

1        **Avoiding attack: How dune wasps leverage colour and motion to detect their**  
2 **cryptic spider predators**

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### 16 ABSTRACT

17

18 Ambush predators depend on cryptic body colouration, stillness and a suitable  
19 hunting location to optimise the probability of prey capture. Detection of cryptic  
20 predators, such as crab spiders, by flower seeking wasps may also be hindered by wind  
21 induced movement of the flowers themselves. In a beach dune habitat, *Microbembex*  
22 *nigrifrons* wasps approaching flowerheads of the *Palafoxia lindenii* plant need to evaluate  
23 the flowers to avoid spider attack. Wasps may detect spiders through colour and  
24 movement cues. We tracked the flight trajectories of dune wasps as they approached  
25 occupied and unoccupied flowers under two movement conditions; when the flowers  
26 were still or moving. We simulated the appearance of the spider and the flower using  
27 psychophysical visual modelling techniques and related it to the decisions made by the  
28 wasp to land or avoid the flower. Wasps could discriminate spiders only at a very close  
29 range, and this was reflected in the shape of their trajectories. Wasps were more prone  
30 to making errors in threat assessment when the flowers are moving. Our results suggest  
31 that dune wasp predation risk is augmented by abiotic conditions such as wind and  
32 compromises their early detection capabilities.

33

34 Keywords: visual sensitivity, flight trajectory, Anti-predator strategies, predator  
35 camouflage.

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### 37 INTRODUCTION

38 Prey strategies to avoid attack by ambush predators are more effective in the  
39 early part of the predation sequence (Pembury Smith and Ruxton, 2020; Ruxton et al.,  
40 2018). Ambush predators are often cryptic, with their body colouration matching their  
41 environment (Anderson and Dodson, 2015); they are very still since movement can  
42 break their crypsis (González and Rodríguez-Gironés, 2013); they often have venom to  
43 debilitate their prey (Schwantes et al., 2018) and most importantly they hunt at a  
44 moment when the prey is vulnerable, i.e., during foraging or mating -- when prey  
45 awareness is compromised (Pembury Smith and Ruxton, 2020). Therefore, for a prey to  
46 overcome an ambush predator's strategy, evaluation of a risky site is crucial.

47 A prey's ability to detect an ambush predator is constrained by its perceptual  
48 capabilities either through chemical or visual mechanisms (González and Rodríguez-  
49 Gironés, 2013). Visual detection of a predator depends on the spectral sensitivity of the  
50 prey's eye (the ability of the eye to respond to specific wavelengths of the light  
51 spectrum; Cronin et al., (2014)), spatial acuity (the capacity to discriminate shape and  
52 pattern details; Caves et al., (2018)) and temporal resolution (time taken to process  
53 visual information; Cronin et al., (2014)). Furthermore, abiotic factors such as wind or  
54 obstacles can add to the visual clutter in a habitat (Burnett et al., 2020; Hennessy et al.,  
55 2020) and consequently hinder predator detection.

56 The problem of detecting ambush predators is commonly faced by pollinating  
57 insects that approach flowers harbouring crab spiders (Araneae: Thomisidae) (Morse,  
58 1986). Crab spiders are famously cryptic -- their body colouration blends into the  
59 background of the flowers (They and Casas, 2009); some species are capable of  
60 changing their colour to match the flower (Oxford and Gillespie, 1998) and others are  
61 mottled in various shades (Rodríguez-Morales et al., 2018). This crypsis may serve to  
62 avoid detection by potential prey (Gavini et al., 2019; Morse, 1986), perhaps by  
63 interfering with search image formation. However, there is still controversy whether the  
64 intended receivers of the crypsis are prey or predators. Crypsis was found to be  
65 ineffective when considering the entire community of flower visiting potential prey  
66 (Brechtbuhl et al., 2010) and a recent study argued that crypsis in crab spiders reduce

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67 their risk of predation by birds (Rodríguez-Gironés and Maldonado, 2020). Though  
68 some crab spiders can increase the number of potential pollinators approaching the  
69 flower using deceptive signalling that exploit an insect's ability to perceive UV  
70 colouration (Heiling et al., 2003; Llandres and Rodríguez-Gironés, 2011; Vieira et al.,  
71 2017), several studies have shown that the presence of a spider on a flower deters  
72 pollinators (Robertson and Maguire, 2005; Yokoi and Fujisaki, 2008). Clearly, some  
73 pollinators are capable of detecting these spiders (Defrize et al., 2010; Reader et al.,  
74 2006) and minimise their risk by evaluating the flower before landing (Ings and Chittka,  
75 2008). What is not known, especially in natural conditions, is if insects can respond to a  
76 predation risk by altering their flight trajectories before landing and whether motion of  
77 the flowers affects their evaluation.

78 In this study, we evaluated the predator detection strategies of dune wasps  
79 (*Microbembex nigrifrons*; Hymenoptera: Crabronidae) as they approached a spider  
80 occupied *Palafoxia lindenii* flowerhead under two conditions of wind induced  
81 movement, i.e., when the flower was still and when it was moving. We measured the  
82 appearance of the flower and spider using psychophysical visual modelling from the  
83 perspective of a hymenopteran visual system and related the appearance to changes in  
84 wasp flight trajectories and landing decisions. If a wasp can detect the presence of the  
85 spider, we expected that their flight characteristics would reflect it and that the wasp  
86 would be able to detect spiders more easily when the flowers were still.

87

### 88 METHODS

#### 89 Study site and species

90 The study was conducted in February and May 2019 at the Centro de  
91 Investigaciones Costeras La Mancha (CICOLMA), situated on the coast of the Gulf of  
92 Mexico (19° 36' N and 96° 22' W). *Palafoxia lindenii* A. Gray (Asteraceae) is an endemic  
93 dune pioneer species with white and purple inflorescences (hereafter 'flowerhead';  
94 (Álvarez-Molina et al., 2013). *Mecaphesa dubia* (Araneae: Thomisidae) is a colour-  
95 polymorphic spider that is frequently found on these flowerheads, either on top or to  
96 the side (i.e., on the receptacle). The most frequent colour morphs were white and

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97 purple (Rodríguez-Morales et al., 2018). *Microbembex nigrifrons* (Hymenoptera:  
98 Crabronidae) nests in dunes near vegetation (Evans et al., 2009), and feed on the pollen  
99 and nectar of *P. lindenii* flowers. These wasps are known to use visual cues to locate  
100 their nests and adult wasps provision their nests with dead arthropods (Alcock and  
101 Ryan, 1973).

### 102 Visual Modelling

103 We quantified the visual appearance of the spiders as perceived by the wasp visual  
104 system at different distances using multispectral standardized images of female  
105 *Mecaphesa dubia* (n = 8) spiders positioned on the side and the top of the *Palafoxia lindenii*  
106 flowerhead. To do so, we took photos of the spider in both parts of the flowerhead  
107 using an Olympus Pen E-PM2 camera (converted to full-spectrum) with a UV  
108 transmitting EL-Nikkor 80 mm f/5.6 lens attached. We took two type of photos: one  
109 using a Baader Venus UV pass and the other with UV/IR cut filters, to obtain images in  
110 the ultraviolet (~ 300–400 nm) and in the human visible part of the spectrum (~ 400–700  
111 nm) respectively. Each photo included two reflectance standards of 93% and 7% as well  
112 and a scale, and for a light source, we used an Iwasaki EYE Color arc lamp (70 W 1.0 A;  
113 Venture Lighting Europe Ltd., Hertfordshire, UK) with the UV block filter manually  
114 removed. The photos were saved in RAW format and processed using the Multispectral  
115 Image Calibration and Analysis (MICA) toolbox (Troscianko and Stevens, 2015) for  
116 ImageJ (v 1.52a), resulting in multispectral files with reflectance values of the spiders in  
117 the different position of the flowerhead.

118 Each multispectral file was converted to quantum catch files used in an integrative  
119 analysis by means of Quantitative Pattern Colour Analysis (QCPA) of the MICA  
120 toolbox. This is a framework based on the Receptor Noise Limited (RNL) model  
121 (Vorobyev and Osorio, 1998) and includes spectral sensitivity and visual acuity (Cronin  
122 et al., 2014). Since there is no information about the visual system of *M. nigrifrons* with  
123 respect to the visual traits mentioned above, we created a model wasp visual system  
124 using the data available for closely related species.

125 Thus, for the colour vision we used a reconstruction of the spectral sensitivity of  
126 *Philanthus triangulum* Fabricius (Sphecidae) with sensitivity peaks at: UV = 344, SW =

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127 444, and MW = 524 (Peitsch et al., 1992). For the RNL model, we used the Weber  
128 fraction ( $w = 0.13$ ) and the relative density for each receptor class (1:0.471:4.412 ratios for  
129 the UV:SW:MW receptors, respectively) based on the honeybee vision (Defrize et al.,  
130 2010). To model the visual acuity, we used the minimal resolvable angle value reported  
131 for *Bembix palmata* Smith (Crabronidae) equal to 1.22 cycles per degree (Feller et al.,  
132 2021).

133 We used the 'Colour Maps' approach to represent and delimit the entire visual scene  
134 combining visual acuity and spectral sensitivity data in a perceptually calibrated  
135 Hymenopteran trichromatic colour space (van den Berg et al., 2019). We estimated the  
136 portion of overlap between the spider and the flowerhead as perceived by the bee. The  
137 higher the overlap, the less likely it is for the viewer to perceive differences between the  
138 spider and the flowerhead. Finally, to have a representation of the noise reduction  
139 subsequent to visual acuity correction (Ligon et al., 2018) and recovering chromatic and  
140 luminance edge information, we included a RNL Ranked Filter based false colour  
141 image which is a representation of the colours using the wasp visual system we created.  
142 However, due to a lack of behavioural validation of the detection thresholds in the  
143 wasp, we use this image for visualisation purposes only. We compared the perceptual  
144 overlap of the colour maps generated for the spider and the flowerhead at different  
145 distances, in each position, by means of a Kruskal-Wallis test with a *Post-Hoc* Wilcoxon  
146 test done in the R statistics package.

147

148 Flight trajectories of *M. nigrifrons*

149 We filmed wasps approaching *P. lindenii* flowerheads with a high-speed camera  
150 (Chronos 1.4, 500 fps, Krontech.com) with two wind treatments (Moving or Still) and  
151 the following conditions: 1. Flowerheads without spiders (Control, Moving:  $n = 9$ ; Still,  
152  $n = 6$ ), 2. Flowerheads with live spiders tethered on the side (Side, Moving:  $n = 6$ ; Still,  $n$   
153  $= 8$ , Fig. 1A), 3. Flowerheads with live spiders tethered on the top (Top, Moving:  $n = 8$ ;  
154 Still,  $n = 6$ , Fig. 1B). Spiders were tethered to the flowerheads by means of a dental floss  
155 strand affixed to their ventral side with a non-toxic glue and placed into position with a  
156 pin. We stabilized flower stalks with a stick for the Still treatment and used freely

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157 moving stalks for the Moving treatment. This ensured that the constant sea breeze  
158 generated flower movement in the Moving treatment, but we did not control for extent  
159 of movement. The mean fluctuation of the flowers, as measured by the distance  
160 between the centre of the flower between frames, was significantly lower (Mann  
161 Whitney test statistic = 78,  $p < 0.0001$ ) in the Still treatment in comparison with the  
162 Moving treatment. The cameras were placed at a distance of 1 m above the flowerheads,  
163 with the focal flower always centred; and the number of flowerheads per plant were  
164 similar. From the videos, the position of the centre of the flowerhead, head and  
165 abdomen of the wasp were manually tracked in 2D, using the MTrackJ plugin in ImageJ  
166 (Meijering et al., 2012). We recorded the following variables: Decision distance (i.e., the  
167 point where the wasp decides to land on or avoid the flower; this was recorded by  
168 visual inspection by one observer of the high-speed video in a frame-by-frame manner;  
169 see the red dot in Fig. 1 for an example), Inspection time (duration of flower  
170 observation, i.e., zig-zag flight, at close range), Outcome (whether the wasp avoided the  
171 flower or landed). From the coordinates of wasp position, we calculated the following  
172 metrics: Sinuosity index (a measure of deviation from a straight line) using the R  
173 package *trajr* (McLean and Skowron Volponi, 2018), the wasp's body axis angle with  
174 respect to the flower ( $0^\circ$  implies that the wasp was pointing directly at the flower) and  
175 speed.

176 Distance profile curves, i.e., distance between the wasp's position and the flower's  
177 position at every point of the trajectory, were compared with an unsupervised cluster  
178 analysis based on the Dynamic Time Warping distance method which retains shape  
179 information (Fu et al., 2008; Hu et al., 2013; Keogh and Ratanamahatana, 2005) using  
180 Mathematica ver. 12. In order to compensate for differences in length of trajectories (i.e.,  
181 some wasps flew for a longer time than others), we interpolated them such that all  
182 trajectories were of the same length. Trajectory data were coloured according to the  
183 distance to the flower, identifying four circular regions (at 2 cm, 5 cm, 10 cm, >10 cm)  
184 centred at the flower's position (Fig. 1). We then analysed the frequency of distance  
185 profile shapes with respect to the different treatments with contingency tests.

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186 To determine the direction of flight, we generated a line extending from the wasp's  
187 abdomen and head (in the direction of the head; i.e., body axis). We subsequently  
188 compared the body axis angles of wasps approaching still and moving spider-occupied  
189 flowers with a Watson-Wheeler Two sample test using the *circular* package in R  
190 (Pewsey et al., 2013).

191

### 192 RESULTS

#### 193 Visual modelling

194 We generated pseudo-colour images of the spiders on the flowerhead (Fig. 2A) that  
195 took into account both spectral sensitivity as well as visual acuity. The log Receptor  
196 Noise Limited (RNL) cluster modelling of the chromatic distances ( $\Delta S$ ), perceptual  
197 thresholds (1 Just-Noticeable Difference), and visual acuity of the wasp visual system  
198 showed that spiders may be detected only at a distance of around 5 cm from the  
199 flowerhead (Fig. 2B).

200 When comparing the overlap of the colour maps (Fig. S2) that represent the  
201 perception of the spider on the flowerhead by the wasp visual system with respect to  
202 the spider position, we found that the perceptual overlap is higher when the spider is  
203 on the top of the flowerhead ( $F = 19.7$ ,  $df = 1$ ;  $p < 0.001$ ) and at a larger distance away  
204 from the flowerhead ( $F = 5.23$ ,  $df = 3$ ;  $p = 0.004$ ; Fig. 2C). When the overlap is higher, the  
205 wasp would find it harder to visually separate the spider from the flower background.  
206 The interaction between position and distance was not significant. Thus, the perceptual  
207 overlap was significantly higher between 2 cm and 15 ( $p = 0.014$ ) or 10 cm ( $p = 0.004$ ),  
208 while there is no difference between the other pairwise comparisons.

#### 209 Wasp behaviour

210 Dune wasps approached flowers in a typical zig-zag flight (Fig. 3; see S1 for a video  
211 and S3 for a plot of all trajectories). Wasps were significantly more likely to land on  
212 flowers that were moving, irrespective of the presence of a spider (GLM, Logit Link,  $\chi^2$   
213 = 9.1,  $df = 1,37$ ,  $p = 0.003$ ; Fig. 4A) whereas spider location ( $\chi^2 = 3.2$ ,  $df = 2,37$ ,  $p = 0.193$ )  
214 and the interaction ( $\chi^2 = 1.3$ ,  $df = 2,37$ ,  $p = 0.512$ ) were not significant. There was no  
215 significant effect of spider or wind treatment on the distance at which they made a



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216 decision to avoid or land on the flower (GLM, Identity link function, Gamma  
217 distribution, Spider:  $\chi^2 = 0.0006$ ,  $df = 1,38$ ,  $p = 0.97$ ; Movement:  $\chi^2 = 1.39$ ,  $df = 1,38$ ,  $p =$   
218  $0.24$ ; Interaction:  $\chi^2 = 0.17$ ,  $df = 1,38$ ,  $p = 0.67$ ; Moving: Mean  $\pm$  S.D. =  $5.14 \pm 2.91$  cm,  
219 Still:  $6.45 \pm 3.16$  cm, Fig. 4B). However, there seems to be a trend that shows that wasps  
220 make their decisions earlier when approaching moving flowers. There was no effect of  
221 spider location (ANOVA:  $\chi^2 = 2.77$ ,  $df = 2,37$ ,  $p = 0.25$ ), movement ( $\chi^2 = 0.54$ ,  $df = 1,37$ ,  $p$   
222 =  $0.463$ ) or the interaction ( $\chi^2 = 1.99$ ,  $df = 2,37$ ,  $p = 0.36$ ) on inspection time.

### 223 Distance profiles

224 Spider location, flower movement and their interaction significantly influenced  
225 wasp distance profile sinuosity (GLM, Identity link function, Spider:  $\chi^2 = 7.75$ ,  $df = 2,37$ ,  
226  $p = 0.021$ ; Movement:  $\chi^2 = 10.87$ ,  $df = 1,37$ ,  $p < 0.001$ ; Interaction:  $\chi^2 = 7$ ,  $df = 2,37$ ,  $p =$   
227  $0.030$ ). Sinuosity was higher when the spider was on the side of the flowerhead in the  
228 still treatment, suggesting that wasps could respond to the presence of the spider in this  
229 condition.

230 The unsupervised DTW cluster analysis showed that the distance profiles (see Fig.  
231 3a1, 3b1 for examples) of all wasp trajectories separated into two main clusters  
232 (designated accordingly as *Sinuuous* and *Straight*; Fig. 5, see Fig. S4 for the distance  
233 matrix of the dendrogram). Contingency analysis of the frequency of type of distance  
234 profile showed that wasps had a straighter profile while approaching flowers without  
235 spiders and moving flowers with spiders (Fisher's Exact Test;  $p = 0.012$ ; Fig. 5 inset).

### 236 Body axis

237 Wasps consistently maintained a body axis angle centred on the flower (e.g., Fig.  
238 3a2, 3b2, see orange lines in Fig. 3A,B) in both treatments (Still angle in radians: Mean  $\pm$   
239 S.D =  $0.0066 \pm 0.50$ , Rayleigh Test of uniformity =  $0.88$ ,  $p < 0.001$ ; Moving angle in  
240 radians: Mean  $\pm$  S.D =  $-0.034 \pm 0.53$ , Rayleigh Test of uniformity =  $0.86$ ,  $p < 0.001$ ).  
241 Wasps approaching moving spider-occupied flowers were more likely to maintain their  
242 body axis angle on the flower location with higher peaks in the angle histogram  
243 (Watson's Two-Sample Test of Homogeneity, Test statistic =  $0.5872$ ,  $p < 0.001$ ; Fig. 6).

### 244 Speed

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245 Wasps slowed down as they approached the flower (e.g., Fig. 3 a3, b3), and the  
246 average slowdown in speed was significantly different between the wind treatments  
247 (Fig. 7A). Wasps approaching moving flowers reduced their speed at a steeper slope  
248 than those approaching still flowers (Linear Regression:  $R^2 = 0.828$ ,  $F_{1,1999} = 9613.74$ ,  $p =$   
249  $0.046$ ). Contrast post hoc analysis showed that wasps approaching still flowers were  
250 significantly faster than those approaching moving flowers at >10, 10 and 5 cm  
251 distances, whereas wasps approaching still flowers were significantly slower only at the  
252 2 cm distance (ANOVA,  $df = 7$ ,  $F_{2,1999} = 4809$ ,  $p < 0.0001$ ; Fig. 7B).

253

### 254 DISCUSSION

255 Dune wasps evaluate flowers for crab spider predators based on colour and motion  
256 cues, and their flight characteristics reflect their decision-making process. We found that  
257 though dune wasps locate and approach the flower from a distance, their decisions to  
258 land or avoid the flower occurs at a very close distance and this is due to the constraints  
259 of their perceptual system. When approaching moving flowers, wasps were more likely  
260 to land, had a straighter distance profile, steeper speed reduction and higher peaks in  
261 their body axis angle distribution targeting the flower.

262 Flight trajectories of insects are a useful window into their decision making process  
263 and can be used to understand their response to predation risk (Ings et al., 2011;  
264 Robertson and Maguire, 2005). For example, bumblebees that were trained to approach  
265 artificial flowers with cryptic or conspicuous artificial spiders showed a decrease in  
266 flight speed and an increase in inspection time after their first encounter with an attack  
267 (Ings et al., 2011). Bees were equally likely to avoid cryptic or conspicuous flowers, but  
268 their inspection times were longer for cryptic spiders (Ings et al., 2011). Wasp flight has  
269 so far been studied extensively, but largely from the perspective of learning flights, i.e.,  
270 how a wasp learns the position of its nest (Collett and Zeil, 1996; Stürzl et al., 2016; Zeil  
271 et al., 1996) and comparatively little information is available about foraging decisions in  
272 free flying wasps. Wasps probably use the motion of the typical zig-zag flight to acquire  
273 visual depth information of the object in question (Egelhaaf, 2012; Lehrer, 1996; Lehrer  
274 and Campan, 2004). In hoverflies, the zig zag flight (termed 'hesitation behaviour') was

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275 more often seen when they approached flowers with a dead spider, and the authors  
276 attribute this to wasp flight mimicry, but it is more likely that this flight pattern allows  
277 the insect to gather more visual information regarding the predator (Nityananda et al.,  
278 2014; Yokoi and Fujisaki, 2008) and the motion parallax generated which would also aid  
279 the insect in range estimation (Kral and Poteser, 1997).

280 We expected that wasps would detect the presence of the spider at a larger distance  
281 when approaching still flowers. We did not find a statistically significant effect but in  
282 general the trend suggests that wasps do have difficulty in evaluating moving flowers.  
283 However, our study was based on 2D trajectories and a 3D reconstruction of flight  
284 trajectories should give better measurements of distances. Furthermore, the fact that  
285 wasps responded to the presence of the spiders at a very close distance suggests there  
286 might be multimodal processes at play here, such as chemical detection. In an  
287 experiment looking at honeybee response to spider occupied flowers, it was shown that  
288 bees were less likely to land on flowers that had been previously been exposed to spider  
289 cues, even when the spider was not present at the time of approach (Reader et al., 2006).  
290 The spider's crypsis may be overcome by chemical detection, but since there is likely to  
291 be substantial variation in odour plume range and strength in natural conditions, a  
292 multimodal detection strategy is essential.

293 From the point of view of the spiders, there is an extensive literature on the effect  
294 of crab spider crypsis on potential pollinators (Dukas, 2019). The main lines of thought  
295 are as follows (*sensu* Brechbuhl et al. (2010)): 1. Spiders are cryptic to prey, 2. They are  
296 cryptic to predators, 3. They attract prey due to deceptive signalling, or 4. They can be  
297 detected and avoided by prey (i.e., no effect of crypsis). There is evidence for and  
298 against all four hypotheses, but using different crab spider species and different prey  
299 types. This variation in insect response to crab spiders (Rodríguez-Morales et al., 2019)  
300 can be attributed to the diversity in perceptual systems of the insects themselves. One  
301 would expect that if the main prey is of hymenopteran origin, then there would be a  
302 higher likelihood of successful evasion of predation in comparison to other insects that  
303 do not perform an inspection behaviour such as certain flies. Our study emphasises the

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304 need to take a species centric approach (*sensu* von Uexhill's *umwelt* (Caves et al., 2019;  
305 Uexküll, 2013)) to understand these interactions at a fine scale.

306 One of the unexpected results from our study was the relatively low frequency of  
307 wasp landings on unoccupied still flowers. We suggest that wasps are evaluating  
308 flowers, using both visual and olfactory cues (which we did not test), perhaps for traces  
309 of earlier visits by conspecifics or predators. Evaluating flowers for predation risk is  
310 significantly influenced by flower motion, suggesting that the cognitive processes  
311 needed to integrate all this information is compromised under certain abiotic conditions  
312 (Nityananda et al., 2014).

313 Our study shows that prey response to predators occurs at fine scales and the prey's  
314 perceptual biases play a significant role in assessing risk. To avoid an attack, wasps  
315 need to detect the predator at a close range and then respond by manoeuvring out of  
316 range before the attack occurs in order to maximise their escape rate.

317

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324

### 325 COMPETING INTERESTS

326 The authors declare no competing interests.

327

### 328 AUTHOR CONTRIBUTIONS

329 Data Collection - DRM, LRO

330 Writing Original Draft - DR

331 Writing & Revision- DR, DRM, HTM, LRO

332 Analysis - DR, DRM, HTM, LRO

333 Visualisation - DR, HTM, LRO

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- 334 Funding Acquisition - DR
- 335 Conceptualisation - DR, DRM
- 336 Project Administration DR, DRM
- 337
- 338

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### 339 FIGURE LEGENDS

340

341

342 Fig 1: Sample trajectory of a *Microbembex nigrifrons* wasp approaching an  
343 unoccupied *Palafoxia lindenii* flowerhead as seen from the top. Wasp positions are  
344 subsampled for clarity. The point when the wasp made a decision (in this case to avoid  
345 the flower) is highlighted in red. Circles around the flowerhead represent the different  
346 distances used in the visual modelling analysis. The insets **A** and **B** show the *Mecaphesa*  
347 *dubia* spiders tethered above and to the side of the flowerhead respectively.

348

349 Fig 2: Colour modelling analysis summary of the Hymenopteran visual perception  
350 of *Mecaphesa dubia* spiders when located in the side or in the top part of the *Palafoxia*  
351 *lindenii* flowerhead at different observation distances (2, 5, 10, 15 cm). (A) False colour  
352 image simulating the perception of the wasp visual system. The image of the spider in  
353 the different parts of the flower were created for visualization purposes by assigning  
354 the colour blue, green and red for the UV, SW, and MW photoreceptor, respectively. (B)  
355 These panels show the results of a Receptor Noise Limited filter method, which  
356 performs noise reduction after the acuity control based on Gaussian filters while  
357 preserving chromatic and luminance edges, simulating spectral sensitivity and visual  
358 acuity of the wasp visual system at different distances of the spider located in the  
359 different parts of the flowerhead. (C) Using the wasp visual system created, we  
360 estimated the proportion of perceptual overlap between the spider and the flowerhead  
361 in the Hymenopteran colour space (higher overlap implies that it is more difficult for  
362 the viewer to perceive differences).

363

364 Fig. 3: Sample trajectories in two movement treatments: A: Still and B: Moving, showing  
365 body axes in orange lines. Grey circle shows the extent of flower movement. Time  
366 series of Distance profile (a1, b1), Speed (a2, b2) and Body axis angle (a3, b3) of the  
367 sample trajectories. All curves are colour coded according to the proximity to the flower  
368 with Grey (> 10 cm), Blue (10-5 cm), Green (5-2 cm) and Orange (< 2 cm)

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369 Fig 4A: Frequencies of wasps that landed on or avoided flowerheads. Moving flowers  
370 with spiders were more likely to be visited than still flowers with spiders. 4B: The  
371 distances at which wasps decided to avoid or land at the flower.

372

373 Fig. 5: Results of a Dynamic Time Warping cluster analysis of distance profiles (a proxy  
374 for the trajectory shape) of all wasps approaching flowerheads with no spider (green  
375 lines), a moving flower with a spider (orange lines) and a still flower with spider (blue  
376 lines). The frequencies of sinuous and straight profiles are shown in the inset. Wasps  
377 approaching moving flowers with spiders were more likely to show a straighter  
378 distance profile.

379

380 Fig. 6: Frequency distribution of all wasp body axis angles as they approached moving  
381 (orange bars) or still (blue bars) flower heads with spiders. 0 degrees implies that the  
382 wasp's body axis angle coincided with the flowerhead. Note that since wasps never  
383 turned around, the maximum extent of the body axis angle was always lesser than  $\pm$   
384  $90^\circ$ . Body axis angle distributions were significantly different between the two  
385 conditions, with higher peaks when wasps approached the moving flowerheads with  
386 spiders.

387

388 Fig. 7A: Normalised speed profiles of all wasps that approached moving (orange lines)  
389 and still (blue lines) flowerheads with spiders. The mean speed is shown with thicker  
390 lines. Wasps slowed down at significantly different rates as they approached the  
391 flowerheads. 7B: Boxplots showing median speed (notches) and mean confidence  
392 interval diamonds at different distance categories. Speeds were significantly greater in  
393 wasps approaching still flowers with spiders at the >10, 10 and 5 cm categories,  
394 whereas speed was greater in wasps approaching moving flowers at the 2 cm category.

395

396

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- 513 Supplementary files
- 514 S1: A sample video showing a wasp approaching an unoccupied still flowerhead.
- 515 S2: Colour maps that show the degree of overlap between the spider (a1), the  
516 flowerhead (f1) using the Hymenopteran colour space. See text for details.

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517 S3: All trajectories of wasp approaches to Moving (orange lines) and Still (blue lines)  
518 flowers. Note that the flowerhead is for illustrative purposes and not to scale.

519 S4: Distance matrix of the Dynamic Time Warp based unsupervised classification of  
520 distance profile of wasp trajectories.

521

# Figure 1



Figure 2

A

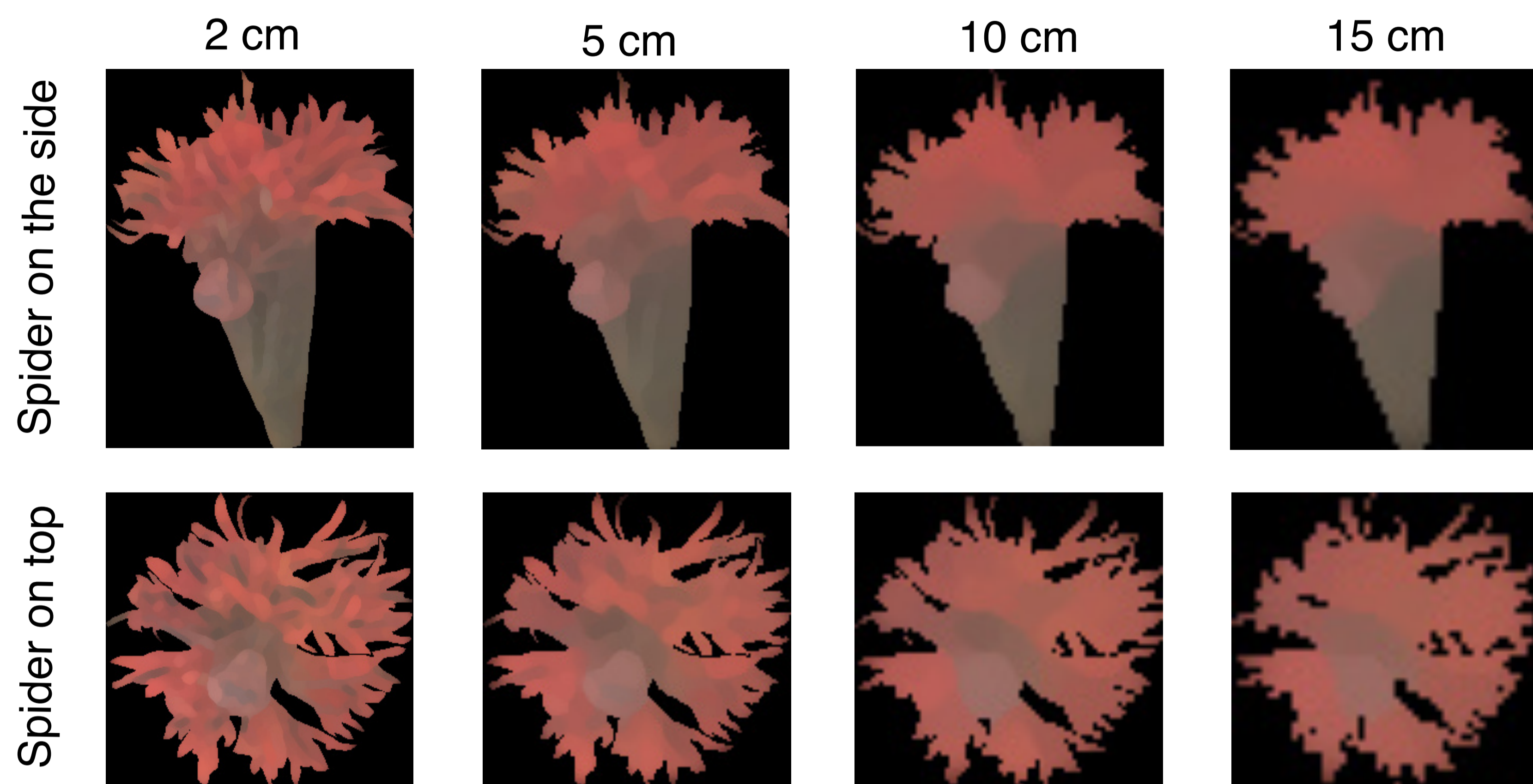


Spider on the side

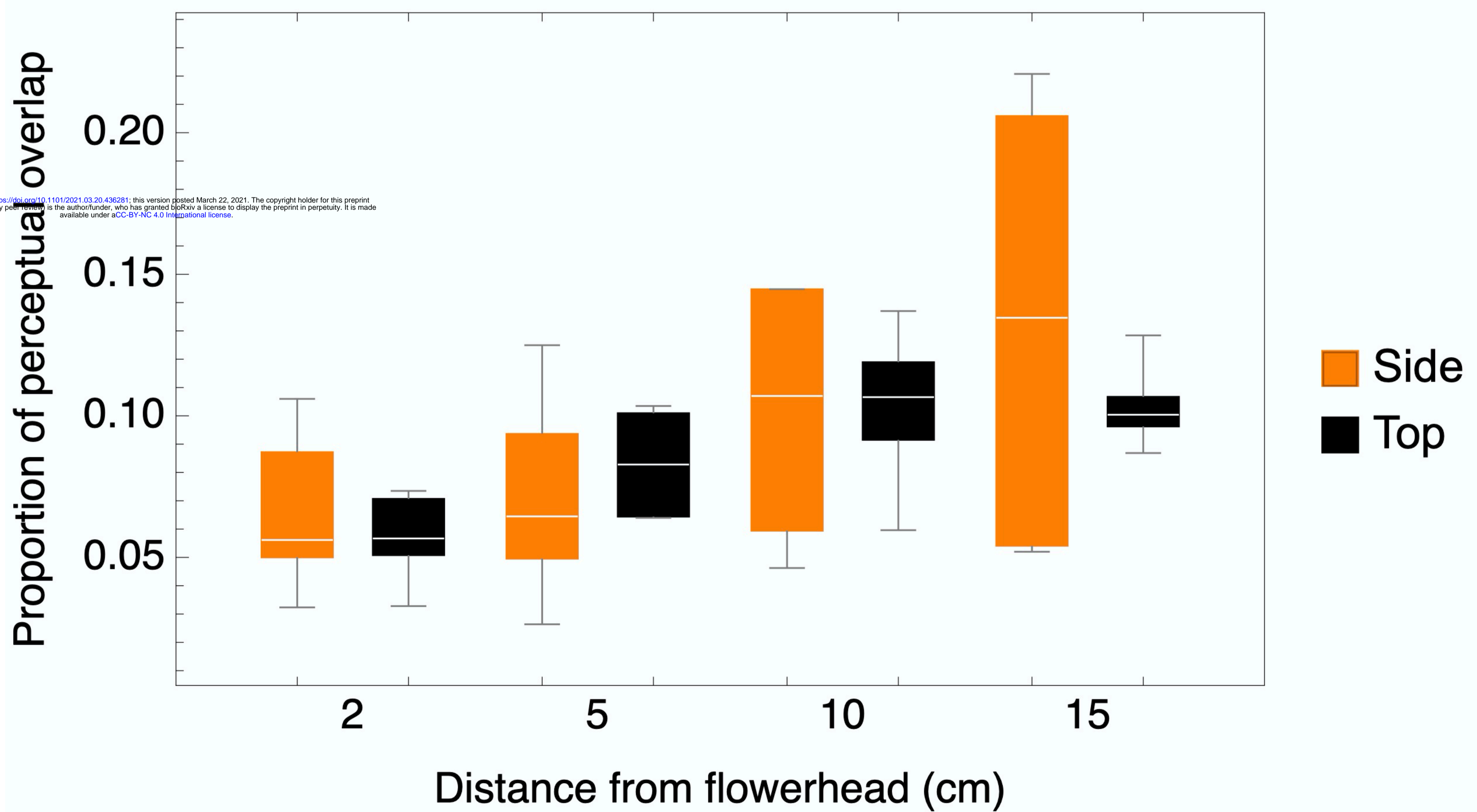


Spider on top

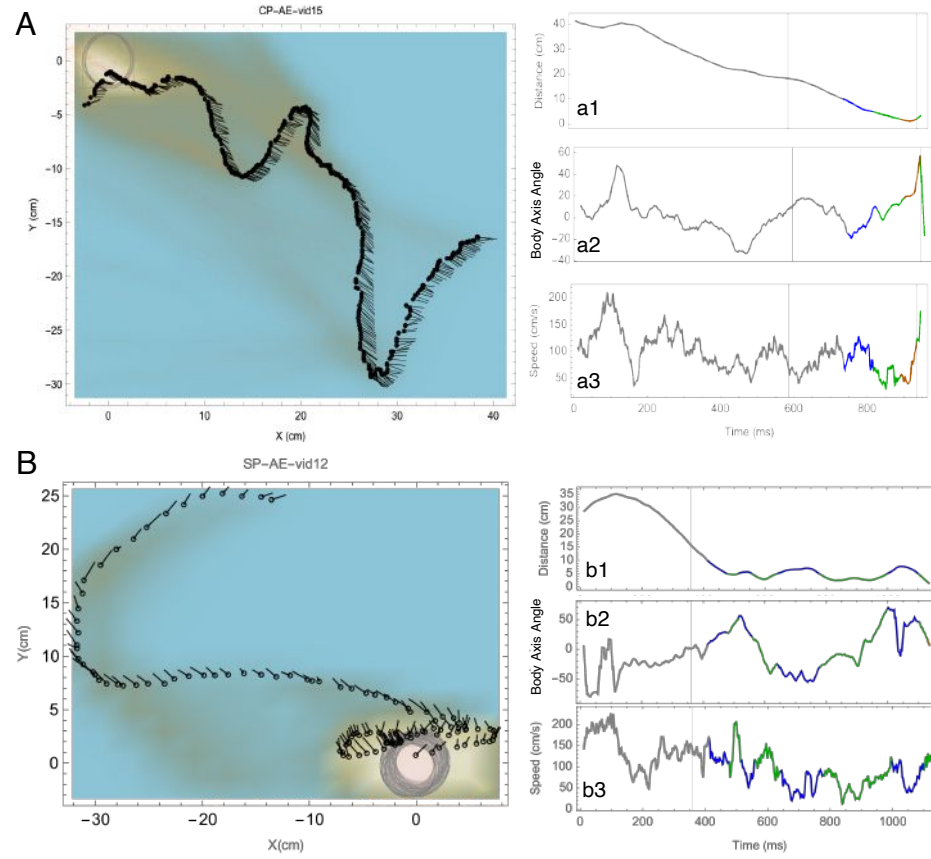
B



C



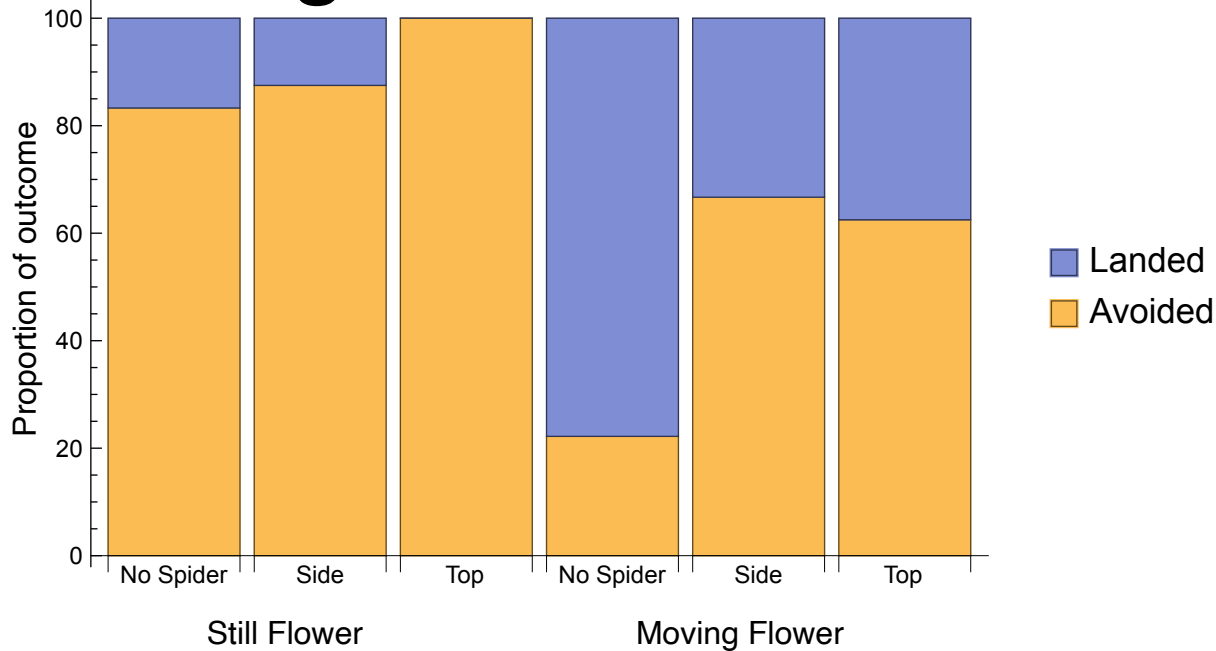
# Figure 3





# Figure 4

A



B

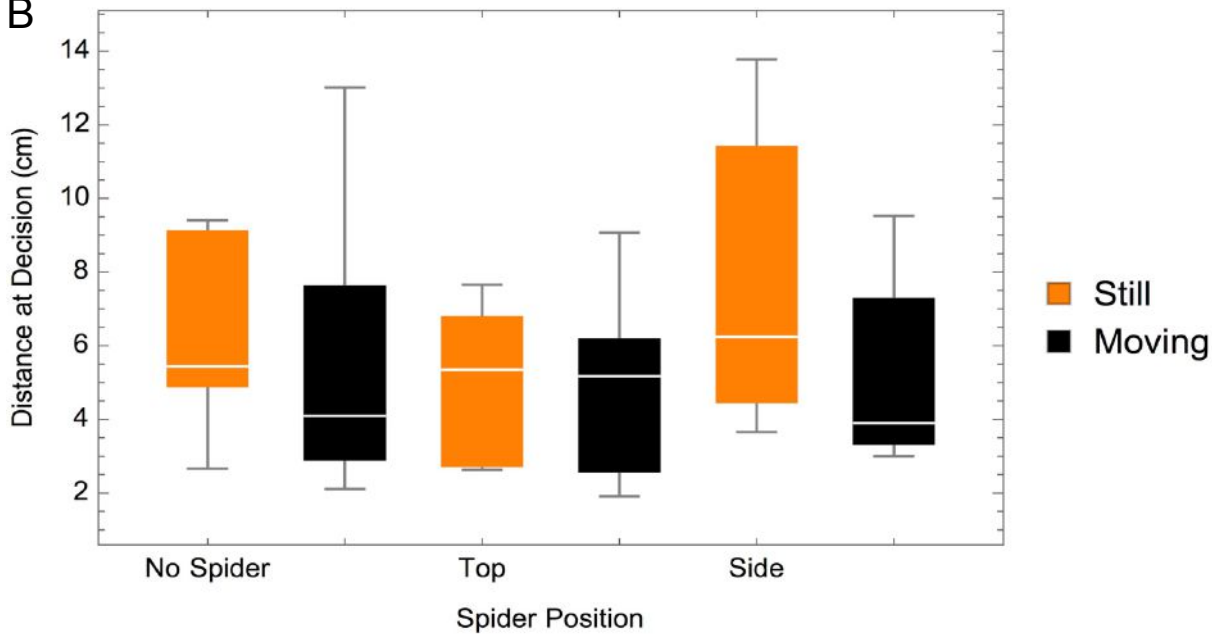
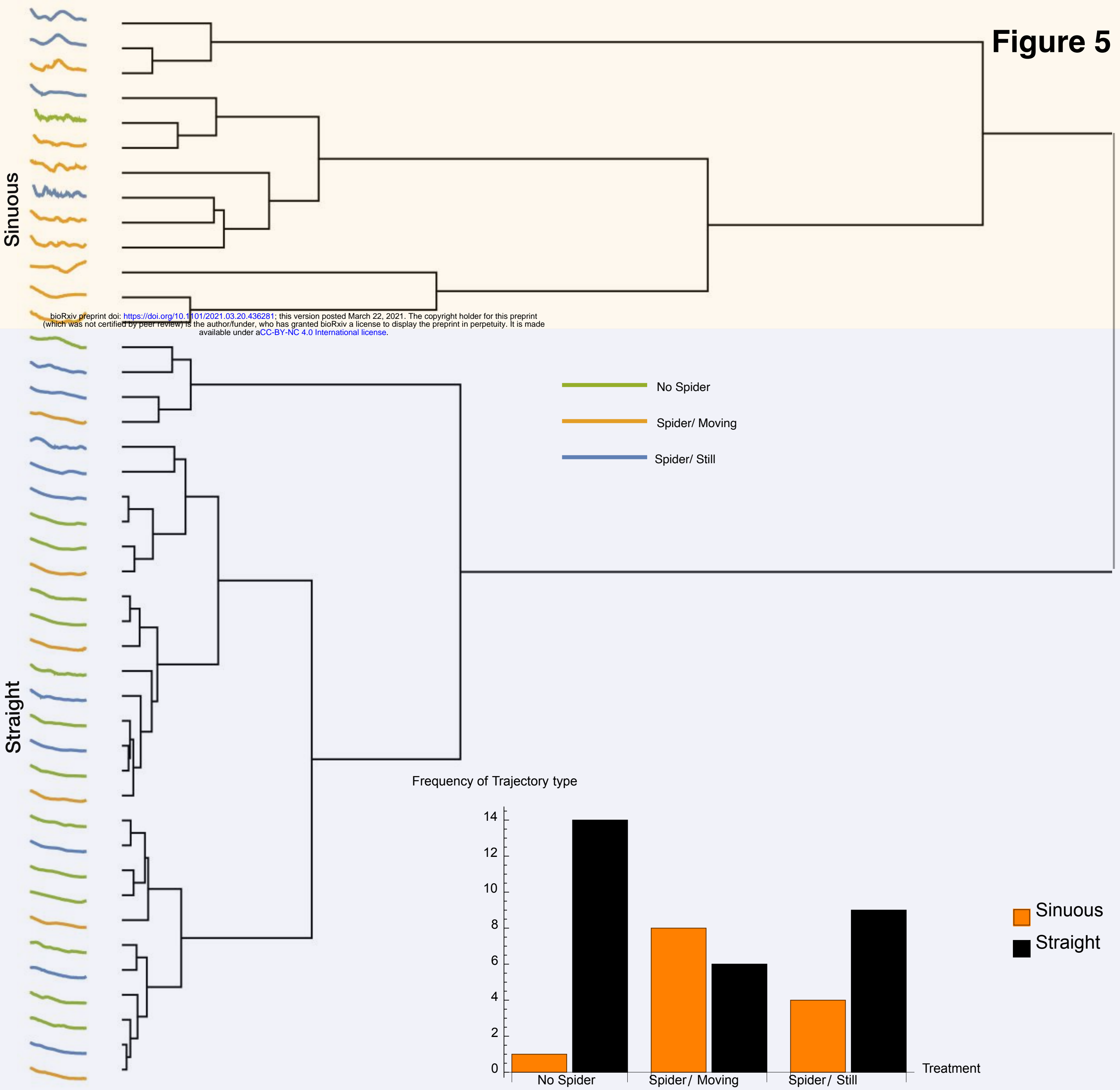


Figure 5

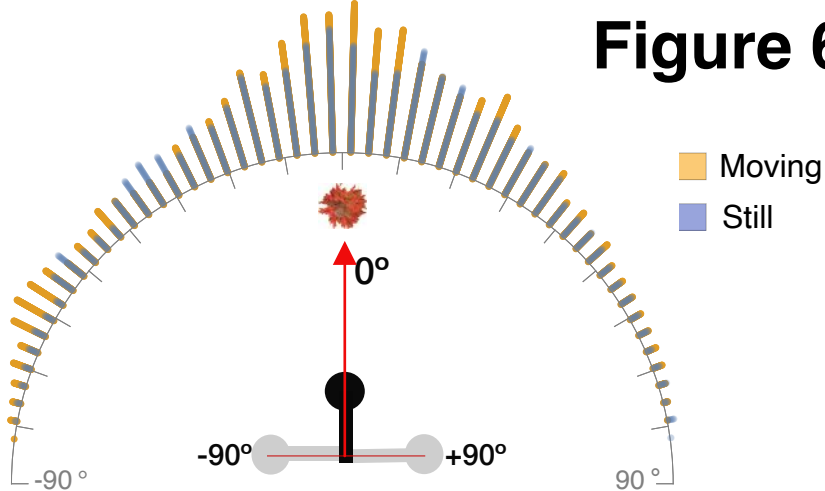
Sinuuous

Straight

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# Figure 6



# Figure 7

