

1 **Title:** Landmark navigation in a mantis shrimp

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6

7 **Summary:**

8 Mantis shrimp are predatory crustaceans that commonly occupy burrows in shallow,
9 tropical waters worldwide. Most of these animals inhabit structurally complex, benthic
10 environments where many potential landmarks are available. Mantis shrimp of the species
11 *Neogonodactylus oerstedii* return to their burrows between foraging excursions using path
12 integration, a vector-based navigational strategy that is prone to accumulated error. Here we
13 show that *N. oerstedii* can navigate using landmarks in parallel with their path integration
14 system, offsetting error generated when navigating using solely path integration. We also report
15 that when the path integration and landmark navigation systems are placed in conflict, *N.*
16 *oerstedii* will orient using either system or even switch systems enroute. How they make the
17 decision to trust one navigational system over another is unclear. These findings add to our
18 understanding of the refined navigational toolkit *N. oerstedii* relies upon to efficiently navigate
19 back to its burrow, complementing its robust, yet error prone, path integration system with
20 landmark guidance.

21

22 **Key Words:** navigation, path integration, landmark navigation, visual guidance, mantis shrimp,
23 stomatopod, homing, marine biology

24

25 **Introduction:**

26 Stomatopods, better known as mantis shrimp, are benthic crustaceans renowned for their
27 ballistic strikes and complex visual systems. As adults, most mantis shrimp species reside in
28 shallow tropical marine waters, environments that are often structurally varied and therefore
29 contain many potential visual landmarks [1]. In these environments, mantis shrimp typically
30 occupy small holes or crevices for use as burrows, where they reside concealed for most of the
31 day. During foraging, many stomatopod species leave the safety of their burrows for extended
32 excursions, where they become vulnerable to predation [2-5]. Returning to the burrow efficiently
33 is critical to minimize predation risk and to also reduce the chance that the vacated burrow will
34 be claimed by another animal.

35 Mantis shrimp of the species *Neogonodactylus oerstedii* employ path integration to
36 efficiently navigate back to their burrows between foraging bouts [5]. During path integration, an
37 animal monitors the distances it travels in various directions from a reference point (usually
38 home) using a biological compass and odometer. From this information, a home vector (the most
39 direct path back to the reference point) is continuously calculated, allowing the animal to return
40 to its original location [6-8]. As animals update their home vectors during excursions, small
41 errors in odometric and orientation measurements are made. Over the course of an animal's
42 travel, these small errors accumulate in its path integrator. Therefore, with longer outward paths,
43 increased errors of home vectors are expected [7, 9]. Path integration using idiothetic cues (those

44 informed by stimuli anchored internal to the body) are particularly prone to accumulated error.
45 As theory suggests, path integration in *N. oerstedii* is prone to this accumulated error [10]. To
46 reduce this error, many path-integrators use landmarks to accurately pinpoint their goal [9, 11-
47 14]. We hypothesized that in addition to path integration, *N. oerstedii* uses landmarks when
48 available during navigation. The benthic habitats *N. oerstedii* occupy are structurally complex
49 with an abundance of sponges, coral, rock, and seagrass to serve as potential visual landmarks
50 (Fig. 1). Using landmarks during navigation would allow *N. oerstedii* to correct for error
51 accumulated while path-integrating during foraging paths away from the burrow.

52

53 **Results:**

54 ***Neogonodactylus oerstedii* uses landmarks during navigation**

55 We placed *N. oerstedii* individuals in relatively featureless circular arenas filled with
56 sand and sea water in a glass-roofed greenhouse. Vertical burrows were buried in the sand so that
57 they were hidden from view when experimental animals were away. Snail shells stuffed with
58 small pieces of shrimp were placed at one of two fixed locations approximately 70 cm from the
59 location of the burrow in the arena (Fig. 2A). Foraging paths to and from the location of the food
60 were video recorded from above.

61 As described by Patel and Cronin (2020a,b) [5,10], we observed that animals would make
62 tortuous paths away from the burrow until they located the food placed in the arena. After
63 animals located the food, they would usually execute a fairly direct home vector towards the
64 burrow. If the burrow was not found using the home vector, animals would initiate a stereotyped
65 search behavior (Fig. 2C and Extended Data Video 1).

66 To determine if *N. oerstedii* use landmarks during homeward navigation when available,
67 a 2-cm diameter, 8-cm tall vertical cylinder with alternating 1-cm thick horizontal black and
68 white stripes was placed adjacent to the burrow to serve as a landmark. Stripe cycles of the
69 landmark would appear to span approximately 0.8 cycles/degree at the location of the food,
70 approximately twice the visual resolving limit of *Gonodactylus chiragra* [15], a closely related
71 mantis shrimp that can be slightly larger than *N. oerstedii*. Trials with the landmark present were
72 compared to the results of previous experiments in which the landmark was absent [5].

73 Return trips in the presence of the landmark were more direct than trips in the landmark's
74 absence ($P < 0.05$; Fig. 2C-D and 3, and Extended Data Videos 1 and 2), supporting the
75 hypothesis that *N. oerstedii* uses landmarks during navigation. This was primarily due to the
76 virtual elimination of stereotyped search behaviors at the ends of homeward paths in the presence
77 of the landmark. Instead, short directed searches for the burrow around the landmark were
78 observed. Return trips were initially oriented similarly between the two groups (Groups were
79 oriented: $P < 0.001$ for both groups; Orientations were not significantly different between
80 groups: $P > 0.5$; All statistical outcomes are presented in Tables 1-3). However, during trials in
81 the presence of the landmark, individuals appeared to correct for their initial homeward error
82 over the course of the homeward path ($P < 0.05$), in contrast to what we observed in the absence
83 of the landmark ($P > 0.5$; Fig. 2D-F). These results indicate that in the presence of a landmark, *N.*
84 *oerstedii* uses both path integration and landmark navigation to navigate back to its burrow.

85

86 **Mantis shrimp exhibit varied homeward paths when landmark navigation and path**
87 **integration are placed in conflict**

88 In light of the above results, we were interested in the confidence *N. oerstedii* places in its
89 landmark navigation system when it is in conflict with its path integrator. In order to create this
90 situation, homeward paths were observed when a landmark adjacent to the burrow was displaced
91 to a new location in the arena while experimental individuals were away foraging. The landmark
92 remained at roughly the same distance from the food location both before and after displacement.
93 If *N. oerstedii* navigates using landmarks and trusts a landmark's location over the location
94 designated by its path integrator when homing, animals should orient towards the displaced
95 landmark rather than the burrow's location (Fig. 2B).

96 Homeward paths were less direct ($P < 0.05$; Fig. 3) and were differently oriented ($P <$
97 0.05 ; Fig. 2D-F) when landmarks were displaced compared to when they were left in place,
98 further supporting the hypothesis that *N. oerstedii* navigate using landmarks. Some individuals
99 oriented towards the displaced landmark while others ignored the displaced landmark, orienting
100 towards the burrow (Fig. 2C and Extended Data Videos 3 and 4). Several individuals initially
101 oriented towards the displaced landmark, but broke away from their initial trajectories during
102 their homeward paths, orienting towards the burrow instead (Fig. 2D). Overall, however,
103 differences observed between initial path orientations and the orientations of homeward paths at
104 the end of the home vector were not statistically significant when the landmark was displaced (P
105 $= 0.36$; Fig. 2E-F). One individual initially oriented its homeward path towards the landmark,
106 only to turn around and return to the food location before adopting a revised homeward path
107 oriented towards the burrow (Fig. 2D). These observations suggest that the path integrator of *N.*
108 *oerstedii* is continually updated during foraging, even after homeward paths are initiated.

109 As just described, when landmarks were displaced some animals adopted paths initially
110 oriented towards the displaced landmark while others ignored the displaced landmark

111 completely, orienting towards the burrow. These results demonstrate that *N. oerstedii* must make
112 decisions when the navigational strategies it relies on are in conflict and raise the question of
113 how these decisions are made.

114 Due to errors inherent in path integration, *N. oerstedii* exhibit growing home vector errors
115 with increased outward path lengths [10]. When the landmark was displaced, individuals may
116 have evaluated this accumulated error during foraging, choosing to trust the position of the
117 landmark when the accumulated error of the path integrator was high (i.e. confidence in the path
118 integrator was low). However, we found that the orientations of homeward paths during
119 landmark displacement experiments were not significantly correlated with the outward path
120 lengths from the burrow to the food location ($P = 0.16$; Fig. 4A); nonetheless, the effect size of
121 this relationship was fairly strong ($r = -0.48$), suggesting this hypothesis should not be
122 completely discounted.

123 Cataglyphid desert ants are model terrestrial species for studying navigation using path
124 integration and visual landmarks. In experiments with these ants, when their path integrators are
125 placed conflict with their surrounding landmark panorama, displaced desert ants will orient
126 toward either the location indicated by their path integrator or toward a local landmark array
127 depending on their distance from their nest, not on the error accumulated in their path
128 integrators. These ants will orient using their home vectors, ignoring local landmarks, when
129 displaced from at a distance greater than three meters from their nest; however, they will orient
130 using the local landmark array when displaced from near the nest. When displaced from a
131 distance of one meter from their nest, desert ants will orient with a mean vector not clearly
132 directed at either their home vectors derived from path integration or the local landmark
133 panorama, but somewhere in between [16]. Interestingly, orientation results of the desert ants

134 displaced from roughly one meter from the nest are similar to those of *N. oerstedii* during the
135 landmark displacement experiments described above. Stomatopods in those experiments were
136 around 0.7 m from their burrows when initiating their homeward paths (Fig. 3E). These
137 observations suggest that a cue integration mechanism resembling that employed by desert ants
138 may also be present in mantis shrimp.

139 As an alternative hypothesis to account for the variation observed in homeward paths
140 during experiments when the landmark was displaced, the deviation between the home vector
141 and the landmark's perceived position may have been at a preference threshold for either of the
142 two navigation systems. For example, if the landmark was displaced further away from the
143 burrow, the majority of animals may have trusted their home vector, while if the landmark was
144 not moved as far from the burrow, the animals may have been more likely to trust the landmark's
145 position. However, when homeward path orientations during landmark displacement
146 experiments were compared to the distance of landmark displacement along the track during
147 those trials, no correlation was observed ($P=0.92$, $r = -0.04$; Fig. 4B). This suggests that the
148 degree of landmark displacement did not influence the decision to orient toward the home vector
149 or the displaced landmark during these trials.

150 Finally, we hypothesized that animals that may have observed the landmark's
151 displacement were more likely to disregard its location than those that may not have noticed
152 displacement of the landmark. To investigate this hypothesis, we measured the orientations of all
153 animals' body axes with respect to the landmark while it was displaced, sampled at a rate of 0.2
154 seconds. We compared the means of these body axis orientations to the orientations of
155 homeward paths and found no correlation ($P = 0.604$, $r = 0.19$; Fig. 4C). This suggests that either
156 animals did not notice the landmark's displacement or that observing the landmark's

157 displacement did not influence an animal's decision to determine the burrow's location by using
158 the displaced landmark's position or by using its home vector.

159

160 **Discussion:**

161 Our results demonstrate that *Neogonodactylus oerstedii* uses landmark navigation
162 together with path integration while navigating back to its burrow while foraging. Landmarks are
163 reliable references which can be used to correct for error accumulated by path integration; this is
164 especially important during idiothetic path integration, which *N. oerstedii* uses when allothetic
165 cues become unreliable [5].

166 Landmarks were used in a very basic situation during our experiments— as a beacon to
167 home towards. Many other questions about how landmarks may be used by mantis shrimp arise
168 from this work: Can mantis shrimp estimate the relative position of a goal to multiple
169 landmarks? Do stomatopods use a snapshot mechanism like that employed by some insects to
170 learn landmark arrays [13,17]? Do they possess cognitive maps akin to those thought to exist in
171 mammals [18]? Do mantis shrimp learn to recognize landmarks encountered during foraging
172 routes, exhibiting “trapline foraging”? Further, mantis shrimp are famed for possessing complex
173 color vision, linear polarization vision in two spectral channels, and circular polarization vision
174 [19]. Besides spatial vision alone, do stomatopods use these visual channels to identify
175 landmarks? If so, how?

176 Mantis shrimp occupy a wide variety of marine habitats and depths, from structurally
177 complex reefs to nearly featureless mud flats. Stomatopod species that occupy landmark-rich
178 environments may weigh the importance of landmarks more heavily during navigation than

179 stomatopods which occupy benthic environments relatively void of landmarks. Further, visual
180 information rapidly attenuates with distance underwater due to extreme scattering of light in
181 water. Therefore, the relative importance of landmark navigation over path integration may differ
182 for mantis shrimp species occupying waters of different depths and turbidities.

183 Taken together with our previous work on mantis shrimp navigation [5, 10], this work
184 offers an opportunity to study the neural basis of navigation, learning, memory, and decision
185 making in stomatopods. Mushroom bodies, centers for arthropod learning and memory, are
186 thought to play a prominent role in landmark learning in insects [20-23]. Prominent
187 hemiellipsoid bodies, homologues of insect mushroom bodies, exist in stomatopod eyestalks
188 [24]. As in insects, these neuropils may be crucial for navigation and landmark learning in
189 mantis shrimp. A separate brain region, the central complex, plays a role in landmark orientation
190 in *Drosophila melanogaster*. Here, landmark orientation is neurally based in the ellipsoid body
191 of the central complex [25]. Stomatopods themselves possess a highly developed central
192 complex composed of a collection of neuropils anatomically very similar to those found in
193 insects [26]. Investigation of the function of stomatopod brain regions in light of our work may
194 have implications for the evolutionary origins of navigational strategies and the neural
195 architecture of the brain within the ancient Pancrustacean clade, a taxon which includes all
196 insects and crustaceans [27], as well as in other arthropods.

197 In summary, *N. oerstedii* possesses a robust navigational toolkit on which it relies to
198 efficiently navigate back to its burrow. First, *N. oerstedii* relies on path integration using multiple
199 redundant compass cues to navigate back to its home [5]. If path integration does not lead *N.*
200 *oerstedii* directly to its burrow, it relies on a stereotyped search behavior which is scaled to the
201 amount of error it accumulates during its outbound foraging path to locate its nearby lost target

202 [10]. Finally, the stomatopod will use landmarks, if available, to quickly pinpoint its target,
203 offsetting error accumulated during path integration.

204

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208 **Author Contributions:** R.N.P. designed and conducted all research, analyzed all data, and
209 prepared the manuscript. T.W.C. provided guidance and research support.

210 **Competing Interests:** The authors declare no competing financial interests.

211 **Data and Materials Availability:** The data that support the findings of this study are available
212 from the corresponding author upon reasonable request. Correspondence and requests for
213 materials should be addressed to R.N.P. (e-mail: [rickpl@umbc.edu](mailto:rnickpl@umbc.edu)).

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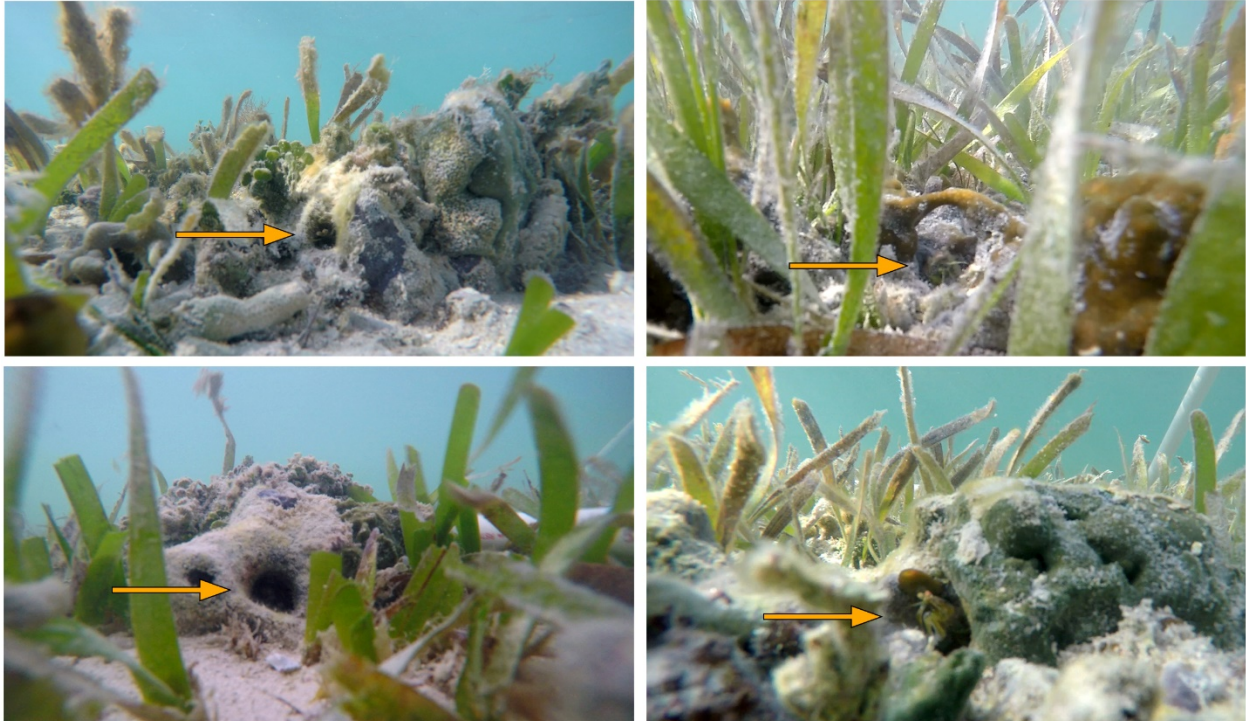
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221 **Figures:**

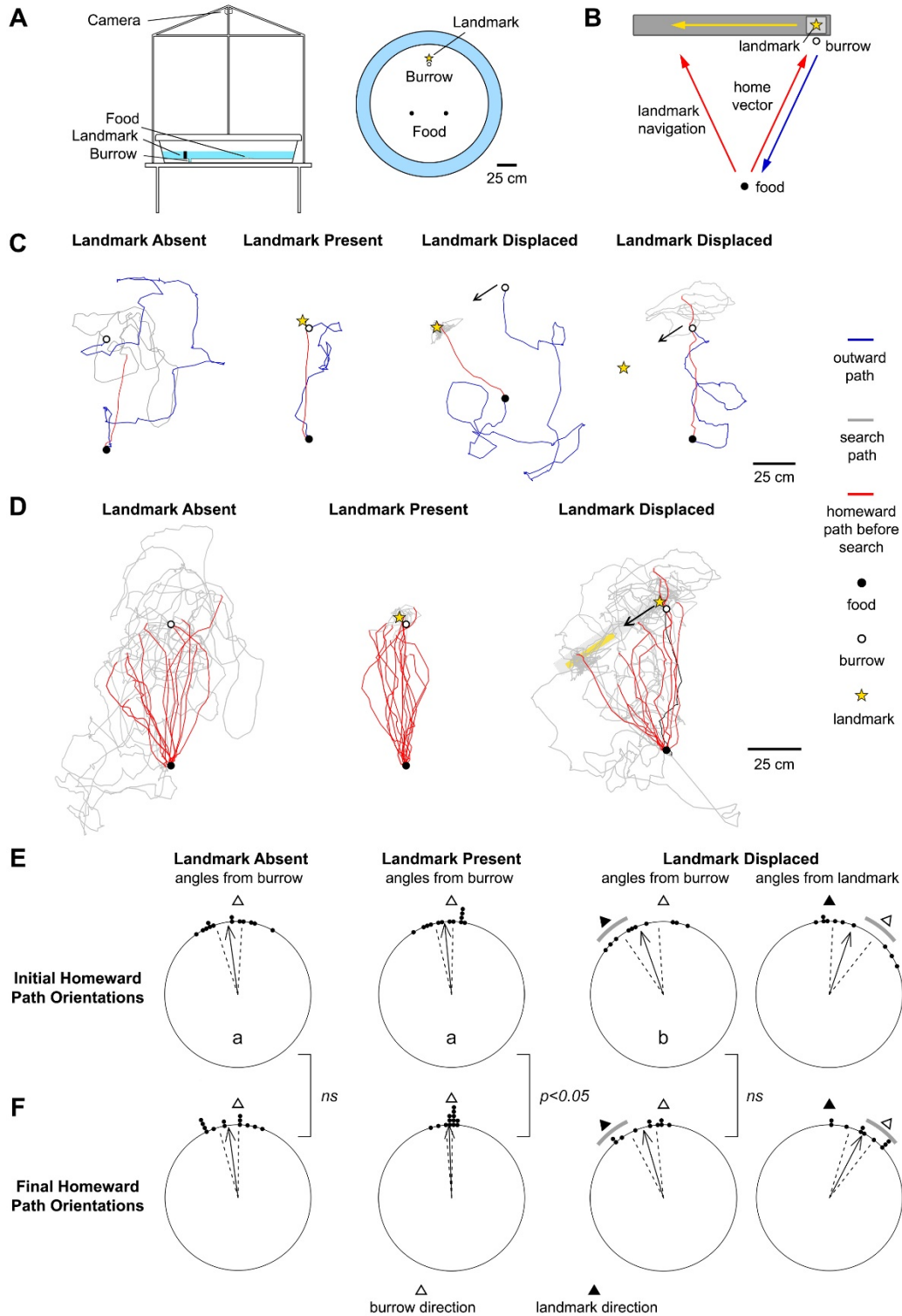
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224 **Figure 1. *Neogonodactylus oerstedii* inhabits shallow waters that offer an abundance of**
225 **potential landmarks.** Burrows are indicated by orange arrows. Note the abundance of potential
226 landmarks, including marine vegetation, sponges, coral fragments, and rock rubble, available in
227 the scenes. Stomatopods can be seen in their burrows in all except the bottom left panel, in which
228 the photograph was taken when the animal had left its home.

229



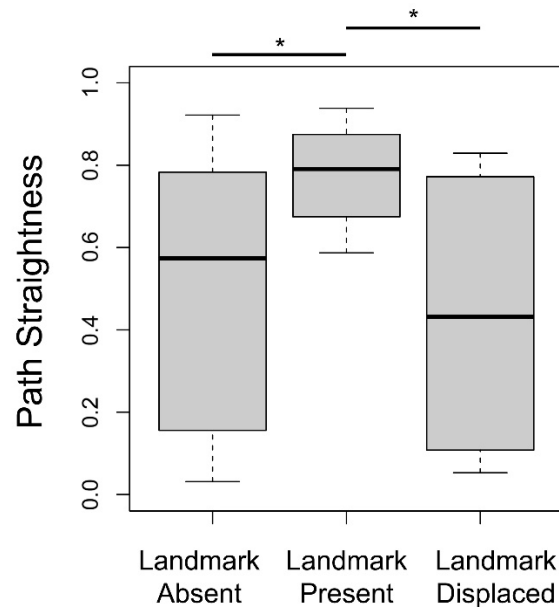
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231 **Figure 2. *Neogonodactylus oerstedii* uses a landmark to navigate back to its burrow while**

232 **foraging. (A) Navigation arenas. Each arena was 150 cm diameter. A vertical burrow was set**

233 into the base of the arena 30 cm from the edge of the pool so it was invisible at range (empty
234 circle). A landmark was placed adjacent to the burrow during some experiments (gold-filled
235 star). Food was placed in one of two locations near the center of the pool (filled circles).
236 Behaviors were video recorded from above. **(B)** Landmark displacement experimental design.
237 Homeward paths were observed when a landmark adjacent to the burrow was displaced to a new
238 location in the arena while experimental individuals were away foraging. **(C)** Examples of
239 foraging paths from and to the burrow during the three experimental conditions. Blue lines
240 represent outward paths from the burrow while red lines represent homeward paths before search
241 behaviors were initiated. Grey lines represent homeward paths after search behaviors were
242 initiated. Empty and filled circles represent the location of the burrow and food, respectively.
243 Gold-filled stars represent the location of the landmark. Arrows represent paths of landmark
244 displacements. **(D)** Data from all homeward paths. Lines and filled circles represent the same as
245 in (C). The grey rectangle represents the track along which the landmark was displaced. The gold
246 rectangle marks the range of locations to which the landmark was displaced during landmark
247 displacement trials. The black tracing in the “landmark displaced” group marks the homeward
248 path of an individual on its second run which, after orienting its initial homeward path towards
249 the displaced landmark (in red), it returned to the food location and oriented towards the burrow
250 (in black). **(E)** Orientations of homeward paths at one-third the beeline distance from the location
251 of the food to the burrow (initial orientations). Each point along the circumference of the circular
252 plot represents the orientation of the homeward path of one individual with respect to either the
253 actual position of the burrow (empty triangle) or displaced landmark’s position (filled triangle).
254 Grey arcs in the “Landmark Displaced” orientation plots represent the range of the directions of
255 the either the displaced landmark or the burrow from at the location of the food. Arrows in each

256 plot represent mean vectors, where arrow angles represent vector angles and arrow lengths
257 represents the strength of orientation (\bar{R}). Dashed lines represent 95% confidence intervals.
258 Different letters within orientation plots denote a significant difference between groups ($p < 0.05$).
259 “Landmark Absent” data were obtained from Patel and Cronin (2020a) [5]. **(F)** Homeward path
260 orientations of groups same as in (E) measured immediately before search behaviors were
261 initiated (final orientations).
262

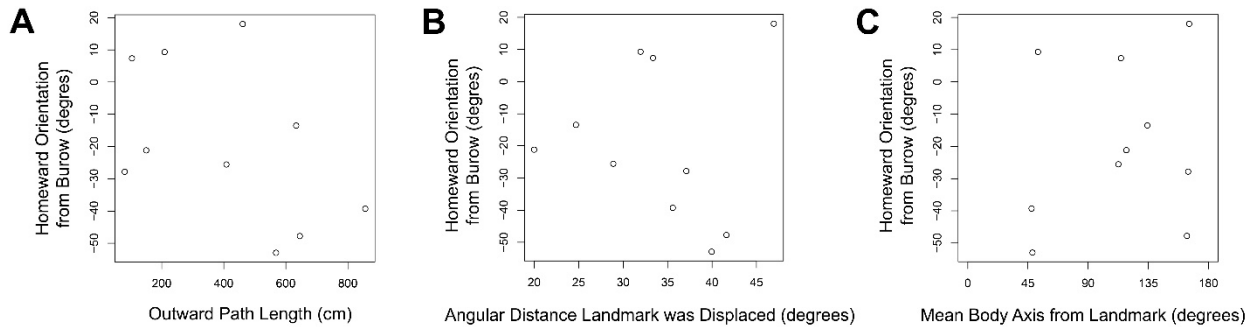


263
264 **Figure 3. Homeward paths were more direct when a fixed landmark was present during**
265 **navigation than when the landmark was absent or displaced to a new location in the arena**
266 **during foraging.** Straightness of homeward paths from the location of food to the burrow during
267 trials when the landmark was present, absent, and displaced. Larger path straightness values
268 indicate straighter paths with a value of one being a completely straight path from the food
269 location to the burrow (a beeline path). Bars represent medians, boxes indicate lower and upper
270 quartiles, and whiskers show sample minima and maxima. Asterisks indicate significant

271 differences in path straightness between groups ($P \leq 0.05$; Landmark Absent: $n = 13$, Landmark
272 Present: $n = 13$, Landmark Displaced: $n = 10$).

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274



275

276 **Figure 4. It is unclear why *N. oerstedii* chose to trust either the landmark or the home**
277 **vector while navigating during landmark displacement experiments. (A)** The orientations of
278 homeward paths when the landmark was displaced was not significantly correlated with the
279 length of outward paths from the burrow to the location of food ($P = 0.16$, $n = 10$, $r = -0.48$). **(B)**
280 The orientations of homeward paths when the landmark was displaced was not correlated with
281 the angular distance of landmark displacement along the track when viewed from the location of
282 the food ($P = 0.92$, $n = 10$, $r = -0.04$). **(C)** Homeward path orientations were not correlated with
283 body axis orientations of animals with respect to the landmark during its displacement ($P =$
284 0.604 , $n = 10$, $r = 0.19$). Each point represents the mean body axis orientation of an individual
285 with respect to the landmark measured at a sampling rate of 0.2 seconds during the landmark's
286 displacement.

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289

290 **Tables:**

291

292 **Table 1: Statistical outcomes of orientation analyses for all experimental groups.**

293 Orientations of homeward paths were measured relative to the burrow at one-third the beeline
 294 distance from the location of the food to the burrow (initial orientations) and were measured
 295 immediately before search behaviors were initiated (final orientations). Rayleigh tests of
 296 uniformity with Holm-Bonferroni multiple testing corrections were used to determine if groups
 297 were oriented. Data from this table can be viewed in Figure 2E and F.

Experiment	P-value (uncorrected)	Holm-Bonferroni (corrected P-value)	n	\bar{R}	Mean Vector Orientation \pm S.E.M.
Landmark Absent (Initial)	<0.0001	<0.001	13	0.949	354.4° \pm 3.76°
Landmark Present (Initial)	<0.0001	<0.001	13	0.974	352.2° \pm 5.36°
Landmark Displaced (with respect to burrow position; Initial)	<0.0001	<0.001	10	0.920	340.54° \pm 7.76°
Landmark Displaced (with respect to landmark position; Initial)	<0.0001	<0.001	10	0.894	18.79° \pm 8.93°
Landmark Absent (Final)	<0.0001	<0.001	13	0.966	352.32° \pm 4.31°
Landmark Present (Final)	<0.0001	<0.001	13	0.996	358.03° \pm 1.47°
Landmark Displaced (with respect to burrow position; Final)	<0.0001	<0.001	10	0.960	343.73° \pm 5.44°
Landmark Displaced (with respect to landmark position; Final)	<0.0001	<0.001	10	0.956	27.54° \pm 5.74°

298

299

300 **Table 2: Summary of homogeneity of means circular statistical tests for orientation data.**

301 Comparisons of orientation groups in rows without an asterisk were analyzed using a Watson-
 302 Wheeler Test of Homogeneity of Means (test statistic is F). Comparisons of groups in rows with
 303 an asterisk (*) were analyzed using a non-parametric Watson's Two-Sample Test of

304 Homogeneity (test statistic is U^2) since they did not adhere to the assumptions of a Watson-
305 Wheeler Test. A P-value of less than 0.05 indicates a significant difference between groups. Data
306 from this table can be viewed in Figure 2E and F.

Experiment	P-value	Holm-Bonferroni	Test Statistic
Landmark Absent (Initial) vs Landmark Present (Initial)	0.7355	0.7355	0.1168
Landmark Present (Initial) vs Landmark Displaced (with respect to burrow; Initial)*	<0.02	<0.04	0.2227
Landmark Absent: Initial vs Final	0.9827	1	0.000048
Landmark Present: Initial vs Final*	<0.005	<0.015	0.3373
Landmark Displaced: Initial vs Final	0.7414	0.7414	0.11234

307

308

309 **Table 3: Summary of homogeneity of means statistical tests for path straightness data.** The
310 comparison in the row without an asterisk was analyzed using a paired T-test (test statistic is t).
311 Since the “landmark displaced” group did not adhere to the requirements of a T-test, the row
312 with an asterisk (*) was analyzed using a non-parametric paired Wilcoxon Signed-Rank Test
313 (test statistic is V). The straightness of paths from groups within each comparison were
314 significantly different from one another ($P < 0.05$). The data from this table can be viewed in
315 Figure 3.

Experiment	P-value	Holm-Bonferroni	Test Statistic
Landmark Absent vs Landmark Present	0.0216	0.0432	2.64
Landmark Present vs Landmark Displaced*	0.027	0.0432	49

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318

319 **Materials and Methods:**

320

321 Animal Care

322 Individual *Neogonodactylus oerstedii* collected in the Florida Keys, USA were shipped to
323 the University of Maryland, Baltimore County (UMBC). Animals were housed individually in 30
324 parts per thousand (ppt) sea water at room temperature under a 12:12 light:dark cycle. Animals
325 were fed whiteleg shrimp, *Litopenaeus vannamei*, once per week. Data were collected from 13
326 individuals (5 male and 8 female). All individuals were between 30 and 50 mm long from the
327 rostrum to the tip of the telson.

328

329 Experimental Apparatuses

330 Four relatively featureless, circular navigation arenas were constructed from 1.5 m-
331 diameter plastic wading pools that were filled with pool filter sand and artificial seawater (30
332 ppt; Fig. 2A). Arenas were placed in a glass-roofed greenhouse on the UMBC campus. The
333 spectral transmittance of light through the greenhouse glass was nearly constant for all
334 wavelengths, excluding the deep-UV-wavelength range (280 to 350 nm; Extended Data Fig. 1A).
335 Celestial polarization information was transmitted through the glass roof of the greenhouse
336 (Extended Data Fig. 1B-D). Vertical burrows created from 2 cm outer-diameter PVC pipes were
337 buried in the sand 30 cm from the periphery of the arena so that they were hidden from view
338 when experimental animals were foraging. Vertical 2 cm diameter, 8 cm high PVC columns with
339 alternating 1 cm thick black and white horizontal stripes were placed adjacent to the burrows to
340 function as removable landmarks. Stripe cycle widths of the landmarks were approximately

341 twice the visual resolving limit of *Gonodactylus chiragra* (0.8 cycles/degree [13]), a closely
342 related mantis shrimp that can be slightly larger than *N. oerstedii*, when viewed from the food
343 location in the arena (a distance of 70 cm). Trials were recorded from above using C1 Security
344 Cameras (Foscam Digital Technologies LLC) mounted to tripods placed above the arenas.
345 During landmark displacement experiments, a thin 11 x 82 cm acrylic track with a movable
346 platform was placed adjacent to the burrow (Fig. 2B). A landmark identical to the one used in
347 trials in which the landmark was static, was mounted to the movable platform.

348

349 Experimental Procedures

350 Individual *N. oerstedii* were placed in each arena and were allowed to familiarize
351 themselves to the arena for 24 hours. During familiarization, the striped landmark was placed
352 adjacent to the burrow, marking it during the animals' initial explorations of the arena.

353 After familiarization, the landmark was either removed for trials in which the landmark
354 was absent or left in place for trials in which the landmark was present. Empty *Margarites sp.*
355 snail shells stuffed with pieces of food (whiteleg shrimp) were placed at one of two locations 50
356 cm from the periphery of the burrow. Each animal was allowed three successful foraging
357 excursions (i.e. food placed in the arena was found) before foraging paths were used for
358 analyses. If an individual did not successfully locate food within one week in the arena, it was
359 replaced with a new individual.

360 During landmark displacement experiments, the landmark was carefully displaced along
361 the track to a new location in the arena by the pulling of a thin fishing line tethered to the

362 platform when animals were foraging away from their burrows. The distance from the food
363 location to the landmark remained relatively constant while the landmark was displaced.

364

365 Data and Statistical Analyses

366 Foraging paths to food locations and from them to the burrow were video recorded from
367 above. In order to differentiate homeward paths from continued arena exploration, paths from the
368 food locations were considered to be homeward paths when they did not deviate more than 90°
369 from their initial trajectories for at least one-third of the beeline distance (the length of the
370 straightest path) from the food location to the burrow. From these homeward paths, search
371 behaviors were determined to be initiated when an animal turned more than 90° from its initial
372 trajectory.

373 Paths were traced at a sampling interval of 0.2 seconds using the MTrackJ plugin [28] in
374 ImageJ v1.49 (Broken Symmetry Software), from which the output is given as Cartesian
375 coordinates. From these data, the inbound and outbound path lengths, beeline distances from
376 food to burrow, and inbound and outbound indices of path straightness were calculated, where

$$377 \text{ Path Straightness} = \frac{\text{beeline distance}}{\text{path length}} = \frac{\sqrt{(x_n - x_1)^2 + (y_n - y_1)^2}}{\sum_{k=1}^n \sqrt{(x_{k+1} - x_k)^2 + (y_{k+1} - y_k)^2}}$$

378 n = the last coordinate of the path

379 Additionally, the orientations of homeward paths when animals were both, at one-third of
380 the beeline distance from the food source to the burrow (at which point the orientation of the
381 home vector was usually observed) and at the end of the home vector (when search behaviors
382 were initiated) were recorded using ImageJ.

383 We also measured the orientations of the body axes of all animals in respect to the
384 landmark while it was displaced. These body axis orientations were sampled at a rate of 0.2
385 seconds. From these body axis orientations a mean body axis orientation was calculated for each
386 individual.

387 Data from the “Landmark Absent” group in this study were taken from the “Not
388 Manipulated” trials of the greenhouse experiments published in Patel and Cronin (2020a) [5].

389 All statistical analyses were run on R (v3.3.1, R Core Development Team 2016) with the
390 “CircStats”, “circular”, “Hmisc”, and “boot” plugins. Orientation data were analyzed using the
391 following procedures for circular statistics [29]. All reported mean values for orientation data are
392 circular means. All circular 95% confidence intervals were calculated by bootstrapping with
393 replacement over 1000 iterations.

394 As reported in Patel and Cronin (2020a) [5], no significant difference was observed
395 between homeward orientations of males and females during experiments in the absence of a
396 landmark ($P > 0.5$; Extended Data Fig. 2)), so data from both sexes were pooled for all
397 experiments.

398 Rayleigh tests of uniformity were used to determine if homeward paths were oriented
399 within a group for all trials. Parametric Watson-Williams tests for homogeneity of means were
400 used to determine if those group orientations were significantly different from one another. The
401 orientations of groups which did not fit the assumptions of the Watson-Williams test were
402 instead compared using the non-parametric Watson’s two sample test of homogeneity. These
403 tests were also used to compare differences between initial homeward path orientations

404 (orientations at one-third the beeline distance from the food to the burrow) and final homeward
405 path orientations (orientations at the initiation of search behaviors) for each group.

406 Homeward path lengths of trials in which the landmark was present were compared to
407 those in which the landmark was absent using a paired T-test. A paired Wilcoxon signed-rank
408 test was used to compare homeward path lengths of trials in which the landmark was static to
409 those in which the landmark was displaced.

410 Pearson's correlation tests were used for all correlative analyses.

411 Holm-Bonferroni multiple testing corrections were used for all tests when applicable.

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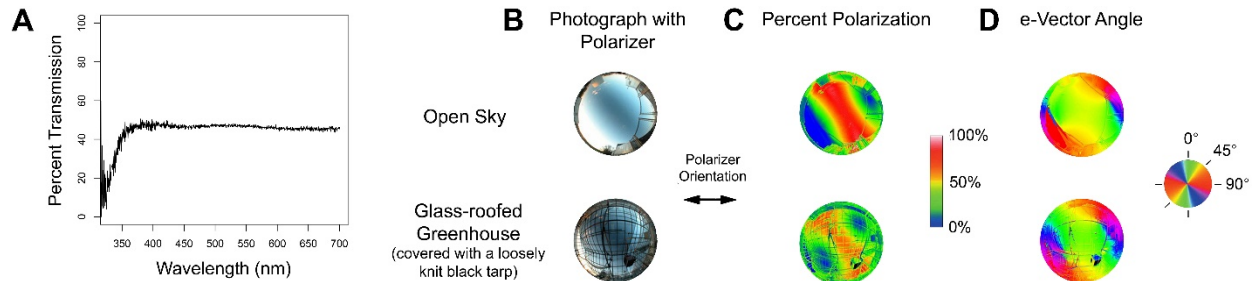
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423 **Extended Data Figures:**

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427 **Extended Data Figure 1. Photonic conditions in the greenhouse where experiments were run.**

428 **(A)** Transmission of irradiance spectra through the glass-roof of the experimental greenhouse

429 near sunset. The spectral transmittance of light through the glass roof of the greenhouse is nearly

430 constant for all wavelengths greater than ~ 360 nm. **(B-D)** Celestial polarization patterns are

431 transmitted through the glass roof of the greenhouse. **(B)** Photographs of the sky at sunset on a

432 day with very few clouds (November 24, 2015) using a fisheye lens and linear polarizer set in the

433 east-west direction (as indicated by the arrow to the right of the photos). Photos were taken

434 inside and outside the glass-roofed greenhouse used for experiments. **(C)** Percent polarization.

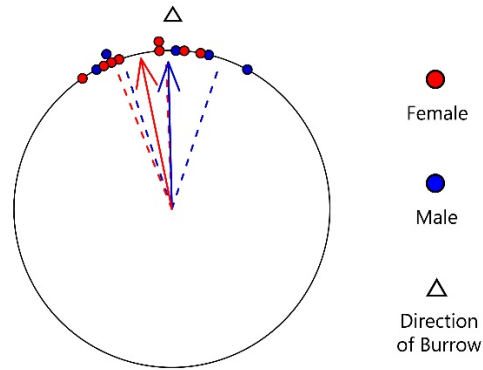
435 Warmer regions in the images indicate higher percent polarization and cooler regions indicate

436 lower percent polarization (see key). **(D)** e-Vector angle, indicated by the color corresponding

437 the key to the right of the images. From Patel and Cronin (2020a) [5].

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441 **Extended Data Figure 2. Male and female *N. oerstedii* orient towards home equally well**

442 **while foraging.** Homeward orientations of male and female individuals during experiments in

443 the greenhouse when animals were not manipulated. Each point along the circumference of the

444 circular plot represents the orientation of the homeward path of one individual with respect to

445 position of the burrow (empty triangle). Blue-filled circles represent males while red-filled

446 circles represent females. Arrows represent mean vectors, where angles of the arrows represent

447 the mean vector angles and arrow lengths represent the strength of orientation in the mean

448 direction (\bar{R}). Dashed lines represent 95% confidence intervals. Males (n=5) and females (n=8)

449 both exhibited significant orientations ($p < 0.01$ for both groups). No significant difference in

450 orientation was observed between males and females ($p > 0.5$). From Patel and Cronin (2020a)

451 [5].

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459 **Video 1. Foraging behavior of *Neogonodactylus oerstedii* showing homing in the absence of**
460 **a landmark near the burrow.** Outward path is in blue, home vector path is in red, and search
461 path is in grey. Filmed at 30 frames per second. Replay speed is indicated in the bottom-right
462 corner of the video.

463

464 **Video 2. Foraging behavior of *Neogonodactylus oerstedii* showing homing in the presence of**
465 **a landmark near the burrow.** Outward path is in blue and homeward path is in red. Filmed at
466 30 frames per second. Replay speed is in real time.

467

468 **Video 3. Foraging behavior of *Neogonodactylus oerstedii* showing homing after a landmark**
469 **near the burrow had been displaced to a new location in the arena.** During this trial, the
470 animal homed towards the displaced landmark. Outward path is in blue, home vector path is in
471 red, and search path is in grey. Filmed at 30 frames per second. Replay speed is indicated in the
472 bottom-right corner of the video.

473

474 **Video 4. Foraging behavior of *Neogonodactylus oerstedii* showing homing after a landmark**
475 **near the burrow had been displaced to a new location in the arena.** During this trial, the
476 animal homed towards its burrow. Outward path is in blue, home vector path is in red, and search
477 path is in grey. Filmed at 30 frames per second. Replay speed is indicated in the bottom-right
478 corner of the video.

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