

1 **Unpredictable movement as an anti-predator strategy**

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26 Prey animals have evolved a wide variety of behaviours to combat the threat of predation,  
27 and these have been generally well studied. However, one of the most common and  
28 taxonomically widespread antipredator behaviours of all has, remarkably, received almost  
29 no experimental attention: so-called 'protean' behaviour. This is behaviour which is  
30 sufficiently unpredictable to prevent a predator anticipating in detail the future position or  
31 actions of its prey. In this study, we used human 'predators' participating in 3D virtual reality  
32 simulations to test how protean (i.e. unpredictable) variation in prey movement affects  
33 participants' ability to visually target them as they move (a key determinant of successful  
34 predation). We found that targeting accuracy was significantly predicted by prey movement  
35 path complexity, although, surprisingly, there was little evidence that high levels of  
36 unpredictability in the underlying movement rules equated directly to decreased predator  
37 performance. Instead, the specific movement rules differed in how they impacted on  
38 targeting accuracy, with the efficacy of protean variation in one element depending on the  
39 values of the remaining elements. These findings provide important insights into the  
40 understudied phenomenon of protean antipredator behaviour, which are directly applicable  
41 to predator-prey dynamics within a broad range of taxa.

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43 **Keywords:** predator-prey interactions, anti-predator defence, unpredictability, virtual reality

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## 54 Introduction

55 Prey organisms have evolved a wide diversity of behavioural mechanisms to combat the  
56 threat of predation. These range from avoiding detection (for example through nocturnality  
57 [1-3], cryptic colouration [4] or living underground [5, 6]), to actively warding off attack (for  
58 example via thanatosis [7] or startle displays [8-10]), to fleeing away from a predator [11].  
59 Many antipredator behaviours, including those described above have received considerable  
60 empirical and theoretical attention and are generally well understood in terms of their  
61 function and mechanistic underpinning [12]. However, one of the most commonly observed  
62 and taxonomically widespread antipredator behaviours of all has, remarkably, received  
63 almost no experimental investigation: so-called 'protean' behaviour [13].

64 Protean behaviour is broadly defined as behaviour which is sufficiently unpredictable to  
65 prevent a predator from anticipating the future position or actions of its prey [13], and there  
66 are many anecdotal examples of animals engaging in this behaviour upon the detection of a  
67 predator. For instance, the erratic 'zig-zagging' behaviour observed in the dwarf blaasop  
68 pufferfish (*Torquigener flavimaculosus*) [14] and the wedge-snouted desert lizard (*Meroles*  
69 *cuneirostris*) [15], or the sharp turns and powered dives by the male budwing mantis  
70 (*Parasphendale agrionina*) [16] have all been hypothesised to make it harder for a predator  
71 to anticipate the animal's subsequent location, and hence make it harder to catch [13].  
72 These are potential examples of active protean movement (i.e. behaviour in which prey  
73 engage when they are aware of an immediate predatory threat), although, protean  
74 behaviour may also be displayed in a passive context as 'insurance'. By continuously  
75 displaying protean movement, prey animals may deter or unknowingly evade attacks from  
76 undetected predators [13]; for example many fly and butterfly species incorporate protean-  
77 like elements in their normal flight [17, 18]. However, despite the almost universal presence  
78 of putatively protean behaviour in the animal kingdom, only one study has empirically  
79 investigated whether this behaviour actually increases the chance of escaping [19].

80 In their study, Jones et al. [19] found, using human subjects 'preying upon' computer-  
81 generated moving prey, that individual prey items were harder to catch when their turning  
82 angles were drawn randomly from a relatively wide angular range (which they classed as  
83 'protean') than when their turn angles were selected (also randomly) from a relatively  
84 narrow angular range (which they classed as 'predictable'). This elegant study therefore

85 provides clear evidence that incorporating protean elements into an animal's movement  
86 can have positive anti-predator benefits, although by focussing solely on turning angle it  
87 does not consider that an animal's movement could be considered protean in various  
88 different ways. For example, animals may show unpredictable changes in speed or the  
89 distance travelled before turning, alongside (or even instead of) unpredictable turning  
90 angles; both of which would be predicted to make an animal's future position harder to  
91 predict. Furthermore, because in Jones et al.'s [19] study all prey items incorporated some  
92 element of unpredictability into their turns, it is unclear what would happen if prey moved  
93 in predictable, but non-trivial, ways, such as spiralling. This has been highlighted as a  
94 putatively protean escape behaviour in the take-off flight of Chironomid midges [13] and  
95 could occur, for instance, if movement parameters such as turning angle had fixed, rather  
96 than protean, values. Pulling apart the effects of these different movement elements is  
97 crucial to furthering our understanding of how a broad range of species respond to  
98 potential, and real, threats of predation.

99 In this study, we used human 'predators' playing a 3D virtual reality (VR) simulation to test  
100 how protean variation in one or more of these three movement elements (speed, the  
101 distance travelled between turns, and turn angle) influenced a predator's ability to target  
102 the prey item as it moved (a key determinant of successful predation; [20]), relative to prey  
103 that exhibited movement elements with fixed (and hence potentially predictable) values.  
104 We predicted that, as the number of movement elements that exhibited protean variation  
105 increased, this would result in increasingly unpredictable prey movement paths which  
106 would be more difficult to target.

107

## 108 **Methods**

### 109 Simulations

110 All simulations were created in the Unity3D game engine (Unity Technologies, San Francisco,  
111 USA), and built to run on a Samsung Galaxy S7 smartphone using the Samsung Gear VR  
112 system. Unlike simulations on a standard computer screen, where movement is confined to  
113 a restricted 2D space, within VR the participant can observe a full 360° 3D environment. This  
114 allows both a greater range of motion (e.g. objects can potentially move behind as well as in

115 front of the participant) and, crucially, the third dimension (allowing objects to be perceived  
116 as moving away from the participant). Simulations consisted of a black sphere (the 'prey')  
117 moving in a 3D virtual space centred on the participant. The prey had a radius of 0.1 m and  
118 was presented against a homogenous white background to maximise contrast. The high  
119 contrast between the prey item and its background, combined with the lack of visual clutter  
120 in the virtual environment, minimises the likelihood of attentional lapses (e.g. by excluding  
121 the possibility that attention is involuntarily drawn to salient features of the background)  
122 [21].

123 Prey movement consisted of a series of steps during each of which it travelled in a straight  
124 line in 3D space before turning and moving off on a different trajectory. This pattern of  
125 movement is commonly used in animal movement models and is characteristic of the  
126 movement patterns of a wide variety of species [22-24]. Movement of prey in the  
127 simulation was therefore determined by three parameters: the distance travelled in a  
128 straight line between turns (hereafter termed 'distance'), the time taken to travel over this  
129 distance ('speed') and the angle turned within a cone centred on the prey's direction of  
130 travel ('angle'). We considered that each of these parameters could be either 'fixed' (that is,  
131 the value assigned to a given prey item was randomly chosen but remained constant  
132 throughout a trial; see below) or 'protean' (the parameter value was randomly chosen each  
133 time the prey performed a particular behaviour, e.g. each time it turned). The specific values  
134 used were based on those obtained from pilot experiments, and were as follows: distance  
135 could take fixed values of either 1 m or 5 m (termed 'short' and 'long', respectively) or a  
136 protean value drawn from a uniform distribution on [1 m, 5 m]; speed could take fixed  
137 values of either 1 ms<sup>-1</sup> or 3 ms<sup>-1</sup> (termed 'slow' and 'fast', respectively) or a protean value  
138 drawn from a uniform distribution on [1 ms<sup>-1</sup>, 3 ms<sup>-1</sup>]; and angle could take fixed values of  
139 either 0.1π radians or 0.5π radians (termed 'narrow' and 'wide', respectively) or a protean  
140 value drawn from a uniform distribution on [0.1π radians, 0.5π radians]. In total, this  
141 resulted in 27 possible combinations of fixed/protean movement elements (e.g. short  
142 distance, fast speed and protean angle, and so on).

143 Within the simulation, participants were free to look around the virtual environment. A  
144 small, red circle (the reticle) was superimposed onto the centre of the participants' field of  
145 view and provided a point of reference for the participant to facilitate targeting, allowing

146 them to interact with moving prey objects in real time. We use the term ‘targeting’ to  
147 emphasise the similarities between this process and, for example, maintaining a target  
148 within a rifle’s sights (a process that requires the participant to move their head to maintain  
149 alignment with the target), although note that eye movements will be required to fine-tune  
150 tracking accuracy [21, 25]. Quantifying targeting accuracy using head movements alone is  
151 therefore likely to suffer from reduced stability (greater jitter), result in slightly slower  
152 response times, and be less sensitive to minor attentional lapses than when also considering  
153 eye movements [21], although importantly our simulated prey were not making subtle  
154 movements that could be tracked solely with the eyes (cf. [21, 25, 26]). Instead, they moved  
155 rapidly around the virtual environment, requiring participants to constantly move their head  
156 in order to keep the prey within their field of view. Targeting, as measured using head  
157 movements, therefore provides a useful overall measure of a participant’s ability to follow a  
158 fast moving prey item, while providing a measure of biological realism in the context of  
159 predator-prey interactions (where animals often align their head with the target before  
160 attack; e.g. [27, 28]).

161

## 162 Experimental protocol

163 A total of  $n = 40$  participants took part in this study (20 females and 20 males, with a mean  
164 age of 20.7 [range, 18 to 28]), all of whom were students of the University of Lincoln. Before  
165 providing consent to take part in the study, participants were given written information on  
166 the general aims of the study (although not the specific hypotheses being tested), what they  
167 would be asked to do, and the approximate time required to complete the study. Their age  
168 and gender were noted, but not linked to their experimental data.

169 When participants put on the headset to begin the simulation they were presented with a  
170 series of simple text instructions to familiarise them with the VR environment and  
171 demonstrate how to interact with objects within it. Each experimental trial presented the  
172 participant with one prey item to target. At the start of each trial, the prey was coloured red  
173 and appeared at a fixed default position (5 m directly in front of the participant) and  
174 trajectory (facing directly away from the participant). To start each trial, the participant used  
175 their head movements to position the reticle over the prey for 3 s. The prey item then  
176 turned from red to black to indicate that the trial had started, and began to move based on

177 the combination of fixed/protean movement rules it had been allocated for that particular  
 178 trial. Participants were instructed that their task was to constantly target the prey item, by  
 179 maintaining the reticle as close to its centre as possible as it moved around the virtual  
 180 environment. Each trial lasted 10 s and there were 27 trials in total per participant (one for  
 181 each possible combination of fixed/protean parameter values). The order of these trials was  
 182 randomised for each participant.

183

#### 184 Data collection

185 Data on prey location (its Cartesian coordinates in 3D space) and the participant's head  
 186 orientation (a 3D vector passing through a point between the participant's eyes and towards  
 187 the reticle) were collected every 0.02 s throughout each trial, and stored in anonymised text  
 188 files. At each time step, we subsequently calculated the minimum distance between a 3D  
 189 point representing the centre of the prey and a ray indicating the participant's head  
 190 orientation; if the reticle was directly over the centre of the prey this distance would be 0,  
 191 and would increase with as the reticle moved further away from the prey's centre. This  
 192 distribution of distance values was used to calculate the mean distance from the centre of  
 193 the prey over the 10 s of each trial, as a measure of overall targeting accuracy (where a  
 194 lower mean distance indicates better overall accuracy) and therefore the overall  
 195 effectiveness of prey 'behaviour' in terms of avoiding predation.

196 We also used the data on prey location to compute a measure of prey movement path  
 197 complexity in each trial, using the information-theoretic approach described by Herbert-  
 198 Read et al. [29]. This method assigns a numeric value to each path, such that more complex  
 199 paths receive higher values, and so provides an objective measure of how 'protean' each  
 200 movement path was. In brief, we constructed an embedding matrix  $\mathbf{M}$  containing the 3D  
 201 positions of the prey over the time window  $t, t + 1, \dots, t + n$  (where here  $n$  was simply the  
 202 total number of positions recorded during each 10 s trial). The  $x$  component of the  
 203 embedding matrix  $\mathbf{M}_x$  was derived from the  $x$  coordinates of the positions, such that

$$\mathbf{M}_x = \begin{bmatrix} x_t & x_{t+1} & \cdots & x_{t+n/2} \\ \vdots & \vdots & \ddots & \vdots \\ x_{t+n/2} & x_{t+n/2+1} & \cdots & x_{t+n} \end{bmatrix}, \quad (1)$$

204 with  $\mathbf{M}_y$  and  $\mathbf{M}_z$  derived similarly from the  $y$  and  $z$  coordinates, respectively. The full  
205 embedding matrix is then simply given by  $\mathbf{M} = [\mathbf{M}_x \mathbf{M}_y \mathbf{M}_z]$ . We next subtracted the mean  
206 from each column of  $\mathbf{M}$ , before extracting the vector of singular values  $s$  from its singular  
207 value decomposition. Each singular value was normalised by dividing it by the sum of all  
208 singular values, to give  $\hat{s}$ , and the complexity of the movement path,  $H$ , taken as the  
209 entropy of the distribution of the singular values

$$H = - \sum_{i=1}^n \hat{s}_i \log_2 \hat{s}_i. \quad (2)$$

210 Representative movement paths, of varying complexity, are given in Figure 1.

211

### 212 Statistical analysis

213 All analyses were conducted using general linear mixed-effects models (glmm) in R version  
214 3.3.2, using the lmer function in the lme4 package [30]. We first tested whether path  
215 complexity predicted targeting accuracy, regardless of the specific movement rules  
216 underpinning each path. Log<sub>10</sub>-transformed targeting accuracy was included as the  
217 dependent variable, with path complexity as a continuous predictor and trial order as a  
218 covariate to control for possible learning or fatigue effects over consecutive trials. Each  
219 participant's anonymous identifier was included as a random effect to control for repeated  
220 data from the same individual. Significance was determined by comparing the full model to  
221 a reduced model lacking the term of interest using a likelihood ratio test [31]. The validity of  
222 the model assumptions was confirmed by visually assessing the normality of the model  
223 residuals.

224 We next considered how the number of protean elements making up the movement rules  
225 for each path (which could range from 0, when all three movement parameters had fixed  
226 values, to 3, when all three parameters were protean) affected both path complexity and  
227 participant performance. Either log<sub>10</sub>-transformed targeting accuracy or log<sub>10</sub>-transformed  
228 path complexity was included as the dependent variable, with the number of protean  
229 movement elements as a fixed factor. As above, we also included trial order as a covariate  
230 and each participant's anonymous identifier as a random effect. As we would predict



231 systematic trends in the dependent variable as the number of protean movement elements  
232 increased, we additionally fitted polynomial (linear, quadratic and cubic) contrasts over  
233 successive levels of the fixed factor. For the analysis involving targeting accuracy, we tested  
234 whether the mean targeting distance was significantly different from 0.1 (the radius of the  
235 prey's body) by including an offset of 0.1 in the model and testing the significance of the  
236 intercept.

237 Finally, we considered whether the values assigned to the movement parameters predicted  
238 participant performance. Each model included  $\log_{10}$ -transformed targeting accuracy as the  
239 dependent variable, and the three movement parameters (distance, speed and angle, each  
240 with three levels), along with their three- and two-way interactions, as fixed factors. As  
241 above, we included trial order as a covariate and each participant's anonymous identifier as  
242 a random effect. In each case, a global model was initially fitted containing all explanatory  
243 variables and their interactions. A final model was then determined by stepwise exclusion of  
244 the least significant terms, starting with the non-significant highest order interactions and  
245 then non-significant main effects. The resulting minimum adequate model is presented. For  
246 significant factors we also tested for differences between factor levels using planned  
247 treatment contrasts, in which protean movement (the reference group) was compared to  
248 each of the other two levels. This allowed us to specifically test the relative efficacy of  
249 protean, compared to fixed, movement strategies.

250

## 251 **Results**

### 252 Path complexity

253 The complexity of prey movement paths significantly predicted participant performance,  
254 with participants exhibiting poorer accuracy (i.e. having a greater mean distance from the  
255 prey's centre) as path complexity increased (glmm:  $\chi^2(1) = 88.01$ ,  $p < 0.001$ ; Figure 2a).  
256 Moreover, path complexity itself was significantly predicted by the number of protean  
257 elements in the movement rules underpinning it ( $\chi^2(3) = 956.01$ ,  $p < 0.001$ ), with an  
258 increasing number of protean elements resulting in increased path complexity (cubic  
259 contrasts:  $p < 0.001$ ; Figure 2a,b). This in turn had a significant (although modest) effect on  
260 participants' ability to accurately target prey ( $\chi^2(3) = 24.07$ ,  $p < 0.001$ ; Figure 2a,c), with the

261 mean distance from the prey's centre increasing linearly (and targeting accuracy thereby  
262 reducing linearly) as the number of protean movement elements rose (linear contrasts:  $p =$   
263  $0.002$ ; Figure 2c). There was, however, considerable variation within these categories. In  
264 particular, even though prey with 0, 1 or 2 protean movement elements contained  
265 exemplars that were comparatively easy to target (i.e. on average participants were able to  
266 maintain the targeting reticle within the prey's 'body'; Figure 2c), targeting accuracy was  
267 comparatively poor for the majority of prey items across all categories (including the  
268 category with 0 protean movement elements). As such, the mean targeting distance was  
269 considerably outside the prey's body in each category, on average (all  $p < 0.001$ ; Figure 2c).  
270 This suggests that rather than targeting accuracy being simply a function of movement path  
271 complexity, the specific movement rules underpinning them may be important.

272

### 273 Movement rules

274 When considering the specific movement rules underpinning prey movement, and hence  
275 contributing to the observed variation in path complexity, targeting accuracy was  
276 significantly predicted by a single interaction between the speed at which the prey moved  
277 and the angle at which it turned ( $\chi^2(4) = 22.06$ ,  $p < 0.001$ ). Specifically, regardless of whether  
278 turning angle was narrow, protean or wide, accuracy was always significantly poorer for  
279 prey moving at high speeds than those exhibiting protean variation in speed (treatment  
280 contrasts: all  $p < 0.001$ ) and significantly poorer for protean speeds compared to low speeds  
281 (all  $p < 0.001$ ) (Figure 3). However, the relationship between targeting accuracy and turning  
282 angle differed depending on the speed of movement: at low speeds, accuracy was  
283 significantly poorer when prey turned at protean compared to narrow angles ( $p < 0.001$ ); at  
284 protean speeds, there was no difference in accuracy between turn angles; while at high  
285 speeds accuracy was significantly poorer when prey turned at protean angles compared to  
286 both narrow ( $p < 0.001$ ) and wide angles ( $p = 0.024$ ) (Figure 3).

287

### 288 **Discussion**

289 Previous studies have found that prey exhibit increased movement path complexity  
290 following a simulated threat (e.g. [29, 32]) with the (untested) assumption being that this

291 increased complexity makes targeting the prey harder, resulting in a reduced chance of  
292 predation. Here, we tested this assumption directly by quantifying the ability of human  
293 predators to target virtual prey which differed in the unpredictability of their underlying  
294 movement rules, and hence exhibited variation in their resultant movement path  
295 complexity. Our results provide direct empirical support for the overall prediction that  
296 increased path complexity results in a reduced ability to accurately target prey, although,  
297 surprisingly, there was little evidence that high levels of unpredictability in the underlying  
298 movement rules equated directly to decreased predator performance. Indeed, prey items  
299 that displayed no protean variation in their movement elements at all (and which typically  
300 travelled along a putatively 'predictable' spiralling path; e.g. see Figure 1) were found to be  
301 as difficult to target as prey exhibiting protean variation in all three movement elements  
302 (which moved along far more tortuous paths). This may explain the evolution of spiralling  
303 take-off behaviours observed in some insect species [13], which may be as effective as the  
304 more classically 'protean' erratic zig-zag-type behaviours in evading predators. It also  
305 suggests that the mathematical predictability of movement (as encompassed here by our  
306 measure of movement path complexity), while a good general predictor of predator  
307 performance, ignores the importance of specific movement parameters. Interestingly, here  
308 we found that the interaction between movement speed and turn angle was the best  
309 predictor of predator performance, while the distance between turns was of limited  
310 importance (and not included in the minimum adequate model). More specifically, the  
311 relative efficacy of turning behaviour (i.e. whether turns were narrow, protean or wide)  
312 differed as a function of speed, with the most effective protean behaviour involving a mix of  
313 protean and fixed elements (in this case high speeds and protean turn angles, regardless of  
314 distance travelled). This demonstrates that in terms of efficacy, the 'most protean'  
315 behaviour may not always be as effective as combinations of protean and fixed elements.

316 Our understanding of prey escape decisions has been advanced greatly by considering the  
317 fitness costs and benefits of escape, and economic models of escape behaviour have been  
318 used to provide qualitative predictions about aspects of escape behaviour [33]. In these  
319 models, the costs of escaping typically refer to the lost opportunities of engaging in other  
320 behaviours (such as feeding and engaging in social activities including courtship, mating and  
321 territorial defence), and the costs of escape are often considered relatively insignificant [34].

322 However, the energetic and/or cognitive costs of maintaining behaviours at the extremes of  
323 an animal's abilities, such as travelling at high speeds or turning at wide angles [34-36], or,  
324 in the case of protean behaviour, behaving unpredictably [19, 37] could be considerable.  
325 Animals may therefore be expected to optimise the trade-off between the increased  
326 chances of avoiding predation and the costs of engaging in protean behaviour. Our results  
327 suggest that engaging in escape behaviour that is potentially less cognitively or energetically  
328 challenging, but equally efficacious in terms of predator avoidance (such as spiralling), may  
329 offer animals a solution to this trade-off. However, the specific ecological conditions that  
330 allow the evolution of these different types of behaviour are still to be established.

331 Literature examples of real world predator–prey pursuits show a great variation in strategies  
332 that vary based on several factors (e.g. the type of predator [solitary or pack hunters] or the  
333 difference in size between predator and prey). For example, prey pursued by a single  
334 predator tend to use sharp turns [38] while prey fleeing from multiple predators will often  
335 make few or no turns and try to outrun them [39, 40]. However, active evasion of predators  
336 may not be the only successful strategy: for example, in a recent study Combes et al. [17]  
337 reported that fruit flies (*Drosophila melanogaster*) attacked on the wing by dragonflies  
338 (*Libellula cyanea*) rarely responded with evasive manoeuvres; instead, the flies performed  
339 routine, erratic turns during flight (i.e. passive protean behaviour; *sensu* [13]) which were  
340 responsible for more failed predation attempts than active evasive manoeuvres. We note,  
341 though, that whether prey adopt a constitutive or induced anti-predator strategy may  
342 depend strongly on the prevailing environmental conditions: the former is likely to be better  
343 when predation pressure is constant, or at least predictable; the latter when predation is  
344 variable or difficult to predict. The fact that the results from our virtual study into protean  
345 behaviour are in agreement with those from a real-life system highlights the benefits of a  
346 virtual approach in the study of adaptive prey behaviour. For example, the use of easily  
347 manipulable artificial prey circumvents animal welfare concerns and allows the rapid  
348 generation of large sample sizes. Furthermore, our novel approach to this study through the  
349 use of VR allowed targeting within a three-dimensional space, allowing prey to flee *away*  
350 from a predator (the most common behavioural response of a fleeing animal [12], thereby  
351 conferring a greater degree of realism over previous two-dimensional approaches (e.g.  
352 [19]), at least for simulated animals that 'fly' or 'swim' within a three-dimensional

353 environment. In our study, participant performance was assessed by their ability to  
354 consistently and accurately target moving prey items using head movements alone,  
355 although in humans (and most likely many other animals) visual attention is in fact a  
356 function of both head movements and accompanying eye movements [26, 41]. Our  
357 approach, while providing sufficient resolution to uncover clear relationships between  
358 protean movement and participant performance, may nonetheless benefit by  
359 simultaneously considering the movement of the eyes, particularly in terms of reducing  
360 noise, recording faster response latencies, and detecting subtle attentional lapses of the  
361 sort that may be important in the precise local tracking of an erratically moving target [26].

362 In summary, we can draw several general conclusions about protean behaviour from this  
363 study. Firstly, incorporating protean variation into a prey's movement can improve the  
364 chances of escaping predators; however, more important with respect to avoiding predation  
365 were the interactions between these different movement rules. Interestingly, here we  
366 found that the 'most protean' behaviour was not the most effective at avoiding predation.  
367 In fact the most effective behavioural strategy incorporated a combination of protean and  
368 fixed elements. To put the results of this study into a broader context, here we have  
369 provided strong experimental support for the widely-held assumption that protean  
370 strategies can reduce chances of predation, and have determined how the individual  
371 behavioural rules that make up prey movement can interact to affect the overall efficacy of  
372 protean behaviour. Our virtual methodology into the study of adaptive behaviour,  
373 combined with the parallels between our results and those from real-world systems  
374 demonstrates the utility of this approach.

375

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379

### 380 **Data accessibility**

381 Data used in the analyses reported here are available from the Dryad data repository  
382 (doi:10.5061/dryad.9h95737).

383

384 **Ethics**

385 This project was approved by the College of Science ethics committee at the University of  
386 Lincoln (reference CoSREC265).

387

388 **Competing interests**

389 The authors declare that they have no competing interests.

390

391 **Author contributions**

392 All authors designed the study, G.R. collected the data, G.R. and T.W.P. conducted the  
393 statistical analysis, and all authors wrote the paper.

394

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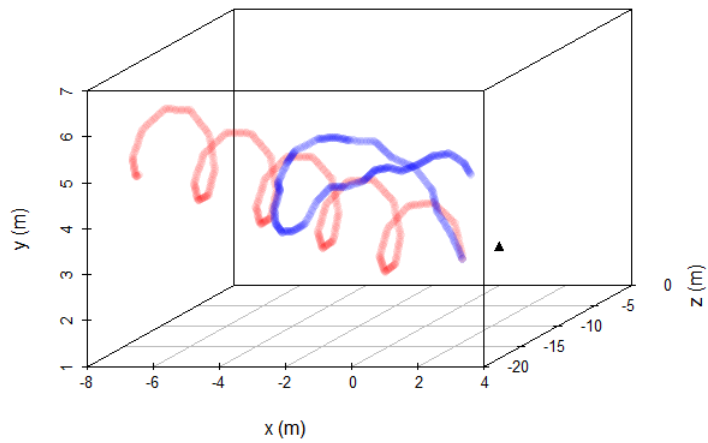
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498 Figure 1. Representative movement paths from a prey with all fixed movement parameters  
 499 (red; which has a path complexity of 1.53) and a prey with all protean movement  
 500 parameters (blue; which has a path complexity of 2.29). The black triangle denotes the  
 501 location of the participant's head in each case, and all prey start from the same position.

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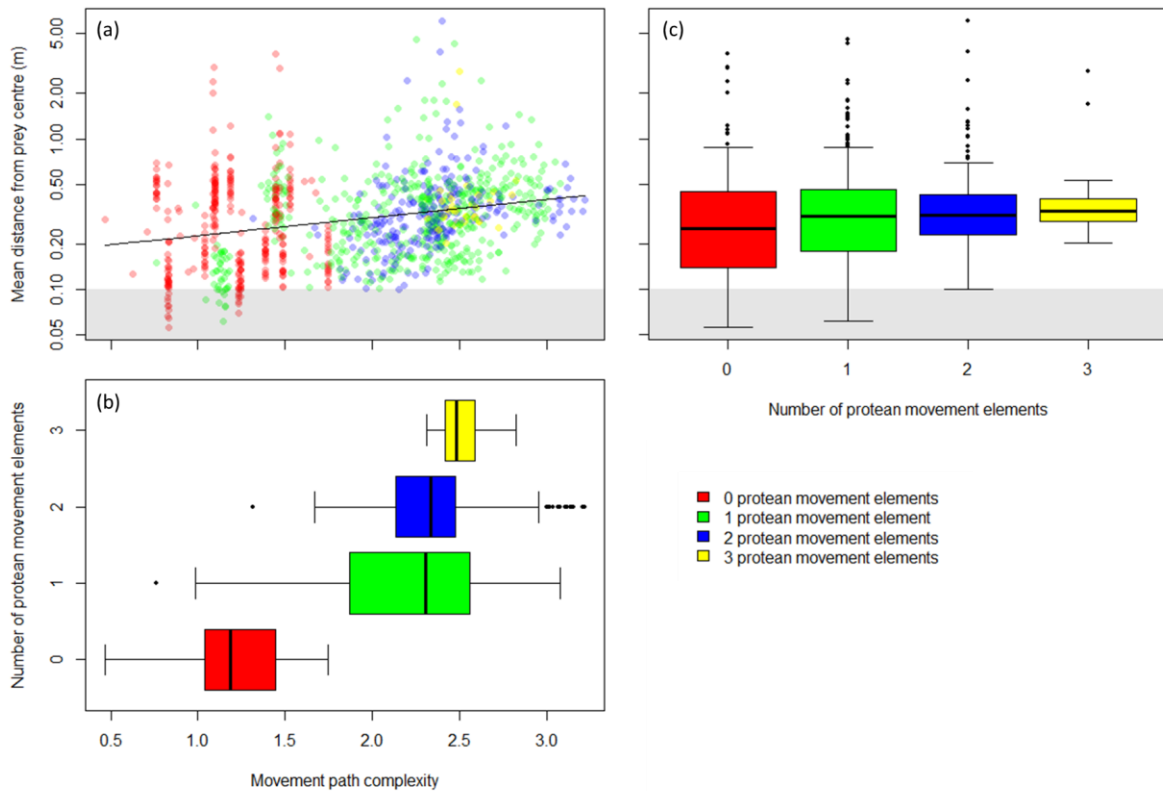
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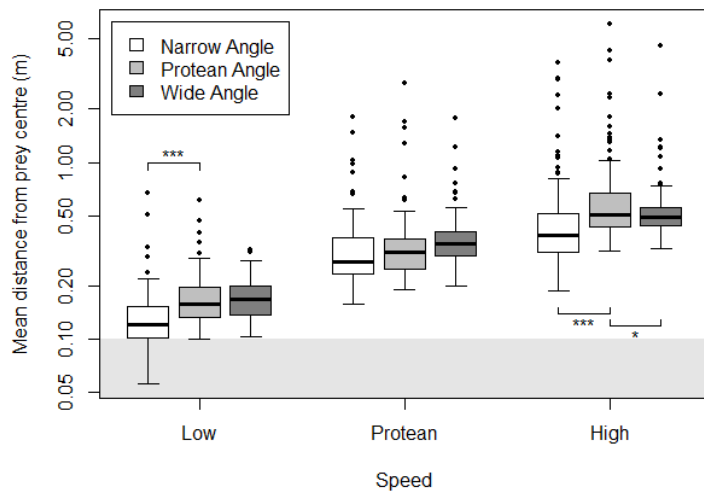


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518 Figure 2. (a) Targeting accuracy (measured as the mean distance from the centre of the prey  
 519 item over the course of a trial) as a function of movement path complexity. Higher values  
 520 along the x-axis denote more complex movement paths, while higher values along the y-axis  
 521 denote poorer targeting accuracy. Note the log scale on the y-axis. Each data point  
 522 represents a single simulated prey item, and is coloured according to how many protean  
 523 movement elements it had. The solid line denotes the glmm model fit, and the grey shaded  
 524 area indicates distances within the 'body' of the prey item. For any data point within this  
 525 shaded area, participants therefore managed to maintain the targeting reticle over the  
 526 prey's body throughout the entire trial, on average. (b) Movement path complexity as a  
 527 function of the number of protean movement elements, and (c) targeting accuracy as a  
 528 function of the number of protean movement elements. Thick lines denote the median,  
 529 boxes the interquartile range, lines the range of the data, and dots denote potential  
 530 outliers.

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534 Figure 3. Targeting accuracy (measured as the mean distance from the centre of the prey  
 535 item over the course of a trial) as a function of Speed (which was categorised as Low,  
 536 Protean or High) and Angle (which could be either Narrow, Protean or Wide); please see  
 537 text for full details. Higher values along the y-axis denote poorer targeting accuracy (note  
 538 the log scale). Thick lines denote the median, boxes the interquartile range, lines the range  
 539 of the data, and dots denote potential outliers. The grey shaded area indicates distances  
 540 within the 'body' of the prey item. Asterisks (\*) denote significant differences between  
 541 levels of Angle at each given level of Speed: \*  $p < 0.05$ ; \*\*\*  $p < 0.001$ .