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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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Manuscripts

1 **How do foragers decide when to leave a patch? A test of alternative**

2 **models under natural and experimental conditions**

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16

17

18 **Abstract**

19

20 1. A forager's optimal patch-departure time can be predicted by the prescient marginal value

21 theorem (pMVT), which assumes they have perfect knowledge of the environment, or by

22 approaches such as Bayesian-updating and learning rules, which avoid this assumption by

23 allowing foragers to use recent experiences to inform their decisions.

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

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2

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

3

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 & Gegear 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   <u>Study Site</u>

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 Cowlishaw & 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 (Cowlishaw 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 – 9a.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 ± 10 hours, mean ± s.d., per individual) containing 6,175 patch

186   visits (112 ± 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. Cowlishaw, 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 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 x 10^{-5} (transect area of 50m^2

203   = 5 x 10^{-5} 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 m^2 (patches B and C in Fig. 1) and three at 80 m^2 (patches A, D and E) for the

213   small troop, producing a total per-animal feeding area of 8.5 m^2 (280 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 m^2 and 96 m^2 for the large troop, producing a total per-animal feeding area of 8.3 m^2 (342

216   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 ± 0.3 g/m^2, mean ± 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 ± 0.4 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 $222 \pm 1g$ (mean ± 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   (g/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; $n_{large} = 2391$, $n_{small} = 1931$) using Matman 1.1.4 (Noldus Information

247   Technology 2003). Hierarchies in both troops were strongly linear (Landau's corrected linearity

248   index: $h'_{large} = 0.71$, $h'_{small} = 0.82$, $p < 0.001$ 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   <u>Analysis</u>

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

11

273   current physical and social characteristics of both the patch and the forager, in the case of c, and

274   the foraging habitat's characteristics, in the case of 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 = $f(c)$ (model 1), recent experience, PRT = $f(t)$ (m2) and

281   habitat characteristics, PRT = $f(h)$ (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 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 = $f(c + h)$ (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    $\text{PRT} = f(c + t)$ (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: $\text{PRT} = f(c + t + h)$ (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    $\text{PRT} = f(c + t + h_{sd} + t \times h_{sd})$ (m7)

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

313

314   Here, 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 c, h and h_{sd} were as follows. In models predicting natural PRTs,

318   the forager's current experience, c, was described by the patch size, food species and handling

319   time. In models predicting experimental PRTs, 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, 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, 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^2; 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, h_{sd} described the standard deviations around the

330   estimates of both the mean number of food items per patch and patch density (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 (Biernaskie et al. 2009; Lima 1984; Valone 1992). These alternative

393   hypotheses may coincide, since less variable environments may also be more predictable – but

16

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   Vásquez 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; Vásquez 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

19

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

518   **Data Accessibility**

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

520   10.5061/dryad.3vt0s).

521

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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 ± 0.1 grams/m^2 (low, first 14-day period)

646   and 16.7 ± 0.1 g/m^2 (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^2 (a = 10 m, b

650   = 10 m, c = 6 m) for the small troop and 96 m^2 (10, 12, 6) for the large troop. Small patches (C

651   and D) were set at 20m^2 (5, 5, 3) for the small troop and 27 m^2 (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, ΔAIC = difference between AIC score and lowest AIC score, w_i = Akaike's model

654   weight

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	29323.18	981.02	0.00		null	49200.07	789.32	0.00

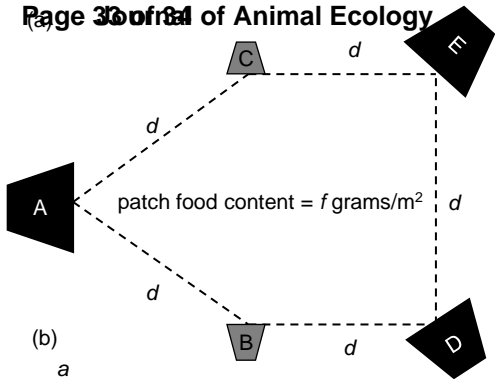|				
	configuration			
2	fixed rule based on recent foraging experience	29521.79	1179.64	0.00
	null	29543.59	1201.43	0.00

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 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	inter-patch distance (m)	0.10 ± 0.04

658

(a)

C

d

E
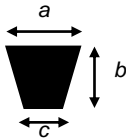
d

d

A

patch food content = *f* grams/m²

d

d

B

d

D

(b)

a

b

c

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