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# Wild chacma baboons *(Papio ursinus)* remember single foraging episodes

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## Abstract

Understanding animal episodic-like memory is important for tracing the evolution of the human mind. However, our knowledge about the existence and nature of episodic-like memory in nonhuman primates is minimal. We observed the behaviour of a wild male chacma baboon faced with a trade-off between protecting his stationary group from aggressive extra-group males and foraging among five out-of-sight platforms. These contained high-priority food at a time of natural food shortage. In 10 morning and 8 evening trials, the male spontaneously visited the platforms in 5 and 4 different sequences, respectively. In addition, he interrupted foraging sequences at virtually any point on eight occasions, returning to the group for up to 2 hours. He then visited some or all of the remaining platforms and prevented re-visits to already depleted ones, apparently based on his memory for the previous foraging episode about food value, location and time. Efficient use of memory allowed him to keep minimal time absent from his group while keeping food intake high. These findings support the idea that episodic-like memory offers an all-purpose solution to a wide variety of problems that require flexible, quick, yet precise decisions in situations arising from competition for food and mates in wild primates.

Key words: foraging, episodic-like memory, baboons, feeding platforms, flexibility

## Introduction

Declarative memory systems offer potential solutions to two distinct kinds of challenge for a foraging animal, both of which are fitness-relevant. On the one hand, a semantic memory system would provide information about environmental regularities (Tulving 1983), such as the aboveground aspect of plants with palatable bulbs, the spatial location of a water hole, and the animal's social status relative to others. On the other hand, an episodic memory system would provide detail about entire events that are likely to occur in the same form only once: human episodic (Tulving 1983) and animal episodic-like (Clayton and Dickinson 1998; see Beran 2014 for alternative terminology) memories have been viewed as integrated representations of several co-occurring percepts that allow remembering the broader context in which an important event was embedded (e.g. an entire scenario). For example, in addition to remembering a leopard attack with information about its location, a baboon may remember that all other group members had been out-of-sight, that the sun had just disappeared behind the horizon, and that a flock of crested guinea fowls had been foraging in a nearby thicket. Although none of these percepts alone are directly linked to leopard attacks, they may together indicate an increased likelihood of an attack, and in the baboon evoke the corresponding episodic memory. Episodic(-like) memory shares neural substrates in humans and animals (Allen and Fortin 2013), and therefore is likely to also share an evolutionary past (Raby and Clayton 2012; Allen and Fortin 2013). Understanding the nature and circumstances in which episodic memories are formed by animal minds is thus crucial for understanding the human mind.

Animal episodic-like memories were initially demonstrated in scrub jays by Clayton and Dickinson (1998). They were viewed as integrated memories for content ("what"), location ("where") and time ("when"), leaving aside the much-disputed role of a sense of subjective experience (e. g. resulting from autonoetic consciousness, Tulving 1983, 2005; mental time travel, Schwartz et al. 2005; or autobiographical memory, Fivush 2011) as an additional, compulsory component. At the same time, a language-trained chimpanzee was reported to spontaneously recall the nature ("what") and locations ("where") of objects several hours or days after they had been hidden outside her cage, even though she witnessed the corresponding hiding event only once (Menzel 1999; 2005). Clearly, these behaviours could not be explained by the traditional view that animal memory is confined to environmental regularities. This sparked a hefty controversy about the relation between animal and human episodic(-like) memory (e. g. Tulving 1983, 2005; Suddendorf and Corballis 2007; Suddendorf and Busby 2003; Roberts and Feeney 2009; Raby and Clayton 2012 for reviews). Although the role of self-consciousness in human episodic memory still remains unclear to date, it was the "when" component that has been particularly questioned as a valid indicator of episodic-like memory in animal studies (Roberts 2002; Crystal 2010; Raby and Clayton 2012): it was suggested that animals can distinguish two events that occurred in the past with relatively simple cognitive mechanisms, for example based on relative familiarity (Crystal 2010) or memory trace strength estimation (e. g. Friedman 1993; Roberts 2002; but see Schwartz et al. 2005 for an example of gorilla palinscopy). It was pointed out that these time estimation mechanisms can be performed in the present, but fail to reflect a "sense of pastness". For example, scrub-jays may use the state of their memory trace of the location where they have previously cached worms to semantically predict whether or not the worms are decayed, whereby, for example, a weaker memory trace meant decayed worms, a stronger memory trace meant fresh worms (Roberts 2002; Schwartz 2005).

However, it has also been pointed out that the time component of human episodic memories can be rudimentary (Zentall et al. 2001) or entirely absent (Friedman 1993). For example, humans may distinguish two past dinners out with the same friend by binding each episode to the different contexts provided by the two restaurants (Clayton et al. 2007). Thus, time has been proposed to consist of just one of several possible "occasion specifiers" that are used by humans and animals alike to distinguish similar episodes (Eacott and Norman 2004; Eacott et al 2005). As a consequence, episodic-like memory has been re-defined as integrated long-term memories for events (one or several "what" components) in context ("which", such as "where", "when", "who", or other details, see also Menzel 2005), to support adaptive behaviour in novel situations (Allen and Fortin, 2013; Clayton et al. 2003; Clayton et al. 2007).

Episodic-like memory has been claimed for several species (e. g. scrub jays: Clayton and Dickinson 1998; rats: Eacott and Norman 2004, Eacott et al. 2005, Babb and Crystal 2005, 2006; chickadees: Feeney et al. 2009; magpies: Zinkivskay et al. 2009; cuttlefish: Jozet-Alves et al. 2013; meadow voles: Ferkin et al. 2008; chimpanzees: Menzel 1999; Menzel 2005; orang-utans and bonobos: Martin-Ordas et al. 2010; minipigs: Kouwenberg et al. 2009; adult humans: Holland and Smulders 2011, human children: Scarf et al. 2013; hummingbirds: Gonzalez-Gomez et al. 2011). Surprisingly, monkeys have to date not shown convincing evidence of episodic-like memory (Hampton et al. 2005; Hoffman et al. 2009; Basil and Hampton 2011), alongside of pigeons (Zentall et al. 2001). The experimental paradigms used by Hoffman et al. (2009) and Basil and Hampton (2011) used delays of seconds and thus examined working-memory. This raises doubt about whether a link of the results to the concept of episodic memory can be made with confidence. In contrast, the monkeys *(Macaca mulatta)* tested by Hampton et al (2005) failed to show that they differentiated between short and long delays ("when"). The authors concluded that their subjects were not sensitive to the time of learning where preferred food was hidden in a room, and that their memory was restricted to the "what" and the "where" component. Thus, convincing evidence that monkeys use episodic-like memory is still lacking, and our understanding of the factors under which episodic-like memory may be beneficial in natural settings is at best vague.

The daily lives of wild savannah baboons, as those of many other animal species, contain a large number of re-occurring event sequences. Baboons feed on a wide variety of stationary food sources, and their re-visit rate to particular food patches and water holes is high. They possess excellent memory skills for the locations of different food types. They anticipate the value of out-of-sight food they will obtain up to two hours later (Noser and Byrne 2007; 2010). Also, there is evidence that they infer food value of out-of-sight resource sites from the movement directions of group members alone (Stolba 1979; King et al. 2008, Figure S4). This impressive knowledge about resource value and location allows them to take important, but re-occurring foraging decisions during social and ecological stability, allowing them to survive and reproduce in areas of low food density.

However, baboons also regularly face a wide variety of unpredictable or novel events, such as the sudden appearance of an intra-group competitor, a competing group or a predator, causing a deviation of their usual foraging routine. Do they link such an event with additional details surrounding the scenario, and use this information in the future? To answer this question, we examined whether a wild alpha male chacma baboon under naturally occurring but unusually high time pressure spontaneously formed a memory for single foraging episodes. Stressor was the highly unusual presence of close-by extra-group males that for him generated a trade-off between two fitness-relevant tasks: foraging for highly valuable fruit (orange) among five out-of-sight feeding platforms during a time of food shortage, when the most valuable naturally occurring fruit type consisted of tiny, dry and at best mildly sweet berries *(Grewia spp)* located at much larger distances (Noser and Byrne 2007); and protecting his females and offspring from aggression and take-over by these males (e.g. Palombit et al. 2000). We hypothesised that knowledge about the spatial locations of platforms (i.e. a cognitive map of some form; "where") and their contents ("what"; resource value) would allow him to forage for some or all orange sites at a time, and perhaps to keep short overall foraging distance. In contrast, only by integrating a cognitive map and contents with an episodic-like memory of temporal or categorical information of single platforms could he tell recent foraging episodes apart from older ones, and as a result, predict which platforms were still baited after foraging had been unexpectedly disrupted. If available, this form of memory would allow him to flexibly switch between the two tasks given by the trade-off, and ultimately to coordinate his foraging with the group's behaviour, adjusting the timing and extent of foraging to the current social requirements of a particular situation while maximising foraging benefit.

## Methods

This experiment was part of a larger study that we carried out in the woodland savannah at Blouberg Nature Reserve (BNR; 22° 58'S, 29°09' E), Limpopo Province, South Africa between August 2000 and August 2002 with a group of chacma baboons *(Papio ursinus;* see Noser and Byrne, 2007 for details). The group consisted of the adult alpha male, an adolescent male, and of 8 adult females with offspring, totalling 24 individuals. At the time of the test phase, they had been followed on foot daily by a team of two human observers for 23 months and thus were well habituated to our presence. The alpha male had been dominant over an additional male who had emigrated from the group at an earlier stage of the study, and thus was likely to have fathered a large number of offspring present in the group. The group used a single sleeping site throughout the study, and as a consequence, could be regularly met in the adjacent area in the early mornings and late afternoons.

Between August 2001 and May 2002 we habituated the group to the presence of novel feeding platforms, commercial oil barrels (approx 88 cm in height, 60 cm in diameter), with the outer steel walls painted in brown. We filled the barrels with heavy rocks to ensure stability, and occasionally baited them with two slices of peeled orange each so that the oranges could only be seen by a baboon when sitting on the platform, or when standing on the hind legs in front of them, but not when walking on the ground. The relatively small platform diameter enabled single baboons to monopolise a platform. All group members could reach the oranges.

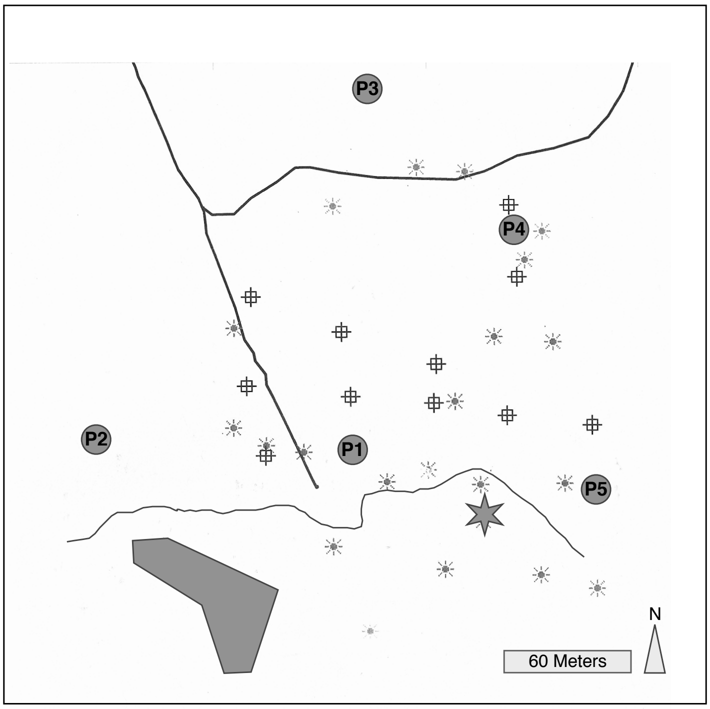

**Figure 1**
Map of experimental setting. Five monopolisable feeding platforms P1 - P5 (grey circles), situated next to the sleeping site (large grey area) were baited with two slices of peeled orange each. The foraging behaviour of subjects was monitored from an elevated observation point (large star). Thick grey lines are car tracks, thin grey line is line of most pronounced change in elevation. Small symbols (suns and crossed rectangles) represent landmarks.

In May 2002, we placed a total of five platforms (P1 - P5) in the vicinity of the sleeping site (Figure 1), so that two criteria were met, 1) the platforms were out of sight of each other, and 2) all the platforms as well as the sleeping site area were well visible from an elevated observation point (large star in Figure 1). We excluded inter-platform visibility: two persons stood each next to a platform, one waving a white plastic bag on a stick at the height of the upper platform rim, and the other one determining with binoculars from which point along the line connecting the two platforms the flag became visible through the bushes. This revealed that platforms became visible from a distance of 40 m or less. The sleeping site area was out of sight from P3, P4 and P5, and partly visible from P1 and P2. We took GPS readings of the sleeping site area, the platforms and of prominent landmarks in the experimental area (car tracks, a fire break, a dry riverbed, tall trees, rock outcrops) and plotted maps of this layout.

The learning phase took place between May and July 2002, for a total of 21 trials, and ended when at least one individual had discovered all platforms. Learning trials were carried out opportunistically, either in the mornings before the group left the sleeping site, or in the evenings when they re-approached it for the night. To indicate that the platforms had been baited, we placed two slices of orange on the ground at a distance of approximately 5 m from P1, so that they were visible from the sleeping site. Note that as a result, the value of P1 (with 2 orange slices on the platform and 2 next to it) was larger than the value of P2 - P5 (each containing 2 slices). For morning trials, platforms were baited before dawn, at around 5 am, when the group was still asleep. For evening trials, baiting took place at around 3 pm, when the group still foraged far from the experimental area.

The sleeping site had been used exclusively and at a daily basis by the focal group for at least 21 months (August 2000 - May 2002). This, together with our observation that our focal group's day journey lengths were large in comparison with those observed at other baboon study sites (Noser and Byrne, unpublished), suggested that the Blouberg baboon groups competed intensely for suitable sleeping sites. Indeed, an additional unknown baboon group consisting of approximately 35 individuals (two adult males, 11 adult females) suddenly started to co-use our focal group's sleeping site during the learning phase (June 2002). From this point onward, the two groups shared the site every night, using a small vertical elevation in the cliff as a natural visual barrier to separate the groups' actual sleeping ledges. At dawn (approx. 6 am), both groups climbed the cliff. This was the point when aggressive inter-group interactions started, including emission of a large number of male aggressive inter-group calls ("roar-grunts"), alarm calls ("wahoos", "barks"), many herding bouts and screaming. We did not observe any friendly interactions between any of the two groups' members. Aggressive displays persisted in the mornings until one of the groups left the area at around 8 am to forage separately and out-of-sight of the other during the day. In the evenings, the two groups returned from their foraging trips at around 5 pm. Aggressive displays were taken up immediately. They lasted until around 6:30 pm, when the two groups entered the actual sleeping ledges. The novel group was unhabituated to observers and platforms, and never participated in trials.

The test phase started in July 2002, during the dry season. Due to poor quantity and quality of naturally occurring fruit during this time of year, the study group regularly traveled for up to 2 hours each morning at high speed to breakfast on small, dry Grewia berry *(Grewia spp)* situated at distances of 5 - 6 km from the sleeping site. This was the turning point of their journey after which they returned to the sleeping site while slowly travel-feeding on abundant dry matter such as pods and kernels (Noser and Byrne 2007). Both, the natural fruit scarcity and the associated natural foraging behaviour suggested that our baited platforms constituted extremely valuable food resources to these baboons. The test phase comprised a total of 18 trials (10 morning, 8 evening trials). During this time, none of the focal group's females were in oestrus.

Two observers watched the experimental area from the observation point (Figure 1): one continuously followed the alpha male's behaviour, the other observer scanned the experimental area for additional baboons using the platforms. The following variables were spoken onto a voice recorder: identity of individuals that foraged for oranges (thereafter "subjects"), time when subjects climbed individual platforms P1 - P5, and whether or not they found and ingested oranges. We reconstructed the routes that subjects had taken by additionally recording the time when they passed by the prominent landmarks in the experimental area (Figure 1). Maps of these routes were drawn from the recordings after returning to the research camp the same day. Since travel among platforms was essentially linear, we used the order of platform visits to assess spatial flexibility (Figure 2).

We viewed a trial as "split" into two parts when a subject interrupted and then resumed orange foraging. This resulted in a "first part" and a "second part" of orange foraging, with either of two types of behaviour occurring intermittently: returning to the sleeping site to socialise or engage in group defense, and climbing trees to inspect the area. During the second part of orange foraging, one ore more platforms were visited. Foraging time for oranges was the time (accurate to 1 min) when a subject crossed the imaginary outer lines of the experimental area connecting the platforms.

A baboon was viewed as absent from the group when he was engaged in orange foraging while the majority of the group stayed in the sleeping site area (mornings; see Figure 1 for distances) or foraged for natural foods far from the experimental area (evenings; unknown distances between forager and other group members), thereby temporally losing sight of them. In contrast, subjects were viewed as present when they coordinated their behaviour with their own group, so that orange foraging occurred during the time when their group crossed or passed by the experimental area, and spatial proximity to their group was retained.

We used R software (R Core Team 2013) for statistics. We performed a hypothesis test with a linear mixed model fit by maximum likelihood (lme4 package, Bates et al. 2014), comparing a null model with an extended model using BIC and Anova. After depletion of a given orange site, subjects needed to decide which platform to visit next. We viewed long-term memory to be involved in this choice when a "split" occurred between depletion of platform n and choice for platform n+1. For these cases, we devised a random choice model each for the third, the fourth and the fifth platform simulating 1000 decisions from random numbers. We determined the likelihood that the observed number of choices to unvisited platforms was due to chance.

## Results

The alpha male participated in 18 test trials (100 %) and obtained 0.68 ± 0.48 orange slices per min spent in the experimental area (mean ± SD). In comparison, the adolescent male participated only in three trials, and obtained only 0.14 ± 0.27 slices per min. Two additional group members, an adolescent male and an adult female, spent 1 min and 12 min in the experimental area, but did not obtain any oranges at all. For the rest of this study, we focus on the performance of the alpha male only.

Within-trial re-visits to platforms occurred three times: twice in the learning phase, and once in the test phase, with a delay between the two visits of 14, 28, and 14 min respectively, and intermittent visits to additional platforms. Inter-trial intervals ranged between 8.3 and 37.7 h (median 18.7 h), and some or all platforms that had been visited in trial x were re-visited in trial x+1.

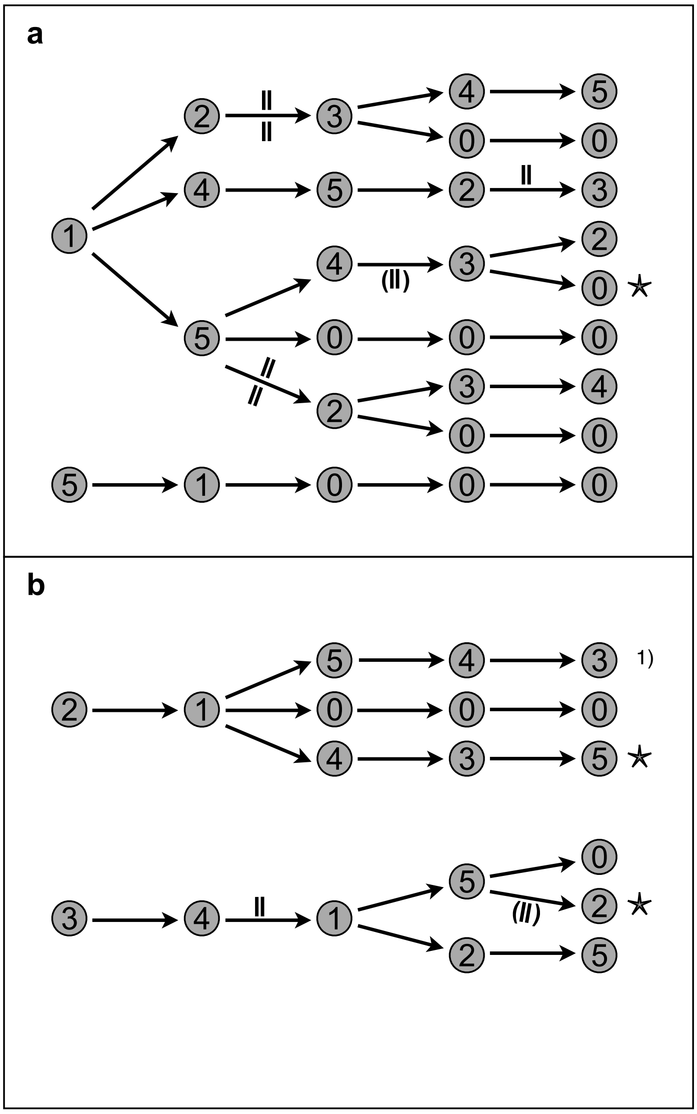

**Figure 2**

Flexibility in number, order and timing of visits to platforms in 18 trials. In the mornings (a; N=10), when the sleeping site was the starting point of orange foraging, the alpha male first visited P1 on 9 occasions, and then visited either P2, P4, or P5. He then either left the experimental area to entirely abandon orange foraging (indicated by three 0 for the remaining platforms), or to resume orange foraging, sometimes after returning to the sleeping site and spending 8 - 113 min with the group (**II**, occurrence of a "split", see text). Note that a split applies to upper of two path legs when the sign is located above arrow, and to lower path when the sign is below. Stars indicate identical number and order of visits in two trials. (**II**) indicates that only one of two otherwise identical sequences of orange foraging was split. In the evening trials (b; N = 8), P2 and P3 were the first platforms visited, corresponding to the overall direction from where the sleeping site was approached after natural foraging. 1) A single within-trial re-visit to a platform was recorded in an evening trial, with the order of visits P2-P1-P5-P4-P3-P1-sleeping site.

The alpha male's spatial and temporal decisions during orange foraging exhibited a high degree of variation (Figure 2). It is reasonable to assume that trials in which he left one or several platforms unvisited (indicated by 0 in the platform symbols; N = 8) as well as split trials (a split in a sequence of visits is indicated by **II**; N = 8; Figure 2) reflect socially-induced interruptions of a given trip. Thus, they can be interpreted as parts of intended, but unfinished full trips. Taking this view, the alpha male exhibited five spatial variants of orange foraging in the mornings, and four in the evenings. Abandoning orange foraging after only two platform visits without later resumption occurred in three trials; it remains open whether these trips, if finished, would have resulted in additional variants.

Splits occurred after visits to two, three or four platforms. One, two or three platforms were visited after resumption of orange foraging in the second part of split trials. Splits never occurred during the learning phase, but appeared for the first time during the third test trial. Re-visits to platforms did not occur in split trials. Median time elapsed between the end of the first and the beginning of the second part of orange foraging in split trials was 92.5 min (range 8 -113 min). The onset of the second part was triggered by the spatial displacement of the focal group in 7 of 8 split trials: the alpha male re-entered the experimental area when the group either finished socialising/engaging in aggressive displays (mornings) or feeding (evenings) and started moving by either directly crossing the experimental area or passing by at a short distance. In the remaining case, the adolescent male entered the experimental area shortly after the alpha male had interrupted orange foraging. This caused the alpha male to re-enter the area after only 8 min, and to resume orange foraging.

Overall, the alpha male stayed in the experimental area for 14.4 ± 5.8 min per trial (mean ± SD). However, he stayed absent from the group for only 10.1 ± 5.1 min, due to his ability to split trials. Statistically, splitting orange foraging into two parts significantly reduced duration of absence from the group (linear mixed null model: fixed effect = number of barrels visited, random effect = date (with two or only one experimental trials per date), BIC = - 8.3; full model: fixed effects = Number of platforms visited, occurrence of split (yes/no), random effect = date, BIC = -18.7, ChiSq = 12.4, $P < 0.001$, Figure 3).

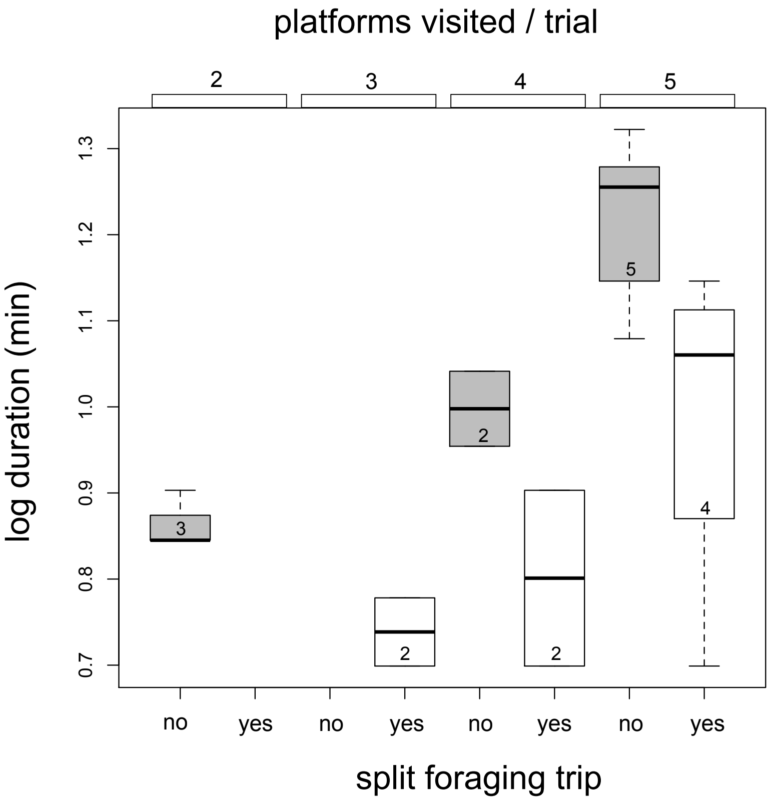

**Fig. 3**

Duration of absence from group was shorter when the alpha male split the foraging trip split into two parts (white) and longer when a split did not occur (grey), irrespective of the number of platforms visited per trial. Numbers within boxes are numbers of observations.

Were the platform choices during the second parts of split trials informed by memory? Splits after depletion of two platforms occurred on five occasions (Figure 2). The random choice model revealed a likelihood of subsequently targeting an unvisited platform on five occasions (e.g., without targeting an already depleted platform in one or several trials) of P = 0.093. In contrast, a split after three visited platforms occurred in a single trial, and the corresponding likelihood of targeting an unvisited platform after the split was P = 0.386. A split after visits to four platforms occurred twice, and the likelihood of targeting the single unvisited platform after the splits was P = 0.033. Thus, when splitting the orange foraging into two parts, the likelihood of never targeting an already visited platform after the splits in a total of eight trials by pure chance, without involvement of long-term memory was highly significant (P = 0.001). This suggests that the alpha male used a memory of earlier platform visits when resuming orange foraging after a split.

## Discussion

During ten morning and eight evening experimental trials, a wild male chacma baboon faced two mutually exclusive tasks: the presence of extra-group males next to his group required him to engage in group defense and to stay next to the group, while obtaining rare high-priority food at distant out-of-sight feeding platforms early (see Noser and Byrne 2007: Janmaat et al. 2014) required him to leave. In this situation, the male applied a flexible spatial and temporal strategy. He visited five baited platforms in several different sequences, with the visit order possibly depending on the behaviour and spatial location of extra-group males in a given trial. In addition, he interrupted some of these sequences at virtually any point to re-join the social group after having depleted only a fraction of the platforms. Later, he returned to visit some or all remaining platforms, apparently by choosing a time when he could coordinate his own foraging behaviour with the general movement of his group. This strategy allowed him to significantly reduce duration of absence from the group, but required long-term memory for previous specific foraging episodes to avoid redundant re-visits to platforms.

The flexibility of the order of platform visits as well as the ability to resume a randomly interrupted trip after a delay without re-visits to depleted platforms implies that he did not primarily pursue a distance minimising strategy, but rather reflects a disposition to adapt to an unpredictable and unstable social environment, perhaps while keeping overall-distance short. Indeed, a short-term maximisation foraging strategy, predicting choice of the next best option at each decision point is expected under such circumstances (Sayers and Menzel 2012 and references therein). On a cognitive level, semantic knowledge about resource value and location cannot entirely explain the high degree of behavioural flexibility required in such situations. When interrupting and then resuming orange foraging, the alpha male baboon never re-visited an already depleted platform. This suggests an additional temporal memory component that was specific to a particular foraging episode and allowed him to differentiate between long and short delays of previous visits to individual platforms: already visited platforms were empty after short, but not after long delays.

How might he have achieved this? Using an external cue such as time of day cannot account for our findings, due to the irregular nature of our experiment. Neither is interval timing (Friedman 1993; Roberts 1998) a likely explanation, since this mechanism has only been documented for time estimates considerably shorter than those involved in the present study. Relative familiarity and memory strength estimation are two mechanisms often proposed as providing humans and animals with cues to distinguish more recent from older memories when directly perceiving an item. In the present experiment, recent memories were built 92.5 min ago on average, and older ones 18.7 hours ago, theoretically allowing a clear distinction. However, when the alpha male started approaching the remaining platforms after a split, he was unable to see them until he was close by (i.e. 40 m or less apart). Thus, relative familiarity cannot account for his performance unless we assume he compared mental representations of familiarity or memory trace strengths for several platforms.

A more parsimonious view is that upon visiting a platform, the alpha male may have "tagged" it as "depleted", internally checking it off a represented list or a cognitive map containing all platforms, and holding a memory of the platforms that remained baited. In each experimental trial, he would then have used a represented map with different locations still active after the delay. This assumption would not necessarily assume a memory for the actual event of depleting a platform, or a "sense of pastness"; rather, it assumes an integrated memory that (semantically) encodes food value and location of several resource places, and an additional flexible component that regulates a categorical "tag" for each location that temporally and individually devalues platforms once they are visited. This "tag" would need to become inactive after a minimum of 2 hours to allow re-visits of all platforms during a later trial.

How does do this idea match the natural foraging behaviour of baboons? During our 2-year study with this baboon group, most naturally occurring fruit resources were visited only once a day, leaving the possibility of a tagging mechanism intact. However, this was not true for one naturally occurring food source, the Mountain Fig *(Ficus glumosa):* our focal group did re-visit particularly productive Mountain Fig tree specimens after delays of 111 min minimally (median 221 min), with 6 within-day re-visits to two trees recorded on 12 days of observation (Noser and Byrne, unpublished). Other trees, however, were visited only once a day, and yet others after longer time periods. In contrast to the present study, the decision to re-visit a fig tree was likely taken on the basis of differential renewal rates of individual trees, with trees that were ideally exposed to the summer sun producing ripe figs at shorter time intervals. In the present study, renewal rate was identical for all platforms, but orange feeding (i.e. visiting and depleting one platform after the other) was interrupted by another baboon group. As a consequence, the baboon male needed to remember which platforms he had already visited, and which ones remained baited. In this situation, the longest delay between the two parts of a "split" trial was 116 min, yet no re-visit occurred. These observations combined are at odds with the idea that a single, rigid "tagging" mechanism governs re-visits to resource places in baboons, which would obviously lead to a rigid re-visit pattern. Instead, we need to assume that different tags exist for different food types, and in the case of fig foraging, also for different specimens within a species. Given that our baboon group consumed at least 27 fruit species in addition to a wide variety of non-fruit food (Noser and Byrne, unpublished), this would imply an extensive body of semantic knowledge about renewal patterns (or a large number of different "tags"). Any advantage of parsimony is thus lost.

Clearly, a more elegant way to solve the problem posed in this study, and in foraging in large-scale space under uncertain social conditions in general, is holding an integrated memory containing information about food value (or profitability) at multiple locations, about how to get there (e.g. Noser and Byrne 2007; Janson 1998), and an egocentric memory component that stores information about own behaviour to reveal the locations already visited and those that are still available. This cognitive toolbox allows for choosing the next best option at each decision point ("short-term rate maximisation", see Sayers and Menzel 2012). This idea converges with the observations of captive chimpanzees who recover hidden bags in the order of profitability rather than in the order of the hiding process (Sayers and Menzel 2012), and of wild capuchin monkeys who visit feeding platforms in the order of profitability (Janson 1998). In fact, there is growing neuroanatomical evidence that this ability may extend to simian primates in general (Genovesio et al. 2014).

In summary, we have presented data on an adult male baboon whose foraging journey among five out-of-sight platforms containing high-priority food was repeatedly disrupted due to extra-group males staying in proximity to his females and offspring. The fact that he continued any disrupted journey after several hours, thereby never re-visiting an already depleted platform suggested that he had formed an episodic-like memory for the value and location of high-priority food and for the locations that still contained food after a single foraging episode. These findings highlight the adaptive value of episodic-like memory in the wild when flexible, quick, yet precise decisions must be taken in a complex foraging and social environment.

Our findings raise the question whether all foraging episodes, only those for high-priority foods, or only foraging episodes that are coupled with elevated stress levels leave behind episodic-like memory traces in baboon brains. Evidence for the latter comes from the finding that human and rat declarative memory consolidation co-varies with stress hormones levels: experienced stress at the time of learning leads to increased long-term memory performance (Sandi and Pinelo-Nava 2007; Wolf 2009), and humans often form vivid episodic memories in stressful or emotionally otherwise prominent situations (Joels et al. 2006; Pause et al 2013). For example, a need to bring an unaccomplished task to an end ("ungestilltes Erledigungsbedürfnis") has been suggested to trigger human episodic memory formation (Zeigarnik 1927). Future research may also examine whether the ability of nonhuman primates to integrate an episodic component into existing semantic memory extends to contexts other than foraging, for example social or predatory, and thus, whether episodic memory may be a multi-purpose tool suitable for solving a wide variety of problems that arise daily in the lives of primates.

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