PUTTING MECHANISMS IN FORAGING THEORY: the role of computational mechanisms in optimal decision making

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1 Castellano Sergio

2 Department of Life Sciences and Systems Biology, University of Turin, Via Accademia

3 Albertina 13, 10123, Torino

4 Email: sergio.castellano@unito.it

Abstract

6 Classic optimization models explain adaptive behaviours in terms of optimal cost-benefit trade-offs. They

7 assume flexibility and make testable predictions about what animals should do in order to maximize their

8 fitness. But they usually do not ask how animals can do it. Since flexible behaviours can be globally optimal

9 but locally sub-optimal, the optimality models should directly focus on the underlying mechanisms of

10 behavioural flexibility, such as learning and decision making. In this paper, I use the classic "diet" model of

11 Optimal Foraging Theory (OFT) to investigate the evolution of decision-making mechanisms at both the

12 computational and the algorithmic level. At the computational level, I define benefits (the expected rate of

13 net energy intake) and costs (lost opportunity) and formalize the decision rule. At the algorithmic level, I

14 present two sequential-sampling models, which differ in the way information is internally represented and

15 used. The first model represents the prospective items along a one-dimension scale of values (benefit-cost

16 differences) and it uses a fixed amount of sensory information (and time) to make decisions. The second

17 model represents items in the 2-dimension plane of benefits and costs, and it uses a variable amount of

18 information. I test the models along a gradient of resource abundance. In each environment, I use OFT to

19 classify resources as either profitable or unprofitable, and describe the model performance in terms of

20 decision time and accuracy. At high resource density, both models predict foraging choice to be more

21 selective, but less accurate than at low density, because decisions are strongly biased in the false-positive

22   direction. At low resource density, the 2-dimension model performs better than the 1-dimension

23   alternative, because it takes less time to make more accurate decisions. These differences, however,

24   disappear when resources are abundant.   2

25

26   **Keywords:** behavioural plasticity, decision-making, evo-mecho, heuristics, speed-accuracy trade-offs

27

28   Perhaps the most glaring attribute of behaviour is flexibility, which makes animals capable to cope with the

29   uncertainty and the unpredictability of their lives. What permits animals to behave flexibly are the decision

30   mechanisms, implemented in their nervous system, which allows them to use internal and external stimuli

31   when choosing among alternative behaviours (Fawcett et al. 2013). While classic ethology was mainly

32   interested on the mechanistic aspects of these behaviours (Dewsbury 1989), behavioural ecology shifted

33   the focus on their ultimate functions. Behavioural ecologists started investigating the adaptive roles of

34   behaviours and, doing so, they settled the bases for a new paradigm, which was based on the economic

35   consideration of costs and benefits of alternative actions (Krebs and Davies 1978).

36   Undoubtedly, the greatest success of this new approach was due to the tight link between theoretical and

37   empirical research, which allowed testable predictions of adaptive behaviours. An emblematic example of

38   such a success is Optimal Foraging Theory (OFT) (Stephens and Krebs 1986; Krebs and Kacelnik 2007;

39   Stephens et al. 2007). OFT uses normative models to predict foraging strategies that maximize the rate of

40   net energy intake. For example, the "diet-model" (Stephens and Krebs 1986) predicts clear-cut foraging

41   decisions, which are flexibly adjusted to the environment where choice is made. Specifically, in a given

42   environment, the model predicts that a consumer that optimizes the long term rate of energy intake should

43   choose to feed on a resource only when the rate of benefits of this resource exceeds that of the diet

44   comprised only with items with higher values (Stephens and Krebs 1986, and see below). Although the

45   "diet model" was based on some unrealistic assumptions (i.e. no uncertainty and no errors in resource

46   assessment), it made testable predictions and, most importantly, it helped the empirical research to focus

47   on the right questions and, thus, it contributed to broaden and deepen the field (Krebs and Kacelnik 2007).

48   The "diet model", as well as many other OFT models, by focusing on the functional aspects of behavioural

49   flexibility, paid very little attention to its underlying psychological and cognitive mechanisms (Kacelnik

50   2012). This neglecting of causal mechanisms has been dubbed the "behavioural gambit" (Giraldeau and

51   Dubois 2008; Fawcett et al. 2013), because, like the "phenotypic gambit" (Grafen 1984), it makes the

52   simplifying assumption that mechanisms play a marginal role in the adaptive evolution of phenotypes.

53   However, there are several reasons why it might not be worth it to make such an improbable bet. First, for

54   flexible behaviours, the rules that govern flexibility are the indirect target of selection and, thus, the

55   optimality approach should focus on their function rather than on the function of single behaviours

56   (McNamara and Houston 2009). Second, decisions are made under uncertainty and they are prone to error.

57   Optimal behaviours depend on the effective use of uncertainty, that is, on the optimal trade-offs between

58   the risks and the costs of different type of errors (Johnson et al. 2013). Finally, to limit the costly effects of

59   uncertainty, animals need to process large amounts of information from the environment. But this takes

60   time and thus optimality depends also on the mechanisms of information processing and on the trade-offs

61   between speed and accuracy in decision making (Chittka et al. 2009).

62   Behavioural ecologists have long been aware of the risks that neglect of mechanisms might weaken the

63   functional analysis of behaviour. In deterministic OFT models, such as the "patch model", researchers find

64   optimal decisions by computing first derivatives on the curve of diminishing returns (Stephens and Krebs

65   1986), whereas in stochastic OFT models (i.e. foraging decisions under uncertainty, Stephens 2007) they

66   apply Bayesian computation of prior and posterior probabilities. But animals do not have access to

67   computational devices that can implement algorithms of such a level of complexity. Nevertheless they

68   manage to solve these problems effectively. How can animals be functionally optimal if they can afford only

69   limited computational resources?

70   One of the first attempts to answer to this question and resolve the function-mechanism dichotomy, in

71   behavioural ecology, has been the rules-of-thumb approach (RoT), which assumes natural selection to

72   favour the evolution of simple rules that approximate the optimal strategies identified by theoreticians

73   through optimisation (Kacelnik 2012). Interestingly, a similar approach, the heuristic research program, has

74   been adopted by cognitive psychologists to study human decision making (Gigerenzer et al. 2002).

75   Heuristics and RoTs have evolved under natural selection and, as all adaptive traits, they are expected to

76   perform optimally (or satisfactorily) in the ecological context where they have been selected. In this sense,

77   they are expression of "ecological rationality" (Goldstein and Gigerenzer 2002, Stephens 2008). Since the

78   heuristic and the RoT approaches do not consider the mechanisms underlying decision rules, they

79   contributed to reinforce the idea that cognitive mechanisms can be justifiably ignored, because natural

80 selection somehow or other will be able to implement context-dependent optimal rules in the neural

81 machinery of decision makers (Bateson and Healy 2005). However, by ignoring the psychological

82 mechanisms of decision making, proponents of this approach failed to provide convincing evidence that

83 these rules do actually exist.

84 More recently, McNamara and Houston (2009) proposed a new line of research, named 'evo-mecho', which

85 approaches the function-mechanism dichotomy from a different perspective. Instead of focusing on

86 narrow-domain rules, which are implicitly assumed to evolve 'ex-novo' and solve specific tasks under

87 simple environmental conditions, they suggest to focus on simple, general mechanisms that perform well in

88 complex and variable environments (Fawcett et al. 2014). Like anatomical traits that show adaptive

89 variation on a common structural plan, the psychological mechanisms that control behaviour can be tuned

90 by natural selection to solve specific tasks, but maintain the same general structure, which may reflect

91 either constraints or adaptations at the anatomical level of the cognitive machinery. Unlike the RoT

92 approach, the 'evo-mecho' model does not view mechanisms and functions as independent levels of

93 behavioural analysis, but as the two interconnected components of a multi-level approach. The "evo-

94 mecho" approach not only addresses questions about the functional role of behavioural flexibility, but also

95 about the functional role of the rules that govern behavioural flexibility, and the functional role of the

96 psychological mechanisms that implement such rules (McNamara and Houston 2009). According to

97 Castellano (2015), in the "evo-mecho" models, the optimality approach should still play a central role and

98 should be applied at all levels of analysis, in a way similar to that proposed by Marr's pioneering work in the

99 neurosciences (Marr 1982). In the present paper, I adopt this approach to study optimal decisions in

100 foraging. By focusing on the "diet model" (Stephens and Krebs 1986), I explore how this fundamental

101 model could be used to address multi-level functional questions on the computational mechanisms of

102 foraging decisions.

The model

103

104 Imagine an insect hovering above a meadow searching for nectar. While flying, it approaches a brightly

105 yellow flower, which captures its attention. The insect begins to collect sensory information about the

106 prospective source of food and, after a while, it lands on the flower and starts foraging. The insect decides

107 to exploit the flower because it recognizes it as a worthy source of food, and it does so because it has a

108 cognitive machinery that is adapted to process noisy sensory information effectively and to provide

109 economically valuable decisions.

110 To model the insect's cognitive machinery of decision making, I adopt the approach suggested by Marr

111 (1982) and analyse the information-processing system at two distinct levels: (i) at the computational-theory

112 level, by responding to the questions of 'what is being computed' and 'why the computation is carried out'

113 and (ii) at the algorithm level, by addressing the questions of 'how information is represented' and 'which

114 algorithms are used'.

115 **THE COMPUTATIONAL-THEORY LEVEL**

116 To understand what type of computation the insect should carry out in order to maximize its long-term

117 fitness benefits, I first make the following assumptions: (i) during foraging, the insect encounters N flowers,

118 sequentially, each flower is a potential resource, that is, an item that can be exploited by the insect (notice

119 that throughout the paper, I use "resource" and "item" as synonyms) ; (ii) searching and exploiting are

120 mutually exclusive; (iii) the optimal decision rule depends only on the economic values of the available

121 resources and it is independent of both the state of the foraging insect and of the predation risk it faces

122 when foraging.

123 Let us assume that the N items are randomly distributed in the foraging patch. Let s be the average

124 searching time and T_s the total searching time ($T_s = N\bar{s}$). The economic value of an item i is assumed to

125 depend on two attributes (Stephens and Krebs 1986): h_i, its expected handling, and q_i, its expected net

126 energy*,* if the insect decided to exploit the item *i.* Natural selection is assumed to favour the evolution of

127 decision rules that maximize the rate of net energy intake:

128

129 $$W = \frac{\sum_i^N p_i q_i - \gamma T_s}{T_s + \sum_i^N p_i h_i},$$ (Eq. 1)

130

131 where p_i is the probability that the item *i* is exploited (Stephens and Krebs, 1986), and γ is the cost of

132 search per unit time. OFT shows that, within the set of the *N* available resources, the probability p_i must be

133 either 0 (rejection) or 1 (acceptance).

134 Let the *N* resources be ranked by their "profitability" such that $\frac{q_1}{h_1} > \frac{q_2}{h_2} > \cdots > \frac{q_r}{h_r} > \cdots > \frac{q_N}{h_N}$. When the

135 insect adopts, as a decision rule, the threshold $\left(\theta_{OFT}^k\right)$, it is expected to exploit only the first *k* items of the

136 list and to reject the others. In this case, the expected rate of energy intake is:

137 $$W(k) = \frac{\sum_r^k q_r - \gamma T_s}{T_s + \sum_r^k h_r}.$$ (Eq. 2)

138 Natural selection is expected to favour the evolution of a decision rule that maximizes *W*. Suppose the

139 insect knew the maximum rate of energy intake in a given environment (W^*). In this case, the optimal

140 decision rule would be to exploit only those items with profitability (q_r/h_r) equal to or higher than

141 $\theta_{OFT}^* = W^*$ (Stephens and Krebs 1986). In the real world, however, two problems are likely to reduce the

142 effectiveness of foraging decisions. The first problem is uncertainty. When the insect evaluates an item, the

143 sensory information it processes is prone to error. The insect can reduce error and improve accuracy by

144 processing several independent pieces of information. But this requires time and an increase in the

145 assessment time inevitably reduces the rate of energy intake. For this reason, to make optimal decisions,

146 the insect should be able to control not only the decision threshold, but also the decision time. How can it

147 do this? The second problem is flexibility. Since the optimal decision threshold (θ_{OFT}^*) depends on the

148 entire set of the available resources, which varies over time and space, the insect should be able to adjust

149 the threshold to the local conditions. How can it do this?

150 To answer to the questions of uncertainty and flexibility, I impose two constraints on the decision model.

151 The first is the inevitability of uncertainty. This means that when the insect is evaluating the *i* item, with

152 quality q_i and handing time h_i, the sensory information it receives is described by the stochastic variables

153     $Q_i = q_i(1 + \varepsilon_q)$ and $H_i = h_i(1 + \varepsilon_h)$, where ϵ_q and ϵ_h are two normally distributed stochastic variables

154   with zero mean, zero covariance, and ${\sigma_q}^2$ and ${\sigma_h}^2$ variances. The second constraint concerns what the

155   insect "knows" about the available resources. As mentioned above, OFT assumes that animals "know" the

156   optimal threshold, which depends on the position of each resource along the ordinal scale of profitability.

157   This means that when the insect visits a new habitat with unknown resource distribution, to adjust its

158   decision threshold, it should acquire information on the entire new set of the available resources. To

159   provide flexibility to the decision rules, I assume the insect to adjust the decision threshold on the basis of

160   three, easily assessable descriptors of the distribution of both profitable and unprofitable resources: the

161   average quality ($\bar{q}$), the average handling time ($\bar{h}$), and the average searching time ($\bar{s}$).

162   Suppose the insect encounters a random sequence of the prospective resources 1, 2, …, N, with quality q_1,

163   q_2…, q_N and handling time h_1, h_2…, h_N. Given the available information, I assume that the insect exploits the

164   resource i if the following inequality is true:

165     $$\frac{E[Q_i]}{E[H_i]} > \frac{\bar{q} - \gamma \bar{s}}{\bar{s} + \bar{h}}. \qquad\qquad\qquad\qquad\qquad \text{(Eq. 3)}$$

166   On the left-hand side of the inequality, there is the expected rate of energy intake (profitability) if the

167   insect decided to exploit the i item. On the right-hand side, there is the expected rate of energy intake if it

168   decided NOT to exploit the i item (i.e. the opportunity costs): the numerator is the expected quality of the

169   next-encountered (i+1) item (that is, the average quality $\bar{q}$), discounted by the costs of finding it, the

170   denominator is the expected time needed to find ($\bar{s}$) and to handle ($\bar{h}$) the next encountered item.

171   **THE REPRESENTATION-ALGORITHM LEVEL**

172   To model the decision process at the algorithmic level, we need to make some biologically plausible

173   assumptions about two issues. The first is about how information is handled and internally represented by

174   the cognitive machinery of decision making. The second issue is about uncertainty. Since sensory

175   information is uncertain and prone to error, how can the cognitive machinery integrates independent

176   pieces of information over time to increase reliability?

177   I start with the representation issue. In Eq. 2 and Eq. 3, the variables involved in the decision process are

178   expressed in Watts (Joules/s). This follows the assumptions that the rate of the long-term energy intake is

179   what natural selection maximizes and that the rate is also the criterion to compare the efficacy of

180   alternative decision strategies. Although the ultimate function of the decision process is to maximize rates

181   of energy intake, I assume that the algorithm of decision making is not based on a comparison of rates and

182   that benefits and costs are internally represented in terms of relative differences between perceived and

183   expected values of energy and time. By defining $\tilde{q} = \bar{q} - \gamma\bar{s}$ and by using simple algebra, Eqn. 3 can be

184   rearranged in the equivalent form of Eqn. 4, which shows, on the left hand side, the relative difference

185   between the perceived and the expected value of a resource, whereas, on the right hand side, it shows the

186   relative difference between the perceived handling time of the inspected resource and the expected time

187   to find and handle another resource (see also the supplementary materials for more details):

188
$$E\left[\frac{Q_i - \tilde{q}}{\tilde{q}}\right] > E\left[\frac{H_i - (\bar{s} + \bar{h})}{\bar{s} + \bar{h}}\right]. \qquad\qquad \text{(Eq. 4)}$$

189   I assume that, when the insect assesses the value of a resource *i*, it sequentially collects several pieces of

190   sensory information relative to the energetic quality $(Q_i(1), Q_i(2) \ldots Q_i(\vartheta))$ and the handling time

191     $(H_i(1), H_i(2) \ldots H_i(\vartheta))$ of the resource,. Each piece of information $Q_i(j)$ and $H_i(j)$ is then converted, by

192   two linear filters into a context-dependent representation of the energetic benefits $\left(B_i(j) = \frac{Q_i(j) - \bar{q}}{\bar{q}}\right)$ and

193   opportunity costs $\left(C_i(j) = \frac{H_i(j) - (\bar{s} + \bar{h})}{\bar{s} + \bar{h}}\right)$. The insect perceives as "useful" a resource if $E[B_i] > E[C_i]$, that

194   is, if its benefits are greater than its costs.

195   As mentioned above, since sensory information is noisy, the insect is expected to integrate several pieces of

196   information to obtain a reliable evaluation of benefits and costs. My next assumption is thus about how

197   such an integration is carried out. Specifically, I consider two computational mechanisms.

198   The first, is the one-dimension-static-sampling model of decision making (1-DSS). The mechanism (Fig. 1a)

199   views decisions as the outcome of a three-step process: deliberation, commitment, and motor response. In

200   terms of abstract neural computation, the model can be described as a three-layer neural circuit. The first

201   layer is composed by two neural modules, the *b-* and *c*-module, which linearly transform sensory

202   information into the perceived benefits $(B = b(Q))$ and costs $(C = c(H))$. The pieces of sensory

203   information are then sent to a second-layer module (*U*), which integrates them over time: the input from

204   the *b*-module increases the neural activity of *U*, whereas the input from the *c*-module decreases the neural

205   activity of *U*. The number of pieces of information (J_{max}) and the decision time ($\vartheta = J_{max}/\tau$, where τ is the

206   rate at which information is collected) are fixed and independent of the value of the resource. Once all the

207   pieces of sensory information have been collected, the neural activity of the *U* module will be proportional

208   to the difference between the perceived benefits and costs of an item and, thus, *U* is the internal

209   representation of its economic value, which I call "utility":

210    $$U_i = \sum_j^{J_{max}} B_i(j) - \sum_j^{J_{max}} C_i(j). \qquad \text{(Eqn. 5)}$$

211   U_i is a stochastic variable with expectation $E[u_i] = J_{max}\left(\frac{q_i}{\tilde{q}} - \frac{h_i}{(\bar{h} + \bar{s})}\right)$ and with variance

212    $Var[u_i] = J_{max}\left(\frac{{\sigma_q}^2}{\tilde{q}^2} + \frac{{\sigma_h}^2}{(\bar{s} + \bar{h})^2}\right)$ (Fig. 2a,b). The coefficient of variation of *u* (the ratio between

213   its standard deviation and mean) decreases with J_{max} and the accuracy of decisions increases.

214   The second step of the decision process is commitment. It involves a third-layer of gate-neurons, which

215   compare *U* with an internal standard θ: if $U \geq \theta$, then the resource is accepted; if $U < \theta$, it is rejected. The

216   third and final step of the decision process is action: once the decision is made, the insect prepares and

217   carries out the appropriate motor response to accomplish the established goal. In the 1-DSS, decision time

218   is fixed and cannot be flexibly adjusted to the difficulty of choice. If the insect has evolved such a static

219   decision mechanism, it is expected to spend the same amount of decision time independent of the quality

220   of the resource being inspected.

221   The second model I consider belongs to the class of sequential sampling models (reviewed by Bogacz et al.

222   2006), which views decisions as the accumulation over time of noisy information that lasts until evidence is

223   so strong that it crosses a pre-defined threshold. In the sequential sampling models, the number of samples

224   (and the decision time) is not fixed, but it depends on the items under assessment. I call the second model

225   the "2-Dimension Sequential Sampling" model of decision making (2-DRW), because it no longer assumes

226   that the insect makes a 1-dimension internal representation of the resource economic value, rather, that it

227   integrates information of benefits and costs independently into the two neural modules, the *b*- and the *c*-

228   module, as described by the following recursive equations:

229
$$\begin{cases} B_i(j) = B_{i,}(j-1) + \frac{Q_i(j)-\tilde{q}}{\tilde{q}} \\ C_i(j) = C_i(j-1) + \frac{H_i(j)-(\bar{h}+\bar{s})}{\bar{h}+\bar{s}} \end{cases}.$$
(Eq. 6)

230   The 2-DRW considers that the *b*- and the *c*-module have lower ($\theta_B^l = f(C), \theta_C^l = f(B)$) and upper ($\theta_B^u =$

231    $f(C), \theta_C^u = f(B)$) thresholds, which are described by the following set of equations:

232
$$\begin{aligned} \theta_B^u &= T + C_i \\ \theta_C^l &= -T + B_i \\ \theta_B^l &= -L + C_i \\ \theta_C^u &= L + B_i \end{aligned}.$$
(Eq. 7)

233   Where *T* and *L* are parameters of the model and represent the thresholds for either the acceptance or the

234   rejection when no information has been yet acquired. Mathematically speaking, the 2-DRW describes a

235   random walk in the Cartesian plane defined by the *C* and *B* axes (Fig. 2c, d). After processing the first piece

236   of information of the item *i*, the random walk reaches the point [*C$_i$(1)*, *B$_i$(1)*]. At this stage, the acceptance

237   thresholds are $\theta_C^l(1) = -T + B_i(1)$ and $\theta_B^u(1) = T + C_i(1)$, whereas the rejection thresholds are $\theta_C^u(1) =$

238    $L + B_i(1)$ and $\theta_B^l(1) = -L + C_i(1)$. The acceptance and the rejection thresholds define two consensus

239   areas, one for the acceptance (where both $x \le \theta_C^l(1)$ AND $y \ge \theta_B^u(1)$) and one for the rejection of the

240   resource (where both $x \ge \theta_C^u(1)$ AND $y \le \theta_B^l(1)$). If the random walk falls into one of these areas, then

241   the assessment terminates and the choice is made, otherwise a new piece of information is collected.

242   Suppose now that the item is indeed useful and, thus, that the amount of evidence for the benefits

243   increases faster than the amount of evidence for the costs. The random walk and the acceptance-

244   consensus area move closer to each other and, after *j* pieces of information, they eventually converge to a

245   point on the threshold line $y = T + x$, where $\theta_C^l(j) = -T + B_i$ and $\theta_B^u(j) = T + C_i(j)$. At this exact

246   moment, the decision is made and the resource is chosen (see also the IPython Notebook in the

247   supplementary materials). *T* and *L* directly affects decision time and, thus, the speed-accuracy trade-off in

248   decision making. If the insect sets the thresholds close to zero, decisions will be quick, but inaccurate. In

249   contrast, if it sets the thresholds far from zero, decisions will be slow, but much more accurate.

250 It must be noticed that the 2-DRW can be converted into a one-dimension random walk by rotating the

251 axes clockwise by 45° with respect to the origin, so that the decision thresholds are parallel to the rotated

252 y-axis. The x-coordinates of the rotated random-walk are $\frac{B_i(j)+C_i(j)}{\sqrt{2}}$, whereas the y-coordinates are

253 $\frac{B_i(j)-C_i(j)}{\sqrt{2}}$. Since displacements along the x-axis do not affect decision time, the dynamics of the decision

254 process can be described as the bounded random walk $U(j) = U(j) + (B(j) - C(j))/\sqrt{2}$, with decision

255 thresholds $T' = T/\sqrt{2}$ and $L' = L/\sqrt{2}$. While the one- and the two-dimension decision mechanisms are

256 equivalent in terms of computational efficiency (the $\sqrt{2}$ parameter is a scale factor and has no effects on

257 decision time), they are not equivalent in biological terms. In fact, the one-dimension random walk

258 mechanism requires an additional neural layer (U) for integrating benefits and costs and, thus, it is "neuro-

259 anatomically" less efficient than the 2-DRW (Fig. 1).

260 **OPTIMAL DECISION STRATEGIES**

261 I define with *S* the decision strategy of the foraging insect. In the 1-DSS model, *S* depends on the decision

262 threshold θ and on the decision time τ, which is independent of the resource qualities, $S = s(\theta, \tau)$. In

263 contrast, in the 2-DRW, the insect controls the decision time only indirectly, by adjusting the two decision

264 thresholds. For this reason, decision time is no longer fixed, but it depends on the qualities of the resources

265 and on the thresholds. The decision strategy is thus a function of the two decision thresholds (see Eqn. 7):

266 $S = s(T, L)$.

267 Let *P* be the probability that the foraging insect exploited a resource. *P* is a function of both *S* and the

268 characteristics of the resource (i.e. $P = p(S, q, h)$). Let *A* and *R* be the decision time, respectively, to accept

269 and to reject an option. Since the sensory information is acquired at a constant rate, *A* and *R* are

270 proportional to the number of pieces of information used to make decision. In the 1-DSS, *A* and *R* depend

271 on the decision strategy and have the same value ϑ independent of the resource being assessed. In

272 contrast, in the 2-DRW, *A* and *R* are a function of *S*, *q*, and *h* (i.e. $A = a(S, q, h)$, $R = r(S, q, h)$).

273 I define with $W(S)$ the fitness benefits of a decision strategy. I assume that during its daily foraging activity,

274 the insect inspects *N* items. Each item *i* is fully described by its attributes q_i and h_i. For the sake of

275 simplicity, I also assume that q and h are statistically independent of each other. $W(S)$ is the ratio between

the total caloric intake and the total foraging time (i.e. the time spent for searching, handling, and for

deciding either to or not to exploit a resource). The expected fitness of both the 1-DSS and 2-DRW is

derived from Eqn. 1:

$$W\big(S(\theta,\tau)\big) = \frac{\sum_i^N p(S,q_i,h_i)\cdot q_i - \gamma\cdot N\cdot\bar{s}}{N\cdot(\bar{s}+\tau)+\sum_i^N p(S,q_i,h_j)\cdot h(j)}, \qquad\qquad \text{(Eq. 8a)}$$

$$W\big(S(T,L)\big) = \frac{\sum_i^N p(S,q_i,h_i)\cdot q_i - \gamma\cdot N\cdot\acute{s}}{N\cdot\bar{s}+\sum_i^N\big[p(S,q_i,h_i)\cdot(a(S,q_i,h_i)+h_i)+(1-p(S,q_i,h_i))\cdot r(S,q_i,h_i)\big]} \qquad \text{(Eq. 8b)}$$

The optimal strategy, S^*, is the one that maximizes $W(S)$, so that $W(S^*) > W(S)$ for all possible decision

strategies.

SOLUTION PROCEDURE

The optimal solutions were derived numerically. In order to compute choice probabilities and acceptance

and rejection decision times, for each type of resource, I run 5000 random-walk simulations, each with a

maximum number of time steps J_{max}. This set of simulations was used to compute the optimal decision

strategy and the expected maximum rate of energy intake for both the 1-DSS and 2-DRW.

To find the optimal 1-DSS strategy, I first created a list of evenly spaced threshold values

$(\theta = [\theta_1, \theta_2 \dots \theta_{max}])$ and decision times $(\tau = [\tau_1, \tau_2 \dots \tau_{max}])$, which define the set of feasible strategies

to be optimised. Then, for each threshold in θ, for each time in ϑ, and for each type of resource i, I

computed the choice probability $P(i,\theta,\tau) = p(S(\theta,\tau), q_i, h_i)$ as the frequency of random-walk

simulations with $U_i \geq \theta$. The P values were used in the Eq. 8a to calculate $W(S)$ and derive $W(S^*)$.

To find the optimal 2-DRW strategy, I created not one, but two lists of evenly spaced thresholds: the list of

acceptance thresholds $(T = [T_1, T_2 \dots T_{max}])$, with $0 \leq T_j \leq T_{max}$, and the list of rejection thresholds

$(L = [L_1, L_2 \dots L_{max}])$, with $0 \leq L_j \leq L_{max}$. For all possible combinations of T and L, I computed the

relative frequencies of simulations that reached the acceptance threshold T_j and I assumed them to be

equivalent to the choice probabilities $P(T_j, L_k, i) = p(S(T_j, L_k), q_i, h_i)$. I further assumed that the rejection

probabilities was $1 - P$ and thus that absence of evidence to support acceptance was evidence to support

rejection. For each simulation, I also computed either the acceptance or the rejection time and averaged

300   them over the 5000 simulations to obtain, respectively $a\big(S(T_j, L_k), q_i, h_j\big)$ and $r\big(S(T_j, L_k), q_i, h_j\big)$ to be

301   used in Eqn. 8b.

Results

303   OFT assumes information to be complete and free of errors and costs. My model has been designed to

304   investigate what happens when these implausible assumptions are relaxed. To this purpose, I had to

305   impose some constraints on the model and to make specific assumptions on how information is internally

306   represented and processed. The first question that I address, thus, is about the effects of these

307   assumptions. Specifically, I ask how the assumed representation affects the ranking of resource profitability

308   and the ability to discriminate between profitable and unprofitable items.

309   In Figure 3 and 4, I analyse the relationship between profitability (q_i/h_i) and utility $(B_i - C_i)$ under two

310   different foraging conditions. The energetic quality (q) and the handling time (h) were generated from two

311   independent, random, uniform distributions (ranges: q = (100, 2000); h = (10, 200)). The profitability and

312   the utility of the items were computed by setting the mean searching time ($\bar{s}$) either equal to (Figure 3, $\bar{s} \cong$

313     $\bar{h}$) or much lower than the mean handling time (Figure 4, $\bar{s} \cong 0.2\bar{h}$). I used Eqn. 2 and Eqn. 4 to discriminate

314   between acceptable and unacceptable items according to the criteria of profitability (vertical lines) and

315   utility (horizontal lines). The two thresholds divide the plane in four regions. (i) In the top-left area, there

316   are the items that are perceived useful, but which are actually unprofitable. Since they will be erroneously

317   included in the diet, I call this region the area of false positives. (ii) In the bottom-right region, there are the

318   items that are profitable, but perceived as useless. This is the region of false negatives. (iii) The top-right

319   and (iv) the bottom-left regions include, respectively, the true positives (items that are both profitable and

320   useful) and the true negatives (items that are both unprofitable and useless). Although utility increases

321   monotonically with profitability, the ranking along the two ordinal scales differ markedly and the

322   differences increases at the extremes of the distributions. Profitability is a context independent property of

323   a resource, whereas utility depends on the average quality and on the average handling and searching time

324   of the entire sample of available resources. Moreover, independent of the context, utility often provides a

325   biased representation of profitability. In fact, two resources that differ in quality and handling time, but

326   that have the same profitability (i.e. $q_1/h_1 = 10/5$ and $q_2/h_2 = 100/50$) differ in their perceived utility,

327   because the item with the highest energetic quality (i.e. U_2 with $q_2 > q_1$) will always be of higher perceived

328   utility than the other.

329   Despite these marked differences, the utility and profitability representations may lead to very similar

330   foraging behaviours, in particular, when the environment favours unselective foraging strategies. In the

331   simulation of Figure 3, the optimal foraging strategy makes the insect to choose about 70% of the available

332   resources and reject the remaining 30% (i.e. moderate choosiness). In this case, no items fall into the false-

333   positive and false-negative regions (Figure 3a). Both the 1-DSS (Fig. 3b) and the 2-DRW (Fig. 3c) discriminate

334   accurately between profitable and unprofitable resources. When the environment favours choosiness,

335   however, the performance of both models decreases and discrimination becomes much less accurate.

336   Figure 4 shows results of a simulation that assumes a highly selective environment (where the searching

337   time is much shorter than the handling time). The OFT model predicts the insect to be much choosier than

338   before and to include in the diet only 40% of the available resources. Under these strong selective

339   conditions, many unprofitable items are perceived as useful (they reside in the false-positive region of Fig

340   4a) and the optimal decision strategy of both the 1-DSS (Fig. 4B) and 2-DRW (Fig. 4C) models provides a less

341   accurate discrimination between profitable and unprofitable items.

342   The next issue that I consider is performance. Specifically, I ask how the assumed internal representation of

343   benefits and costs (see Eqn. 3) affects the optimal energy intake predicted by the 1-DSS and the 2-DRW. I

344   compare the two models along a cline of resource density, from a high-density condition, where an

345   unselective insect would spend about than 10% of the total foraging time in searching (that is, when

346    $\bar{s}/(\bar{s} + \bar{h}) = 0.1$), to a low-density condition, where it would spend most of its foraging time in searching.

347   Figure 5 shows the optimal performance predicted by the 1-DSS, by the 2-DRW and by the no-choice

348   strategy (when all the resources are exploited indiscriminately). For each decision model and

349   environmental condition, I calculated the optimal rate of energy intake and divided it by W_{OFT} , the

350 optimal rate predicted by Eqn. 2, under the unrealistic assumptions that foraging decisions were always

351 correct and that decision time was always negligible. These ratios were used as a measure of the relative

352 efficiency of the decision strategy. When the percentage of searching time increases, the relative efficiency

353 of all decision strategies increases as well. The efficiency will reach its maximum when the high searching

354 costs will make all items profitable. The reason of this becomes clear when we consider the expected

355 benefits and costs (Eqn.5). An increase in searching time reduces the average quality of the resources ($\bar{q} -$

356 $c\bar{s}$) and thus increases the expected benefits of the item that is being assessed, $(q_i - \bar{q} + c\bar{s})/(\bar{q} - c\bar{s})$.

357 Moreover, the increase in searching time, by reducing the average encounter rate, reduces also the

358 opportunity costs of a resource. As a consequence, the portion of useful items (for which benefits

359 overcome costs) tends to increase with increasing searching time. While this trend is evident in both 1-DSS

360 and 2-DRW, their patterns are slightly different. For very short searching time, 1-DSS and 2-DRW show

361 similar efficiency, but 1-DSS becomes less efficient than 2-DRW when searching time increases. Wald and

362 Wolfowitz (1948) demonstrated that, among all the sample decision methods, the sequential tests are the

363 most efficient, because they minimize random error rates with respect to the number of samples used. At

364 low searching time, however, we have seen that a benefit-cost representation introduces a systematic

365 error that increases the risk of false positives (Fig 4a). The effect of this bias increases with the decreasing

366 of uncertainty in decision making (that is, with the decreasing of random errors). For this reason, in the

367 absence of representation biases, the 2-DRW is (slightly) more efficient than the 1-DSS, because it needs

368 less time to make similarly accurate decisions. But when representation biases are present (i.e. at low

369 searching times, when the risk of false-positive errors is high), the higher precision of the 2-DRW (i.e. the

370 ability to control random errors) plays against its ability to make accurate decisions and both models

371 perform in a similar way.

372 So far, I have emphasized the differences between the 1-DSS and the 2-DRW. These differences in

373 performance, however, are admittedly small and one may ask whether selection can discriminate between

374 the mechanisms. From a computational point of view, in fact, the models implement two different

375 algorithms that both provide a "satisfactory" and flexible solution to the problem of optimal foraging.

376   Figure 6 shows how such flexible solutions are attained. When the resource density is high and the

377   proportion of searching time is low, the decision thresholds are asymmetrically distributed to control for

378   the high risk of false positives (Fig. 6a). Nevertheless, under these conditions, false positives are still more

379   likely than false negatives (Fig. 6b), probably because of the "utility bias", which overestimates profitability

380   when resources are abundant. When the same type of resources are dispersed over a larger area, the

381   searching time increases and the opportunity costs decreases. Since the expected benefits do not change,

382   the increase of searching time causes an increase of the proportion of profitable resources and,

383   consequently, a decrease of the risk of false positives. In these cases, the acceptance decision threshold of

384   both models is predicted to decrease. In 1-DSS, it converges to zero, whereas in 2-DRW it is positive, but

385   lower (in absolute terms) than the rejection threshold. The decreased asymmetry of the decision

386   thresholds reduces the false-positive bias, which is, however, eliminated (1-DSS) or even slightly inverted

387   (2-DRW) only when resource densities are very low (i.e. for proportion of searching time larger than 50%).

388   With increasing searching time, 1-DSS model predicts no marked differences in decision time (Fig. 6c). In

389   contrast, 2-DRW predicts an increase in decision time when the proportion of searching time decreases and

390   most of the resources become unprofitable. In fact, in these selective environments, to avoid the high

391   opportunity costs of false-positive decisions, the insect must assess expected benefits and costs accurately.

392   **Discussion**

393   "Evo-mecho" models (McNamara and Houston 2009) aim at integrating the functional and the mechanistic

394   approach in the study of animal behaviour. Castellano (2015) argues that the success of this research

395   program will largely depend on its capacity to incorporate a coherent body of theory, which can guide the

396   empirical research. By adopting the "evo-mecho" perspective in the study of mating decisions, Castellano

397   (2015) presents a 2-steps approach, which aims at identifying, first, the optimal computational mechanism

398   and, then, the algorithm that can implement it. These two steps correspond to the first two levels of

399   analysis in the Marr's (1982) neuroscience research program. In the present paper, I extend the 2-steps,

400   "evo-mecho" approach to the investigation of the mechanisms of foraging decisions. In the complex

401 hierarchy of foraging choices (Stephens 2008), my model focuses on the most basic decision, that is,

402 whether an encountered resource should be exploited or dismissed in favour of searching for the next,

403 hopefully better item. The functional aspects of this decision have been thoroughly investigated by the

404 classic "diet model" of the optimal foraging theory (Stephens and Krebs 1986). My model can thus be

405 viewed as a mechanistic version of this classic model. Although some of the simplifying assumptions of the

406 "diet model" might appear to constrain the reliability of its predictions (Sih and Christensen 2001), I will

407 argue that they are nevertheless instrumental to the "evo-mecho" approach. In fact, the assumptions of

408 the functional models define the type of information, but not how this information is processed. For

409 example, my "evo-mecho" model shares with the "diet model" the assumption that neither the forager's

410 state nor the predation risk play a role in foraging decisions. To study the effect of predation and condition,

411 these simplifying assumptions should be relaxed and a new fitness function should be defined (see for

412 example Brown 1992; Clark and Dukas 1994). In this new model, the type of information used to define

413 costs and benefits would change, but the computational mechanisms of decision making might remain the

414 same.

415 The "diet model" defines the "computational theory" of foraging decisions, in that it deals with the abstract

416 computations that maximize the fitness of decision makers, expressed as the long-term rate of energy

417 intake. In contrast, the 1-DSS and the 2-DRW define the theory of computational mechanisms, in that they

418 focus on the algorithms used to process sensory information and to make decision. The "diet model"

419 assumes that the sensory information about the quality of items is converted into an internal

420 representation of their profitability, the rate of net energy intake (q/h). From this assumption it derives that

421 the economic value is an intrinsic, context-independent attribute of the items. For example, variation in the

422 relative abundance of items has no effect on their perceived profitability, but only on the decision rules

423 (that is, the decision thresholds). In contrast, both the 1-DSS and the 2-DRW assume that the perceived

424 value of items is context-dependent and, thus, that choice variation can be the consequence not only of

425 flexible decision rules, but also of the flexible use of sensory information. Specifically, the two models

426 assume that sensory information about the energetic value and handling time of a resource is processed in

427   a parallel fashion and converted into two context-dependent representations of benefits and costs.

428   Benefits are the relative difference between the observed and expected energetic value of a resource.

429   Costs are the loss of opportunity, measured as the relative difference between the observed and expected

430   exploitation time. Such a representation of the item economic value is what provides flexibility to the

431   decision mechanism. Suppose, in fact, that the foraging insect moves to a new environment, where the

432   resources are more abundant than before. By direct experience, the insect can adjust its expectations and

433   modify its choice: what in the previous environment was perceived as a profitable resource because it had

434   a larger-than-average energetic income, now it is perceived as unprofitable because it falls below the

435   average. In both environments the decision rule may remain the same, but the foraging behaviour changes.

436   Expected benefits and costs are not abstract concepts invented by theoreticians to provide a formal

437   description of complex decision processes. In recent years, in fact, several neuro-economics studies have

438   been providing convincing evidence for their biological role (review in Glimcher 2011): humans, for

439   example, have physically distinct neural representations of expected benefits (in the pre-frontal cortex) and

440   expected costs (in the cingulate cortex) (Grabenhorst and Rolls 2011).

441   When the "cost-benefit" and the "profitability" representations are compared, some discrepancies emerge.

442   When resources are abundant and the optimal decision strategy is highly selective (that is, when less than

443   50% of the available resources are included in the optimal diet), the cost-benefit representation tends to

444   over-estimate the values of resources and makes the insect to exploit items that should have been avoided.

445   As a consequence, the maximum rate of net energy intake that can be attained by adopting this type of

446   representation is much lower than that predicted by the more efficient, but biologically less plausible

447   representation of profitability. Furthermore, independent of the relative abundance of resources, the cost-

448   benefit representation tends to weigh proportionally more the benefits than the costs: for example, the

449   profitability representation predicts that two items that have the same rate of energy intake, but differ in

450   their energy value and handling time, will be perceived as having the same economic value. In contrast, the

451   cost-benefit representation predicts that the item with larger energetic value and longer handling time will

452   be perceived of higher economic value than the other. Both these predictions can be experimentally tested

453   and the results may provide useful insights into the information processing mechanisms of decision making.

454   A theory of computational mechanisms must specify not only the type of representation, but also the

455   algorithm used to process information. As for representation, also in this case there may be several

456   possible solutions. Indeed, many researchers in decision science assume that natural selection has provided

457   decision makers with a toolbox of heuristics each performing optimally (or satisfactory) in different

458   contexts (Goldstein and Gigerenzer 2002). These rules and their implementing algorithms are often viewed

459   as evolutionarily independent traits, which can be easily adjusted or ex-novo created by natural selection in

460   response to new challenges. But the algorithms in the brain are not like the list of commands in a computer

461   script. They have a physical and anatomical reality and new anatomical structures usually do not evolve ex-

462   novo, but from the modifications of ancestral traits (Cisek and Pastor-Bernier 2014). In accordance with this

463   parsimonious idea of evolution, the 1-DSS and 2-DRW are actually two variants of the same general

464   mechanism of information processing, which integrates over time independent pieces of information to

465   reduce uncertainty. Despite the similarity, the two models show two important differences with respect to

466   decision time and to the dimensionality of the decision space.

467   As it concerns decision time, the 1-DSS, a variant of signal-detection models (e.g. Green and Sweet 1966,

468   Stephens 2007, Wiley 1994, 2006), assumes decision time to be context independent and under the direct

469   control of the decision maker (see Abbott and Sherratt 2013), while the 2-DRW assumes decision time to

470   be context dependent and only indirectly controlled by the decision maker. The 2-DRW belongs to the

471   category of sequential-sampling models, which were first developed by cognitive psychologists (review in

472   Busemeyer and Townsend 1993, Bogacz et al. 2006, Ratcliff et al. 2016) and then used by neuroscientists to

473   model the neuronal mechanisms of decision making (Gold and Shadlen 2001, 2007, Churchland et al. 2008).

474   In these models, decision time depends on both the quality of the item being assessed and the threshold

475   adopted to make decisions. Bogacz et al. (2006) showed that, in terms of decision time, the performance of

476   these models approximates that of the Sequential Probability Ratio Tests (SPRT, Wald 1945), which is

477   computationally optimal, because, for a given error rate, it provides the fastest response (i.e. lowest

478 decision time) (McNamara et al. 2009). To compare the performance of the 1-DSS and the 2-DRW, I have

479 used the OFT as a benchmark. Specifically, I have described the relative efficiency of the two models as the

480 ratio between the maximum rate of energy intake predicted by these models and that predicted by the OFT

481 model. When the food is very abundant (i.e. when only 10% - 20% of foraging time is spent for searching),

482 both efficiencies are relatively low, because the risk of false positives is high and the cost-benefit

483 representation predisposes both models to make this error. When the abundance of food decreases, the

484 risk of false positives decreases as well, and the 2-DRW becomes slightly more efficient than the 1-DSS,

485 because it allows both faster and more accurate responses.

486 Besides decision time, the 1-DSS and the 2-DRW differ in the way costs and benefits are used to make

487 decisions. The 1-DSS assumes that the decision maker integrates the perceived benefits and costs into a

488 single decision variable, which represents the subjective utility of the resource (sensu Savage 1954). In

489 contrast, the 2-DRW supports a novel interpretation of the decision process. According to this view, sensory

490 information is supposed to "influence" rather than to "inform" decision makers (Rendall et al. 2009).

491 Decisions are not based on the internal representation of abstract values, but of action opportunities that

492 compete against each other for execution (Cisek 2007, Cisek and Pastor-Bernier 2014): exploitation is

493 supported by the accumulating evidence of benefits, exploration by the accumulating evidence of handling

494 costs. The perceived benefits and costs can be viewed as two independent decision variables or, in

495 geometrical terms, as the two axes of a multi-dimension decision plane. The assumption that alternative

496 options are ordered along an ordinal scale of expected utilities implies that animals are rational decision

497 makers and that their behaviours obey to the principles of transitivity (if A is preferred over B, and B over C,

498 then A should be preferred over C) and independence (if A is preferred over B in the absence of C, A should

499 be preferred over B also in the presence of C). By relaxing this assumption, we could develop new models

500 of decision making, which help us to understand why animals (and humans as well) behave irrationally,

501 when they are expected to do it, and which are the computational mechanisms underlying the cognitive

502 biases responsible for irrational behaviours. In the process, these models could also provide insights into

503 the unsolved question of the evolutionary significance of irrational behaviours (Houston et al. 2007,

504 Trimmer 2013, McNamara et al. 2014). In the present paper, the 2-DRW has been used to model one-

505 choice decisions, that is, decisions between alternative actions in response to a single option. The same

506 decision mechanism, however, can be used in multiple-choice contexts, that is, to model choice among

507 alternative actions in response to multiple options. While in one-choice context, the 2-DRW predicts

508 rational behaviours, it may no longer do it under multiple-choice contexts (Castellano 2019).

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605

606

FIGURE CAPTIONS

608 **Figure 1**. Schematic representations of the neural circuits underlying (*a*) the one-dimension-static-sampling

609 model (1-DSS) and (*b*) the two-dimension random walk model (2-DRW) of decision making. Sensory

610 information about the energetic quality and the handling time of a resource is linearly transformed by,

611 respectively, the benefit (B) and the costs (C) neurons. In the 1-DSS, the B- and C-neurons are connected

612 with the U recursive neurons, which integrate information and accumulate neural activity for a fixed

613 assessment time. The neural activity of the U-neurons represents the decision variable and they provide an

614 internal representation of the economic value of the resource. Once assessment terminates the U

615 integrators activate the gate-neurons (triangles) controlling for the motor response: they elicit acceptance

616 if their neural stimulation is greater than a threshold value, they elicit rejection if it is below the threshold.

617 In the 2-DRW, U-neurons are missing and the B- and C-neurons play the role of recursive integrators.

618 Assessment has not a fixed duration, but it terminates as soon as the difference in the activity of B- and C-

619 neurons is greater than some pre-determined values (*T* for acceptance, *L* for rejection, Eqn 7). The

620 mechanism does not compute such difference, though it behaves as it did. Metaphorically speaking, the

621 mechanism resembles a cycling pursuit race. In this type of races, two cyclists start simultaneously from

622 opposite positions along the track and each of them rides as fast as he can to reach the opponent. The race

623 terminates when the difference between the distances covered by the faster and the slower riders equals

624 their starting distances. Similarly, in the 2-DRW, B- and C-neurons (the cyclists) accumulate independent

625 pieces of evidence over time, supporting either the acceptance (B) or the rejection (C) response. Due to

626 neural modulation, an increase in the B activity causes an increase of the C threshold, whereas an increase

627 of the C activity causes an increase of the B threshold. As in the pursuit race, If B increases faster than C, B

628 gets closer to its upper threshold and C to its lower threshold. When B will finally reach its upper threshold,

629 the difference between B and C will be exactly *T* (Eqn. 7). In contrast, if C increases faster than B, the upper

630 threshold of C will be reached and when this happens, the difference between C and B will be *L* (Eqn. 7).

631

632   **Figure 2**. A graphical representation of the one-dimension-static-sampling model (1-DSS) and the two-

633   dimension random walk model (2-DRW) of decision making. (a) The resources perceived utilities (U) are

634   assumed to be normally distributed. An optimal decision maker should choose to exploit only resources

635   with a positive value ("true" positives, green area) and avoid those with a negative value ("true" negatives,

636   red area). The frequency of valuable resources is always larger than that of invaluable resources and the

637   difference increases with the relative increase of searching time (see main text). (b) Since assessment is

638   prone to error, the perceived distributions of "true" negatives and of "true" positives approximate two

639   overlapping normal distributions. The probabilities of false-positives (red area) and false-negatives (green

640   area) depend on the decision threshold. (c) In the 2-DRW, the internal representation of resources is a

641   point in a 2-dimension plane, described by the costs and benefits axes. In this example, resources show a

642   bi-normal distribution. The optimal decision maker should exploit the resources above the B = C line (green

643   area) and avoid those below this line (red area). (d) Since assessment is uncertain (unsaturated red and

644   green areas), decision makers collect a sequence of sensory information over time. The decision process is

645   analogous to a random-walk (grey lines) in the two-dimension plane, bounded by an upper (green) and a

646   lower (red) threshold line. Decision is made as soon the random walk reaches one of the two thresholds

647   (i.e. the blue path).

648

649   **Figure 3**. (a) Profitability and perceived utilities of a sample of items, randomly selected from a population

650   with uniformly distributed energetic quality (q range: 10-2000 caloric units) and handling time (h range: 10-

651   200 time units), with average searching time of 100 time units, and with a cost of search per unit time, γ =

652   0.002. All profitable items (whose q/h was higher than the acceptance threshold predicted by the Optimal

653   Foraging Theory) show positive utilities (benefits minus costs). The profitability and utility representations

654   provides highly consistent choice criteria and no items falls either in the false-positive or false-negative

655   regions. (b) Choice probabilities of the 100 items predicted by the 1-DSS model of decision making. (c)

656   Choice probabilities predicted by the 2-DRW model of decision making.

657

Figure 4. (a) Profitability and perceived utility of the same 100 items of Figure 3, under a much shorter

average searching time ($\bar{s} = 20$ time units) . Some items, which are just below the profitable threshold

(θ_{OFT}), fall just above the benefit-cost threshold and are positively selected by the insect. (b) Choice

probability of the 100 items predicted by the Signal-detection-model (1-DSS). (c) Choice probabilities

predicted by the 2-Dimension-Dynamic Model (2-DRW) of decision making.

663

Figure 5. A comparison of the relative efficiency of the 1-DSS (red line) and the 2-DRW (black line) as a

function of the resource abundance (expressed as the percentage of the total foraging time spent in

searching). The relative efficiency is computed as the ratio between the predicted maximum rate of net

energy intake and that predicted by the optimal foraging theory (assuming no uncertainty and zero

decision time). The no-choice line (green line) shows the relative efficiency expected when all the available
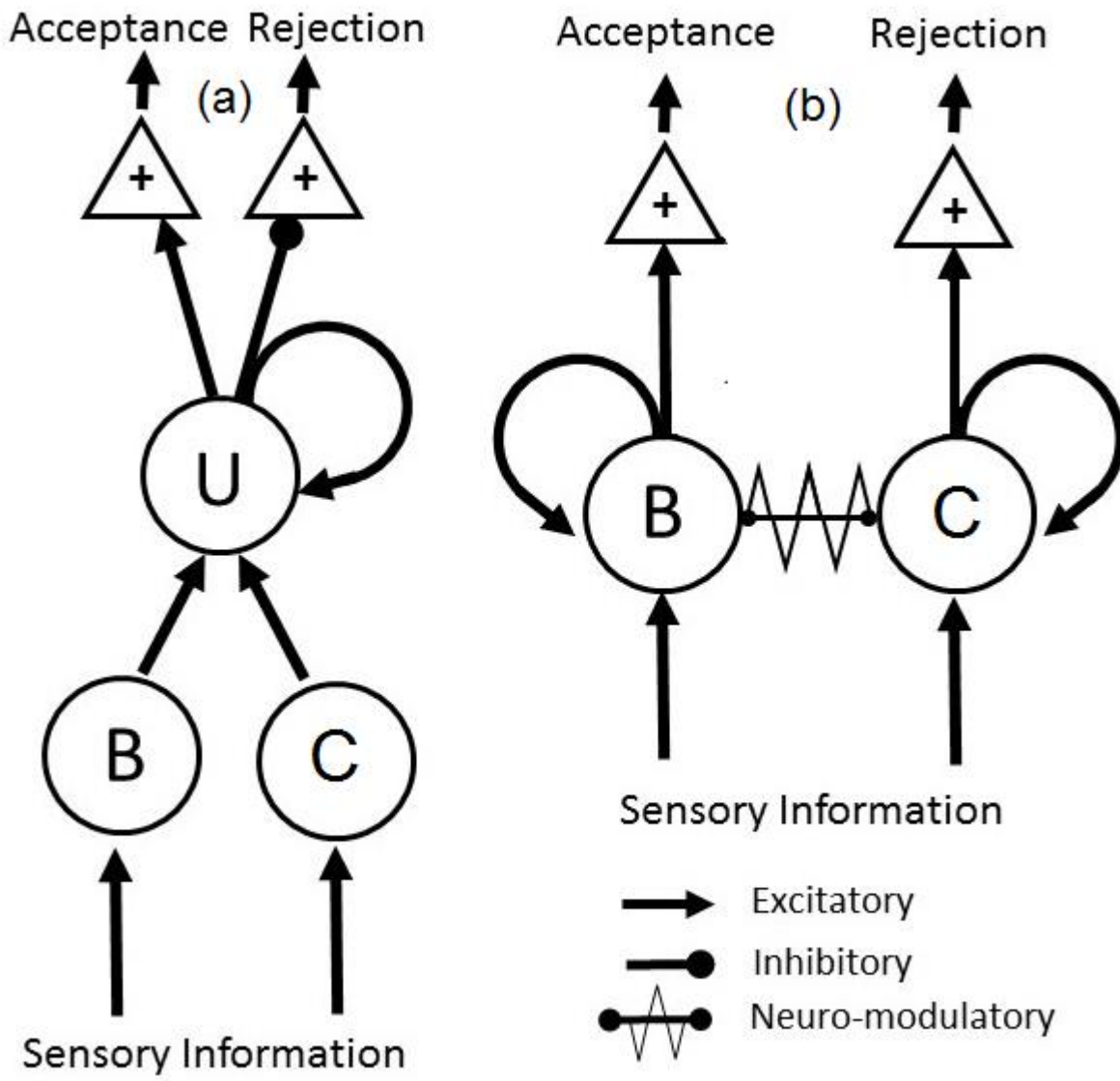
resources are indiscriminately exploited.

Figure 6. Optimal decisions rules under different relative searching times (%searching = $\bar{s}/(\bar{s} + \bar{h}) \cdot 100$).

(a) At low searching time, when the risk of false positives is much higher than the risk of false negatives, the

decision thresholds are strongly asymmetrical. In 1-DSS (red-filled squares), the threshold is positive and

converges to zero only for searching time longer than 50%. In the 2-DRW (black-filled squares), the

acceptance threshold is, in absolute, larger than the rejection threshold, but it becomes smaller when the

increase of searching time, by making most of the resources profitable, also increases the risk of false

negatives. (b) When searching is lower than 50%, false positives (solid lines) are more likely than false

negatives (dashed lines) in both the 2-DRW (black dots) and the 1-DSS (red squares). When searching time

increases, false positives and false negatives are equally likely (1-DDS) or false negatives are slightly more

likely than false positives (2-DRW). (c) In the 2-DRW (black dotted line), the insect is predicted to decrease

decision time when searching time increases, whereas, in the 1-DSS (red-square line), decision times is

681   independent of searching time. Vertical bars the standard errors. They have been computed by replicating

682   100 times the entire sets of simulations.
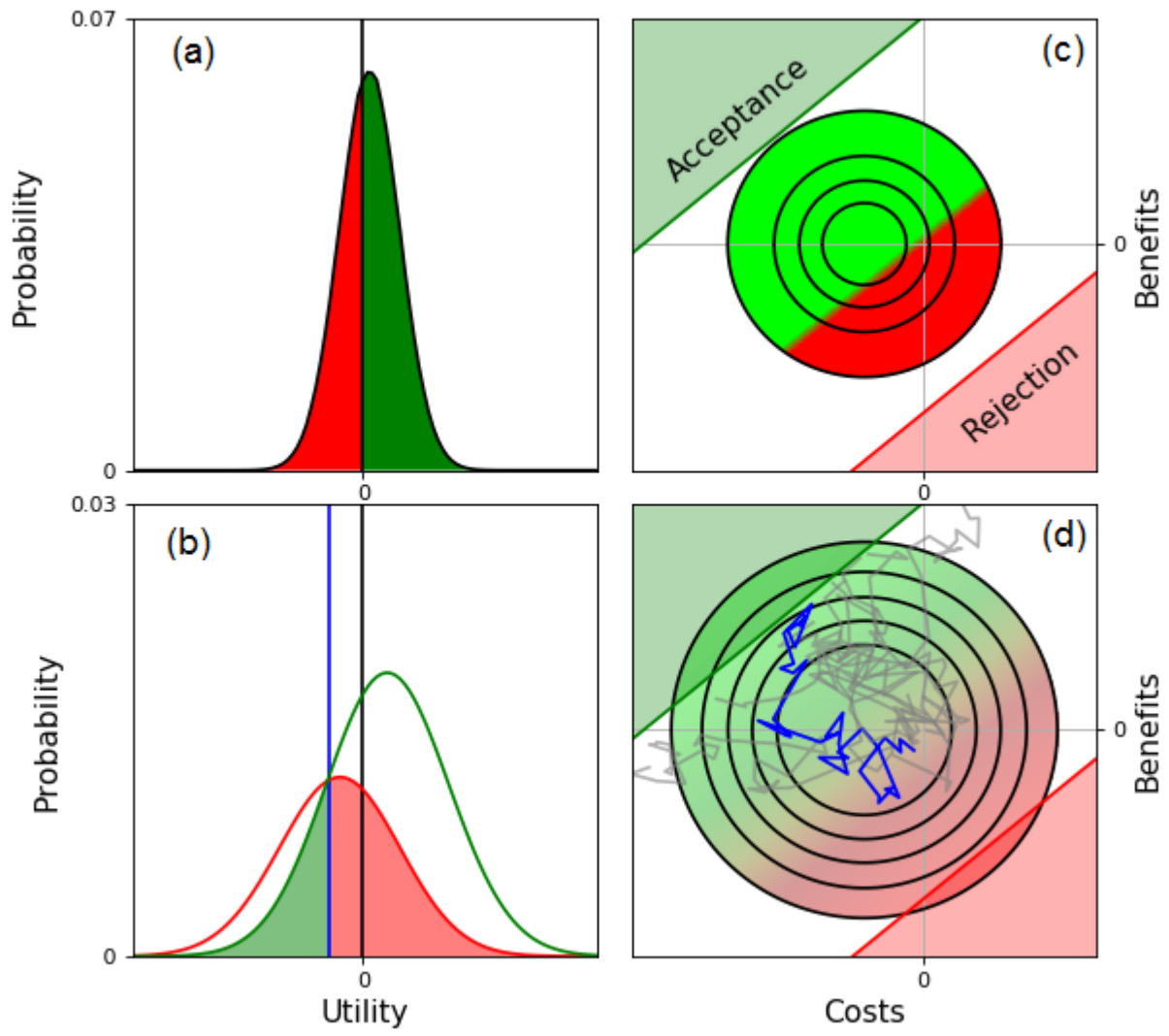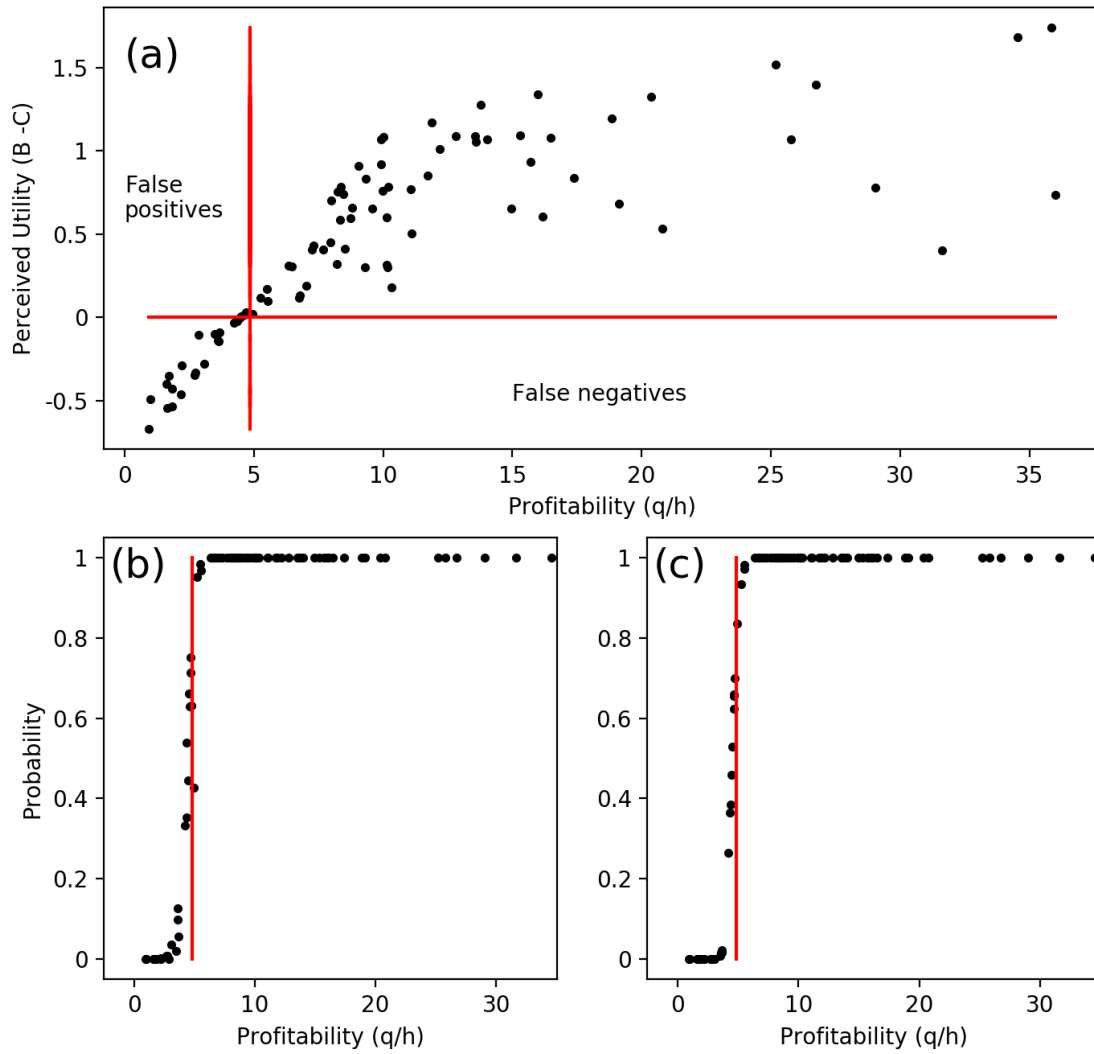
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684 **FIGURE 1**

685
686

Acceptance Rejection (a)

Acceptance Rejection (b)

B C

U

B C

Sensory Information

Sensory Information

→ Excitatory
—● Inhibitory
●—〜—● Neuro-modulatory
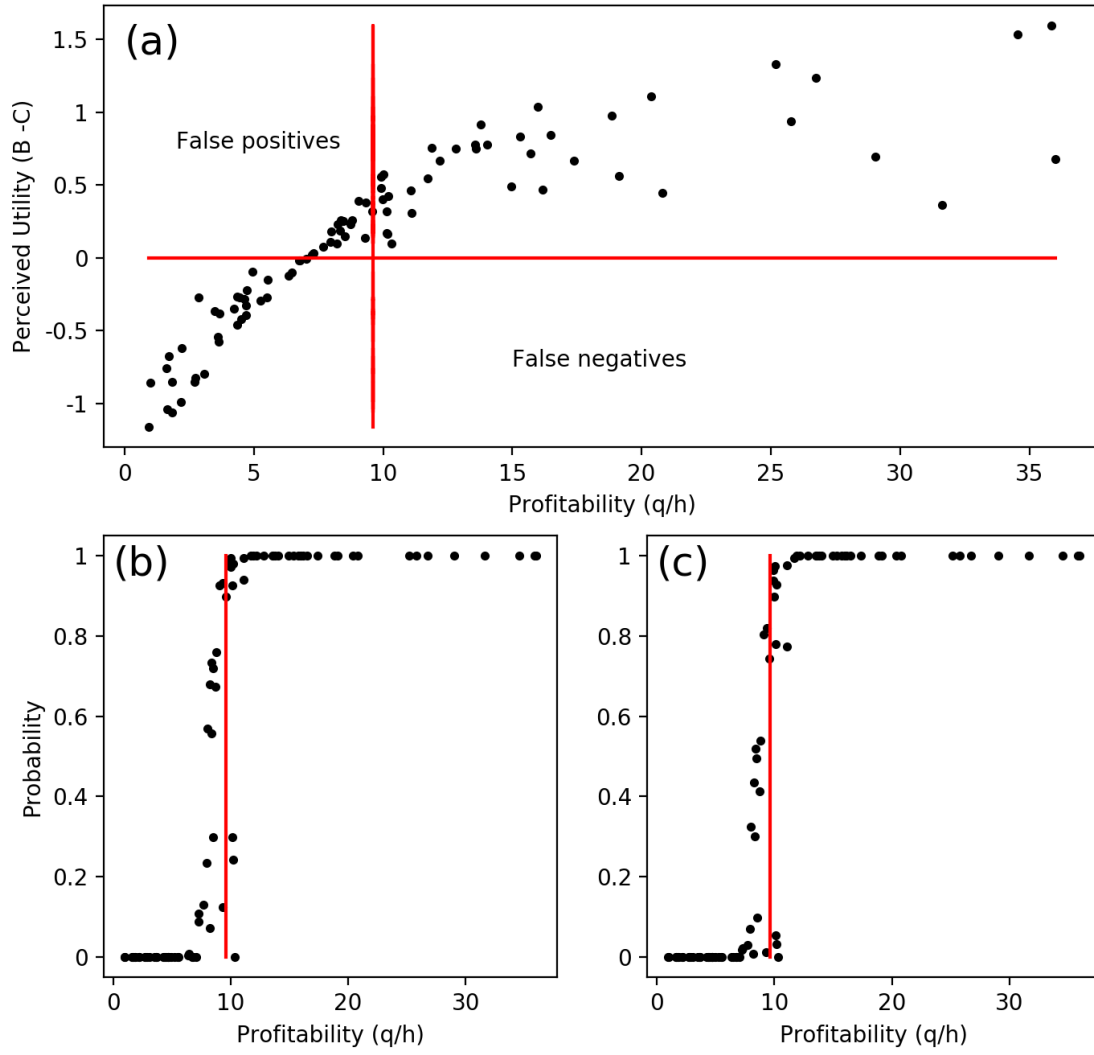
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FIGURE 2

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FIGURE 3

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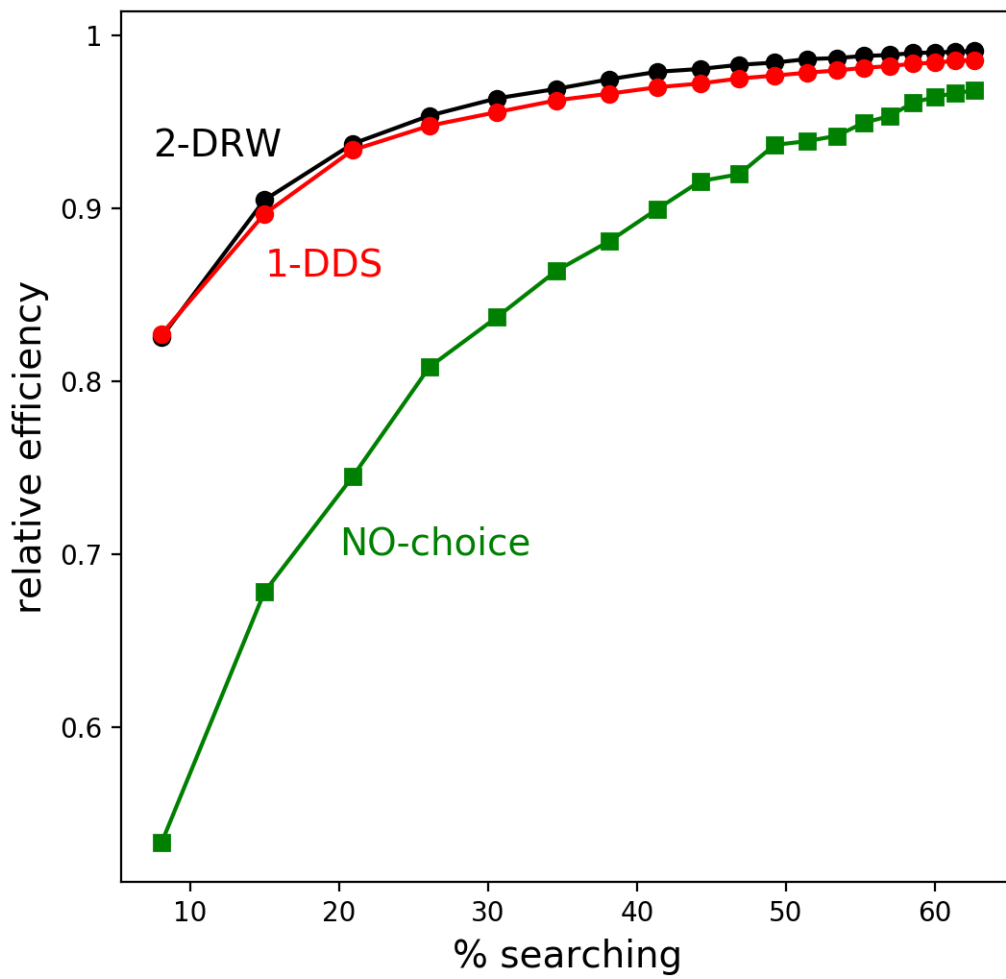697

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FIGURE 4

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FIGURE 5

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FIGURE 6