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Overstaying in patchy foraging can be explained by behavioral variability

Tyler Cash-Padgett and Benjamin Hayden

Department of Neuroscience,
Center for Magnetic Resonance Research, and
Center for Neuroengineering
University of Minnesota,
Minneapolis MN 55455

Corresponding author:

Tyler Cash-Padgett
Department of Neuroscience
University of Minnesota
Minneapolis, MN, 55455
Email address: tcashpadgett@gmail.com

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Competing interests

The authors have no competing interests to declare.

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ABSTRACT

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Foragers often systematically deviate from rate-maximizing choices in two ways:

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in accuracy and precision. That is, they both use suboptimal threshold values and show

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variability in their application of those thresholds. We hypothesized that these biases are

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related and, more specifically, that foragers' widely known accuracy bias – over-staying –

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could be explained, at least in part, by their precision bias. To test this hypothesis, we

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analyzed choices made by three rhesus macaques in a computerized patch foraging task.

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Confirming previously observed findings, we find high levels of variability. We then show,

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through simulations, that this variability changes optimal thresholds, meaning that a

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forager aware of its own variability should increase its leaving threshold (i.e., over-stay) to

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increase performance. All subjects showed thresholds that were biased in the predicted

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direction. These results indicate that over-staying in patches may reflect, in part, an

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adaptation to behavioral variability.

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KEYWORDS

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foraging; decision making; macaque; patch-leaving; over-staying

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61 **INTRODUCTION**

62 Foraging theory provides normative guides for decisions that will maximize long-
63 term reward intake rate in foraging contexts (Charnov 1976; Stephens and Krebs, 1986).
64 Many foragers roughly approximate rate-maximizing behavior (Bixter and Luhmann,
65 2013; Krebs et al., 1977; McNamara and Houston, 1997; Houston and McNamara, 2014;
66 Kacelnik 1997). Two major apparent deviations from rate-maximizing behavior stand out.
67 **First**, foragers tend to exhibit much more behavioral variability than they should (Charnov,
68 1976; Cowie, 1977; Kacelnik, 1984; Lima, 1984; Munger, 1984). This is true even in
69 carefully controlled computerized tasks (Hayden et al., 2011; Blanchard and Hayden,
70 2014; Eisenreich et al., 2019). A decision-maker that shows variability will harvest less
71 reward than one that does not, because even if their average threshold is correct, it is often
72 incorrect on individual trials. **Second**, foragers tend to have systematically suboptimal
73 average thresholds and, particularly in patch-leaving contexts, tend to over-stay (Hayden et
74 al., 2011; Blanchard and Hayden, 2015; Cassini et al. 1990; Cassini et al. 1993;
75 Constantino and Daw 2015; Kamil et al. 1988; Kane et al. 2018; Nonacs 2001).

76 Variability has several potential explanations. One possibility is that there is some
77 factor we are not measuring or considering. These may include internal factors such as
78 deliberate exploration, sensory or motor variability, and cognitive noise (Daw et al. 2006;
79 Evans and Raine 2014; Pyke 1978; Todd and Kacelnik 1993; Ebitz et al., 2019). They may
80 include external factors, such as a limitation in our measurement of foragers' behavior or
81 our inability to accurately quantify the statistical properties of the environment to which
82 the forager is responding (Brown 1988; Houston and McNamara 1990; Lima and Dill

83 1990; McNamara and Houston 1987). It can be difficult to disambiguate these possibilities
84 in field studies because much of the information that drives foraging decisions is difficult
85 to measure (Houston and McNamara 2014).

86 The systematic error in thresholds is more mysterious (Nonacs 2001). Here we
87 propose a new hypothesis, that foragers' use of suboptimal thresholds may be a rational
88 response to their own variability, and may thus be less costly than it appears. Specifically,
89 if foragers are intrinsically variable and foraging payoff curves are asymmetric (as they
90 typically are), the optimal strategy may be to use a threshold biased in the direction of the
91 shallower slope of the payoff curve. If the forager is both aware of its own variability and
92 unable to reduce it, then the forager may potentially increase its harvest rate by altering its
93 thresholds. Or, more specifically, the forager may be able to mitigate the loss in reward
94 caused by variability by strategically adjusting its threshold.

95 Here, we examined a dataset consisting of choices made by three foraging
96 macaques in a computerized foraging task (Blanchard and Hayden, 2015). All subjects
97 lived in highly controlled laboratory environments with stable food provisioning and were
98 over-trained on their tasks for months to reduce their subjective uncertainties about task
99 structure as much as possible. All subjects nonetheless showed high behavioral variability,
100 consistent with observations from less controlled field studies. They also showed over-
101 staying. These results suggest that subjects have the flexibility to adjust strategies to
102 account for their own variability.

103

104

METHODS

105 Three macaque subjects performed a *patch-leaving task* during the collection of
106 data for previously published studies (Blanchard and Hayden 2015; Hayden et al. 2011;
107 Ramakrishnan et al., 2019) and were trained on the task for several months prior. All
108 procedures were approved by the University Committee on Animal Resources at the
109 University of Rochester and were designed and conducted in compliance with the Public
110 Health Service’s Guide for the Care and Use of Animals. Subjects had never previously
111 been exposed to foraging decision-making tasks. Previous training history for these
112 subjects included several types of gambling tasks (Azab and Hayden, 2017 and 2018;
113 Heilbronner and Hayden, 2016; Farashahi et al., 2017) and, in one case, a cognitive set-
114 shifting task (Sleezer et al., 2016).

115

Patch-leaving task

116 Stimuli were colored rectangles on a computer screen. A rectangle’s color indicated
117 reward available from that option, and its size represented the delay associated with
118 choosing it. On each trial, subjects acquired fixation on a central point stimulus and were
119 then presented with two targets representing the ‘stay’ in patch and ‘leave’ patch options
120 respectively. After 100 ms, subjects were free to select either target by shifting their gaze
121 to it. Targets shrank in size at a constant rate once selected so that their height provided an
122 unambiguous cue to the delays associated with the two options on every trial. Staying in
123 the current patch always resulted in a 0.6 s “handling time” delay, while the “travel time”
124 associated with leaving varied randomly from patch to patch between 0.5 s and 10.5 s.
125

126 If subjects chose to stay in the current patch, a water reward was delivered
127 following the delay. This reward would decrement on each subsequent ‘stay’ decision but
128 would reset upon arrival in a new patch. The initial reward amount for subject C was 200
129 μL and was decremented by 13 μL for every ‘stay’ decision. The initial reward amounts
130 for subjects E and O were 230 μL and were decremented stochastically, between 12.7 and
131 15.5 μL per trial, with a mean decrement of 14.1 μL . Further description of the task is
132 available in Hayden et al. (2011).

133

134 *Patch-leaving data analysis*

135 We aggregated 14,413 trials across 33 sessions from subject C, 2,010 trials across 4
136 sessions from subject E, and 1,717 trials across 4 sessions from subject O. In order to
137 control for slight differences in travel times and handling times between the two datasets,
138 we analyzed the subjects’ foraging behavior in terms of the number of ‘stay’ decisions per
139 patch. Mean patch residence time was defined as the mean number of trials spent in-patch
140 across all patches. Reward rate was defined as the mean amount of water received per
141 patch across all trials.

142

143 *Patch-leaving task simulation*

144 To calculate the impact of noise on a subject’s optimal threshold value, we
145 constructed a simulation of the patch-leaving task as described above. Each simulated
146 subject ran 10,000 behavioral sessions of 439 trials (the average number of trials per
147 session over all three datasets). Patch-leaving thresholds ranged from 1 to the maximum

148 number of rewarded trials depending on initial reward and decrement size (18 for subject
149 C, 17 for subjects E & O). We uniformly distributed the possible thresholds across the
150 patches in each session. The expected reward rate for a given threshold (Figure 2B) was
151 calculated as the average reward rate from all patches, in all sessions, where that threshold
152 was in effect.

153 The total accumulated reward in a given patch was based on the number of ‘stay’
154 decisions, initial reward, and reward decrement amount. We therefore normalized the
155 reward rate to the number of trials, rather than raw time, spent in-patch. Travel time was
156 normalized by dividing, for each patch residence duration, the mean and standard deviation
157 of travel times observed during behavioral testing, respectively, by total patch residence
158 time. Travel time for each simulated patch was then drawn from a normal distribution
159 based on the empirically observed mean and standard deviation for that particular
160 normalized patch residence duration. Since we lacked precise timing information for
161 subject C, this normalized travel time function was calculated based on behavioral data
162 from subjects E and O.

163 To simulate the effect of threshold noise on its optimal value, we interpolated the
164 reward curve twenty-fold and performed trapezoidal numerical integration for a Gaussian-
165 distributed matrix centered on each candidate threshold value. For standard deviations
166 ranging from zero to one half of the maximum number of rewarded trials, we calculated
167 the noise-adjusted threshold value that maximized the area under the reward rate curve.

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170 **RESULTS**

171 Three macaques (subjects C, E, and O) performed a series of trials in which they
172 chose between remaining in a patch or leaving it. Remaining led to a short “handling time”
173 (delay of 600 ms) and leaving led to a longer “travel time” (delay of 0.5 to 10.5 seconds,
174 see **Methods** for details). Travel time varied randomly between patches and was signaled
175 unambiguously within each patch. To control for slightly differing travel and handling time
176 regimens between our three subjects, we defined patch residence time as the number of
177 decisions to stay in a patch.

178 Both subjects showed residence times that were close to, but longer than, the
179 dictates of foraging theory (Stephens and Krebs, 1986), which yields an optimal patch
180 residence time of **4.01 (± 0.74) trials** for subject C’s version of the task and **4.16 (± 0.78)**
181 **trials** with subject E and O’s slightly different version of the task. In practice, all three
182 subjects’ mean patch residence times were significantly longer than optimal: **5.84 (± 0.08)**
183 **trials** for subject C, **9.26 (± 0.41) trials** for subject E, and **12.09 (± 0.42) trials** for subject
184 O (all significant, two-sided Student’s t-test, $p < 0.0001$)

185 Subjects’ trial-to-trial behavior in this task showed significant variability, which
186 was costly. A forager with no variability would have obtained a reward rate of **168.4**
187 **$\mu\text{L}/\text{patch}$** with subject C’s observed threshold. Subject C’s actual reward rate, however,
188 was **128.4 $\mu\text{L}/\text{patch}$** . Similarly, a forager with no variability would have obtained a reward
189 rate of **174.4 $\mu\text{L}/\text{patch}$** with subject E’s observed threshold, but the subject’s actual reward
190 rate was **161.0 $\mu\text{L}/\text{patch}$** . Finally, while a forager with no variability would have obtained

191 a reward rate of **147.1 $\mu\text{L}/\text{patch}$** with subject O's observed threshold, the subject's actual
192 reward rate was **135.1 $\mu\text{L}/\text{patch}$** .

193 We calculated the trial-to-trial variability in each subject's patch leaving behavior
194 as the standard deviation in its threshold over a large sample of bootstrapped 500-trial bins.
195 Based on an empirical threshold standard deviation of **4.15 trials/patch**, Subject C's
196 uncertainty-adjusted optimal patch residence threshold was **7.40 trials**. In other words,
197 optimizing given his variability can account for some of his observed rate adjustment
198 (**+1.84 trials**) relative to optimal, assuming no variability (**+3.40 trials**). A similar pattern
199 held for subjects E and O, with respective standard deviations of **6.02 trials per patch** and
200 **5.04 trials per patch** both suggesting a compensatory increase in threshold. While their
201 behavioral adjustments are in the same direction as suggested by accounting for
202 uncertainty, however, the observed adjustments are actually larger than optimal (**+4.26**
203 **trials/patch** observed vs. **+3.05** predicted for subject E, and **+7.09 trials** observed vs. **+2.95**
204 **trials** predicted for subject O).

205 **DISCUSSION**

206 We examined previously collected datasets of rhesus macaques performing a
207 computerized patch foraging task (Blanchard and Hayden, 2015). Macaques showed two
208 behavioral patterns that are characteristic of many foragers. First, they showed a systematic
209 deviation from an optimal foraging threshold by over-staying. Second, they showed a
210 strong and costly variability in behavior. We propose that these two phenomena are at least
211 partly related. First, we conjecture that behavioral variability is for some reason
212 unavoidable (and our results do not offer any explanation for it). Given this unavoidability,
213 we show that the reward-maximizing threshold increases. We then show that all three
214 subjects showed changes in the direction that yielded improved harvest rates.

215 Previous studies of foraging behavior have suffered two limitations that ours
216 avoids. First, many studies are limited by data quantity. By using well-trained macaques
217 performing a computerized task, we were able to analyze several thousand trials. Second,
218 many studies have sources of unmeasurable noise. These include difficulty quantifying the
219 details of the environment and difficulty knowing that the forager has had sufficient
220 experience with the environment to make the same calculations we as observers would.
221 The carefully controlled nature of our computerized task enables us to fix all relevant task
222 variables and ensure overtraining on those specific tasks. We were further able to reduce
223 unmeasured variability by controlling animals' learning environment in their juvenile and
224 adult lives and by ensuring a relatively stable food supply over that entire period of time.

225 It is perhaps surprising that subjects' behavioral variability on this task was so high
226 despite the stable environment and months of preparatory task training. This result

227 replicates a classic finding from a seminal study (Charnov, 1976). Our own study does not
228 shed any light on the source of behavioral variability. A long tradition in foraging theory
229 emphasizes the importance of “informational constraint” on suboptimal behaviors
230 (Eisenreich et al. 2017; Fernández-Juricic et al. 2004; Pearson et al. 2010; Stephens 2002).
231 Other factors may also be relevant, including information-seeking (Blanchard et al. 2015;
232 Bromberg-Martin and Hikosaka 2009), temporal discounting (Kane et al. 2018), curiosity
233 (Wang and Hayden 2019), computational noise, or exploratory behavior (Ebitz et al. 2018;
234 Pearson et al. 2009; Wilson et al. 2014). Whatever the source, our results highlight an
235 intriguing fact about monkeys’ variability: they have adjusted their behavior as if they have
236 learned to reduce its costs. This suggests that they may be unable or unwilling to directly
237 change it, but flexible enough to adjust surrounding aspects of their behavior.

238 Foraging is a major driver of the animal brain (Calhoun and Hayden 2015; Hayden
239 2018; Murray and Rudebeck 2013; Passingham and Wise 2012; Pearson et al. 2014). As
240 such, a science of the neural basis of choice ought to go hand in hand with an
241 understanding of foraging psychology. Systematic deviations from optimal foraging
242 provide an important measure of the forces of evolution; because they are costly, they
243 likely reflect the existence of tradeoffs that are not obvious to evolutionary biologists.
244 Many of these likely come from constraints on the costs of computing foraging strategies
245 in full.

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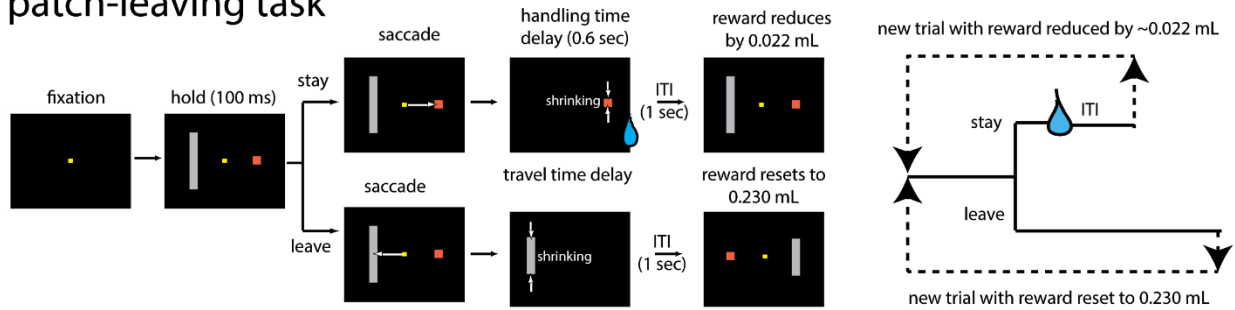
247

FIGURES

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249 **FIGURE 1**

patch-leaving task



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251 **Figure 1. Task.** After fixation, the subject views two targets, and chooses one by shifting

252 gaze to it. Choice of the orange rectangle (stay in patch) yields a short delay and reward

253 whose value diminishes by 13 μL /trial. Choice of the gray rectangle (leave patch) yields no

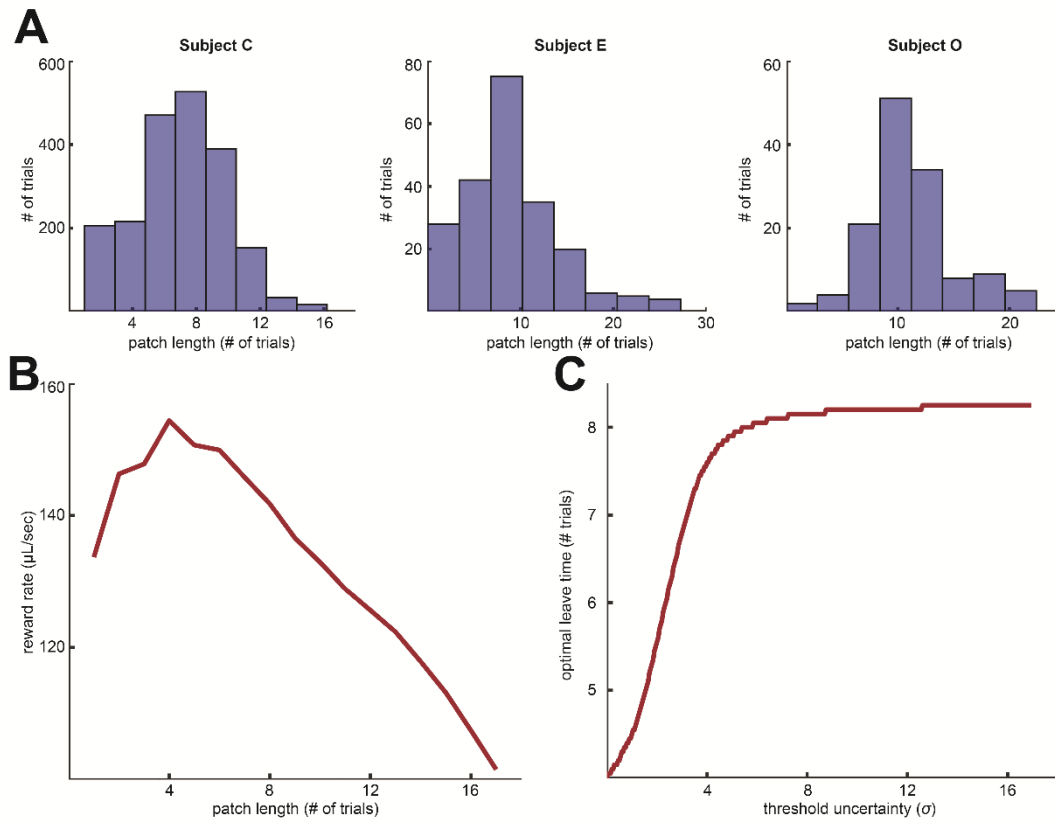
254 reward and a long delay (travel time) whose duration is indicated by the height of the bar,

255 and resets the value of the orange rectangle at 230 μL . Patch travel time varies randomly

256 from patch to patch between 0.5 to 10.5 s.

257

258 **FIGURE 2**



259

260 **Figure 2. Patch-leaving behavior and simulation. (A)** Patch length distributions for each
261 subject denoted by number of trials ('stay' decisions). **(B)** The reward rate available via
262 behavioral policies of leaving after a threshold number of trials, per simulation. **(C)** The
263 optimal patch leaving threshold as a function of a set amount of Gaussian noise applied to
264 the threshold (quantified by the standard deviation σ).

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AUTHORS' CONTRIBUTIONS

270 *TCP performed all data analysis, designed the simulations, and drafted the manuscript.*

271 *BYH posited the study's hypothesis and critically revised the manuscript. Both authors*

272 *gave final approval for publication and agree to be held accountable for the work*

273 *performed therein.*

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