

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.

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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^{-1} or 3 ms^{-1} (termed 'slow' and 'fast', respectively) or a protean value
138 drawn from a uniform distribution on [1 ms^{-1} , 3 ms^{-1}]; 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. Log₁₀-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 log₁₀-transformed targeting accuracy or log₁₀-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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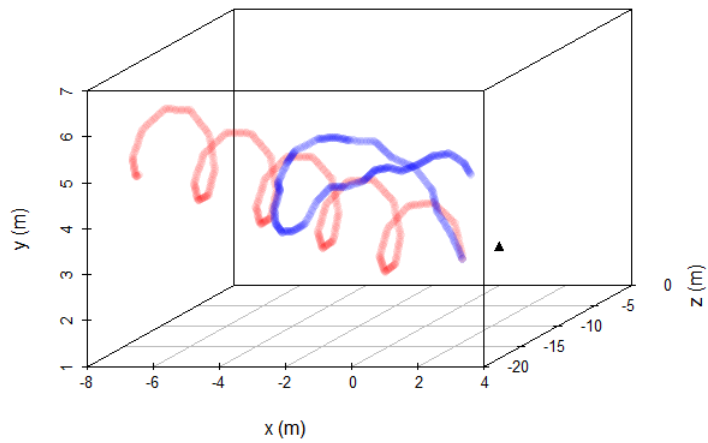
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498 Figure 1. Representative movement paths from a prey with all fixed movement parameters
 499 (red; which has a path complexity of 1.53) and a prey with all protean movement
 500 parameters (blue; which has a path complexity of 2.29). The black triangle denotes the
 501 location of the participant's head in each case, and all prey start from the same position.

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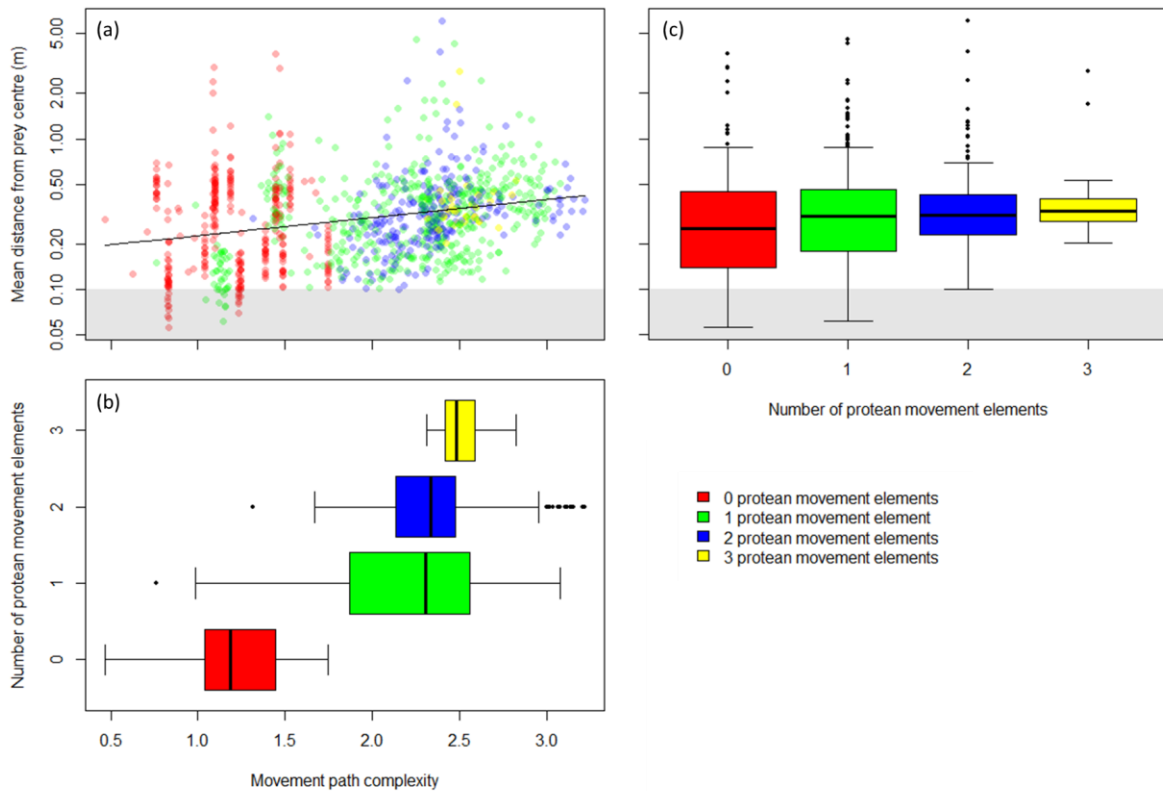
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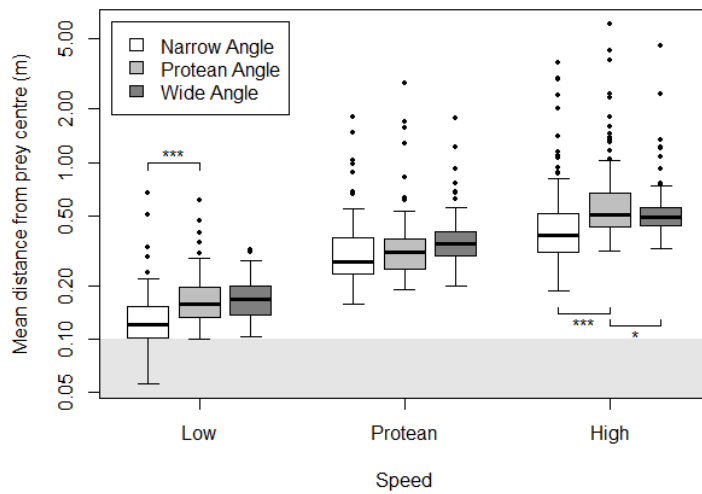


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518 Figure 2. (a) Targeting accuracy (measured as the mean distance from the centre of the prey
 519 item over the course of a trial) as a function of movement path complexity. Higher values
 520 along the x-axis denote more complex movement paths, 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: * $p < 0.05$; *** $p < 0.001$.