental design, I included in the Choice analysis the identity of the destination sites as an independent variable, analogous to a separate-intercepts model in a random-effects GLMM. If a more complex model did not fit significantly better than the simpler model, the simpler model was considered the most parsimonious model for the data. To account for multiple testing, I used an experiment-wise $\alpha$ of 0.05 with a simple but conservative Bonferroni procedure, yielding a comparison-wise $\alpha$ of $0.05/c$, where $c$ (either 2 or 4) is the number of tests performed. Type I error rates are reported as one-tailed values for sequential tests of increasingly complex profitability measures; otherwise they are two-tailed.

## (d) Profitability measures

I calculated, at the moment of the group's departure from each site, the profitability of visiting each of the other seven sites in the design. Using the moment of departure from a site as the time of decision is reasonable because the monkeys nearly always move between feeding sites using highly goal-directed and rapid travel

[10]; intervals between departure and arrival at the next site were typically less than 20 min, not enough to change the expected reward at the destination. I calculated profitability for each destination site as the expected reward there divided by distance to the site. In the null model (H0), the reward was indexed only by the site-specific intercepts, to account for any preferences for specific sites that were independent of the feeding regime. In the base profitability model (H1), I used as the expected reward the number of banana pieces associated with a constant 24 h delay; this value is close to the observed mean reward for each site while removing the effect of actual time interval elapsed since the last visit to a site.

After the base model H1, I fitted and tested two more profitability models. Model H2 calculates the expected reward at each destination site based on the actual elapsed time since the previous visit to that site, at the moment the group leaves the current feeding site. If H2 provides a significantly better fit to the observed movements than does H1, it appears that the monkeys are sensitive to elapsed time at each destination relative to the current time and place. Model H3 calculates profitability from a two-step model [28] that integrated expected rewards across cumulative distance for every pair of destination sites (based on earlier results from this population [20]). For this two-step model, each destination site was associated with seven values of profitability (one for each of the remaining other sites that could be the destination on the second step); of these seven values, I chose the path with the highest profitability and assigned that path profitability to the (first) destination site.

To compare predicted and actual destinations visited, I needed to convert the multinomial statistical model into destination-specific likelihoods of being visited. I used the fitted parameters from the multinomial logistic for each profitability measure (H1, H2 or H3) separately to calculate the expected utility of visiting each site $j$ in the $i$th choice ($U_{ij}$). From these utilities, the expected probability of visiting each site is given by formula (2.1) [27]:

$$P_{ij} = \frac{e^{U_{ij}}}{\sum_{j=1}^{\max} e^{U_{ij}}}. \tag{2.1}$$

## (e) Spatio-temporal movement models

I performed simulations to predict the sites chosen in this experiment if a memory for elapsed time were not present. The question of interest in these simulations is whether inclusion of the actual elapsed time since the previous visit to a site would help to explain the pattern of simulated site choices, even though elapsed time was not part of the profitability measure. There are many models available to simulate or interpret small-scale movements of animals [29], but these only secondarily incorporate landscape-level features of attraction or repulsion. In this experimental context, I ignore small-scale movements, as capuchin groups in Iguazú move in nearly perfectly straight lines between the feeding sites [10], and so I am concerned only with the features of feeding sites that affect the choice of the next destination. Based on previous studies [20], I initially assumed that sites would be visited in proportion to their H1 profitability (expected reward at 24 h, divided by distance from the current site). This measure of profitability does not depend on the elapsed time since the previous visit to each destination site, so in principle elapsed time should not help to predict the movement of simulated animals. To predict the movements of simulated groups, I used a two-part process. First, I used the expected probabilities $P_{ij}$ of visiting destinations sites (from equation 1) based on profitability H1. Second, to add realistic constraints on group movements, I biased the simulated movements depending on the turning angle $\theta$, defined as the angle the group needed to turn from their previous direction (arriving at a given feeding site) to reach each destination. Larger angles were deemed less likely, based on
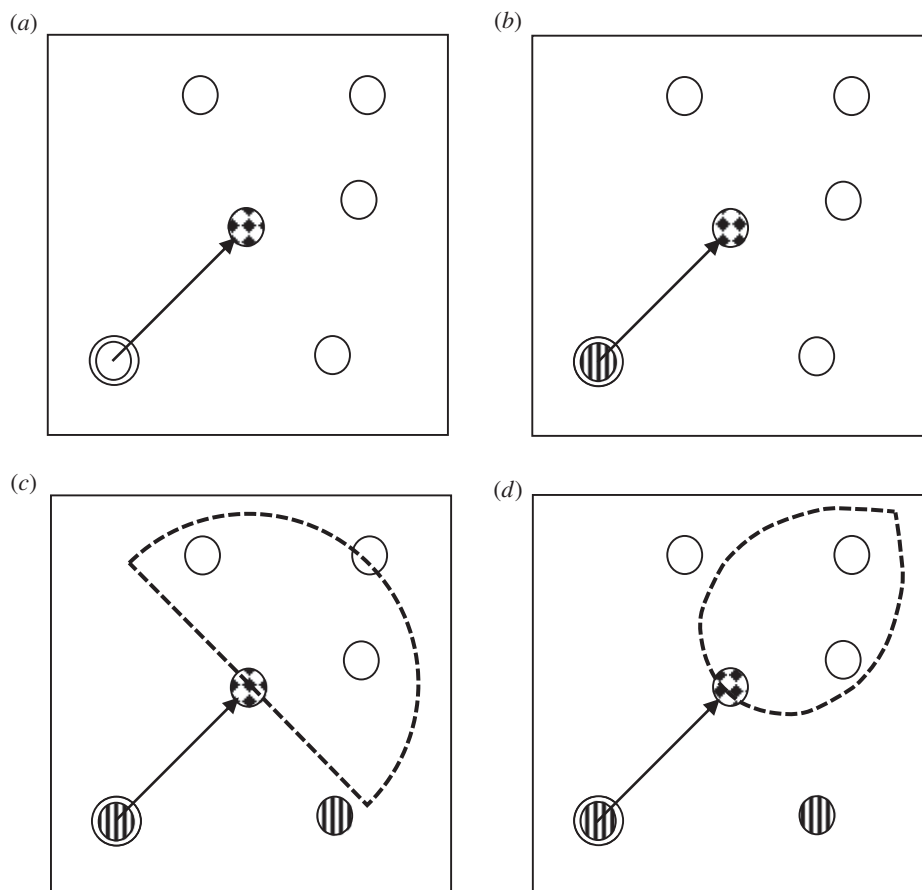
**Figure 2.** Diagram of simulated movement models. In each panel, the previous site is the double circle, the current site is checkered, all available choice sites are in white, and all excluded sites are striped. The initial travel path from the previous site to the current one is shown as an arrow. (*a*) No restriction except the current site: backtracking from the current to the previous site is allowed. (*b*) No backtrack: any site is available except the current and previous sites. (*c*) Forward uniform: sites within $\pm 90°$ of the initial travel path are equally available. (*d*) Forward linear bias: same as (*c*), but the probability of choosing a given forward angle is inversely proportional to the difference from straight-forward movement.

previous results [10]. I simulated four angular biases, the first with no directional bias and the rest with increasingly forward-biased movements (figure 2). The relative likelihood of moving in a particular direction for each such 'null' model is denoted by $L(\theta)$. Therefore, each destination site $j$ had a relative likelihood of being chosen equal to $R_{ij} = L(\theta_j)P_{ij}$. The probability of choosing site $j$ is given by

$$P_{ij}^* = \frac{R_{ij}}{\sum_{j=1}^{\max} R_{ij}}. \tag{2.2}$$

If no site fell within the restricted set of directions for a given model (all $L(\theta_j) = 0$), the simulated monkeys chose among sites according to equation (2.1). I used the resulting probabilities $P_{ij}^*$ to simulate choices of sites $j$ for each of the 212 observed starting sites $i$. I then used the resulting set of simulated choices in the multinomial Choice analysis in JMP to generate fitted parameters for distance, treatment and elapsed time that best predict the simulated choices; of particular interest was the slope for elapsed time. I repeated this procedure 1000 times to generate an expected distribution of the slope for elapsed time from the Choice model under the different forward-biased movement assumptions. I then compared the distribution of simulated slopes for elapsed time from each of the various null movement models to the Choice model's slope for elapsed time of the observed movements in this experiment. To check whether this simulation procedure would give realistic results under the conditions of the experiment, I repeated the simulations using H2 as the profitability measure, in which the food amount at each site depends on elapsed time in the same way as the experimental protocol.

## (f) Bootstrap procedure

I could not use conventional measures of model fit (e.g. *F*-test) to decide if a given measure of profitability fitted the observed movement data significantly better than another measure. The several tested models were not nested; for instance, H2 does not 'contain' H1 in the sense of using additional parameters to fit the data. In the case of non-nested models, any difference in model fit reveals only if one of the models is better, not whether the improved fit is greater than one would expect by chance (as one of the two models must necessarily fit better than the other). Therefore, I used a bootstrap procedure to calculate the likelihood of any observed improvement in fit from one model to the next more complicated one. I implemented the bootstrap procedure as follows. I used the output of the Choice analysis to calculate the expected probabilities $P_{ij}$ of choosing each destination site $j$ in a given choice $i$ using formula (2.1). I summed the $\ln(P_{ij})$ corresponding to the actual destination site observed in each choice across all $i$, yielding a single statistic, $T$. $T$ is directly proportional to the likelihood of the observed data with respect to the fitted model. The higher (less negative) the value of $T$, the greater the correspondence between the observed choices and the predicted probabilities of the observed choices by the model. For each model $H$, there is a corresponding $T$; for instance, H1 produces T1. I simulated the variability in $T$ for a given model by making random simulated choices of site $j$ in proportion to the $P_{ij}$ for each choice $i$, then using the Choice platform in JMP to generate a new set of simulated $P_{ij}$, which I named $SP_{ij}$. I summed the $\ln(SP_{ij})$ corresponding to each random 'observed' choice as before to generate a simulated test statistic $ST_i$; I repeated this simulation 10 000 times and stored

**Table 1.** Results of multinomial logistic analyses of feeding site choice based on simulated movement data, under increasingly restrictive assumptions about forward-biased movement (figure 2). The effect of interest is that of elapsed time interval in helping to explain variation in site choice; the values below are the slopes for ln(time interval). Because four tests of the same hypothesis (H1 profitability) are performed, a Bonferroni correction is applied to the experiment-wise type-1 error rate of 0.05, resulting in comparison-wise confidence intervals including $100(1 - 0.05/4) = 98.75\%$ of the simulated data. In each case, simulations were based on 1000 replicates. The slope of ln(time interval) for the same statistical model applied to the observed choices was 0.7293, which lies outside the confidence interval for the simulations based on H1, but inside the confidence interval for simulations based on H2.

| movement restrictions modelled | confidence interval of fitted slope of ln(time interval) in analysis of simulated site choice | |
| --- | --- | --- |
| | profitability model = H1 | profitability model = H2 |
| no immediate return to starting site (figure 2a) | −0.0129, 0.1907 | 0. 5663, 0.9319 |
| no backtrack to previous site (figure 2b) | 0.1793, 0.3860 | 0.6212, 0.9804 |
| forward uniform (figure 2c) | 0.3729, 0.6082 | 0.6679, 1.0232 |
| forward linear bias (figure 2d) | 0.3991, 0.6335 | 0.6775, 0.9944 |

the results as a cumulative distribution CD(ST). I started with model H1, generating CD(ST1). I then fitted the next model (H2) to the data and calculated T2. If the model corresponding to T2 was no better able to predict the observed choices than the model corresponding to T1, then T2 should not differ markedly from the median value of ST1. If T2 had a value that was significantly above the median of ST1 (specifically, in the upper 5%/2 tests = 2.5% tail of CD(ST1)), then T1 was rejected in the favour of T2. This bootstrap approach was then repeated with H3 versus H2 for a total of two planned tests.

## 3. Results

### (a) Choice of feeding site: space, energy and time

As expected, the group's choice of a next feeding site depended significantly on distance, food renewal treatment and elapsed time interval when the null hypothesis for each variable is zero (electronic supplementary material). The non-zero effects of distance and time could be trivially due to the inevitable spatio-temporal autocorrelation of sequences of animal movements [17]. I have previously shown that capuchins in this study population have highly goal-oriented movements toward feeding sites that are closer and/or have more food, in ways that cannot be duplicated by any reasonable search model of foraging [10]. Therefore, I focus here on assessing the effect of elapsed time.

### (b) Can forward-biased movement explain an apparent memory for elapsed time?

I simulated site choice under successively more restrictive forward-biased movement (figure 2): (i) no restrictions—the group could choose any site, except the present one it was leaving from; (ii) no backtrack—the group could visit any site except the present site and the site it had left to arrive at the present site; (iii) forward uniform—they could choose with equal likelihood any site the lay within $\pm 90^{\circ}$ of the direction between the previous site and the current one; (iv) forward linear bias—as (iii), but with the relative likelihood of choosing a site being inversely proportional to the angular deviation from $0^{\circ}$. The distribution of turning angles of actual site-to-site movements is closest to situation (iv) [10]. As expected, the slope of elapsed time on site choice did not differ significantly from zero when there were no angular

restrictions on movements and profitability did not depend on actual elapsed time (table 1); in this case, the spatio-temporal correlation of movements should be close to zero. However, in all other cases, including the simplest of avoiding only the immediately previously visited site (figure 2b), elapsed time was a highly significant predictor of site choice (the confidence limits of its slope are bounded well away from zero). Thus, even when elapsed time is not part of the profitability measure used to choose feeding sites, an apparent effect of elapsed time can be statistically prominent in the analysis of sites chosen (cf. [18]).

Given the strong statistical effect of elapsed time on simulated forward-biased site choices when destination profitability did not include elapsed time, could the effect of elapsed time on observed choices be due simply to forward-biased movement? If monkeys choose to travel towards sites with longer actual delays since the previous visit, then the statistical effect of elapsed time on site choice should be quantitatively stronger for observed choices than in the preceding simulated choices that do not include elapsed time. I performed the statistical analysis in table 1 using the observed choices rather than simulated ones. As expected, the contribution of elapsed time in the statistical model for observed choices (slope = 0.7293) was significantly greater than in the comparable models for forward-biased simulated movements that use time-independent profitability H1.

A sceptic might argue that I chose the wrong class of movement models or that the particular degrees of forward bias in my simulations produced these results that differ from the observed choices (table 1, H1), even though some other movement parameters might have fitted better. To discover if the movement models I used to simulate choice can produce realistic results under appropriate conditions, I repeated the previous simulations but with choice depending on profitability measure H2, which includes actual elapsed time since the previous visit to each site at the moment of decision. For the same set of four movement rules (figure 2), all sets of simulations using H2 produced slopes for elapsed time that are consistent with the effect of elapsed time for the observed choices (table 1, H2). This outcome was true even when the group could have backtracked to the site they had just left, and therefore was independent of any forward bias of group movements. Thus, the observed site-to-site movement data are consistent with a simple preference to visit sites with

**Table 2.** Results of observed versus simulated choices under several sequential models assuming integration of more kinds of information or across more feeding sites (steps) into the profitability measure. $T$ is a test statistic proportional to the likelihood of the data given the hypothesis. The probability of $Ti$ is the fraction of the distribution of simulated $ST(i-1)$ that was greater than $Ti$ (see the text).

| model ($i$) | observed $Ti$ | simulated $STi$ (min, median, max, s.d.) | P($Ti$), one-tailed | % agreement of observed versus predicted (highest utility) choices |
|---|---|---|---|---|
| base model H1: site-specific intercepts and 24 h reward (based on renewal rate treatment) divided by distance | −318.53 | −372.41, −317.3, −266.27, 13.12 | <0.0001 | 42.9 (91/212) |
| H2: as H1 but site rewards based on elapsed time since previous visit | −273.69 | −330.96, −271.6, −220.44, 14.04 | 0.00035 | 51.9 (110/212) |
| H3 = H2 plus 2-step planning | −254.34 | −326.4, −260.66, −216.89, 13.36 | 0.1 | 58.5 (124/212) |

higher expected food rewards when these increase predictably with elapsed time since the previous visit.

## (c) What movement rule do the monkeys appear to use?

Having established that including elapsed time helps to explain the monkeys' observed choices among renewing feeding sites, it is of interest to ask which of several profitability measures predicts the observations most parsimoniously. I fitted a series of models using increasingly complex temporal and/or spatial cognition as the basis for evaluating the profitability of different site choices. The profitability measure H1, which does not depend on elapsed time, along with site-specific intercepts, gave a significantly better fit than a null model (H0) using only site-specific intercepts (likelihood ratio $\chi^2 = 187.8$, d.f. = 1, $p < 0.0001$, one-tailed). The use of actual elapsed time interval to calculate expected site-specific profitability (H2 versus H1) significantly increased the fit of the model to the observed movements (table 2; $p = 0.00035$, one-tailed). Calculating time-dependent profitability over pairs of sites (H3) increased the fit over H2, but not quite significantly so (table 2, $p = 0.10$, one-tailed). The fraction of site choices predicted correctly (using the destination with the highest utility) parallels the patterns of model fit (table 2). The highest fraction is from H3 (58.5% of cases), followed by H2 (51.9%) and H1 (42.9%). The difference between H2 and H1 is significant (Fisher's exact test, $p = 0.04$, one-tailed), as is that between H3 and H1 ($p = 0.0009$, one-tailed), but that between H3 and H2 is not ($p = 0.10$, one-tailed).

## 4. Discussion

The behaviour of the capuchin monkeys in this study strongly suggests that they incorporate site-specific elapsed-time delays into their choice of what feeding sites to visit, along with each site's distance to their current location, and the rate of food renewal of the site. They visited the eight feeding sites in their home range in a pattern that is most consistent with a simple decision rule (H2): move to the most profitable food source (the one with the highest ratio of expected reward to distance). They may also stop at less rewarding intermediate sites that lie close to the straight-line path to more rewarding sites (H3), although the pattern is less striking here than in a previous study [20]. Thus, wild capuchins monkeys at this study site appear to perceive and use information on elapsed time since the last visit to a site, along with the site's distance to their current location and its productivity. Based on their observed behaviours, they appear to have used these integrated and dynamic memories of the site characteristics to anticipate which site would have the highest expected profitability; they chose the sites with the highest profitabilities in a majority of cases (table 2). Correctly anticipating time-varying rewards at distant feeding sites might be consistent with the idea of 'mental time-travel', a cognitive ability often associated with episodic memory [4,5].

This experiment provides a more rigorous test of the cognitive bases of monkey movement rules than any previous study on wild primates. Because my assistants and I controlled the food provided at each destination site according to an established rule, the profitability measures used here could be defined without reference to the monkeys' current behaviour and were known with precision. Previous observational studies on wild primates based feeding site quality either on rough gauges of expected productivity based on the size of tree or estimated fruit crop [9], or the realized feeding success of the group when they visited a given visit [30]. In addition, because I did not provide the food until the group had already committed to its movement towards a given feeding site, there is no possibility that the monkeys could cue directly on the size of the food reward to make their decision. Both simpler and more complex cognitive models did not fit the data better, and in some cases did significantly worse, than the model using elapsed time to predict site-specific profitability. While it is possible that some other untested model would fit the data better, I have made every effort to eliminate simpler models as the cause of the observed patterns.

## 5. Conclusion

The results of this study suggest that wild capuchin monkeys can remember three characteristics of each of their feeding sites in this experiment (distance to the site, elapsed time since the previous visit, the rate of food renewal of the site) and can integrate them into a measure of profitability that they compared among sites and perhaps even along multi-destination routes spanning pairs of sites. They appeared to choose the next site to visit using a simple rule of strongly preferring the site with the highest expected profitability at the moment they left the previous site. Such flexible and integrated

cognition is remarkable and conforms well to the foraging challenges suggested by Milton [16] as the selection pressure favouring advanced cognition in primates.

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