

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

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

29 3. We tested the patch-departure rules predicted by fixed-rule, pMVT, Bayesian-updating and  
30 learning models against one another, using patch residency times recorded from 54 chacma  
31 baboons (*Papio ursinus*) across two groups in natural ( $n = 6,175$  patch visits) and field-  
32 experimental ( $n = 8,569$ ) conditions.

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

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

44

45 **Keywords:** Bayesian-updating, habitat predictability, learning, marginal value theorem,  
46 primate, patch-departure-rules

47

48

## 49 **Introduction**

50

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

58

59 Early work on this topic tended to search for the departure rule that would result in a forager  
60 leaving a patch at the optimal time (Stephens & Krebs 1986), but did not tackle the question of  
61 how a forager would judge when it had reached this optimal departure point, often implicitly  
62 assuming the forager had perfect knowledge of its environment (as highlighted by Green 1984;  
63 Iwasa, Higashi, & Yamamura 1981; Olsson & Brown 2006; van Gils et al. 2003). Two well-  
64 recognised examples of this work include the use of simple fixed rules and the original, and  
65 prescient, version of the marginal value theorem (pMVT, Charnov 1976). Fixed-rule foragers, as  
66 the name suggests, leave patches at a fixed point, such as after a fixed amount of time since  
67 entering the patch has elapsed (e.g. Nolet, Klaassen, & Mooij 2006; Olsson & Brown 2006). The  
68 pMVT predicts that foragers should leave a patch when the return they receive (the instantaneous  
69 intake rate) is reduced by patch depletion so that it is more profitable to accept the travel costs of  
70 leaving the patch in search of a new one. This threshold intake rate is known as the 'marginal  
71 value' and is set by the habitat's long-term average intake rate, which is a function of the average  
72 patch quality and density. The pMVT assumes foragers have perfect knowledge (i.e. are  
73 prescient) of the habitat's patch quality and density and so can judge when their intake rate has

74 reached the marginal value, resulting in patch residency times being shorter in habitats where  
75 patches are closer together and better quality. In addition to perfect knowledge, the pMVT also  
76 assumes that foragers gain energy in a continuous flow, rather than as discrete units, and that  
77 there is no short-term variation in the marginal value (reviewed in Nonacs 2001). Consequently,  
78 it has been criticised as unrealistic (van Gils et al. 2003; McNamara, Green & Olsson 2006;  
79 Nonacs 2001), despite receiving some qualitative empirical support for its predictions (Nonacs  
80 2001).

81

82 Further work on patch-departure decisions has addressed the fact that foragers are likely to have  
83 imperfect knowledge of their environment, and so will need to use their past foraging experiences  
84 to estimate the optimal patch departure time. Two such approaches which have received  
85 particular attention are Bayesian-updating (Green 1984; Oaten 1977) and learning-rule models  
86 (Kacelnik & Krebs 1985). In the case of Bayesian-updating, these models were developed in  
87 direct response to the above criticisms of the pMVT (e.g. Green 1984; reviewed in McNamara et  
88 al. 2006). In these models, individuals make foraging decisions as an iterative process, using their  
89 foraging experiences to update their perception of the available food distribution (their “prior”  
90 knowledge), making decisions on the basis of this updated perception (their “posterior”  
91 knowledge), and then using the outcome of this decision to further update their perception, and so  
92 on. Learning-rule models (Kacelnik & Krebs 1985) appear to have developed separately to  
93 Bayesian models, but similarly describe foragers using information from past experiences in their  
94 current foraging decisions. They differ from Bayesian models, however, in that they describe past  
95 experiences accumulating in a moving average representing a perceived valuation of the  
96 environment (Kacelnik & Krebs 1985), rather than a perceived distribution of the relative  
97 occurrence of different patch qualities as in Bayesian models (Dall et al. 2005; McNamara et al.  
98 2006). A learning-rule forager then makes a decision about whether to leave a patch or not by

99 combining its moving average valuation of the environment up to the last time step with  
100 information gathered in the current time step (e.g. Beauchamp 2000; Groß et al. 2008; Hamblin &  
101 Giraldeau 2009).

102

103 Compared to this considerable amount of theoretical work, empirical tests of these models'  
104 predictions are relatively limited and have mainly focussed on the pMVT (reviewed in Nonacs  
105 2001; but see Valone 2006). In those few cases where models of perfectly informed foragers have  
106 been empirically compared against either Bayesian or learning models (i.e. models of foragers  
107 with imperfect information), perfect-information models provided a relatively poor explanation  
108 of the foraging behaviour observed (Alonso et al. 1995; Amano et al. 2006; van Gils et al. 2003,  
109 but see Nolet et al. 2006). For example, Bayesian updating models explained foraging behaviour  
110 better than other models, including a prescient forager model, in red knots (*Calidris canutus*) (van  
111 Gils et al. 2003). We know of no empirical study, however, that has compared the performance of  
112 Bayesian, learning and perfect-information models, such as the pMVT, in the same analysis.  
113 Furthermore, there is evidence that a forager's use of past experiences in its patch-departure  
114 decisions, within either the Bayesian or learning framework, can be dependent on the  
115 characteristics of the foraging habitat (Biernaskie, Walker & Gegeer 2009; Devenport &  
116 Devenport 1994; Lima 1984; Valone 1991, 1992). However, most studies to date have only  
117 compared foraging behaviour between captive environments or differing configurations of  
118 artificial food patches (but see Alonso et al. 1995). Therefore, to fully understand how a forager  
119 uses previous experiences in its decision-making, a simultaneous comparison of perfect-  
120 information, Bayesian-updating and learning-rule models, ideally involving both natural and  
121 experimental conditions (in which the characteristics of the foraging habitat can be manipulated),  
122 would be extremely valuable.

123

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

132

### 133 **Materials and Methods**

134

#### 135 Study Site

136

137 Fieldwork was carried out at Tsaobis Leopard Park, Namibia (22°23'S, 15°45'E), from May to  
138 September 2010. The environment at Tsaobis predominantly consists of two habitats: open desert  
139 and riparian woodland. The open desert, hereafter 'desert', is characterised by alluvial plains and  
140 steep-sided hills. Desert food patches mainly comprise small herbs and dwarf shrubs such as  
141 *Monechma cleomoides*, *Sesamum capense* and *Commiphora virgata*. The riparian woodland,  
142 hereafter 'woodland', is associated with the ephemeral Swakop River that bisects the site.  
143 Woodland food patches are large trees and bushes such as *Faidherbia albida*, *Prosopis*  
144 *glandulosa* and *Salvadora persica* (see Cowlshaw & Davies 1997 for more detail). At Tsaobis,  
145 two troops of chacma baboons (total troop sizes = 41 and 33 in May 2010), hereafter the 'large'  
146 and 'small' troop, have been habituated to the presence of human observers at close proximity.  
147 The baboons at Tsaobis experience relatively low predation risk as their main predator, the  
148 leopard (*P. pardus*, Linnaeus 1758), occurs at low densities, while two other potential predators,

149 lions (*Panthera leo*, Linnaeus 1758) and spotted hyenas (*Crocuta crocuta*, Erxleben 1777), are  
150 entirely absent (Cowlshaw 1994). We collected data from all adults and those juveniles over two  
151 years old ( $n = 32$  and  $22$ ), all of whom were individually recognisable (see Huchard et al. 2010  
152 for details). Individuals younger than two were not individually recognisable and so were not  
153 included in this study.

154

### 155 Data Collection

156

#### 157 *Natural foraging behaviour*

158

159 Baboon behaviour was observed under natural conditions using focal follows (Altmann 1974),  
160 and recorded on handheld Motorola MC35 (Illinois, U.S.A) and Hewlett-Packard iPAQ Personal  
161 Digital Assistants (Berkshire, U.K.) using a customised spreadsheet in SpreadCE version 2.03  
162 (Bye Design Ltd 1999) and Cybertracker v3.237 (<http://cybertracker.org>), respectively. Focal  
163 animals were selected in a stratified manner to ensure even sampling from four three-hour time  
164 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  
165 animal was sampled more than once per day. Focal follows lasted from twenty to thirty minutes  
166 (any less than twenty minutes were discarded). At all times we recorded the focal animal's  
167 activity (mainly foraging, resting, travelling or grooming) and the occurrence, partner identity  
168 and direction of any grooming or dominance interactions. We also recorded the duration of  
169 grooming bouts. During foraging we recorded when the focal animal entered and exited discrete  
170 food patches. Entry was defined as the focal moving into and eating an item from the patch (to  
171 rule out the possibility that they were simply passing by or through the patch), and exit defined as  
172 the focal subsequently moving out of the patch. Patches were defined as herbs, shrubs or trees  
173 with no other conspecific plant within one metre (closer conspecifics, which could potentially be



174 reached by the forager without moving, were treated as part of the same patch), and made up the  
175 vast majority of the baboons' diet. At each patch entry we recorded the local habitat (woodland or  
176 desert), the number of other baboons already occupying the patch, the identity of any adult  
177 occupants, and three patch characteristics: the patch size, type, and food-item handling time.  
178 Patch size was scored on a scale of 1-6 in the woodland and 1-4 in the desert, and subsequently  
179 converted into an estimate of surface area ( $m^2$ ) using patch sizes recorded during a one-off survey  
180 of 5,693 woodland patches and monthly phenological surveys of desert patches, respectively. See  
181 below for details of the surveys; for details of the surface area estimations, see Marshall et al.  
182 (2012). Patch type was recorded by species for large trees and bushes in the woodland, and as  
183 non-specified 'herb/shrub' for smaller woodland and all desert patches. Food-item handling time  
184 was classed as high (bark, pods and roots) or low (leaves, berries and flowers). Overall, we  
185 recorded 1,481 focal hours ( $27 \pm 10$  hours, mean  $\pm$  s.d., per individual) containing 6,175 patch  
186 visits ( $112 \pm 71$  visits per individual) for our analyses.

187

188 Temporal variation in habitat quality was estimated by the monthly, habitat-specific, variation in  
189 both the mean number of food items per patch and the patch density. These calculations were  
190 based on monthly phenological surveys in which we estimated the number of food items in  
191 randomly selected food patches. In the woodland, we monitored a representative sample of 110  
192 patches selected from an earlier survey of 5,693 woodland patches (G. Cowlshaw, unpublished  
193 data); in the desert, we monitored 73 food patches that fell within eight randomly placed 50 m x 1  
194 m transects. In both habitats, the monitored patches fell within the study troops' home ranges.  
195 Monthly estimates of patch density were calculated as the mean number of patches containing  
196 food per  $km^2$ . In the woodland, this was calculated by randomly grouping the survey patches into  
197 11 groups of 10, and calculating the proportion of these patches containing food in each group  
198 per month. Each group's proportion was then used to estimate a patch density (the number of the

199 5,693 woodland patches containing food divided by  $9.9 \text{ km}^2$ , the extent of the woodland habitat  
200 in the study area) and the mean of these values taken as the woodland patch density, for any  
201 given month. In the desert, monthly estimates of patch density were calculated from the mean of  
202 the number of patches containing food in each transect divided by  $5 \times 10^{-5}$  (transect area of  $50 \text{ m}^2$   
203  $= 5 \times 10^{-5} \text{ km}^2$ ).

204

#### 205 *Large-scale feeding experiments*

206

207 Our foraging experiments were conducted in an open, flat and sandy area in each troop's home  
208 range. They involved a configuration of five artificial food patches of loose maize kernels  
209 arranged as shown in figure 1. The baboons visiting each patch were recorded using Panasonic  
210 SDR-S15 (Kadoma Osaka, Japan) video cameras on tripods, and so patches were trapezoidal to  
211 maximise the use of their field of view. The five patches were a combination of sizes, two  
212 measuring  $20 \text{ m}^2$  (patches B and C in Fig. 1) and three at  $80 \text{ m}^2$  (patches A, D and E) for the  
213 small troop, producing a total per-animal feeding area of  $8.5 \text{ m}^2$  ( $280 \text{ m}^2$  divided by 33 animals).  
214 We kept the total per-animal feeding area approximately constant by increasing these patch sizes  
215 to  $27 \text{ m}^2$  and  $96 \text{ m}^2$  for the large troop, producing a total per-animal feeding area of  $8.3 \text{ m}^2$  ( $342$   
216  $\text{m}^2$  divided by 41 animals). The experiment was run in two 14-day periods, alternating between  
217 troops. In the first period, patch food content ( $f$  in Fig. 1) was 'low' ( $11.4 \pm 0.3 \text{ g/m}^2$ , mean  $\pm$  s.d.)  
218 while inter-patch distance ( $d$ ) was 'short' (25 m) for the first 7 days and 'long' (50 m) for the  
219 second 7 days. In the second 14-day period, patch food content was increased by 50% to 'high'  
220 ( $17.1 \pm 0.4 \text{ g/m}^2$ ) while inter-patch distance was 'long' for the first 7 days and 'short' for the  
221 second 7 days. The experiments were therefore run over 28 days in total, involving four different  
222 food content – inter-patch distance combinations, for each troop. The amount of food per patch

223 was measured using a standard level cup of maize kernels weighing  $222 \pm 1\text{g}$  (mean  $\pm$  s.d.,  $n =$   
224 20).

225

226 Experimental food patches were marked out with large stones, painted white, and were evenly  
227 scattered with maize kernels before dawn each morning. Video cameras (one per patch, started  
228 simultaneously when the first baboon was sighted) were used to record all patch activity and  
229 trained observers (one per patch) recorded the identity of all individuals entering and exiting the  
230 patch. These patch entry and exit data were subsequently transcribed from the videos to create a  
231 dataset in which each row represented one patch visit and included: the forager ID, the patch ID,  
232 the patch residency time (s), the initial food density of the patch at the start of the experiment  
233 ( $\text{g}/\text{m}^2$ ), the patch depletion (indexed by the cumulative number of seconds any baboon had  
234 previously occupied the patch), the forager's satiation (indexed by the cumulative number of  
235 seconds the focal baboon had foraged in any patch that day) and the number and identity of all  
236 other individuals in the patch. Video camera error on day 11 of the large troop's experiment  
237 meant that data from all patches were not available on that day, resulting in unreliable depletion  
238 and satiation estimates. Data from this day were therefore excluded, leaving 8,569 patch visits  
239 ( $159 \pm 137$  per individual) in the final dataset for analysis.

240

#### 241 *Individual forager characteristics*

242

243 For each focal animal, we calculated its dominance rank, social (grooming) capital, and genetic  
244 relatedness to other animals in the troop. Dominance hierarchies were calculated from all  
245 dominance interactions recorded in focal follows and *ad libitum* (in both cases, outside of the  
246 experimental periods;  $n_{\text{large}} = 2391$ ,  $n_{\text{small}} = 1931$ ) using Matman 1.1.4 (Noldus Information  
247 Technology 2003). Hierarchies in both troops were strongly linear (Landau's corrected linearity

248 index:  $h'_{\text{large}} = 0.71$ ,  $h'_{\text{small}} = 0.82$ ,  $p < 0.001$  in both) and subsequently standardised to vary  
249 between 0 (most subordinate) and 1 (most dominant) to control for the difference in troop sizes.  
250 Social capital was calculated using a grooming symmetry measure as there is growing evidence,  
251 particularly in primates, that asymmetries in grooming interactions can be traded for foraging  
252 tolerance (e.g. Fruteau et al. 2009). This symmetry measure was calculated as the proportion of  
253 grooming time between two individuals that the focal animal was the groomer, minus 0.5 (to  
254 make balanced relationships 0), multiplied by the proportion of total focal time that the focal and  
255 partner were observed grooming together during focal follows. Finally, dyadic relatedness ( $r$ ) was  
256 estimated on the basis of 16 microsatellite loci using Wang's triadic estimator (Wang 2007; see  
257 Huchard et al. 2010 for further details). These data were then used in the analysis of natural and  
258 experimental foraging behaviour to calculate: (1) each forager's rank, mean social capital and  
259 mean relatedness with other troop members, as individual characteristics of the forager that were  
260 constant across patches, and (2) the mean rank difference, social capital and relatedness between  
261 the focal forager and other patch occupants, which were specific for each patch visit.

262

263 Analysis

264

265 We formulated eight models describing the factors predicted to influence patch departure  
266 decisions, and so patch residency times, by our three types of patch-departure model (fixed-rule,  
267 including pMVT, Bayesian-updating, and learning rules: see Introduction). We then compared  
268 these models' performances against each other as explanations of the natural and experimental  
269 patch residency times we observed. These models comprised different combinations of three  
270 groups of variables that described, respectively, the forager's current foraging experience,  $c$ , its  
271 recent foraging experience,  $t$ , and the broader habitat characteristics,  $h$ . Here  $t$  is simply the time  
272 the forager spent in the previous patch, whilst  $c$  and  $h$  are vectors of variables that describe the

273 current physical and social characteristics of both the patch and the forager, in the case of  $\mathbf{c}$ , and  
274 the foraging habitat's characteristics, in the case of  $\mathbf{h}$  (see below for details of the variables  
275 included in each vector).

276

277 The simplest patch-departure models assume that a forager's decision to leave a patch (and so the  
278 time it spends in it) is solely based on a rule fixed by some aspect of their environment. To  
279 explore this approach, our first three models predict patch residency time (PRT) simply from the  
280 forager's current experience, i.e.  $PRT = f(\mathbf{c})$  (model 1), recent experience,  $PRT = f(t)$  (m2) and  
281 habitat characteristics,  $PRT = f(\mathbf{h})$  (m3), respectively. Such fixed-rule models are often  
282 considered to represent the 'floor' on foraging performance (e.g. Olsson & Brown 2006), i.e., the  
283 poorest of performances, so these three models (m1-m3) are intended to act as a baseline against  
284 which the more sophisticated models, that are likely to achieve higher levels of performance, can  
285 be compared (see below). The prescient version of the marginal-value theorem (Charnov 1976),  
286 which assumes foragers are perfectly informed, predicts a forager should leave a patch when their  
287 intake rate in that patch falls below the habitat's long-term average, or 'marginal value'. In this  
288 case, our fourth model predicts PRT from a combination of the forager's current experience and  
289 the habitat characteristics:  $PRT = f(\mathbf{c} + \mathbf{h})$  (m4).

290

291 Bayesian-updating and learning-rule models suggest that foragers use their recent experiences to  
292 inform their patch-departure decisions. In learning models, foragers possess a valuation of their  
293 environment, a moving average of their foraging experiences up to the previous time step, and  
294 information about the foraging conditions in the current time step. Foraging decisions in the  
295 current time step are made by differentially weighting and combining these two elements  
296 (environmental valuation and current information) into a single value for the current patch or  
297 foraging tactic (Beauchamp 2000; Hamblin & Giraldeau 2009; Kacelnik & Krebs 1985). This

298 suggests that, in this study, PRT should be predicted by the previous foraging experience,  
299 representing the forager's valuation of the environment, and the current foraging conditions, or  
300  $PRT = f(\mathbf{c} + t)$  (m5), approximately describing the simplest learning rule, the linear operator  
301 (Kacelnik & Krebs 1985). Bayesian models, in contrast, suggest that foragers have a perception  
302 of the environment's distribution of food (rather than a simple valuation), which they update  
303 using their recent experiences, and then combine this information with current foraging  
304 experiences to make their patch-departure decisions (see Dall et al. 2005; McNamara et al. 2006),  
305 thus suggesting:  $PRT = f(\mathbf{c} + t + \mathbf{h})$  (m6). Finally, there is some evidence that the use of recent  
306 experiences may be contingent on habitat variability, as increases in variability may decrease the  
307 reliability of recent experiences in predicting the next experience, and so informing decisions  
308 (Lima 1984; Valone 1992). Therefore, our final two models develop m5 and m6 further by  
309 including an interaction between the forager's recent experience and habitat variability:

310  
311  $PRT = f(\mathbf{c} + t + \mathbf{h}_{sd} + t \times \mathbf{h}_{sd})$  (m7)

312 and,  $PRT = f(\mathbf{c} + t + \mathbf{h} + \mathbf{h}_{sd} + t \times \mathbf{h}_{sd})$  (m8).

313

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

316

317 The variables included in vectors  $\mathbf{c}$ ,  $\mathbf{h}$  and  $\mathbf{h}_{sd}$  were as follows. In models predicting natural PRTs,  
318 the forager's current experience,  $\mathbf{c}$ , was described by the patch size, food species and handling  
319 time. In models predicting experimental PRTs,  $\mathbf{c}$  comprised the patch's initial food density,  
320 estimated depletion and the focal forager's estimated satiation. Since the social environment can  
321 also influence a forager's current foraging experience,  $\mathbf{c}$  also included (for both natural and  
322 experimental PRT models) the focal forager's rank, mean social capital and mean relatedness to

323 other troop members, and, on a patch-by-patch basis, their mean rank difference, social capital  
324 and relatedness to other patch occupants, plus the number of patch occupants present (linear and  
325 quadratic terms). The variables describing the foraging habitat characteristics,  $\mathbf{h}$ , reflected the  
326 average patch quality and density. In the natural PRT models, these were the monthly habitat-  
327 specific estimates of both food items per patch and food patches per km<sup>2</sup>; in the experimental  
328 PRT models, these were the mean initial weight of food per patch (g) and inter-patch distance  
329 (m). Finally, in the natural PRT models,  $\mathbf{h}_{sd}$  described the standard deviations around the  
330 estimates of both the mean number of food items per patch and patch density ( $\mathbf{h}_{sd}$  was not  
331 explored in the experimental PRT models, since the initial patch quality and density were fixed  
332 with zero variance).

333

334 Models 1 to 8 and a null model (containing no fixed effects) were estimated using generalised  
335 linear mixed models for the natural and experimental PRTs datasets. In both cases, all non-  
336 categorical explanatory variables were standardised to have a mean of zero and standard  
337 deviation of one. Natural models included focal follow number nested within focal animal ID,  
338 nested within troop as random effects. Experimental models included focal animal ID, patch ID  
339 and experiment day cross-classified with each other and nested within troop, as random effects.  
340 To account for overdispersion in the PRT data, all models also included an observation-level  
341 random effect and were fitted as Poisson lognormal mixed effects models using a log link  
342 function (Elston et al. 2001) in the package lmer in R (Bates, Maechler, & Bolker 2011; R  
343 Development Core Team 2011). We assessed these models' performance (nine models in the  
344 natural analyses, seven in the experimental analyses) using Akaike's model weights. These were  
345 calculated from AIC values, since in all models  $n/k > 40$ , where  $n$  is the number patch visits and  $k$   
346 is the number of parameters in the maximal model (Burnham & Anderson 2002; Symonds &

347 Moussalli 2011). The data and R code used in these analyses are available from the Dryad  
348 repository (doi: 10.5061/dryad.3vt0s).

349

350

## 351 **Results**

352

353 The baboons visited food patches for a median of 30 seconds (inter-quartile range = 12 – 79 s, n  
354 = 6,175) in natural foraging conditions and 52 seconds (16 – 157 s, n = 8,569) in experimental  
355 foraging conditions.

356

357 Natural PRTs were best explained by the model containing factors predicted by the prescient  
358 marginal value theorem (Akaike's model weight  $w_i = 0.69$ , Table 1) but also showed some  
359 support for the model containing factors predicted by a Bayesian-updating rule ( $w_i = 0.27$ ). In  
360 contrast, experimental PRTs were best explained by the model containing factors predicted by a  
361 Bayesian-updating rule above all other models ( $w_i = 0.98$ , Table 1). In both conditions, the  
362 influence of the foraging habitat's characteristics on PRTs was consistent with the predictions of  
363 the prescient marginal value theorem (Table 2): the baboons spent less time in food patches when  
364 the environment was characterised by higher quality patches at higher densities. In both  
365 conditions, the model based on a Bayesian-updating rule also showed that baboons stayed longer  
366 in a patch when they had spent more time in the previous patch. The effect of this recent foraging  
367 experience was, however, relatively weak, especially in the natural observations (Table 2).

368



## 369 Discussion

370

371 The use of a patch-departure decision rule consistent with a Bayesian-updating process was  
372 strongly supported by the behaviour of the foragers on the experimental food patches. In contrast,  
373 foraging behaviour under natural conditions, whilst showing some support for the use of  
374 Bayesian-updating, showed greater support for a patch-departure rule based on the prescient  
375 marginal value theorem. Furthermore, in both environments our Bayesian-updating models also  
376 suggested that the influence of a single previous foraging experience was relatively weak. Our  
377 discussion first focuses on why these differences in decision-making between the two  
378 environments might occur and what this might suggest about the animals' abilities to efficiently  
379 exploit different environments. We then consider what these results reveal about how foragers  
380 use their recent experiences in their patch-departure decisions and the implications of these  
381 findings for the modelling of foraging behaviour.

382

383 It is widely appreciated that the collection and use of information by animals is dependent on its  
384 associated costs and benefits (Dall et al. 2005; Danchin et al. 2004). These costs and benefits may  
385 be dependent on individual traits (Koops & Abrahams 2003; Marshall et al. 2012; Webster &  
386 Laland 2011), but also on the characteristics of the surrounding environment and its resource  
387 distribution (Olsson & Brown 2006; Templeton & Giraldeau 1995; Webster & Laland 2008).  
388 Previous work has suggested that differences in the weight a forager places on their most recent  
389 experiences between habitats may be due to these experiences providing more reliable indicators  
390 of future foraging rewards when environments are either more predictable (Devenport &  
391 Devenport 1994; Eliassen et al. 2009; Fortin 2002; Valone 1991; Vásquez, Grossi, & Marquez  
392 2006) or less variable (Birnaskie et al. 2009; Lima 1984; Valone 1992). These alternative  
393 hypotheses may coincide, since less variable environments may also be more predictable – but

394 not always, since some patterns of variation, such as seasonal habitat changes, can also be highly  
395 predictable (Eliassen et al. 2009). Our findings are able to distinguish between these two  
396 hypotheses to some extent, and support the former. If environmental variability had influenced  
397 the baboons' use of recent experiences we would have expected more support for our models  
398 which explicitly incorporated it (models 7 and 8). Instead, the baboons incorporated their most  
399 recent experience into their patch-departure decisions to a greater extent in the more predictable,  
400 i.e. experimental, foraging environment (Table 2). This environment was likely to have been  
401 more predictable as the relative quality and position of each patch remained constant throughout,  
402 and their absolute quality and position only changed once (after 14 days) and three times (after  
403 7, 14, and 21 days), respectively (see Fig. 1, and Methods). In contrast, natural foraging  
404 environments, such as at Tsaobis, where food patches consist of multiple plant species, with  
405 different plant parts, whose phenology varies considerably across the year (not only between  
406 species but also between individuals), are inherently much less predictable.

407

408 An ability to flexibly incorporate recent experience, contingent on its reliability, into decision-  
409 making should allow foragers to maximise the efficiency with which they exploit different  
410 environments (Devenport & Devenport 1994; Koops & Abrahams 2003; Rodriguez-Gironés &  
411 Vázquez 1997; Valone 1991; Valone & Brown 1989). Such an ability appears to be possessed by  
412 the foragers in this study. This flexibility may also be widely distributed across a variety of taxa,  
413 and not limited solely to cognitively advanced animals such as baboons. A model by Holmgren &  
414 Olsson (2000) demonstrated that incorporating recent experiences during Bayesian foraging was  
415 possible using a simple three-neurone network. Furthermore, there is growing evidence, from a  
416 range of taxa, that the incorporation of recent experiences into foragers' decision-making can  
417 vary between environments (insects: Biernaskie et al. 2009, birds: Alonso et al. 1995; Valone  
418 1991, non-primate mammals: Devenport & Devenport 1994; Vázquez et al. 2006).

419

420 The model of forager behaviour predicted by Bayesian-updating was consistently supported over  
421 the model predicted by learning rules. This was true for both natural and experimental  
422 environments. Both Bayesian-updating (Green 1984; McNamara et al. 2006; Oaten 1977) and  
423 learning rules (Beauchamp 2000; Hamblin & Giraldeau 2009; Kacelnik & Krebs 1985) have been  
424 proposed as descriptions of how foragers incorporate past experiences into their decision-making.  
425 Our results seem to suggest that the former is more accurate in our system. This difference in  
426 performance may be explained by the fact that learning rules, particularly the linear operator rule  
427 that our model represents, are often simpler than Bayesian-updating approaches and may be less  
428 responsive to environmental variability (Eliassen et al. 2009; Groß et al. 2008). There is,  
429 however, evidence that the best way for a forager to incorporate previous experiences into their  
430 foraging decisions can be dependent on the underlying resource distribution (Eliassen et al. 2009;  
431 Olsson & Brown 2006; Rodriguez-Gironés & Vásquez 1997). Thus, although our study favours  
432 the Bayesian-updating approach, another study in a different setting might not. Furthermore, in  
433 our study we built each of our candidate models from the general theoretical principles  
434 underlying each approach. However, within each approach, different methods for incorporating  
435 previous experiences have been proposed, e.g. the ‘linear operator’ versus ‘relative payoff sum’  
436 methods for learning rules (Beauchamp 2000; Hamblin & Giraldeau 2009), and the ‘current  
437 value’ versus ‘potential value assessment’ methods for Bayesian updating (Olsson & Holmgren  
438 1998; van Gils et al. 2003). Another study, which was able to test more specifically these  
439 different methods, might find a narrower gap in performance between the learning and Bayesian  
440 approaches.

441

442 The influence of the baboons’ most recent experience on their patch-departure decisions, whilst  
443 generally important, was still relatively small, suggesting that, where foragers inform such

444 decisions with their recent experiences, they do so incrementally (Amano et al. 2006; Beauchamp  
445 2000; Biernaskie et al. 2009; Hamblin & Giraldeau 2009). That is, it is not just the previous  
446 foraging experience that is important but the experiences before that, and so on. This is consistent  
447 with the concept, common across models of imperfectly-informed foragers, that an individual's  
448 estimate of the environment's distribution of resources (Bayesian-updating) or value (learning  
449 rules) is an aggregate of their past experiences, and that individuals are continually updating this  
450 estimate with each subsequent experience (Kacelnik & Krebs 1985; McNamara et al. 2006). If, as  
451 here, the influence of each of these experiences is low, then as an increasing number of previous  
452 experiences are remembered this perceived distribution or valuation will increasingly  
453 approximate the true distribution (Koops & Abrahams 2003), i.e. the perfect knowledge assumed  
454 by the prescient marginal value theorem (pMVT; Charnov 1976). The predicted effects of patch  
455 quality and density characteristics in our best supported models (table 2) were consistent with the  
456 pMVT's prediction, suggesting that the baboons' perception of their environment did incorporate  
457 many past experiences and was a good approximation of perfect knowledge. Once again, there is  
458 reason to believe that this finding is not specific to baboons, since (1) a weak effect of a single  
459 recent experience on foraging decisions has been shown many times previously (Amano et al.  
460 2006; Beauchamp 2000; Biernaskie et al. 2009; Hamblin & Giraldeau 2009), and (2) there is  
461 evidence from other taxa that foragers can incorporate experiences over many days into their  
462 decision-making (birds: Valone 1991; non-primate mammals: Devenport & Devenport 1994;  
463 Vásquez et al. 2006). Furthermore, in theoretical comparisons, prescient (i.e. perfect-knowledge)  
464 foragers perform best (Eliassen et al. 2009; Koops & Abrahams 2003; Olsson & Brown 2006),  
465 and so it would seem likely that there is widespread selection for the ability to retain and use as  
466 many experiences as possible in foraging decision-making.

467

468 The finding that the baboons' perception of their environment included many past experiences  
469 and approximated perfect knowledge has two implications. First, it may provide an extra  
470 explanation for why the pMVT model outperformed the Bayesian-updating model in the natural  
471 foraging conditions. Here, the baboons were assigning very little weight to each foraging  
472 experience, which, as we have argued, is expected in this more natural, unpredictable  
473 environment. The inclusion of the single previous foraging experience variable in the Bayesian-  
474 updating model would therefore have provided very little extra explanatory power over the  
475 pMVT model, where this variable is absent, whilst being penalised 2 AIC points for the inclusion  
476 of the extra parameter. The AIC score difference of 1.9 points between the two models supports  
477 this argument. Thus, the baboons may have been using previous experiences in the natural  
478 foraging habitat, but we were less able to detect this given the relatively low weight assigned to  
479 each foraging experience. Indeed, it is hard to imagine how the baboons would have acquired  
480 sufficient knowledge of their environment to follow the pMVT were it not for the gradual  
481 accumulation of information through a process like Bayesian-updating or learning. It has also  
482 been noted that, where foragers update their information about the environment in such a gradual  
483 manner, distinguishing an updating from a non-updating strategy may be difficult (Eliassen et al.  
484 2009).

485  
486 The second implication is more important. If a forager's perception of its environment  
487 approximates perfect knowledge, then, in theory, its behaviour should also approximate  
488 optimality (Koops & Abrahams 2003), within the scope of its informational or physiological  
489 constraints (Fawcett et al. 2012). Our empirical support for this theoretical prediction suggests  
490 that the assumption of such knowledge by the prescient marginal value theorem may not be so  
491 unrealistic. Indeed, the predictions of the pMVT have received widespread qualitative support  
492 (Nonacs 2001). Modelling any natural process requires researchers to trade-off model accuracy

493 and simplicity (Evans 2012). The present study, and previous research, indicates that models of  
494 patch-departure decisions that consider how foragers incorporate past experiences into these  
495 decisions will usually provide more realism and accuracy than simpler models. However, our  
496 findings also suggest that when attempting to predict foraging behaviour, the prescient marginal  
497 value theorem may provide a simpler approach without sacrificing a great deal of accuracy.  
498

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500

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517

## 518 **Data Accessibility**

519 The data and R code used in this paper's analyses are available from the Dryad repository (doi:  
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521

522 **References**

- 523 Alonso, J.C., Alonso, J.A., Bautista, L.M. & Muñoz-Pulido, R. (1995) Patch use in cranes: a field  
524 test of optimal foraging predictions. *Animal Behaviour*, 49, 1367–1379.
- 525 Altmann, J. (1974) Observational study of behavior: sampling methods. *Behaviour*, 49, 227–267.
- 526 Amano, T., Ushiyama, K., Moriguchi, S., Fujita, G., Higuchi, H., Mano, T.A.A., Shiyama,  
527 K.A.U., Origuchi, S.A.M. & Ujita, G.O.F. (2006) Decision-making in group foragers with  
528 incomplete information: test of individual-based model in geese. *Ecological Monographs*,  
529 76, 601–616.
- 530 Bates, D., Maechler, M. & Bolker, B. (2011) lme4: Linear mixed-effects models using S4  
531 classes. R package version 0.999375-39.
- 532 Beauchamp, G. (2000) Learning rules for social foragers: implications for the producer-scrouter  
533 game and ideal free distribution theory. *Journal of Theoretical Biology*, 207, 21–35.
- 534 Biernaskie, J.M., Walker, S.C. & Gegear, R.J. (2009) Bumblebees learn to forage like Bayesians.  
535 *The American Naturalist*, 174, 413–423.
- 536 Burnham, K.P. & Anderson, D.R. (2002) Model Selection and Multimodel Inference: A Practical  
537 Information-Theoretic Approach. Springer, New York.
- 538 Bye Design Ltd. (1999) SpreadCE version 2.03. Available at [www.byedesign.co.uk](http://www.byedesign.co.uk)
- 539 Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population*  
540 *Biology*, 9, 129–136.



- 541 Cowlshaw, G. (1994) Vulnerability to predation in baboon populations. *Behaviour*, 131, 293–  
542 304.
- 543 Cowlshaw, G. & Davies, J. (1997) Flora of the Pro-Namib Desert Swakop River catchment,  
544 Namibia: community classification and implications for desert vegetation sampling. *Journal*  
545 *of Arid Environments*, 36, 271–290.
- 546 Dall, S.R.X., Giraldeau, L.A., Olsson, O., McNamara, J.M. & Stephens, D.W. (2005)  
547 Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*,  
548 20, 187–193.
- 549 Danchin, É., Giraldeau, L.-A., Valone, T.J. & Wagner, R.H. (2004) Public information: from  
550 nosy neighbors to cultural evolution. *Science*, 305, 487–491.
- 551 Devenport, L.D. & Devenport, J.A. (1994) Time-dependent averaging of foraging information in  
552 least chipmunks and golden-mantled ground squirrels. *Animal Behaviour*, 47, 787–802.
- 553 Eliassen, S., Jørgensen, C., Mangel, M. & Giske, J. (2009) Quantifying the adaptive value of  
554 learning in foraging behavior. *The American Naturalist*, 174, 478–489.
- 555 Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C. & Lambin, X. (2001) Analysis of  
556 aggregation, a worked example: numbers of ticks on red grouse chicks. *Parasitology*, 122,  
557 563–569.
- 558 Evans, M.R. (2012) Modelling ecological systems in a changing world. *Philosophical*  
559 *Transactions of the Royal Society B: Biological Sciences*, 367, 181–190.
- 560 Fawcett, T., Hamblin, S. & Giraldeau, L.-A. (2013) Exposing the behavioral gambit: the  
561 evolution of learning and decision rules. *Behavioral Ecology*, 24, 2–11.

- 562 Fortin, D. (2002) Optimal searching behaviour: the value of sampling information. *Ecological*  
563 *Modelling*, 153, 279–290.
- 564 Fruteau, C., Voelkl, B., Damme, E. van & Noë, R. (2009) Supply and demand determine the  
565 market value of food providers in wild vervet monkeys. *Proceedings of the National*  
566 *Academy of Sciences*, 106, 12007–12012.
- 567 Giraldeau, L.-A. & Caraco, T. (2000) *Social Foraging Theory*. Princeton University Press,  
568 Princeton, New Jersey.
- 569 Green, R.F. (1984) Stopping rules for optimal foragers. *The American Naturalist*, 123, 30–43.
- 570 Groß, R., Houston, A.I., Collins, E.J., McNamara, J.M., Dechaume-Moncharmont, F.-X. &  
571 Franks, N.R. (2008) Simple learning rules to cope with changing environments. *Journal of*  
572 *the Royal Society Interface*, 5, 1193–1202.
- 573 Hamblin, S. & Giraldeau, L.-A. (2009) Finding the evolutionarily stable learning rule for  
574 frequency-dependent foraging. *Animal Behaviour*, 78, 1343–1350.
- 575 Holmgren, N.M.A. & Olsson, O. (2000) A three-neuron model of information processing during  
576 Bayesian foraging. *Perspectives in Neural Computing: Artificial neural networks in*  
577 *medicine and biology. Proceedings of the ANIMAB-1 Conference, Göteborg, Sweden, May*  
578 *13-16, 2000*. (eds H. Malmgren, M. Borga & L. Niklasson), pp. 265–270. Springer, London.
- 579 Huchard, E., Alvergne, A., Féjan, D., Knapp, L.A., Cowlshaw, G. & Raymond, M. (2010) More  
580 than friends? Behavioural and genetic aspects of heterosexual associations in wild chacma  
581 baboons. *Behavioral Ecology and Sociobiology*, 64, 769–781.

- 582 Iwasa, Y., Higashi, M. & Yamamura, N. (1981) Prey distribution as a factor determining the  
583 choice of optimal foraging strategy. *The American Naturalist*, 117, 710–723.
- 584 Kacelnik, A. & Krebs, J.R. (1985) Learning to exploit patchily distributed food. *Behavioural*  
585 *Ecology: Ecological Consequences of Adaptive Behaviour*. (eds R.M. Sibly & R.H. Smith),  
586 pp. 189 – 206. Blackwell Scientific Publications, Oxford.
- 587 Koops, M.A. & Abrahams, M. V. (2003) Integrating the roles of information and competitive  
588 ability on the spatial distribution of social foragers. *The American Naturalist*, 161, 586–600.
- 589 Lima, S. (1984) Downy woodpecker foraging behavior: efficient sampling in simple stochastic  
590 environments. *Ecology*, 65, 166–174.
- 591 Marshall, H.H., Carter, A.J., Coulson, T., Rowcliffe, J.M. & Cowlshaw, G. (2012) Exploring  
592 foraging decisions in a social primate using discrete-choice models. *The American*  
593 *Naturalist*, 180, 481-495.
- 594 McNamara, J.M., Green, R.F. & Olsson, O. (2006) Bayes' theorem and its applications in animal  
595 behaviour. *Oikos*, 112, 243–251.
- 596 Noldus Information Technology. (2003) Matman version 1.1.4. Noldus Information Technology,  
597 Wageningen.
- 598 Nolet, B.A., Klaassen, R.H.G. & Mooij, W.M. (2006) The use of a flexible patch leaving rule  
599 under exploitative competition: a field test with swans. *Oikos*, 112, 342–352.
- 600 Nonacs, P. (2001) State dependent behavior and the Marginal Value Theorem. *Behavioral*  
601 *Ecology*, 12, 71–83.

- 602 Oaten, A. (1977) Optimal foraging in patches: a case for stochasticity. *Theoretical Population*  
603 *Biology*, 12, 263–285.
- 604 Olsson, O. & Brown, J. (2006) The foraging benefits of information and the penalty of ignorance.  
605 *Oikos*, 112, 260–273.
- 606 Olsson, O. & Holmgren, N.M.A. (1998) The survival-rate-maximizing policy for Bayesian  
607 foragers: wait for good news. *Behavioral Ecology*, 9, 345–353.
- 608 R Development Core Team. (2011) R: A language and environment for statistical computing. R  
609 Foundation for Statistical Computing, Vienna.
- 610 Rodríguez-Gironés, M. & Vásquez, R. (1997) Density-dependent patch exploitation and  
611 acquisition of environmental information. *Theoretical Population Biology*, 52, 32–42.
- 612 Stephens, D.W., Brown, J.S. & Ydenberg, R.C. (Eds.). (2007) *Foraging: Behavior and Ecology*.  
613 University of Chicago Press, Chicago.
- 614 Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton,  
615 New Jersey.
- 616 Symonds, M.R.E. & Moussalli, A. (2011) A brief guide to model selection, multimodel inference  
617 and model averaging in behavioural ecology using Akaike's information criterion.  
618 *Behavioral Ecology and Sociobiology*, 65, 13–21.
- 619 Templeton, J.J. & Giraldeau, L.-A. (1995) Patch assessment in foraging flocks of European  
620 starlings: evidence for the use of public information. *Behavioral Ecology*, 6, 65–72.
- 621 Valone, T.J. (1991) Bayesian and prescient assessment: foraging with pre-harvest information.  
622 *Animal Behaviour*, 41, 569–577.

- 623 Valone, T.J. (1992) Information for patch assessment: a field investigation with black-chinned  
624 hummingbirds. *Behavioral Ecology*, 3, 211–222.
- 625 Valone, T.J. (2006) Are animals capable of Bayesian updating? An empirical review. *Oikos*, 112,  
626 252–259.
- 627 Valone, T. & Brown, J.S. (1989) Measuring patch assessment abilities of desert granivores.  
628 *Ecology*, 70, 1800–1810.
- 629 van Gils, J.A., Schenk, I.W., Bos, O. & Piersma, T. (2003) Incompletely informed shorebirds that  
630 face a digestive constraint maximize net energy gain when exploiting patches. *The American*  
631 *Naturalist*, 161, 777–793.
- 632 Vásquez, R.A., Grossi, B. & Marquez, I.N. (2006) On the value of information: studying changes  
633 in patch assessment abilities through learning. *Oikos*, 112, 298–310.
- 634 Wang, J. (2007) Triadic IBD coefficients and applications to estimating pairwise relatedness.  
635 *Genetical Research*, 89, 135–53.
- 636 Webster, M.M. & Laland, K.N. (2008) Social learning strategies and predation risk: minnows  
637 copy only when using private information would be costly. *Proceedings of the Royal Society*  
638 *B: Biological Sciences*. 275, 2869–2876.
- 639 Webster, M.M. & Laland, K.N. (2011) Reproductive state affects reliance on public information  
640 in sticklebacks. *Proceedings of the Royal Society B: Biological Sciences*. 278, 619–627.
- 641

642 **Figures legends**

643

644 Figure 1: Schematic of the foraging-experiment's patch (a) layout and (b) dimensions. For each  
645 troop patch food content,  $f$ , was varied between  $11.1 \pm 0.1$  grams/m<sup>2</sup> (low, first 14-day period)  
646 and  $16.7 \pm 0.1$  g/m<sup>2</sup> (high, second 14-day period) of loose dried maize kernels. Inter-patch  
647 distance ( $d$ ) was varied within each 14-day period. In the first period it was set at 25 m (low) for  
648 the starting 7 days and 50m (high) for the remaining 7 days, and vice versa for the second period.  
649 Patch size was constant within troops. Large patches (A, D and E) were set at 80 m<sup>2</sup> (a = 10 m, b  
650 = 10 m, c = 6 m) for the small troop and 96 m<sup>2</sup> (10, 12, 6) for the large troop. Small patches (C  
651 and D) were set at 20m<sup>2</sup> (5, 5, 3) for the small troop and 27 m<sup>2</sup> (6, 6, 3) for the large troop.

652 Table 1: Model performance in explaining patch residency times, under natural and experimental conditions. Models in bold make up the 95%  
 653 confidence model set. AIC = Akaike's information criterion,  $\Delta AIC$  = difference between AIC score and lowest AIC score,  $w_i$  = Akaike's model  
 654 weight

| <u>natural</u> |  |                 |              |             | <u>experimental</u> |   |                 |              |             |
|----------------|--|-----------------|--------------|-------------|---------------------|---|-----------------|--------------|-------------|
| no.            | patch-departure rule from predictions of :         | AIC             | $\Delta AIC$ | $w_i$       | no.                 | patch-departure rule from predictions of :        | AIC             | $\Delta AIC$ | $w_i$       |
| <b>4</b>       | <b>prescient marginal value theorem</b>            | <b>28342.16</b> | <b>0.00</b>  | <b>0.69</b> | <b>6</b>            | <b>Bayesian updating</b>                          | <b>48410.75</b> | <b>0.00</b>  | <b>0.98</b> |
| <b>6</b>       | <b>Bayesian updating</b>                           | <b>28344.06</b> | <b>1.90</b>  | <b>0.27</b> | 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                | 29323.18        | 981.02       | 0.00        |                     | null  | 49200.07        | 789.32       | 0.00        |

configuration

|   |  |          |         |      |
|---|--|----------|---------|------|
| 2 | fixed rule based on recent foraging experience | 29521.79 | 1179.64 | 0.00 |
|   | null   | 29543.59 | 1201.43 | 0.00 |

655

656 Table 2: The influence of previous foraging experience and foraging habitat characteristics (effect sizes,  $\beta \pm$  s.e.) on patch residency times (PRTs)  
 657 in the best models (95% confidence set, see table 1) under natural and experimental conditions

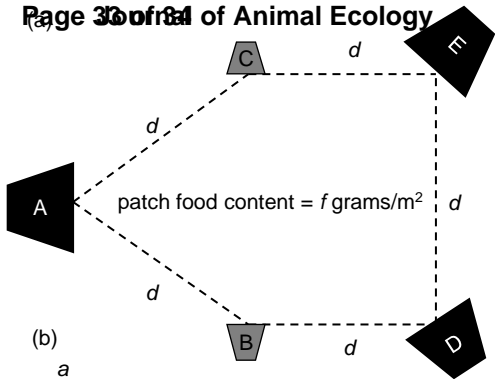
| natural PRT models (model number)                  |   |                            | experimental PRT models (model number) |                            |
|--|---|----------------------------|--|----------------------------|
| predictors   | prescient<br>marginal value<br>theorem (m4) | Bayesian-<br>updating (m6) | predictors                             | Bayesian-<br>updating (m6) |
| time in previous patch<br>(s)                      |   | $0.006 \pm 0.02$           | time in previous patch<br>(s)          | $0.08 \pm 0.02$            |
| mean number of food<br>items per patch             | $-0.11 \pm 0.03$                            | $-0.11 \pm 0.03$           | mean weight of food<br>per patch (g)   | $-0.56 \pm 0.15$           |
| mean number of food<br>patches per km <sup>2</sup> | $-0.16 \pm 0.02$                            | $-0.16 \pm 0.03$           | inter-patch distance<br>(m)            | $0.10 \pm 0.04$            |



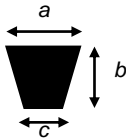
658

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(a)



(b)





Juvenile female chacma baboon (*Papio ursinus*). Photo credit: Harry Marshall/ZSL Tsaobis Baboon Project  
169x254mm (300 x 300 DPI)