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How do foragers decide when to leave a patch? A test of alternative models under natural and experimental conditions

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Summary

1. A forager's optimal patch-departure time can be predicted by the prescient marginal value theorem (pMVT), which assumes they have perfect knowledge of the environment, or by approaches such as Bayesian updating and learning rules, which avoid this assumption by allowing foragers to use recent experiences to inform their decisions.

2. In understanding and predicting broader scale ecological patterns, individual-level mechanisms, such as patch-departure decisions, need to be fully elucidated. Unfortunately, there are few empirical studies that compare the performance of patch-departure models that assume perfect knowledge with those that do not, resulting in a limited understanding of how foragers decide when to leave a patch.

3. We tested the patch-departure rules predicted by fixed rule, pMVT, Bayesian updating and learning models against one another, using patch residency times (PRTs) recorded from 54 chacma baboons (*Papio ursinus*) across two groups in natural ($n = 6175$ patch visits) and field experimental ($n = 8569$) conditions.

4. We found greater support in the experiment for the model based on Bayesian updating rules, but greater support for the model based on the pMVT in natural foraging conditions. This suggests that foragers may place more importance on recent experiences in predictable environments, like our experiment, where these experiences provide more reliable information about future opportunities.

5. Furthermore, the effect of a single recent foraging experience on PRTs was uniformly weak across both conditions. This suggests that foragers' perception of their environment may incorporate many previous experiences, thus approximating the perfect knowledge assumed by the pMVT. Foragers may, therefore, optimize their patch-departure decisions in line with the pMVT through the adoption of rules similar to those predicted by Bayesian updating.

Key-words: Bayesian updating, habitat predictability, learning, marginal value theorem, patch-departure-rules, primate

Introduction

There is a growing appreciation of the need to understand the individual-level mechanisms that drive broader scale ecological and evolutionary patterns (Evans 2012). Two such mechanisms that are being increasingly recognized as important are individuals' foraging behaviour and information use (Giraldeau & Caraco 2000; Danchin *et al.* 2004; Dall *et al.* 2005; Stephens, Brown & Ydenberg 2007). Decisions made by foragers, and particularly the rules governing patch-departure decisions, involve both these mechanisms and are central to optimal foraging

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theory (Giraldeau & Caraco 2000; Stephens, Brown & Ydenberg 2007; Fawcett, Hamblin & Giraldeau 2013).

Early work on this topic tended to search for the departure rule that would result in a forager leaving a patch at the optimal time (Stephens & Krebs 1986), but did not tackle the question of how a forager would judge when it had reached this optimal departure point, often implicitly assuming the forager had perfect knowledge of its environment (as highlighted by Green 1984; Iwasa, Higashi & Yamamura 1981; van Gils *et al.* 2003; Olsson & Brown 2006). Two well-recognized examples of this work include the use of simple fixed rules and the original, and prescient, version of the marginal value theorem (pMVT, Charnov 1976). Fixed rule foragers, as the name suggests, leave patches at a fixed point, such as after a fixed amount of time since entering the patch has elapsed (e.g. Nolet, Klaassen & Mooij 2006; Olsson & Brown 2006). The pMVT predicts that foragers should leave a patch when the return they receive (the instantaneous intake rate) is reduced by patch depletion so that it is more profitable to accept the travel costs of leaving the patch in search of a new one. This threshold intake rate is known as the 'marginal value' and is set by the habitat's long-term average intake rate, which is a function of the average patch quality and density. The pMVT assumes foragers have perfect knowledge (i.e. are prescient) of the habitat's patch quality and density and so can judge when their intake rate has reached the marginal value, resulting in patch residency times (PRTs) being shorter in habitats where patches are closer together and better quality. In addition to perfect knowledge, the pMVT also assumes that foragers gain energy in a continuous flow, rather than as discrete units, and that there is no short-term variation in the marginal value (reviewed in Nonacs 2001). Consequently, it has been criticized as unrealistic (Nonacs 2001; van Gils *et al.* 2003; McNamara, Green & Olsson 2006), despite receiving some qualitative empirical support for its predictions (Nonacs 2001).

Further work on patch-departure decisions has addressed the fact that foragers are likely to have imperfect knowledge of their environment and so will need to use their past foraging experiences to estimate the optimal patch-departure time. Two such approaches that have received particular attention are Bayesian updating (Oaten 1977; Green 1984) and learning rule models (Kacelnik & Krebs 1985). In the case of Bayesian updating, these models were developed in direct response to the above criticisms of the pMVT (e.g. Green 1984; reviewed in McNamara, Green & Olsson 2006). In these models, individuals make foraging decisions as an iterative process, using their foraging experiences to update their perception of the available food distribution (their 'prior' knowledge), making decisions on the basis of this updated perception (their 'posterior' knowledge), and then using the outcome of this decision to further update their perception, and so on. Learning rule models (Kacelnik & Krebs 1985) appear to have developed separately to Bayesian models, but similarly describe foragers using information from past experiences in their current foraging decisions. They differ from Bayesian models, however, in that they describe past experiences accumulating in a moving average representing a perceived valuation of the environment (Kacelnik & Krebs 1985), rather than a perceived distribution of the relative occurrence of different patch qualities as in Bayesian models (Dall *et al.* 2005; McNamara, Green & Olsson 2006). A learning rule forager then makes a decision about whether to leave a patch or not by combining its moving average valuation of the environment up to the last time step with information gathered in the current time step (e.g. Beauchamp 2000; Groß *et al.* 2008; Hamblin & Giraldeau 2009).

Compared to this considerable amount of theoretical work, empirical tests of these models' predictions are relatively limited and have mainly focussed on the pMVT (reviewed in Nonacs 2001; but see Valone 2006). In those few cases where models of perfectly informed foragers have been empirically compared against either Bayesian or learning models (i.e. models of foragers with imperfect information), perfect information models provided a relatively poor explanation of the foraging behaviour observed (Alonso *et al.* 1995; van Gils *et al.* 2003; Amano *et al.* 2006; but see Nolet, Klaassen & Mooij 2006). For example, Bayesian updating models explained foraging behaviour better than other models, including a prescient forager model, in red knots (*Calidris canutus*) (van Gils *et al.* 2003). We know of no empirical study, however, that has compared the performance of Bayesian, learning and perfect information models, such as the pMVT, in the same analysis. Furthermore, there is evidence that a forager's use of past experiences in its patch-departure decisions, within either the Bayesian or learning framework, can be dependent on the characteristics of the foraging habitat (Lima 1984; Valone 1991, 1992; Devenport & Devenport 1994; Biernaskie, Walker & Gegear 2009). However, most studies to date have only compared foraging behaviour between captive environments or differing configurations of artificial food patches (but see Alonso *et al.* 1995). Therefore, to fully understand how a forager uses previous experiences in its decision-making, a simultaneous comparison of perfect information, Bayesian updating and learning rule models, ideally involving both natural and experimental conditions (in which the characteristics of the foraging habitat can be manipulated), would be extremely valuable.

The purpose of this study is, therefore, to empirically test whether patch-departure models that assume foragers' knowledge of their environment are imperfect, such as the Bayesian updating and learning rule approaches, provide a better description of patch-departure decisions than those that assume perfect knowledge. To do this, we consider which aspects of an individual's environment and its foraging experiences these different models predict will play a role in patch-departure decisions and assess the explanatory power of these different factors in the PRTs of wild chacma baboons (*Papio ursinus*, Kerr 1792) in both their natural foraging habitat and in a large-scale field experiment.

Materials and methods

STUDY SITE

Fieldwork was carried out at Tsaobis Leopard Park, Namibia (22°23′ S, 15°45′ E), from May to September 2010. The environment at Tsaobis predominantly consists of two habitats: open desert and riparian woodland. The open desert, hereafter 'desert', is characterized by alluvial plains and steep-sided hills. Desert food patches mainly comprise small herbs and dwarf shrubs such as *Monechma cleomoides*, *Sesamum capense* and *Commiphora virgata*. The riparian woodland, hereafter 'woodland', is associated with the ephemeral Swakop River that bisects the site. Woodland food patches are large trees and bushes such as *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica* (see Cowlishaw & Davies 1997 for more detail). At Tsaobis, two troops of chacma baboons (total troop sizes = 41 and 33 in May 2010), hereafter the 'large' and 'small' troop, have been habituated to the presence of human observers at close proximity. The baboons at Tsaobis experience relatively low predation risk as their main predator, the leopard (*Panthera pardus*, Linnaeus 1758), occurs at low densities, whilst two other potential predators, lions (*P. leo*, Linnaeus 1758) and spotted hyenas (*Crocuta crocuta*, Erxleben 1777), are entirely absent (Cowlishaw 1994). We collected data from all adults and those juveniles over 2 years old ($n = 32$ and 22), all of whom were individually recognizable (see Huchard *et al.* 2010 for details). Individuals younger than two were not individually recognizable and so were not included in this study.

DATA COLLECTION

Natural foraging behaviour

Baboon behaviour was observed under natural conditions using focal follows (Altmann 1974) and recorded on handheld Motorola MC35 (Libertyville, IL, USA) and Hewlett-Packard iPAQ Personal Digital Assistants (Bracknell, Berkshire, UK) using a customized spreadsheet in SpreadCE version 2.03 (Bye Design Ltd 1999) and Cybertracker v3.237 (http://cybertracker.org), respectively. Focal animals were selected in a stratified manner to ensure even sampling from four to three-h time blocks (6–9 a.m., 9 a.m.–12 p.m., 12–3 p.m. and 3–6 p.m.) across the field season, and no animal was sampled more than once per day. Focal follows lasted from twenty to thirty minutes (any <20 min were discarded). At all times, we recorded the focal animal's activity (mainly foraging, resting, travelling or grooming) and the occurrence, partner identity and direction of any grooming or dominance interactions. We also recorded the duration of grooming bouts. During foraging, we recorded when the focal animal entered and exited discrete food patches. Entry was defined as the focal moving into and eating an item from the patch (to rule out the possibility that they were simply passing by or through the patch), and exit defined as the focal subsequently moving out of the patch. Patches were defined as herbs, shrubs or trees with no other conspecific plant within one metre (closer conspecifics, which could potentially be reached by the forager without moving, were treated as part of the same patch), and made up the vast majority of the baboons' diet. At each patch entry, we recorded the local habitat (woodland or desert), the number of other baboons already occupying the patch, the identity of any adult occupants and three patch characteristics: the patch size, type and food-item handling time. Patch size was scored on a scale of 1–6 in the woodland and 1–4 in the desert and subsequently converted into an estimate of surface area (m^2) using patch sizes recorded during a one-off survey of 5693 woodland patches and monthly phenological surveys of desert patches, respectively. See below for details of the surveys; for details of the surface area estimations, see Marshall *et al.* (2012). Patch type was recorded by species for large trees and bushes in the woodland and as non-specified 'herb/shrub' for smaller woodland and all desert patches. Food-item handling time was classed as high (bark, pods and roots) or low (leaves, berries and flowers). Overall, we recorded 1481 focal hours (27 ± 10 h, mean ± SD, per individual) containing 6175 patch visits (112 ± 71 visits per individual) for our analyses.

Temporal variation in habitat quality was estimated by the monthly, habitat-specific, variation in both the mean number of food items per patch and the patch density. These calculations were based on monthly phenological surveys in which we estimated the number of food items in randomly selected food patches. In the woodland, we monitored a representative sample of 110 patches selected from an earlier survey of 5693 woodland patches (G. Cowlishaw, unpublished data); in the desert, we monitored 73 food patches that fell within eight randomly placed 50×1 m transects. In both habitats, the monitored patches fell within the study troops' home ranges. Monthly estimates of patch density were calculated as the mean number of patches containing food per km^2. In the woodland, this was calculated by randomly grouping the survey patches into 11 groups of 10 and calculating the proportion of these patches containing food in each group per month. Each group's proportion was then used to estimate a patch density (the number of the 5693 woodland patches containing food divided by 9·9 km^2, the extent of the woodland habitat in the study area), and the mean of these values taken as the woodland patch density, for any given month. In the desert, monthly estimates of patch density were calculated from the mean of the number of patches containing food in each transect divided by 5×10^{-5} (transect area of $50\ m^2 = 5 \times 10^{-5}\ km^2$).

Large-scale feeding experiments

Our foraging experiments were conducted in an open, flat and sandy area in each troop's home range. They involved a configuration of five artificial food patches of loose maize kernels arranged as shown in Fig. 1. The baboons visiting each patch were recorded using Panasonic SDR-S15 (Kadoma Osaka, Japan) video cameras on tripods, and so patches were trapezoidal to maximize the use of their field of view. The five patches were a combination of sizes, two measuring 20 m^2 (patches B and C in Fig. 1) and three at 80 m^2 (patches A, D and E) for the small troop, producing a total per-animal feeding area of 8·5 m^2 (280 m^2 divided by 33 animals). We kept the total per-animal feeding area approximately constant by increasing these patch sizes to 27 and 96 m^2 for the large troop, producing a total per-animal feeding area of 8·3 m^2 (342 m^2 divided by 41 animals). The experiment was run in two 14-day periods, alternating between troops. In the first period, patch food content (f in

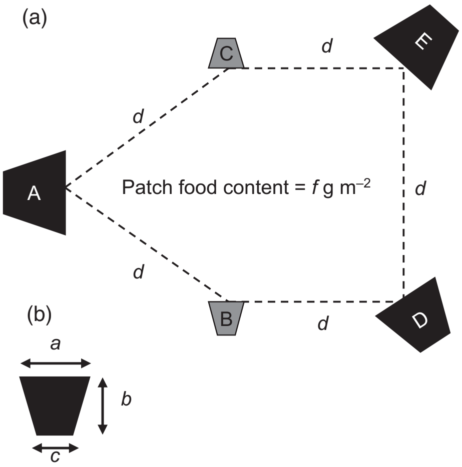

Fig. 1. Schematic of the foraging experiment's patch (a) layout and (b) dimensions. For each troop patch food content, *f*, was varied between $11{\cdot}4 \pm 0{\cdot}3$ g m^{-2} (low, first 14-day period) and $17{\cdot}1 \pm 0{\cdot}4$ g m^{-2} (high, second 14-day period) of loose dried maize kernels. Interpatch distance (*d*) was varied within each 14-day period. In the first period, it was set at 25 m (short) for the starting 7 days and 50 m (long) for the remaining 7 days, and vice versa for the second period. Patch size was constant within troops. Large patches (A, D and E) were set at 80 m^2 (a = 10 m, b = 10 m, c = 6 m) for the small troop and 96 m^2 (10, 12, 6) for the large troop. Small patches (B and C) were set at 20 m^2 (5, 5, 3) for the small troop and 27 m^2 (6, 6, 3) for the large troop.

Fig. 1) was 'low' ($11{\cdot}4 \pm 0{\cdot}3$ g m^{-2}, mean ± SD), whilst interpatch distance (*d*) was 'short' (25 m) for the first 7 days and 'long' (50 m) for the second 7 days. In the second 14-day period, patch food content was increased by 50% to 'high' ($17{\cdot}1 \pm 0{\cdot}4$ g m^{-2}), whilst interpatch distance was 'long' for the first 7 days and 'short' for the second 7 days. The experiments were therefore run over 28 days in total, involving four different food contents – interpatch distance combinations, for each troop. The amount of food per patch was measured using a standard level cup of maize kernels weighing 222 ± 1 g (mean ± SD, $n = 20$).

Experimental food patches were marked out with large stones, painted white, and were evenly scattered with maize kernels before dawn each morning. Video cameras (one per patch, started simultaneously when the first baboon was sighted) were used to record all patch activity, and trained observers (one per patch) recorded the identity of all individuals entering and exiting the patch. These patch entry and exit data were subsequently transcribed from the videos to create a dataset in which each row represented one patch visit and included: the forager ID, the patch ID, the PRT (s), the initial food density of the patch at the start of the experiment (g m^{-2}), the patch depletion (indexed by the cumulative number of seconds any baboon had previously occupied the patch), the forager's satiation (indexed by the cumulative number of seconds the focal baboon had foraged in any patch that day) and the number and identity of all other individuals in the patch. Video camera error on day 11 of the large troop's experiment meant that data from all patches were not available on that day, resulting in unreliable depletion and satiation estimates. Data from this day were therefore excluded, leaving 8569 patch visits (159 ± 137 per individual) in the final dataset for analysis.

Individual forager characteristics

For each focal animal, we calculated its dominance rank, social (grooming) capital and genetic relatedness to other animals in the troop. Dominance hierarchies were calculated from all dominance interactions recorded in focal follows and *ad libitum* (in both cases, outside of the experimental periods; $n_{\text{large}} = 2391$, $n_{\text{small}} = 1931$) using Matman 1·1·4 (Noldus Information Technology 2003). Hierarchies in both troops were strongly linear (Landau's corrected linearity index: $h'_{\text{large}} = 0{\cdot}71$, $h'_{\text{small}} = 0{\cdot}82$, $P < 0{\cdot}001$ in both) and subsequently standardized to vary between 0 (most subordinate) and 1 (most dominant) to control for the difference in troop sizes. Social capital was calculated using a grooming symmetry measure as there is growing evidence, particularly in primates, that asymmetries in grooming interactions can be traded for foraging tolerance (e.g. Fruteau *et al.* 2009). This symmetry measure was calculated as the proportion of grooming time between two individuals that the focal animal was the groomer, minus 0·5 (to make balanced relationships 0), multiplied by the proportion of total focal time that the focal and partner were observed grooming together during focal follows. Finally, dyadic relatedness (*r*) was estimated on the basis of 16 microsatellite loci using Wang's triadic estimator (Wang 2007; see Huchard *et al.* 2010 for further details). These data were then used in the analysis of natural and experimental foraging behaviour to calculate: (i) each forager's rank, mean social capital and mean relatedness with other troop members, as individual characteristics of the forager that were constant across patches; and (ii) the mean rank difference, social capital and relatedness between the focal forager and other patch occupants, which were specific for each patch visit.

ANALYSIS

We formulated eight models describing the factors predicted to influence patch-departure decisions, and so PRTs, by our three types of patch-departure model (fixed rule, including pMVT, Bayesian updating, and learning rules: see Introduction). We then compared these models' performances against each other as explanations of the natural and experimental PRTs we observed. These models comprised different combinations of three groups of variables that described, respectively, the forager's current foraging experience, $\boldsymbol{c}$, its recent foraging experience, t, and the broader habitat characteristics, $\boldsymbol{h}$. Here, t is simply the time the forager spent in the previous patch, whilst $\boldsymbol{c}$ and $\boldsymbol{h}$ are vectors of variables that describe the current physical and social characteristics of both the patch and the forager, in the case of $\boldsymbol{c}$, and the foraging habitat's characteristics, in the case of $\boldsymbol{h}$ (see below for details of the variables included in each vector).

The simplest patch-departure models assume that a forager's decision to leave a patch (and so the time it spends in it) is solely based on a rule fixed by some aspect of their environment. To explore this approach, our first three models predict PRT simply from the forager's current experience, $\text{PRT} = f(\boldsymbol{c})$ (model 1), recent experience, $\text{PRT} = f(t)$ (m2) and habitat characteristics, $\text{PRT} = f(\boldsymbol{h})$ (m3), respectively. Such fixed rule models are often considered to represent the 'floor' on foraging performance (e.g. Olsson & Brown 2006), that is, the poorest of performances, so these three models (m1–m3) are intended to act as a baseline against which the more sophisticated models, that are likely to achieve higher levels of performance, can be compared (see below). The prescient version of the marginal value theorem

(Charnov 1976), which assumes foragers are perfectly informed, predicts a forager should leave a patch when their intake rate in that patch falls below the habitat's long-term average, or 'marginal value'. In this case, our fourth model predicts PRT from a combination of the forager's current experience and the habitat characteristics: PRT = $f(\boldsymbol{c} + \boldsymbol{h})$ (m4).

Bayesian updating and learning rule models suggest that foragers use their recent experiences to inform their patch-departure decisions. In learning models, foragers possess a valuation of their environment, a moving average of their foraging experiences up to the previous time step, and information about the foraging conditions in the current time step. Foraging decisions in the current time step are made by differentially weighting and combining these two elements (environmental valuation and current information) into a single value for the current patch or foraging tactic (Kacelnik & Krebs 1985; Beauchamp 2000; Hamblin & Giraldeau 2009). This suggests that, in this study, PRT should be predicted by the previous foraging experience, representing the forager's valuation of the environment, and the current foraging conditions, or PRT = $f(\boldsymbol{c} + t)$ (m5), approximately describing the simplest learning rule, the linear operator (Kacelnik & Krebs 1985). Bayesian models, in contrast, suggest that foragers have a perception of the environment's distribution of food (rather than a simple valuation), which they update using their recent experiences, and then combine this information with current foraging experiences to make their patch-departure decisions (see Dall *et al.* 2005; McNamara, Green & Olsson 2006), thus suggesting: PRT = $f(\boldsymbol{c} + t + \boldsymbol{h})$ (m6). Finally, there is some evidence that the use of recent experiences may be contingent on habitat variability, as increases in variability may decrease the reliability of recent experiences in predicting the next experience, and so informing decisions (Lima 1984; Valone 1992). Therefore, our final two models develop m5 and m6 further by including an interaction between the forager's recent experience and habitat variability:

$$\mathrm{PRT} = f(\boldsymbol{c} + t + \boldsymbol{h}_{\mathrm{SD}} + t \times \boldsymbol{h}_{\mathrm{SD}}) \quad (\mathrm{m}7).$$

and

$$\mathrm{PRT} = f(\boldsymbol{c} + t + \boldsymbol{h} + \boldsymbol{h}_{\mathrm{SD}} + t \times \boldsymbol{h}_{\mathrm{SD}}) \quad (\mathrm{m}8).$$

Here, $\boldsymbol{h}_{\mathrm{SD}}$ is a vector of variables describing the standard deviation of the mean estimated habitat characteristics (see below for details).

The variables included in vectors $\boldsymbol{c}$, $\boldsymbol{h}$ and $\boldsymbol{h}_{\mathrm{SD}}$ were as follows. In models predicting natural PRTs, the forager's current experience, $\boldsymbol{c}$, was described by the patch size, food species and handling time. In models predicting experimental PRTs, $\boldsymbol{c}$ comprised of the patch's initial food density, estimated depletion and the focal forager's estimated satiation. Because the social environment can also influence a forager's current foraging experience, $\boldsymbol{c}$ also included (for both natural and experimental PRT models) the focal forager's rank, mean social capital and mean relatedness to other troop members, and, on a patch-by-patch basis, their mean rank difference, social capital and relatedness to other patch occupants, plus the number of patch occupants present (linear and quadratic terms). The variables describing the foraging habitat characteristics, $\boldsymbol{h}$, reflected the average patch quality and density. In the natural PRT models, these were the monthly habitat-specific estimates of both food items per patch and food patches per km^2; in the experimental PRT models, these were the mean initial weight of food per patch (g) and interpatch distance (m). Finally, in the natural PRT models, $\boldsymbol{h}_{\mathrm{SD}}$ described the standard deviations around the estimates of both the mean number of food items per patch and patch density ($\boldsymbol{h}_{\mathrm{SD}}$ was not explored in the experimental PRT models, because the initial patch quality and density were fixed with zero variance).

Models 1 to 8 and a null model (containing no fixed effects) were estimated using generalized linear mixed models for the natural and experimental PRTs datasets. In both cases, all non-categorical explanatory variables were standardized to have a mean of zero and standard deviation of one. Natural models included focal follow number nested within focal animal ID, nested within troop as random effects. Experimental models included focal animal ID, patch ID and experiment day cross-classified with each other and nested within troop, as random effects. To account for overdispersion in the PRT data, all models also included an observation-level random effect and were fitted as Poisson lognormal mixed effects models using a log link function (Elston *et al.* 2001) in the package lmer in R (Bates, Maechler & Bolker 2011; R Development Core Team 2011). We assessed these models' performance (nine models in the natural analyses, seven in the experimental analyses) using Akaike's model weights. These were calculated from AIC values, because in all models $n/k > 40$, where n is the number patch visits and k is the number of parameters in the maximal model (Burnham & Anderson 2002; Symonds & Moussalli 2011). The data and R code used in these analyses are available from the Dryad repository (doi: 10.5061/dryad.3vt0s).

Results

The baboons visited food patches for a median of 30 s (interquartile range = 12–79 s, $n = 6175$) in natural foraging conditions and 52 s (16–157 s, $n = 8569$) in experimental foraging conditions.

Natural PRTs were best explained by the model containing factors predicted by the prescient marginal value theorem (pMVT; Akaike's model weight $w_i = 0{\cdot}69$, Table 1) but also showed some support for the model containing factors predicted by a Bayesian updating rule ($w_i = 0{\cdot}27$). In contrast, experimental PRTs were best explained by the model containing factors predicted by a Bayesian updating rule above all other models ($w_i = 0{\cdot}98$, Table 1). In both conditions, the influence of the foraging habitat's characteristics on PRTs was consistent with the predictions of the pMVT (Table 2): the baboons spent less time in food patches when the environment was characterized by higher quality patches at higher densities. In both conditions, the model based on a Bayesian updating rule also showed that baboons stayed longer in a patch when they had spent more time in the previous patch. The effect of this recent foraging experience was, however, relatively weak, especially in the natural observations (Table 2).

Discussion

The use of a patch-departure decision rule consistent with a Bayesian updating process was strongly supported by the behaviour of the foragers on the experimental food patches. In contrast, foraging behaviour under natural conditions, whilst showing some support for the use of

Table 1. Model performance in explaining patch residency times, under natural and experimental conditions. Models in bold make up the 95% confidence model set

Natural					Experimental				
No.	Patch-departure rule from predictions of	AIC	ΔAIC	w_i	No.	Patch-departure rule from predictions of	AIC	ΔAIC	w_i
4	**Prescient marginal value theorem**	**28342·16**	**0·00**	**0·69**	**6**	**Bayesian updating**	**48410·75**	**0·00**	**0·98**
6	**Bayesian updating**	**28344·06**	**1·90**	**0·27**	5	Learning rule	48418·16	7·41	0·02
7	Learning rule dependent on habitat variability	28348·33	6·18	0·03	4	Prescient marginal value theorem	48429·22	18·47	0·00
8	Bayesian updating dependent on habitat variability	28349·61	7·46	0·02	1	Fixed rule based on current foraging condition	48436·57	25·82	0·00
1	Fixed rule based on current foraging condition	28377·87	35·71	0·00	3	Fixed rule based on habitat's patch configuration	49161·69	750·94	0·00
5	Learning rule	28379·16	37·01	0·00	2	Fixed rule based on recent foraging experience	49174·14	763·39	0·00
3	Fixed rule based on habitat's patch configuration	29323·18	981·02	0·00		Null	49200·07	789·32	0·00
2	Fixed rule based on recent foraging experience	29521·79	1179·64	0·00					
	Null	29543·59	1201·43	0·00					

AIC = Akaike's information criterion, ΔAIC = difference between AIC score and lowest AIC score, w_i = Akaike's model weight

Table 2. The influence of previous foraging experience and foraging habitat characteristics (effect sizes, β ± SE) on patch residency times (PRTs) in the best models (95% confidence set, see Table 1) under natural and experimental conditions

Natural PRT models (model number)			Experimental PRT models (model number)	
Predictors	Prescient marginal value theorem (m4)	Bayesian updating (m6)	Predictors	Bayesian updating (m6)
Time in previous patch (s)		0·006 ± 0·02	Time in previous patch (s)	0·08 ± 0·02
Mean number of food items per patch	−0·11 ± 0·03	−0·11 ± 0·03	Mean weight of food per patch (g)	−0·56 ± 0·15
Mean number of food patches per km^2	−0·16 ± 0·02	−0·16 ± 0·03	Interpatch distance (m)	0·10 ± 0·04

Bayesian updating, showed greater support for a patch-departure rule based on the pMVT. Furthermore, in both environments, our Bayesian updating models also suggested that the influence of a single previous foraging experience was relatively weak. Our discussion first focuses on why these differences in decision-making between the two environments might occur and what this might suggest about the animals' abilities to efficiently exploit different environments. We then consider what these results reveal about how foragers use their recent experiences in their patch-departure decisions and the implications of these findings for the modelling of foraging behaviour.

It is widely appreciated that the collection and use of information by animals is dependent on its associated costs and benefits (Danchin *et al.* 2004; Dall *et al.* 2005). These costs and benefits may be dependent on individual traits (Koops & Abrahams 2003; Webster & Laland 2011; Marshall *et al.* 2012), but also on the characteristics of the surrounding environment and its resource distribution (Templeton & Giraldeau 1995; Olsson & Brown 2006; Webster & Laland 2008). Previous work has suggested that differences in the weight a forager places on their most recent experiences between habitats may be due to these experiences providing more reliable indicators of future foraging rewards when environments are either more predictable (Valone 1991; Devenport & Devenport 1994; Fortin 2002; Vásquez, Grossi & Marquez 2006; Eliassen *et al.* 2009) or less variable (Lima 1984; Valone 1992; Biernaskie, Walker & Gegear 2009). These alternative hypotheses may coincide, because less variable environments may also be more predictable – but not always, because some patterns of variation, such as seasonal habitat changes, can also be highly predictable (Eliassen *et al.* 2009). Our findings are able to distinguish between these two hypotheses to some extent and support the former. If environmental variability had influenced the baboons' use of recent experiences, we would have expected more support for our models which explicitly incorporated it (models 7 and 8). Instead, the baboons incorporated their most recent experience into their patch-departure decisions to a greater extent in the more predictable experimental foraging environment (Table 2). This environment was likely to have been more predictable as the relative quality and position of each patch remained constant throughout, and their absolute quality and position only changed once (after 14 days) and three times (after 7,14, and 21 days), respectively (see Fig. 1, and Methods). In contrast, natural foraging environments, such as at Tsaobis, where food patches consist of multiple plant species, with different plant parts, whose phenology varies considerably across the year (not only between species but also between individuals), are inherently much less predictable.

An ability to flexibly incorporate recent experience, contingent on its reliability, into decision-making should allow foragers to maximize the efficiency with which they exploit different environments (Valone & Brown 1989; Valone 1991; Devenport & Devenport 1994; Rodriguez-Gironés & Vásquez 1997; Koops & Abrahams 2003). Such an ability appears to be possessed by the foragers in this study. This flexibility may also be widely distributed across a variety of taxa and not limited solely to cognitively advanced animals such as baboons. A model by Holmgren & Olsson (2000) demonstrated that incorporating recent experiences during Bayesian foraging was possible using a simple three-neurone network. Furthermore, there is growing evidence, from a range of taxa, that the incorporation of recent experiences into foragers' decision-making can vary between environments (insects: Biernaskie, Walker & Gegear 2009; birds: Alonso *et al.* 1995; Valone 1991; non-primate mammals: Devenport & Devenport 1994; Vásquez, Grossi & Marquez 2006).

The model of forager behaviour predicted by Bayesian updating was consistently supported over the model predicted by learning rules. This was true for both natural and experimental environments. Both Bayesian updating (Oaten 1977; Green 1984; McNamara, Green & Olsson 2006) and learning rules (Kacelnik & Krebs 1985; Beauchamp 2000; Hamblin & Giraldeau 2009) have been proposed as descriptions of how foragers incorporate past experiences into their decision-making. Our results seem to suggest that the former is more accurate in our system. This difference in performance may be explained by the fact that learning rules, particularly the linear operator rule that our model represents, are often simpler than Bayesian updating approaches and may be less responsive to environmental variability (Groß *et al.* 2008; Eliassen *et al.* 2009). There is, however, evidence that the best way for a forager to incorporate previous experiences into their foraging decisions can be dependent on the underlying resource distribution (Rodriguez-Gironés & Vásquez 1997; Olsson & Brown 2006; Eliassen *et al.* 2009). Thus, although our study favours the Bayesian updating approach, another study in a different setting might not. Furthermore, in our study, we built each of our candidate models from the general theoretical principles underlying each approach. However, within each approach, different methods for incorporating previous experiences have been proposed, for example, the 'linear operator' vs. 'relative payoff sum' methods for learning rules (Beauchamp 2000; Hamblin & Giraldeau 2009) and the 'current value' vs. 'potential value assessment' methods for Bayesian updating (Olsson & Holmgren 1998; van Gils *et al.* 2003). Another study, which was able to test more specifically these different methods, might find a narrower gap in performance between the learning and Bayesian approaches.

The influence of the baboons' most recent experience on their patch-departure decisions, whilst generally important, was still relatively small, suggesting that, where foragers inform such decisions with their recent experiences, they do so incrementally (Beauchamp 2000; Amano *et al.* 2006; Biernaskie, Walker & Gegear 2009; Hamblin & Giraldeau 2009). That is, it is not just the previous foraging experience that is important but the experiences before that, and so on. This is consistent with the concept, common across models of imperfectly informed foragers, that an individual's estimate of the environment's distribution of resources (Bayesian updating) or value (learning rules) is an aggregate of their past experiences, and that individuals are continually updating this estimate with each subsequent experience (Kacelnik & Krebs 1985; McNamara, Green & Olsson 2006). If, as here, the influence of each of these experiences is low, then as an increasing number of previous experiences are remembered this perceived distribution or valuation will increasingly approximate the true distribution (Koops & Abrahams 2003), that is, the perfect knowledge assumed by the pMVT (Charnov 1976). The predicted effects of patch quality and density characteristics in our best supported models (Table 2) were consistent with the pMVT's prediction, suggesting that the baboons' perception of their environment did incorporate many past experiences and was a good approximation of perfect knowledge. Once again, there is reason to believe that this finding is not specific to baboons, because (i) a weak effect of a single recent experience on foraging decisions has been shown many times previously (Beauchamp 2000; Amano *et al.* 2006; Biernaskie, Walker & Gegear 2009; Hamblin & Giraldeau 2009); and (ii) there is evidence from other taxa that foragers can incorporate experiences over many days into their decision-making (birds: Valone 1991; non-primate mammals: Devenport & Devenport 1994; Vásquez, Grossi & Marquez 2006). Furthermore, in theoretical comparisons, prescient (i.e. perfect knowledge) foragers perform best (Koops & Abrahams 2003; Olsson & Brown 2006; Eliassen *et al.* 2009), and so it would seem likely that there is widespread selection for the ability to retain and use as many experiences as possible in foraging decision-making.

The finding that the baboons' perception of their environment included many past experiences and approximated perfect knowledge has two implications. First, it may provide an extra explanation for why the pMVT model outperformed the Bayesian updating model in the natural foraging conditions. Here, the baboons were assigning very little weight to each foraging experience, which, as we have argued, is expected in this more natural, unpredictable environment. The inclusion of the single previous foraging experience variable in the Bayesian updating model would therefore have provided very little extra explanatory power over the pMVT model, where this variable is absent, whilst being penalized 2 AIC points for the inclusion of the extra parameter. The AIC score difference of 1·9 points between the two models supports this argument. Thus, the baboons may have been using previous experiences in the natural foraging habitat, but we were less able to detect this given the relatively low weight assigned to each foraging experience. Indeed, it is hard to imagine how the baboons would have acquired sufficient knowledge of their environment to follow the pMVT were it not for the gradual accumulation of information through a process like Bayesian updating or learning. It has also been noted that, where foragers update their information about the environment in such a gradual manner, distinguishing an updating from a non-updating strategy may be difficult (Eliassen *et al.* 2009).

The second implication is more important. If a forager's perception of its environment approximates perfect knowledge, then, in theory, its behaviour should also approximate optimality (Koops & Abrahams 2003), within the scope of its informational or physiological constraints (Fawcett, Hamblin & Giraldeau 2013). Our empirical support for this theoretical prediction suggests that the assumption of such knowledge by the pMVT may not be so unrealistic. Indeed, the predictions of the pMVT have received widespread qualitative support (Nonacs 2001). Modelling any natural process requires researchers to trade-off model accuracy and simplicity (Evans 2012). The present study, and previous research, indicates that models of patch-departure decisions that consider how foragers incorporate past experiences into these decisions will usually provide more realism and accuracy than simpler models. However, our findings also suggest that when attempting to predict foraging behaviour, the pMVT may provide a simpler approach without sacrificing a great deal of accuracy.

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Data accessibility

The data and R code used in this study's analyses are available from the Dryad repository (doi: 10·5061/dryad.3vt0s).

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