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► **To cite this version:**

Etienne Sirot, Olivier Pays. On the dynamics of predation risk perception for a vigilant forager.. Journal of Theoretical Biology, 2011, 276 (1), pp.1. 10.1016/j.jtbi.2011.01.045 . hal-00682410

**HAL Id: hal-00682410**

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Submitted on 26 Mar 2012

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## Author's Accepted Manuscript

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PII: S0022-5193(11)00071-3  
DOI: doi:10.1016/j.jtbi.2011.01.045  
Reference: YJTBI6357

To appear in: *Journal of Theoretical Biology*

Received date: 27 August 2010  
Revised date: 13 December 2010  
Accepted date: 28 January 2011

Cite this article as: Etienne Sirot and Olivier Pays, On the dynamics of predation risk perception for a vigilant forager., *Journal of Theoretical Biology*, doi:10.1016/j.jtbi.2011.01.045

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1 **On the dynamics of predation risk perception for a vigilant forager.**

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26 **ABSTRACT**

27 Foraging animals often raise their head to scan for predators. Scanning intervals have variable  
28 durations, and occur more or less frequently, depending on ecological conditions. Our study  
29 relies on the assumption that temporal patterns of vigilance depend on the speed with which  
30 information concerning the likelihood of a predator's presence in the neighbourhood is  
31 gathered when an animal is vigilant, and lost when it is not. Using an analytical model, we  
32 study how the perceived level of risk progressively decreases, when the individual is vigilant  
33 and detects no predator, then increases again, when it lowers its head to feed, thereby losing  
34 most of its detection abilities. The speed of these variations is affected by the likelihood of the  
35 presence of a predator in the whole environment, by the mobility of this predator, and by the  
36 detection capacities of the prey. We show how, combined with the range of risk levels  
37 tolerated by this animal, this dynamics determines the frequency and the duration of its  
38 scanning intervals. The dynamics of risk perception can also explain particular behavioural  
39 patterns, such as the progressive decrease of vigilance that may occur after the arrival into a  
40 novel environment, and the central tendency in the distribution of interscan durations reported  
41 by many studies. Next, we use the model to compute optimal vigilance strategies, taking into  
42 account the trade-off between feeding and limiting exposure to predators. The model predicts  
43 that a forager will scan more often, and for longer periods, when the likelihood a predator's  
44 presence in the surrounding environment is increased. A similar response is expected when  
45 the mobility of the predator is increased. By contrast, when the detection capacities of the  
46 prey are reduced, it will increase its vigilance by scanning for longer periods, but scanning  
47 intervals will be separated by longer interscans.

48

49 **Keywords :** anti-predatory behaviour, information, predation, risk, vigilance

## 50 INTRODUCTION

51 Time-sharing between anti-predatory vigilance and other activities, such as foraging,  
52 reproduction, or sleep, implies that animals have to trade some component of fitness (e.g.  
53 energy gain through feeding) for better security against predators (Elgar, 1989; Quenette,  
54 1990). This trade-off has been studied by mathematical models that derived optimal or  
55 evolutionarily stable vigilance strategies as a function of ecological conditions (e.g. Pulliam et  
56 al., 1982; McNamara and Houston, 1992). The assumption of vigilance models is that  
57 individuals with high vigilance levels have more chance of detecting an approaching predator,  
58 hence more chance of escaping when under an attack. The level of vigilance is represented by  
59 a behavioural variable; namely, the scanning rate (e.g. Pulliam, 1973; Pulliam et al., 1982;  
60 Lima 1987; Rodriguez-Gironés and Vàsquez, 2002), or the proportion of time spent vigilant  
61 (e.g. Packer and Abrams, 1990; McNamara and Houston, 1992; Sirot, 2006).

62 Concurrently, temporal patterns of vigilance have been studied over a wide range of  
63 animal taxa, making the topic of anti-predatory vigilance a particularly fruitful example of  
64 joint development between theoretical and field work (Bednekoff and Lima, 1998). Field  
65 studies do indeed report that the proportion of time dedicated to vigilance varies with  
66 ecological conditions, but, moreover, that the duration of both scanning intervals and non  
67 vigilant intervals (interscans) may be affected by these conditions (e.g. Metcalfe, 1984;  
68 Whittingham et al., 2004; Pays et al., 2007). Measuring scans and interscans allows to  
69 calculate the proportion of time dedicated to vigilance, but also conveys more precise  
70 information, as different scanning rates may lead to the same proportion of time spent vigilant  
71 (e.g. Pöysä, 1994; Pays et al., 2007). A relevant question is thus to ask, not only what  
72 proportion of time should be allocated to vigilance, but also how total vigilance time should  
73 be apportioned among consecutive scans. This question is particularly important because  
74 predatory attacks are very sudden events, and the exact posture of the individual at the onset

75 of an attack may determine its chance of escape (Hilton et al., 1999). This is probably the  
76 reason why animals obey short-term decision rules that dictate the precise moments of head  
77 raising and lowering, as a response to immediate conditions (Bekoff, 1995; Pays et al., 2009).

78 In the present study, we use a behavioural model to study the alternation of scanning  
79 and interscan intervals for an isolated forager on a food patch. The model addresses the  
80 following questions: (1) how long should a forager that does not spot any predator stay  
81 vigilant before resuming food search? and (2) how long should it feed after resumption,  
82 before switching back to vigilance?

83 Our study relies on the assumption that the behaviour of the animal is dictated by its  
84 instantaneous perception of predation risk, which fluctuates as a function of its activity. In the  
85 first part of the article, we describe the dynamics of risk perception over a foraging period  
86 during which no detection occurs, successively considering what happens during feeding and  
87 scanning intervals. In the second part, we consider the trade-off between feeding and limiting  
88 exposure to predators, and derive optimal vigilance strategies.

## 90 **THE MODEL**

91 The model considers an isolated forager on a food patch, which shares its time between  
92 feeding and vigilance, considered as two mutually exclusive activities. The duration of the  
93 whole foraging process,  $T$ , is fixed. Feeding allows the individual to increase its level of  
94 energy reserves, while scanning is used to detect a potential predator. The forager's perception  
95 of risk at time  $t$ ,  $\mu(t)$ , corresponds to the estimated probability of the predator's presence in the  
96 neighbourhood (i.e. within detection range).

97  $P_0$ , initially assumed to be a constant, denotes the probability of the predator's presence  
98 in the whole environment, which encompasses both the neighbourhood of the forager and the  
99 surrounding places, which are not observable by the forager, but from which the predator may

100 arrive. Parameters  $s$  and  $S$  denote the areas of the forager's neighbourhood, and of the whole  
 101 environment, respectively. The initial estimated probability of the predator's presence in the  
 102 neighbourhood, when the forager arrives on the patch and has not yet had the opportunity to  
 103 scan, is :  $\mu_0 = P_0 \times s/S$ . The level of risk that prevails in the forager's neighbourhood may  
 104 nevertheless change with time, because the predator, if present, may move. During a small  
 105 time interval  $dt$ , the predator moves with probability  $mdt$ , where  $m$  is a measure of its  
 106 mobility. When moving, the predator arrives in the neighbourhood of the forager with  
 107 probability  $s/S$ .

108 Interval  $[\mu_1, \mu_2]$  corresponds to the range of risk levels tolerated by the animal. This  
 109 means that the forager switches from vigilance to feeding when its perception of risk  $\mu(t)$   
 110 reaches threshold  $\mu_1$  during a scan, and from feeding to vigilance when  $\mu(t)$  reaches threshold  
 111  $\mu_2$  during an interscan.

112 We first determine the fluctuations of predation risk perception during successive  
 113 scans and interscans, when no detection occurs. Then, we consider the trade-off between  
 114 searching for food and scanning for the predator, and compute optimal vigilance strategies.

115

### 116 **Variations of predation risk estimation during interscans**

117 Here, we consider what happens when the forager keeps its head at ground level to feed, after  
 118 a vigilant period. When the animal begins to feed, its estimation of predation risk is  $\mu_1$ .  
 119 Thereafter, due to its incapacity to track changes in the environment, its estimated level of  
 120 risk changes, as a function of the predator's tendency to move and approach close by.  $t$   
 121 denotes the time elapsed since the animal began feeding, and  $\mu_f(t, \mu_1)$  is its estimation of  
 122 predation risk at time  $t$ . The initial condition is :  $\mu_f(0, \mu_1) = \mu_1$ .

123  $\mu_f(t+dt, \mu_1)$  estimates the probability of the predator's presence in the neighbourhood of  
 124 the forager at time  $t+dt$ . Following the rules for predator movement described above, three

125 different reasons may explain this presence. First, the predator may already be present at time  
 126  $t$ , and be immobile during interval  $dt$ . This happens with probability  $\mu_f(t, \mu_1) \times (1 - mdt)$ .  
 127 Second, the predator may already be present, move, and arrive again in the forager's  
 128 neighbourhood. This happens with probability  $\mu_f(t, \mu_1) \times mdt \times s/S$ . Third, the predator may  
 129 initially be present in another part of the environment, and move into this neighbourhood.  
 130 This event occurs with probability  $(P_0 - \mu_f(t, \mu_1)) \times mdt \times s/S$ . Thus, we finally have :

$$131 \quad \mu_f(t+dt, \mu_1) = \mu_f(t, \mu_1) \times (1 - mdt) + \mu_f(t, \mu_1) \times mdt \times s/S + (P_0 - \mu_f(t, \mu_1)) \times mdt \times s/S \quad (1).$$

$$132 \quad \text{or : } \mu_f(t+dt, \mu_1) = \mu_f(t, \mu_1) \times (1 - mdt) + \mu_0 \times mdt, \text{ as } \mu_0 = P_0 \times s/S \quad (2).$$

$$133 \quad \text{This leads to the differential equation : } d\mu_f/dt \times 1/(\mu_f - \mu_0) = -m \quad (3).$$

$$134 \quad \text{The solution of Eq. (3) is : } \mu_f(t, \mu_1) = (\mu_1 - \mu_0) \times \exp(-mxt) + \mu_0 \quad (4).$$

135 Eq. (4) describes the dynamics of predation risk perception when the animal feeds. It  
 136 shows how the level of risk perceived progressively rises, tending towards its basic level  $\mu_0$ ,  
 137 when the animal keeps its head down. Since the animal switches back to vigilance when the  
 138 level of risk perceived reaches threshold  $\mu_2$ , we have :  $\mu_2 = \mu_f(t_f, \mu_1)$  (5),

139 where  $t_f$  denotes the duration of the current feeding interval.

140

#### 141 **Information gathering during vigilance**

142 Here we study how the level of risk perceived changes over one scanning interval, still under  
 143 the assumption that no detection occurs.  $\mu_v(t, \mu_2)$  is the estimation of predation risk at time  $t$ ,  
 144 the time elapsed since the individual started being vigilant.  $\mu_2$  is the perceived level of risk at  
 145 the beginning of the vigilant period, so we have :  $\mu_v(0, \mu_2) = \mu_2$ . When considering predator  
 146 movements only, predation risk follows the same dynamics as during interscans. Thus, the  
 147 estimated probability of the predator's presence at time  $t+dt$  is given by :  $\mu_v(t, \mu_2) \times (1 - mdt) +$   
 148  $\mu_0 \times mdt$  (see Eq. (2)). However, the level of risk perceived by the forager at time  $t+dt$  is also



149 influenced by the fact that it did not detect the predator during interval  $dt$ . We must then  
 150 compute the probability of the predator's presence, conditional on the absence of a detection.  
 151 Parameter  $D$ , which measures the detection abilities of the forager, is the per time unit  
 152 probability of detection when a predator is present. Thus, the predator, when present, is  
 153 detected during small interval  $dt$  with probability  $Ddt$ , and remains undetected with  
 154 probability  $1 - Ddt$ . When the predator is not present, the absence of detection occurs with  
 155 probability 1. Hence we get, using Bayes' formula :

$$156 \quad \mu_v(t+dt, \mu_2) = \frac{(\mu_v(t, \mu_2) \times (1 - mdt) + \mu_0 \times mdt) \times (1 - Ddt)}{(\mu_v(t, \mu_2) \times (1 - mdt) + \mu_0 \times mdt) \times (1 - Ddt) + (1 - (\mu_v(t, \mu_2) \times (1 - mdt) + \mu_0 \times mdt)) \times 1}$$

157 (6).

158 Eq. (6) is built under the hypothesis that detection prevails over movements, that is, assuming  
 159 that the predator has the same chance of being detected if it moves to or from the forager's  
 160 neighbourhood during interval  $dt$  as if it had spent the whole interval within this  
 161 neighbourhood. This approximation, which concerns only rare events, was made to insure  
 162 coherence with the dynamics of risk perception during interscans, where detection ability is  
 163 cancelled (when  $D = 0$ , Eq. (6) collapses to Eq. (2)). Re-arranging Eq. (6) leads to the  
 164 following differential equation :  $d\mu_v / dt \times 1 / (\mu_v^2 \times D - \mu_v \times (m+D) + \mu_0 \times m) = 1$  (7).

165 The solution of Eq. (7) is :

$$\mu_v(t, \mu_2) = \frac{a + b \times c \times \exp(-(b-a) \times D \times t)}{1 + c \times \exp(-(b-a) \times D \times t)} \quad (8),$$

166 where  $a = \frac{(m+D) - \sqrt{((m+D)^2 - 4 \times \mu_0 \times m \times D)}}{2 \times D}$ ,  $b = \frac{(m+D) + \sqrt{((m+D)^2 - 4 \times \mu_0 \times m \times D)}}{2 \times D}$ , and

167  $c = \left| \frac{\mu_2 - a}{\mu_2 - b} \right|$ . Eq. (8) shows how the level of risk perceived progressively decreases when the

168 forager is vigilant and does not detect the predator. The forager switches back to feeding  
 169 when the level of risk perceived reaches threshold  $\mu_1$ , so we have :  $\mu_1 = \mu_v(t_v, \mu_2)$  (9),

170 where  $t_v$  denotes the duration of the current vigilant interval.

171 **Updating the perception of the overall level of environmental risk**

172 Here, we explore the possibility that the observations made by the forager in its immediate  
 173 neighbourhood also convey information about the likelihood of the predator's presence in the  
 174 surrounding places. Thus, we study the process whereby, if the predator, which is mobile, has  
 175 not been detected for a certain period of time in the neighbourhood, it becomes more likely  
 176 that it is indeed absent from the whole environment.

177 In the model, this means that parameter  $P_0$ , which estimates the probability of the  
 178 predator's presence in the whole environment, also becomes the object of an updating process.  
 179 We assume that this updating process takes place at the end of each scanning interval.  $P_n$   
 180 denotes the estimated probability of the predator's presence in the whole environment  
 181 immediately after scan  $n$ , still conditional on the absence of any detection.  $Q(t_v, P_n)$  denotes  
 182 the probability that the predator is present in the environment, but remains undetected during  
 183 a scanning interval of duration  $t_v$ , when the probability of the predator's presence in the  
 184 environment is  $P_n$  (see Appendix A). Using Bayes formula, we have :

$$185 \quad P_{n+1} = Q(t_v, P_n) / (Q(t_v, P_n) + 1 \times (1 - P_n)) \quad (10).$$

186 Eq. (10) is used to update the value of  $P$  at the end of each scanning interval. The  
 187 dynamics of risk perception during the following interscan and scan is then computed using  
 188 Eqs. (4) and (8), respectively, with this updated value.

189 The situation where parameter  $P$  is the object of an updating process yields relatively  
 190 complex vigilance behaviour, with scans and interscans that progressively vary in duration  
 191 (see Results). In the following section, which is dedicated to the influence of ecological  
 192 parameters on vigilance strategies, we do not consider this effect of time.  $P_0$  is thus treated as  
 193 a constant.

194

195

196 **Optimal vigilance**

197 Here we define a fitness measure which takes into account the advantages of vigilance, in  
 198 terms of reduced exposure to the predator, and its drawbacks, in terms of lost feeding time. In  
 199 the framework of a constantly fluctuating level of perceived risk, the vigilance strategy of the  
 200 forager is associated with the range of tolerated risk levels,  $[\mu_1, \mu_2]$ . The analysis of risk  
 201 perception dynamics presented above shows that, when  $\mu_1$  is not too low and  $\mu_2$  not too high  
 202 (i.e.  $\mu_1 > a$  and  $\mu_2 < \mu_0$ ), we can find one single set of durations for scans and interscans,  
 203 hereafter denoted by  $t_v$  and  $t_f$ , respectively, for which the level of risk perceived by the forager  
 204 describes interval  $[\mu_1, \mu_2]$  during each scan/interscan cycle. These durations verify Eqs. (5)  
 205 and (9). The range of risk levels tolerated by the forager thus induces a single vigilance  
 206 strategy, characterized by feeding and vigilant intervals of constant durations.

207 We assume that the forager always escapes if it detects the predator while vigilant. In  
 208 this situation, the total time lost in the current scan and in the escape,  $T_E$ , only impedes its  
 209 overall feeding rate. The probability that the predator is detected during a scan is :  $P_D = P_0 -$   
 210  $Q(t_v, P_0)$ , since  $Q(t_v, P_0)$  is the probability that the predator is present in the environment, but  
 211 remains undetected during the scan (see Appendix A).

212 For the forager, the total level of exposure to predation risk thus only depends on the  
 213 number and duration of feeding periods, and on the probabilities of the predator's presence  
 214 during these periods. This simplifying assumption conserves the advantages of vigilance,  
 215 namely, the fact that the forager has more chance of escape if attacked while vigilant than  
 216 while feeding, and the fact that it endures a reduced level of risk when returning to feed after  
 217 a vigilant period during which no detection occurred.

218 We consider a given feeding period.  $t$  denotes the time elapsed since the forager  
 219 resumed feeding, and  $P_{NE}(t, \mu_1)$  is the probability that the forager has not been exposed to the  
 220 predator at time  $t$ . We make the per time unit probability of exposure to predation risk equal

221 to the estimated probability of the predator's presence. Since  $\mu_f(t, \mu_1)$  is the probability of the  
 222 predator's presence in the neighbourhood at time  $t$ , we have :

$$223 \quad P_{NE}(t+dt, \mu_1) = P_{NE}(t, \mu_1) \times (1 - \mu_f(t, \mu_1)dt) \quad (11),$$

$$224 \quad \text{which leads to the differential equation : } dP_{NE}/dt \times 1/P_{NE} = - (\mu_1 - \mu_0) \times \exp(-m \times t) - \mu_0 \quad (12).$$

$$225 \quad \text{The solution of Eq. (12) is : } P_{NE}(t, \mu_1) = \exp(-\mu_0 \times t) \times \exp((\mu_1 - \mu_0) \times (\exp(-m \times t) - 1) / m) \quad (13).$$

226 Hence, the probability of not being exposed to the predator's presence during a feeding period  
 227 of duration  $t_f$  is  $P_{NE}(t_f, \mu_1)$ , and the probability of not being exposed to the predator's presence  
 228 during the whole foraging bout is  $P(t_f, t_v) = (P_{NE}(t_f, \mu_1))^n$ , where  $n = T / (t_f + (1 - P_D) \times t_v + P_D \times T_E)$  is  
 229 the total number of feeding periods.

230 The expected energy gain for the whole foraging bout, provided the individual  
 231 survives, is :  $E(t_f, t_v) = n \times (t_f \times g - e)$ , where  $g$  is the energy gain per time unit of feeding, and  $e$   
 232 the energy cost of switching from vigilance to feeding, then from vigilance to feeding.

233 To compute optimal strategies in a way that takes into account both the advantages  
 234 and the drawbacks of vigilance, we use the following quantity to measure fitness :

$$235 \quad F(t_f, t_v) = P(t_f, t_v) \times E(t_f, t_v) \quad (14).$$

236 The individual does indeed increase its probability of not being exposed to the predator,  
 237  $P(t_f, t_v)$ , by being more vigilant, but, at the same time, it reduces its energy gain  $E(t_f, t_v)$ . Fitness  
 238 as defined by Eq. (14) thus allows to study the response to the trade-off between feeding and  
 239 limiting exposure to predators (see Packer and Abrams, 1990; Brown, 1999). The optimal  
 240 vigilance strategy is the set of values  $(t_f, t_v)$  for which  $F(t_f, t_v)$  is maximized. It is derived  
 241 numerically.

242

243 **RESULTS**244 **Fluctuations of risk perception**

245 After a relatively long initial scan following the arrival on the patch, the level of risk  
246 perceived by the animal begins to fluctuate in a periodic way. It increases during each  
247 interscan, then decreases again during the following scan, with dynamics respectively given  
248 by Eqs. (4) and (8) (Fig 1). Excepted for the long initial scan, both scans and interscans have  
249 constant durations, which depend on this dynamics and on the range of risk levels  $[\mu_1, \mu_2]$   
250 tolerated by the forager.

251 Compared to a control situation (dashed line,  $t_v = 5.99$ ,  $t_f = 5.03$ ), the detection  
252 capacity of the forager is increased by increasing the value of parameter  $D$ , which measures  
253 this capacity (full line). As a consequence, the level of risk perceived decreases faster during  
254 scans, while the dynamics of risk perception does not change during interscans. To maintain  
255 the level of risk perceived within the same interval, the forager thus shortens its scans, while  
256 the duration of interscans remains the same (full line,  $t_v = 2.14$ ,  $t_f = 5.03$ ). By contrast, if the  
257 level of danger is decreased by reducing the overall likelihood of the predator's presence in  
258 the environment (i.e. parameter  $P_0$ , dotted line), the dynamics of risk perception is affected  
259 during both scans and interscans, because the arrival of the predator becomes less likely  
260 during both kinds of intervals. The level of risk perceived thus decreases more rapidly during  
261 scans, and increases more slowly during interscans (compare dotted and dashed line). The  
262 forager thus responds to this situation by shortening its scans, and increasing its interscans  
263 (dotted line,  $t_v = 3.5$ ,  $t_f = 8.11$ ). Qualitatively similar results are obtained when the level of  
264 danger is increased by an increased mobility of the predator (data not shown).

265

## 266 **Updating the perception of the overall level of environmental risk**

267 Here we explore the situation where the observations made by the forager in its immediate  
268 neighbourhood contribute to update its estimate of the probability of the predator's presence in  
269 the whole environment.

270 The effect of this updating process is that, over a foraging bout during which the  
271 predator is not detected, the estimated probability of the predator's presence in the whole  
272 environment (i.e.  $P$ ) progressively decreases with time. As a consequence of this declining  
273 perception of the overall level of risk, the level of risk perceived locally decreases more  
274 rapidly during scans, and increases less rapidly during interscans, as predicted when the value  
275 of  $P_0$  is decreased (see Fig 1). The proportion of time dedicated to vigilance thus  
276 progressively declines (see Fig 2).

277 Logically, additional simulations show that when  $s/S$ , the proportion of the whole  
278 environment that is observable by the forager, gets smaller, vigilance decreases more slowly.

## 280 **Optimal vigilance**

281 Here we study how the optimal vigilance strategy varies with ecological conditions. The level  
282 of environmental danger increases when either the likelihood of the predator's presence in the  
283 whole environment,  $P_0$ , or its mobility,  $m$ , increases (Fig 3a,b), and when the detection ability  
284 of the forager,  $D$ , decreases (Fig 3c).

285 In the three situations, the durations of both scans and interscans change as a response  
286 to an increased level of danger, and the proportion of time dedicated to vigilance increases.  
287 The effects of increasing the likelihood of the predator's presence in the environment, or the  
288 mobility of the predator, are similar. In both cases, scans get longer, and interscans shorter  
289 (Fig. 3a,b). By contrast, when the level of exposure increases because the detection capacities  
290 of the prey are reduced, the increase in vigilance only results from the lengthening of scans,  
291 which, as they become longer, also become separated by longer feeding intervals (Fig 3c).

292 **DISCUSSION**

293 In the present article, we study how the alternation of anti-predatory vigilance and feeding  
294 intervals determines the levels of risk successively perceived by a forager, in an environment  
295 potentially occupied by a predator. The model dedicates special attention to the process of  
296 information acquisition during scans, as information gathering is the primary function of  
297 vigilance, and considers the loss of this information during feeding intervals.

298 In the first part of the study, we compute the dynamics of predation risk perception, in  
299 the common situation where no detection occurs. We show how the level of risk perceived  
300 continuously vary with the activity of the animal, decreasing during scans, as the animal  
301 accumulates information about safety in the environment, then increasing again during  
302 interscans, when it is no longer able to detect the possible arrival of the predator. The speed of  
303 these variations, combined with the range of risk levels tolerated by the animal, finally  
304 determines its vigilance strategy, which means that the range of risk levels accepted by the  
305 forager and its vigilance behaviour are both tightly connected to the dynamics of risk  
306 perception. The model shows that this dynamics should tend to make the duration of both  
307 scans and interscans relatively constant. However, the initial scan should always be longer  
308 than the following ones, and, if we take into account the possibility for the forager to learn  
309 about surrounding places through its local observations, the proportion of time dedicated to  
310 vigilance should decline with time. Such progressive decrease in vigilance following the  
311 arrival into a novel environment has been reported in harbour seals, *Phoca vitulina*, attending  
312 haul out sites (Terhune and Brillant, 1996).

313 In real conditions, however, the regular dynamics of predation risk perception  
314 predicted by our model will be disturbed by accidental changes, coming from external events  
315 (such as unidentified shapes or noises; Ruxton and Roberts 1999), or observation of  
316 companions, whose behaviour may convey information about potential predators (Fernández

317 et al., 2003), and influence individual predation risk in several ways (Sirot and Touzalin,  
318 2009). As a consequence, the individual will reach the critical switching values for predation  
319 risk perception at different moments, which will induce some variability in the temporal  
320 patterns of vigilance (see Ruxton and Roberts, 1999).

321 Nevertheless, the mechanism described here, whereby predation risk perception  
322 progressively increases during interscans, until it triggers a switch to vigilance, and  
323 progressively decreases during vigilance, until the level of safety allows the animal to resume  
324 feeding, should contribute to reduce the variability of the duration of both scans and  
325 interscans, and the instantaneous probability of switching should increase with time, during  
326 both kinds of intervals. The model thus proposes an alternative, based on mechanistic and  
327 adaptive reasoning, to the original hypothesis of vigilance studies that scans should be  
328 initiated with a constant rate (that is, with a constant per time unit probability; Pulliam, 1973).  
329 In accordance with our results, several studies demonstrate that the per time unit probability  
330 of looking up increases as an animal feeds, instead of being constant (Hart and Lendrem,  
331 1984; Sullivan, 1985; Lendrem et al., 1986; Beauchamp, 2006; Pays et al., 2010). As a  
332 consequence, both short and long interscans become more rare than under the original  
333 hypothesis of a constant scan initiation rate. Scan duration has received much less attention  
334 than interscan duration (Bednekoff and Lima, 1998). The present model suggests that it  
335 should also be relatively constant. The fact that the efficiency of vigilance declines with time,  
336 because attention cannot be sustained for long periods, should reinforce this tendency (Dukas  
337 and Clark, 1995).

338 In the second part of the study, we derive optimal strategies for the alternation of  
339 scanning and interscan intervals. Doing so, we make several simplifying assumptions. First,  
340 we assume that a feeding individual cannot detect predators, whereas an animal may retain  
341 limited detection capacities when it searches for food (Lima and Bednekoff, 1999). However,



342 even animals with such ability also possess characteristic vigilance attitudes, with erect  
343 postures of the neck or the whole body (Bednekoff and Lima, 2005; Ebensperger and  
344 Hurtado, 2005). This situation could thus be studied under the present framework. Including a  
345 limited detection ability for feeding individuals would quantitatively affect the results of the  
346 model, by slowing the resilience of risk estimation during interscans, but not its general  
347 qualitative predictions. Reciprocally, overtly vigilant individuals may sometimes continue to  
348 feed. For example, birds swallowing seeds raise their heads, which allows them to scan  
349 (Baker et al., 2010), and large herbivores may also become vigilant while chewing (Fortin et  
350 al., 2004). In these conditions, feeding does only partially, or not at all, impede vigilance, and  
351 the temporal pattern of vigilance is dependent on the feeding method. We can hypothesize  
352 that this process should contribute to make interscans more variable in length, as the time  
353 necessary to gather food on the ground is variable, and scans more constant, as the handling  
354 time for one particular type of food should be relatively constant.

355         Second we chose, for the sake of mathematical tractability, to consider the probability  
356 of the predator's presence as a measure of risk, thus assuming that minimizing predation risk  
357 is equivalent to limiting exposure to the predator's presence. In reality, predation risk also  
358 depends on the behaviour of the predator, which could in principle adapt its hunting  
359 behaviour to the vigilance displayed by the prey, thus initiating a game between predator and  
360 prey. The outcome of such a game on temporal patterns of prey vigilance has been studied by  
361 Scannell et al. (2001) and Bednekoff and Lima (2002), who identified two situations. In the  
362 first one, predators are prevented from timing their attack according to the vigilance schedule  
363 of the prey, for example because they have to cross a large portion of open space when  
364 attacking. In this situation, scanning at regular intervals is an advantage. By contrast, scanning  
365 at irregular intervals could be the best strategy against stalking predators that launch their  
366 attacks from close distances (Scannell et al., 2001; Bednekoff and Lima, 2002). The

367 mechanism described in the present study could thus, in some situations, be reinforced by the  
368 necessity to counter the hunting strategy of the predator. In others, the prey should  
369 simultaneously compromise with an efficient handling of the information garnered through  
370 vigilance, and an appropriate response to the tactic of the predator.

371         The levels of risk accepted by an animal are also expected to depend on the level of its  
372 energy reserves, which may fluctuate in a non-deterministic way. For example, an animal may  
373 be prevented from feeding for a part of the day. It will thus have low levels of reserves, and  
374 should become relatively risk tolerant, especially if the end of the foraging period is getting  
375 near (McNamara and Houston, 1986). Reciprocally, an animal with important levels of  
376 reserves could afford to invest more in anti-predatory vigilance (Beale and Monaghan, 2004).  
377 Across a foraging bout, the variations of individual levels of reserves and the Bayesian  
378 updating process concerning the prevailing level of risk could thus have conflicting effects on  
379 the level of vigilance. A model incorporating both a state-dependent approach and a  
380 description of the dynamics of risk perception should allow to study how the range of  
381 tolerated levels of risk could vary, according to current level of reserves of the animals and  
382 the time of the day.

383         In accordance with other models (e.g. McNamara and Houston, 1992; Brown, 1999),  
384 our model predicts higher vigilance in dangerous environments. This increase in vigilance is  
385 achieved by longer and more frequent scans when the likelihood of the predator's presence in  
386 the environment is high, and when the predator is highly mobile. By contrast, scan should  
387 increase in length, but not in frequency, when danger originates from decreased detection  
388 capacities for the prey. Additional simulations show that, when the cost of switching  $e$  is  
389 reduced and tends towards zero, the durations of both scans and interscans also tend towards  
390 zero, while the proportion of time spent vigilant does not change. Thus, we can draw the  
391 prediction that an animal will prefer to alternate between feeding and vigilance at the

392 maximum rate that is compatible with the efficiency of both feeding and vigilance activities.  
393 In this way, it will avoid sporadic periods of high risks, corresponding to high values of  $\mu_2$ .

394 Field studies confirm that vigilance rises during periods of increased predator activity  
395 (e.g. Caraco et al. 1980; Scheel, 1993; Devereux et al., 2005). Vigilance is often measured as  
396 the proportion of time spent vigilant, but the effects of environmental conditions on scan  
397 and/or interscan lengths have also been considered in several studies. The level of risk  
398 endured by the animals generally corresponds to the amount of obstructive cover near the  
399 feeding place, which hinders predator detection (Harkin et al., 2000). In accordance with the  
400 predictions of the model, the proportion of time spent vigilant generally increases with the  
401 proximity of obstructive cover (e.g. Underwood, 1982; Lazarus and Symonds, 1992; Watson  
402 et al., 2007; but see Scheel, 1993), and scanning intervals become longer (Metcalf, 1984;  
403 Goldsmith, 1990; Pöysä, 1994). Interestingly, scans may become more frequent when they get  
404 longer (McVean and Haddlesey, 1980; Metcalf, 1984; Goldsmith, 1990), but this is not  
405 always the case (Pöysä, 1994; Whittingham et al., 2004). Reciprocally, increases in scanning  
406 rate with no concomitant changes of scan duration have also been reported, although these  
407 results concern circumstances that are not considered in the present study (in Lendrem's  
408 (1983) study on house sparrows *Passer domesticus*, an individual could leave its feeding  
409 place to join a better observatory, and in Bertram's (1980) study on ostriches *Struthio*  
410 *camelus*, the increased level of vigilance was a response to a smaller group size). Thus, field  
411 studies show that the duration and frequency of scanning intervals may not always vary  
412 together, and tracking the variations of individual perception of predation risk may provide  
413 the key to understanding these patterns. As an extension of the present model, it would be  
414 interesting to consider how individual perception of risk is modified by the presence and  
415 behaviour of companions in a group, thus using the individual-based approach presented here  
416 to study the role played by social information in collective vigilance.

417 **Acknowledgments**

418 We thank Joël Brown, Peter Jarman, Frédéric Mathéus, Franz Weissing and two reviewers for  
419 helpful comments on previous versions of the model.

420

421 **Appendix A. Probability of not detecting the predator during a scanning interval.**

422 Here we compute  $Q(t_v, P_n)$ , the probability of not detecting the predator during a scanning  
423 interval of duration  $t_v$ , when the probability of the predator's presence in the whole  
424 environment is  $P_n$ . Two cases must be considered.

425 First, the predator may initially be present in the neighbourhood of the forager. This  
426 happens with probability  $\mu_1$ , which corresponds to the level of risk perceived at the end of the  
427 vigilant interval. At time  $t$ , the predator is still present and has remained undetected with  
428 probability  $\exp(-(m+D)xt)$ , since both movements and detection are Poisson processes. If still  
429 present, the predator will be detected during small interval  $dt$  with probability  $Ddt$ . Thus, the  
430 probability of not detecting the predator over the whole scanning interval of duration  $t_v$  when  
431 it is initially present in the neighbourhood, is :

$$432 \quad Q_1(t_v) = 1 - \int_0^{t_v} [\exp(-(m+D)xt) \times D] dt = m/(m+D) + D/(D+m) \times \exp(-(D+m)xt_v) \quad (A1).$$

433 Second, the predator may initially be present in the environment, but not in the  
434 neighbourhood of the forager. This happens with probability  $P_n - \mu_1$ . The arrival of the  
435 predator in the neighbourhood of the forager is then a Poisson process of parameter  $m' =$   
436  $m \times S/S$ . The probability that the predator arrives between time  $t$  and  $t + dt$  is thus  $\exp(-$   
437  $m' \times t) \times m' dt$ , and the probability that it is detected before the end of the scan, that is, during the  
438 time that remains, is given by :  $1 - Q_1(t_v - t)$  (see Eq. (A1)). Thus, the probability of not  
439 detecting the predator if it is initially present in the environment, but not in the neighbourhood  
440 of the forager, is :

441 
$$Q_2(t_v) = 1 - \int_0^{t_v} [\exp(-(m'x t)) \times m'x (1 - Q_1(t_v - t))] dt \quad (A2),$$

442 which leads to :

443 
$$Q_2(t_v) = 1 - m'xD/(m+D) \times ((1 - \exp(-m'x t_v))/m' - 1/(D+m-m') \times (\exp(-m'x t_v) - \exp(-(D+m) x t_v))) \quad (A3).$$

444 We finally have :  $Q(t_v, P_n) = Q_1(t_v) \times \mu_1 + Q_2(t_v) \times (P_n - \mu_1) \quad (A4).$

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Accepted manuscript

594 **LEGENDS**

595

596 **Fig. 1**

597 Fluctuations of risk perception during successive scanning and interscan intervals for a  
 598 foraging bout during which no detection occurs. The dynamics for the estimated probability  
 599 of the predator's presence in the neighbourhood are given by Eqs. (4) and (8) for interscans  
 600 and scans, respectively. Parameter values :  $[\mu_1, \mu_2] = [0.01, 0.03]$ ,  $s/S = 0.1$ , dashed line :  $P_0 =$   
 601  $1$ ,  $m = 0.05$ ,  $D = 0.5$ , full line :  $P_0 = 1$ ,  $m = 0.05$ ,  $D = 0.8$ , dotted line :  $P_0 = 0.7$ ,  $m = 0.05$ ,  $D =$   
 602  $0.5$ .

603

604 **Fig. 2**

605 Fluctuations of risk perception during successive scanning and interscan intervals for a  
 606 foraging bout during which no detection occurs, when the estimated probability of the  
 607 predator's presence in the whole environment is updated after each scanning interval. The  
 608 graph also shows, for each scan/interscan cycle, the proportion of time dedicated to vigilance  
 609 (full line). Parameter values :  $[\mu_1, \mu_2] = [0.01, 0.03]$ ,  $P_0 = 0.8$ ,  $s/S = 0.1$ ,  $m = 0.07$ ,  $D = 0.5$ .

610

611 **Fig. 3**

612 Optimal vigilance strategy, represented by the values of  $t_f$  (length of feeding periods),  $t_v$   
 613 (length of vigilance periods after the initial scan), and  $u$  (proportion of time dedicated to  
 614 vigilance), as a function of an increasing likelihood of the predator's presence in the whole  
 615 environment (panel (a)), an increasing mobility of the predator (panel (b)), and a decreasing  
 616 detection ability for the forager (panel (c)). Parameter values :  $g = 1$ ,  $e = 0.001$ ,  $T = 100$ ,  $s/S =$   
 617  $0.1$ , (a)  $m = 0.05$ ,  $D = 0.5$ , (b)  $D = 0.5$ ,  $P_0 = 1$ , (c)  $m = 0.05$ ,  $P_0 = 1$ .

618

Fig. 1

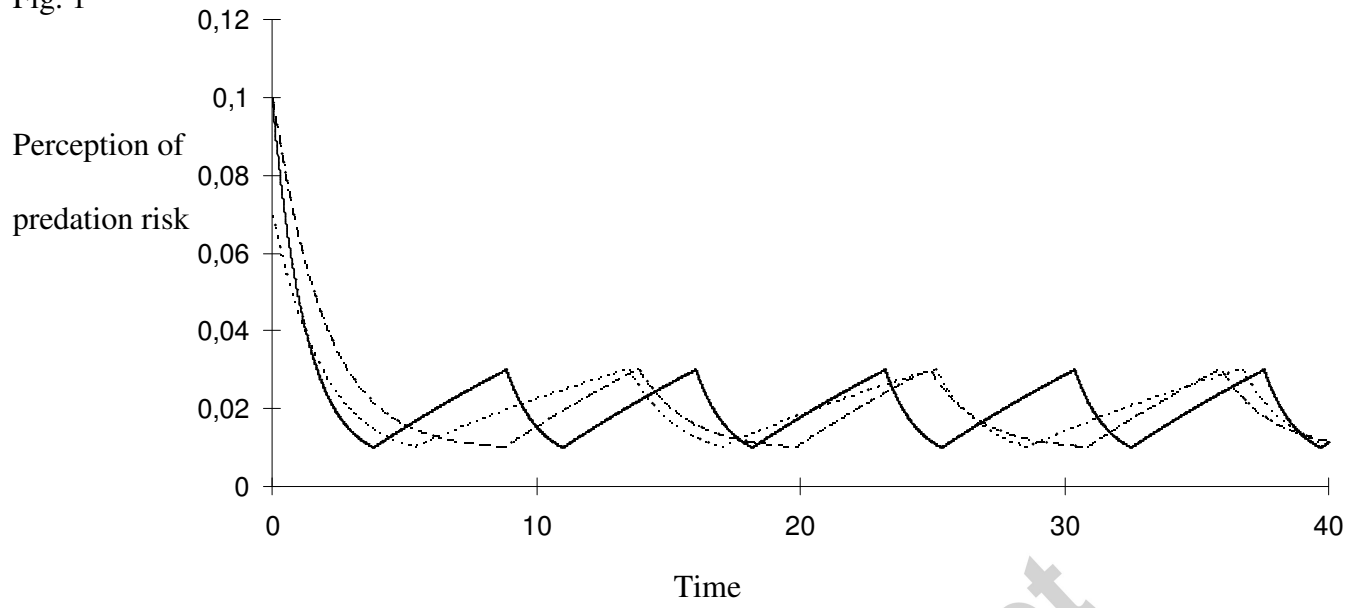


Fig. 2

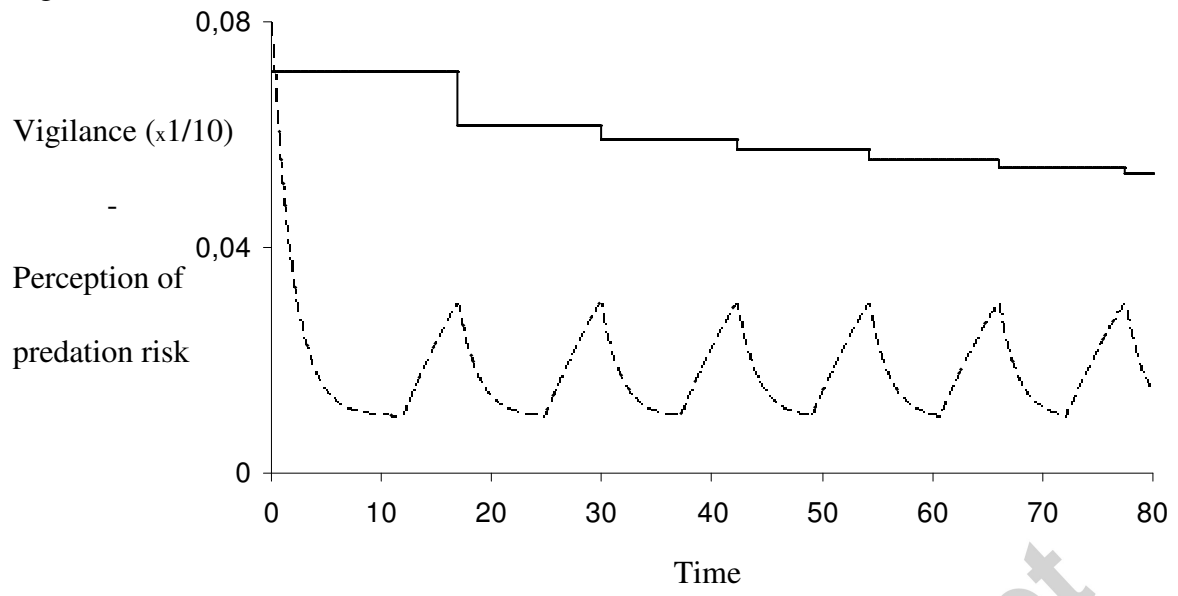


Fig. 3 (a)

