1 Running title: Navigational efficiency in a BCRW model

2 **Navigational efficiency in a biased and correlated random walk model of individual animal**

3 **movement**

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7 **Abstract**: Understanding how an individual animal is able to navigate through its environment is

8 a key question in movement ecology that can give insight into observed movement patterns and

9 the mechanisms behind them. Efficiency of navigation is important for behavioural processes at

10 a range of different spatio-temporal scales, including foraging and migration. Random walk

11 models provide a standard framework for modelling individual animal movement and

12 navigation. Here we consider a vector-weighted biased and correlated random walk (BCRW)

13 model for directed movement (taxis), where external navigation cues are balanced with forward

14 persistence. We derive a mathematical approximation of the expected navigational efficiency for

15 any BCRW of this form and confirm the model predictions using simulations. We demonstrate

16 how the navigational efficiency is related to the weighting given to forward persistence and

17 external navigation cues, and highlight the counter-intuitive result that for low (but realistic)

18 levels of error on forward persistence, a higher navigational efficiency is achieved by giving

19 more weighting to this indirect navigation cue rather than direct navigational cues. We discuss

20 and interpret the relevance of these results for understanding animal movement and navigation

21 strategies.

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1 Introduction

Understanding how and why animals navigate through their environment is one of the key open questions in movement ecology (Nathan, 2008). Animal navigation can occur across various spatio-temporal scales corresponding to a wide variety of behavioural processes, ranging from short-term foraging and home-range exploration (Schultz & Crone, 2001; Fortin et al., 2005; McClintock et al., 2012) to large-scale migration events (Gardiner et al., 2015). Common navigation orientation mechanisms include taxis, where an animal directly orientates in response to external directional cues, and differential klinokinesis (DKK), where the level of turning in the movement path (sinuosity) depends on variations in the magnitude of an external stimulus; both taxis and DKK lead to a long-term directional drift (bias) towards the target (Benhamou & Bovet, 1992). Conversely, the short-term localised bias in movement directions due to the tendency of animals to continue moving in the same direction is known as forward persistence (Benhamou & Bovet, 1992). Empirical studies have considered how a variety of different animals may balance taxis and persistence mechanisms in order to navigate within their local environment, including butterflies (Schultz & Crone, 2001), elk (Fortin et al., 2005), and grey seals (McClintock et al., 2012). Hence it is important to consider a theoretical basis for animal navigation and the underlying mechanisms that may lead to improved navigational efficiency.

Random walk theory has a long history of being used to model individual animal movement and navigation, and as a tool to classify and interpret observed movement data using various path analysis techniques (Jonsen et al., 2005; Codling et al., 2008; Langrock et al., 2012; McClintock et al., 2012). Models of movement based purely on localised forward persistence are known as correlated random walks (CRW) (Kareiva and Shigesada, 1983; Bovet & Benhamou, 1988; Codling et al., 2008). Biased random walks (BRW) are movement models where there is a

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long term directional bias in the direction of movement (Marsh and Jones, 1988; Benhamou, 2006; Codling et al., 2008; Codling et al., 2010). Models that combine both long-term directional bias and forward persistence are known as biased and correlated random walks (BCRW) (Codling et al., 2008).

Benhamou & Bovet (1992) combined taxis and forward persistence to form a vector-weighted BCRW model of movement, and found in a 1000-step random walk that the best navigational strategy was to give approximately 10% weighting to external navigation cues (taxis) and approximately 90% weighting to forward persistence. Such a navigation strategy gave higher navigational efficiency than a movement process based on taxis alone (a pure BRW), although it should be stressed that Benhamou & Bovet (1992) only included error in their external navigation term and not in their forward persistence term. The fact that the most efficient navigation strategy involved giving a high weighting to persistence rather than taxis may seem to be a counter-intuitive result, since movement based purely on persistence is known to be an inefficient navigation strategy when compared to pure taxis (Cheung et al., 2007). A similar result to Bovet & Benhamou (1992) was obtained by Codling & Bode (2014) who found that, in the context of a collective movement model for navigating animal groups, the most efficient navigational strategy was to give a high weighting to indirect navigational cues (copying the movement of other group members) and a low (but non-zero) weighting to direct individual navigational cues (taxis). In a follow-up study, Codling & Bode (2016) included individual forward persistence in the collective movement model and showed that giving a high weighting to indirect cues (copying neighbours or using forward persistence) rather than relying on direct navigational cues gave the highest navigational efficiency.

69   The findings of Benhamou & Bovet (1992) and Codling & Bode (2014, 2016) were

70   based on simulations only and the authors did not give a mathematical explanation for these

71   results. Here we consider a generalised form of the Benhamou & Bovet (1992) BCRW

72   navigation model, that includes error on the persistence term, and derive a mathematical

73   approximation for the expected navigational efficiency. The model predicts that for a reasonably

74   large (and realistic) range of navigation and persistence errors, the highest navigational

75   efficiency is achieved by giving a low weighting to direct navigational cues. We discuss the

76   relevance and implications of these findings in the wider movement ecology context.

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78   **2. Mathematical model**

79   The BCRW model of Benhamou & Bovet (1992) assumes a single random walker starts

80   at the origin, (0,0), and moves through an empty homogenous two-dimensional environment. For

81   simplicity, the target is assumed to be a 'point at infinity' located along the positive x-axis (this

82   effectively means we are only considering the large-scale part of the navigation process when the

83   animal is far from the target). Orientation angles are measured counter-clockwise from the x-

84   axis, and hence the target direction is given by $\Omega_T = 0$. We assume the walker initially starts with

85   no information about the target direction; an initial movement direction, θ_0, is randomly drawn

86   from a uniform circular distribution (this assumption does not affect our results as we will show

87   that the long-term navigational efficiency is independent of θ_0). At each random walk step the

88   components of movement in each direction are given by a weighted vector sum of a navigation

89   term and a persistence term (Benhamou & Bovet, 1992):

90    $$\Delta x_{n+1} = r_{n+1}(w \cos(\Omega_T + \phi_n) + (1 - w) \cos(\theta_n + \delta_n)), \quad (1)$$

91    $$\Delta y_{n+1} = r_{n+1}(w \sin(\Omega_T + \phi_n) + (1 - w) \sin(\theta_n + \delta_n)), \quad (2)$$

4

92   where r_{n+1} is the step length (distance moved) in the current step, $\Omega_T = 0$ is the target direction

93   (which is fixed as the *x*-axis for all steps), θ_n is the direction of movement in the previous step

94   (which varies at each step), δ_n is a persistence error term, ϕ_n is a navigation error term, and

95     $w \in [0,1]$ is the weighting given to navigation (and hence $(1 - w)$ is the weighting given to

96   persistence). In contrast to Benhamou & Bovet (1992) (who only included an error in the

97   navigation term), we include errors on both the navigation and persistence terms. In principle it

98   would be possible to have an even more general BCRW model that includes an additional

99   'output noise/error' term in addition to the navigation and persistence error terms. This output

100   noise could represent either additional movement error because of environmental factors (e.g.

101   turbulence) or could represent a form of 'voluntary' error that the animal may use to modulate its

102   behaviour between behavioural states. However, these more complex model features are beyond

103   the scope of the current work.

104   The additive navigation and persistence random error terms, ϕ_n and δ_n, are drawn from

105   separate zero-centred symmetric circular distributions with respective mean cosine values given

106   by $c_\phi \in [0,1]$ and $c_\delta \in [0,1]$. The level of navigation and/or persistence error is determined by

107   the mean cosine values, c_ϕ and c_δ: a value close to 0 corresponds to very high error, and a value

108   close to 1 corresponds to very low error. We assume that c_ϕ and c_δ are fixed for all steps of the

109   random walk, which implies that direction and persistence errors are independent (no correlation

110   of errors between successive steps) and are not related to spatial location or any other external

111   factor. Hence we do not consider possible changes in navigation cue strength as the animal

112   approaches the target, interactions with other animals, or changes in behaviour and interactions

113   with the environment such as foraging or resting during the navigation process. Note that, as

114   long as c_ϕ and c_δ are defined, the choice of which circular distribution to use is not important

115   since the results only depend on the first trigonometric moment (the mean cosine value); the

116   same results are obtained using common circular distributions such as the wrapped normal, von

117   Mises and wrapped Cauchy (Mardia & Jupp, 1999).

118   Similar to Benhamou & Bovet (1992), we define the navigational efficiency of a single

119   step of the movement process as:

$$\text{Navigational efficiency} = \frac{\text{Net distance moved towards target in } x \text{ direction}}{\text{Total distance moved}}. \quad (3)$$

120   Hence, for the BCRW given by Eqs. (1) and (2) the expected navigational efficiency at a given

121   step is given by $E[\cos\theta_{n+1}]$ since the target direction is the x-axis ($\Omega_T = 0$). In the extreme case

122   of a pure BRW ($w = 1$), navigational efficiency is given exactly by $E[\cos\phi_n] = c_\phi$, while for a

123   pure CRW ($w = 0$), navigational efficiency is given exactly by $E[\cos(\theta_n + \delta_n)] = 0$, since we

124   assume a uniform initial orientation and there is no external navigation cue. More generally for 0

125     $< w < 1$, an expression for $E[\cos\theta_{n+1}]$ is found by normalising Eq. (1) relative to the total step

126   length (noting that r_{n+1} cancels and that $\Omega_T = 0$) and then taking the expectation:

$$E[\cos\theta_{n+1}] = E\left[\frac{w\cos\phi_n + (1-w)\cos(\theta_n + \delta_n)}{\sqrt{w^2 + (1-w)^2 + 2w(1-w)\cos(\phi_n - (\theta_n + \delta_n))}}\right]. \quad (4)$$

127   The expression on the right-hand side of Eq. (4) is non-linear so we cannot directly calculate the

128   expectation. To make progress we use a similar argument to Wu et al. (2000), and assume we

129   can treat the right-hand side of Eq. (4) as if it were linear. We then further assume that θ_n, ϕ_n

130   and δ_n are all independent, and based on a result from Hill & Häder (1997), we assume that in

131   the long-term limit, the distribution of movement directions is stable such that $E[\cos\theta_{n+1}] =$

132     $E[\cos\theta_n] = E[\cos\theta_\infty] \equiv c_\theta$, which is equivalent to the long-term navigational efficiency. This

133   leads to a cubic polynomial for c_θ (see Appendix S1 for full details of the derivation):

$$2w(1-w)c_\phi c_\delta c_\theta{}^3 + (w^2 + (1-w)^2(1-c_\delta{}^2))c_\theta{}^2 - 2w(1-w)c_\phi c_\delta c_\theta - w^2 c_\phi{}^2 = 0. \quad (5)$$

134   It is possible to show that this polynomial has precisely one root in [0,1] for all feasible values of

135   c_ϕ, c_δ and w (see Appendix S2). This root can then be calculated using Cardano's method:

136
$$c_\theta = \sqrt[3]{A + \sqrt{A^2 + B^3}} + \sqrt[3]{A - \sqrt[2]{A^2 + B^3}} - C, \quad (6)$$

137   where A, B, and C are terms involving w, c_ϕ, and c_δ, and are given in Appendix S1.

138

139   **3. Results**

140   We first consider the specific case of zero error on forward persistence, $c_\delta = 1$, which was

141   considered originally by Benhamou & Bovet (1992). In this case Eq. (5) can be simplified and a

142   limiting argument can be used to show that for all $c_\phi > 0$ (i.e. as long as external navigation

143   cues are present) then $c_\theta \to 1$ as $w \to 0$ (see Appendix S3 and Figure 1a-c). It may seem

144   counter-intuitive that more efficient navigation can be obtained by giving a vanishingly small

145   (but strictly non-zero) weighting to direct navigational cues but this is explained by the fact that

146   once a navigating animal is oriented towards the target direction (which is always eventually

147   possible if w is strictly non-zero), it can then maintain this direction of movement indefinitely

148   since there is no persistence error, and hence no further external navigation cues are required.

149   Nevertheless, the higher the level of navigation error (i.e. the lower the value of c_ϕ) the longer it

150   will take (on average) for the animal to orientate itself towards the target direction.

151   Consequently, the apparent navigational efficiency is highly dependent on the number of steps in

152   the observed movement process when there is zero persistence error (Figure 1a-c). Benhamou &

153   Bovet (1992) only considered simulation results for a 1000-step BCRW and hence didn't report

154   this long-term limit result directly. For $w > 0$, the predicted long-term navigational efficiency,

155 c_θ, monotonically decreases as *w* increases, indicating that lower long-term navigational

156 efficiency is obtained when giving a higher weight to external navigation cues. This result is

157 confirmed with the simulation results for the 10,000 step BCRW shown in Figure 1c. In Figure

158 1a and 1b where the BCRW runs for only 100 or 1000 steps respectively, the curves showing the

159 simulated navigational efficiency are non-monotonic: the navigational efficiency is dependent on

160 c_ϕ with a peak for $0 < w < 0.2$ similar to the result reported by Benhamou & Bovet (1992).

161 This indicates that even with zero error on forward persistence, a BCRW with a small number of

162 steps requires external navigational cues for efficient navigation.

163   %% Figure 1 about here %%

164   In the case where there is error on both the navigation and persistence components of the

165 movement process (i.e. $c_\delta, c_\phi < 1$), the solution given in Eq. (6) predicts that as the persistence

166 error increases (c_δ decreases), the navigational efficiency also decreases for all c_ϕ (solid lines in

167 Figure 1c-f). The predicted solution curves are (in general) non-monotonic with a peak indicating

168 a maximum navigational efficiency for an intermediate value of *w*. For low persistence errors

169 ($c_\delta = 0.99, \ 0.95, 0.9$ in Figure 1d-f) the maximum navigational efficiency occurs for $w < 0.5$,

170 and at lower values of *w* when c_ϕ is also small (higher navigation error). As the persistence error

171 increases ($c_\delta = 0.7, \ 0.5, \ 0.1$ in Figure 1g-i) the peak indicating the maximum navigational

172 efficiency shifts to the right corresponding to a larger value of the weighting given to navigation,

173 *w* (Figure 1g-i; Appendix S4). In general, the simulation results shown in Figure 1g-i show the

174 same qualitative behaviour as the predicted solution curves from Eq. (6). In contrast to the case

175 of zero persistence error, for the values of $c_\delta < 1$ considered here, there is very little difference

176 in the model predictions and simulated results for *n* = 100, 1000 and 10,000 steps (see Appendix

177 S5: Figure S1). The inclusion of even a small error on the persistence term means the effective

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178   long-term limiting solutions for navigational efficiency are reached much faster than the case

179   with zero persistence error.

180   %% Figure 2 about here %%

181   The location of the peak corresponding to the maximum navigational efficiency for each

182   of the curves in Figure 1d-i can be calculated directly from Eqs. (5) and (6). More generally, it

183   can be shown that Eq. (6) has precisely one turning point for $w \in [0,1]$, and this turning point

184   corresponds to the maximum predicted navigational efficiency (see Appendix S4). The values of

185   w leading to the theoretical maximum navigational efficiency, together with the predicted values

186   for this efficiency, are calculated from Eqs. (5) and (6) for a range of c_ϕ and c_δ, and are shown in

187   Figure 2a and 2b respectively. Figure 2c and 2d show the equivalent results from simulations of

188   the BCRW, and show a good qualitative match to the theoretical predictions. Figure 2a and 2c

189   highlight the result (also seen in Figures 1d-i) that when the persistence error is high ($c_\delta < 0.1$),

190   the maximum navigational efficiency occurs when giving a higher weighting to the navigation

191   term ($w > 0.9$), and when $c_\delta \approx 0$ this efficiency is given exactly by c_ϕ (Figure 2b and 2d) which

192   corresponds to pure taxis. However, when the persistence error is low ($c_\delta > 0.9$), the maximum

193   navigational efficiency typically occurs for $w < 0.5$ (more weighting on persistence than direct

194   navigation) even if the navigation error is also low (Figures 2a and 2c). Figure 2b and 2d

195   highlight that a high navigational efficiency can be maintained even when the navigation error is

196   large ($c_\phi < 0.5$) because of the weighting given to persistence: the contour corresponding to a

197   long-term navigational efficiency of 0.5 extends well below $c_\phi < 0.5$ (Figures 2b and 2d).

198

199   **4. Discussion**

200   We have developed the model of Benhamou & Bovet (1992) to include persistence error

201   and derived a mathematical approximation for the long-term navigational efficiency of this form

202   of BCRW. We have demonstrated how navigational efficiency depends on the weighting given

203   between navigation and persistence at each step of the movement process and the level of error

204   in each term (Eq. 6; Figure 1d-i). In Figure 2a, the area above the contour line corresponding to

205    $w = 0.5$ indicates the region of the parameter space where giving a lower weighting to direct

206   navigation cues and a higher weighting to persistence leads to the maximum long-term

207   navigational efficiency. Interestingly, the predicted contour line corresponding to $w = 0.5$

208   approaches $c_\phi = 1$ in Figure 2a, indicating that even with close to zero error on the navigation

209   cue, there is little loss of navigational efficiency by giving equal weight to persistence. This

210   potentially hints at some interesting evolutionary advantages for animals that balance forward

211   persistence and external navigation cues in this way: giving a high weighting to persistence can

212   improve overall navigation efficiency if the error on navigation cues is high ($c_\phi < 0.5$), and has

213   little detrimental effect if the error on navigation cues is low ($c_\phi > 0.9$).

214   The vector-weighted BCRW navigation model discussed by Benhamou & Bovet (1992)

215   did not include error on the persistence term and the results given in their paper were for a

216   BCRW with only 1000 steps. We have shown mathematically (Appendix S3 and Figure 1c) that

217   in this scenario the long-term maximum navigation efficiency is actually obtained when the

218   weighting on external navigation cues (taxis) tends to zero, i.e. $c_\theta \to 1$ as $w \to 0$. This may seem

219   like a counter-intuitive result, given that a movement process based purely on persistence with

220   no taxis is known to be a poor navigation strategy (Cheung, 2007). However, this result holds

221   only for the long-term limiting navigation efficiency, where the fact that there is zero error on

222   persistence means an animal can achieve maximum navigational efficiency simply by continuing

223 in the same direction as previously once it is moving in the target direction. At shorter time-

224 scales navigation will not be as efficient (Figures 1a-c), and the observed navigational efficiency

225 is dependent on the number of steps of the BCRW. A possible further extension of this work

226 would be to derive an expression for the navigational efficiency that is valid for a small number

227 of steps and not just the long-term limit. However, Appendix S5: Figure S1 demonstrates how

228 the sensitivity of the navigational efficiency to the number of steps in the BCRW is less when

229 persistence error is non-zero. When referring to the results in Figures 1a-c we are implicitly

230 assuming that a random walk with 1000 steps is 10 times longer than a walk with 100 steps and

231 so on. Instead, an alternative interpretation of the model and results is that the overall path length

232 is fixed and it is the reorientation frequency that changes (so that a single step in a 1000-step path

233 is 10 times shorter than that in a 100-step path). From Figure 1a-c, this then implies that in a

234 noisy environment an animal may improve its navigational efficiency by increasing its rate of

235 reorientation (effectively giving a larger sample size in the navigational averaging process).

236   The BCRW model considered here is deliberately simple but could easily be extended to

237 consider more complex scenarios, although this may come at the expense of analytical

238 tractability, and generalised predictions about navigation efficiency informed by mathematical

239 theory may not subsequently be possible. For example, our model assumes individuals do not

240 interact with conspecifics but the overall conclusions are similar to results observed by Codling

241 & Bode (2014, 2016) who used simulations to demonstrate that in social group navigation, the

242 most efficient navigational strategy was to give a high weighting to indirect cues (copying the

243 movement of other group members or using forward persistence), rather than relying on direct

244 navigational cues (taxis). Our BCRW model assumes a homogeneous environment with a fixed

245 target direction where navigation cues and errors do not vary in space or time. Additionally,

246   individual walkers do not change their movement behaviour over time or when in different

247   spatial locations. Many migrating animals will undertake other behaviours during the large-scale

248   navigation process (such as resting, foraging etc), or may change their behaviour in response to

249   their local environment. Peleg and Mahadevan (2015) developed a random walk model which

250   includes periods of purely persistent behaviour followed by a pause to reorient according to

251   external navigational cues. By repeating this behaviour, a walk which appears to be purely

252   persistent (a CRW) in the short term can then be described as a BCRW in the long term. This is

253   in contrast to our model where we assume the animal is continuously balancing persistence and

254   navigation (taxis) at every step of the movement path. Nevertheless, the relative weighting

255   between navigation and persistence in our model (w) can be directly compared to the relative

256   navigation reorientation frequency in the model of Peleg and Mahadevan (2015) since both

257   effectively give a way to balance persistence and navigation. In the context of group navigation,

258   Bode et al. (2010) used a similar approach and considered a model where the behaviour of an

259   individual at each step was probabilistic and chosen to be either purely persistent or purely local

260   navigation. The probability of choosing persistence against navigation in this model could be

261   directly compared to the relative navigation weighting (w) in our model.

262   Predictions from our model about how animals should (in theory) balance persistence and

263   external navigation cues (taxis) to give the highest navigational efficiency should be tested and

264   compared to observations from empirical data. One of the most interesting model predictions is

265   shown in Figure 2a, where in the parameter region above the $w = 0.5$ contour line (corresponding

266   to values of approximately $c_\delta > 0.8$ for low navigation error, $c_\phi < 0.5$, and $c_\delta > 0.9$ for

267   medium levels of navigation error, $0.5 < c_\phi < 0.9$), it is more efficient to give a higher

268   weighting to persistence than direct navigation cues. Directly comparing empirically reported

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values of c_δ across the literature is known to be difficult since processing and sampling of the data can change the estimated forward persistence of an observed path (Bovet & Benhamou, 1988; Codling & Hill, 2005). Nevertheless, high values for c_δ have been reported for a wide range of species including insects and nematodes ($0.62 \leq c_\delta \leq 0.94$ in Byers, 2001), elk (c_δ=0.68 in Fortin et al. 2005), dolphins (c_δ= 0.8 in Bailey & Thompson, 2006), foraging seabirds ($c_\delta =$ 0.885 for movement mode 3 in Boyd et al. 2014), and reindeer ($c_\delta = 0.84$ for exploratory movement state 2 in Langrock et al. 2014). Hence, it seems clear that many animal species are capable of moving in a highly persistent manner if they choose to do so. The relative weighting between navigation and persistence in the movement behaviour of a prairie butterfly was considered by Schultz and Crone (2001). They found that when returning to within 10-22m of their home habitat they were observed to use a BCRW movement that balanced persistence with navigation with a weighting of $w = 0.38$ (female) and $w = 0.29$ (male). However, the authors did not explore the levels of navigation and persistence error within the observed butterfly movement paths. Fortin et al. (2005) considered the balance between forward persistence and directed movements up-slope in the winter foraging of elk. Using a log-likelihood test, they showed that a BCRW model fitted the data better than the alternative of a pure BRW or a pure CRW, and that the weighting on directional bias was $w = 0.17$, implying that almost five times more weighting was given to persistence than localised up-slope directed movements. The results of Schultz and Crone (2001) and Fortin et al. (2005) provide empirical evidence that some animals do give a high weighting to persistence rather than directed movement, although the contexts are slightly different to our abstracted navigation problem. In contrast, McClintock et al. (2012) used a multi-state generalised BCRW framework to analyse and describe the movements of grey seals near to localised centres of attraction (foraging areas or haul-out sites), and found

292 that when close to the centres of attraction, movement was almost entirely directed ($w > 0.99$).

293 However, the ecological context of their study (short-term foraging within a familiar territory) is

294 different to our problem (large-scale navigation via an external directional cue). In addition,

295 McClintock et al. (2012) didn't directly consider that localised forward persistence and

296 directional bias are often misclassified, especially in a short movement path, a fundamental

297 problem highlighted by Benhamou (2006).

298   A number of studies have considered strategies for maximising movement efficiency in

299 the context of foraging, although these are usually based on minimising energy expenditure

300 rather than optimising navigation efficiency. Fortin et al. (2003) demonstrated how theories from

301 optimal foraging related to energy maximisation did not seem to hold across varying temporal

302 scales, with other factors influencing movement behaviour becoming more important at larger

303 time-scales. Bartoń et al. (2009) used simulations to explore the survival of animals exploring a

304 patchy landscape using a BCRW movement model that balanced persistence with biased

305 movement towards patches of suitable habitat. They found that "…when an organism's ability to

306 detect patches decreases with distance from the patch, dispersal mortality is high if the organism

307 engages in a walk with a low degree of correlation. Thus, even if long distance detection of a

308 patch is poor, an individual can still have a good chance of surviving dispersal if it moves using a

309 more economical, highly correlated walk." Hence, although the model of Bartoń et al. (2009)

310 was based on short-scale localised navigation when foraging, their conclusions seem to be

311 consistent with the findings from our model, which is based on large-scale navigation. Further

312 work is now needed to test our model predictions and to determine in more detail how real

313 animals may balance persistence and taxis (and other possible mechanisms) when navigating

314 efficiently over a range of spatio-temporal scales.

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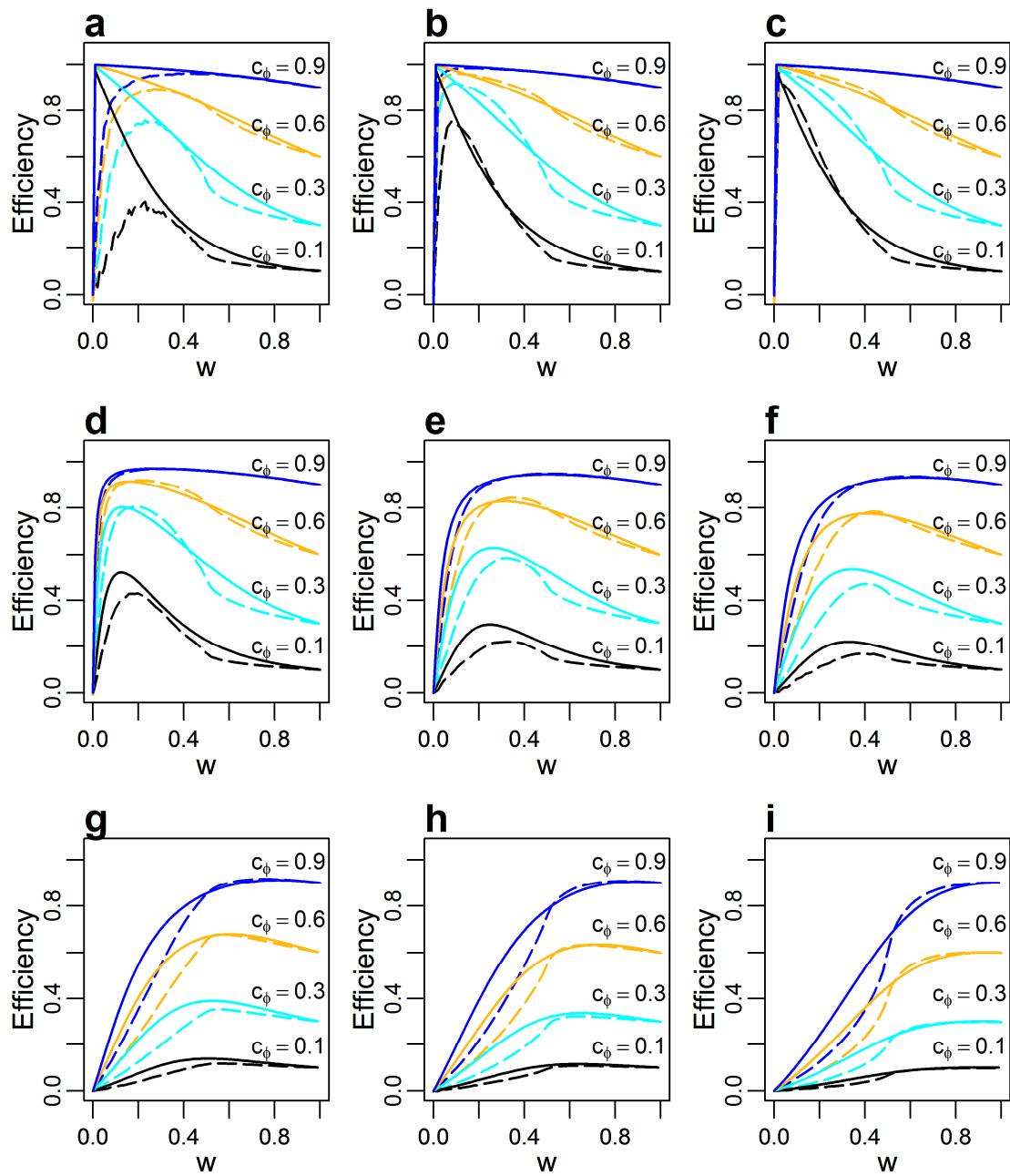
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Figure legends

Figure 1. Navigational efficiency of the vector-weighted BCRW model, c_θ, against weighting

factor on navigation, w, for a range of navigation error levels, $c_\phi = 0.1$ (black), $c_\phi = 0.3$ (cyan),

$c_\phi = 0.6$ (gold) & $c_\phi = 0.9$ (blue). In all plots the solid lines represent the theoretical model

predictions and the dashed lines represent the average results from simulations of 1000

individual random walkers; w ranges from 0 to 1 at 0.01 intervals. Plots (a-c) show results with

zero persistence error ($c_\delta = 1$) for walks with different total number of steps: a) 100, b) 1000, c)

10,000. Plots (d-i) show results for 1000 steps with persistence errors d) $c_\delta = 0.99$, e) $c_\delta = 0.95$,

f) $c_\delta = 0.9$, g) $c_\delta = 0.7$, h) $c_\delta = 0.5$, i) $c_\delta = 0.1$. Navigation and persistence errors were drawn

from zero-centred wrapped Normal distributions with parameters c_δ and c_ϕ respectively.

Figure 2. Heat maps showing (a) the weighting factor on navigation, w, that leads to the

predicted maximum navigation efficiency, and (b) the corresponding maximum navigation

efficiency values. Plots (c) and (d) show the respective average results from simulations of 1000

individual random walkers moving for 1000 steps. In each plot, c_δ and c_ϕ range from 0 to 1 at

0.01 intervals. Values of w ranging from 0 to 1 at 0.01 intervals were used to find the maximum

navigation efficiency for each combination of c_δ and c_ϕ. Navigation and persistence errors were

drawn from zero-centred wrapped Normal distributions with parameters c_δ and c_ϕ respectively.