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, offseting 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.

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22   **Key Words:** navigation, path integration, landmark navigation, visual guidance, mantis shrimp,

23   stomatopod, homing, marine biology

24

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 inherit 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

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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.

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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: rickp1@umbc.edu).

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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.

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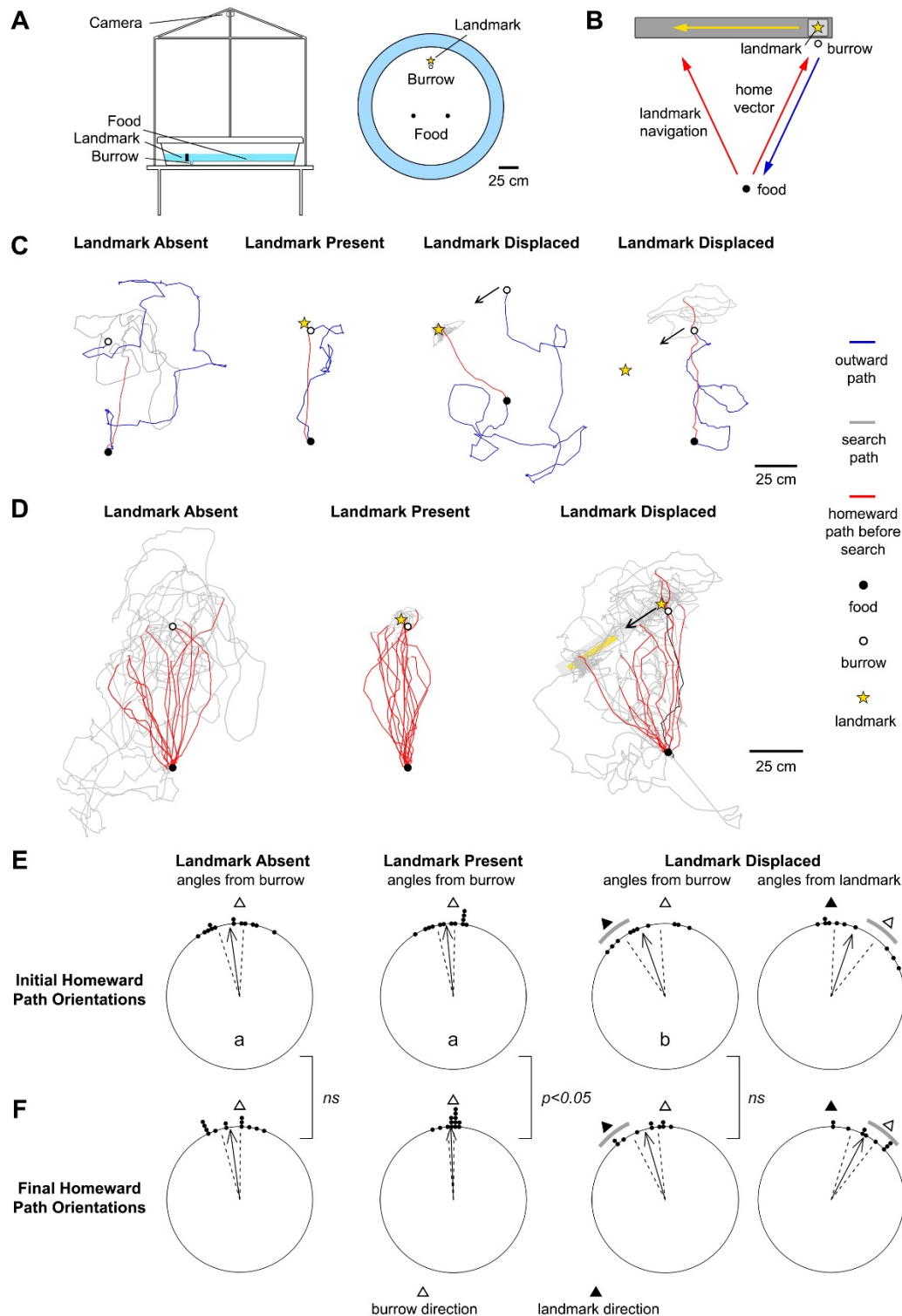
Figure 2. *Neogonodactylus oerstedii* **uses a landmark to navigate back to its burrow while**

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).

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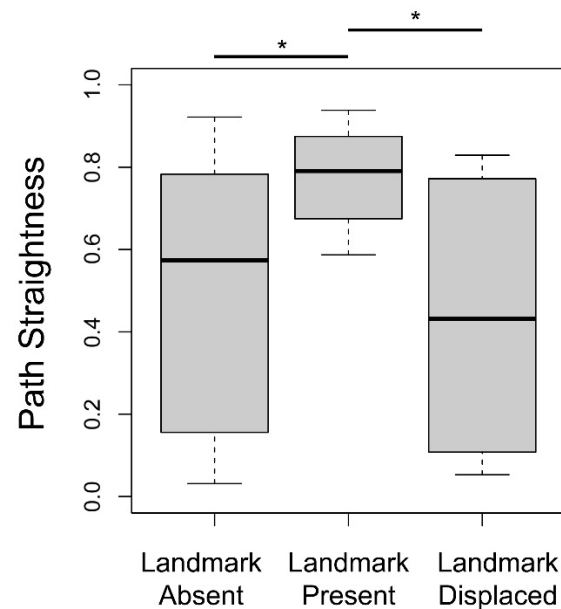
264   **Figure 3. Homeward paths were more direct when a fixed landmark was present during**

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

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271   differences in path straightness between groups (P ≤ 0.05; Landmark Absent: n = 13, Landmark

272   Present: n =13, Landmark Displaced: n = 10).

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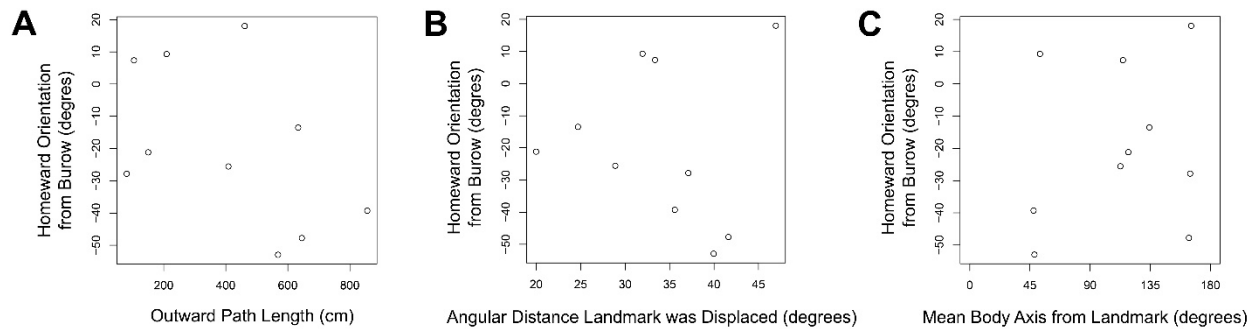
Figure 4. It is unclear why *N. oerstedii* chose to trust either the landmark or the home

vector while navigating during landmark displacement experiments. (A) The orientations of

homeward paths when the landmark was displaced was not significantly correlated with the

length of outward paths from the burrow to the location of food (P = 0.16, n = 10, r = -0.48). **(B)**

The orientations of homeward paths when the landmark was displaced was not correlated with

the angular distance of landmark displacement along the track when viewed from the location of

the food (P = 0.92, n = 10, r = -0.04). **(C)** Homeward path orientations were not correlated with

body axis orientations of animals with respect to the landmark during its displacement (P =

0.604, n = 10, r = 0.19). Each point represents the mean body axis orientation of an individual

with respect to the landmark measured at a sampling rate of 0.2 seconds during the landmark's

displacement.

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290   **Tables:**

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

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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

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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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Materials and Methods:

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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

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

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.

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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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423   **Extended Data Figures:**

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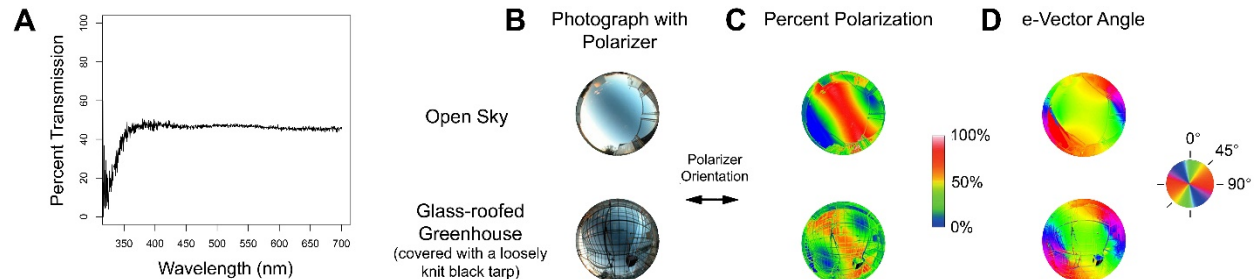
427   **Extended Data Figure 1. Photic conditions in the greenhouse where experiments were run.**

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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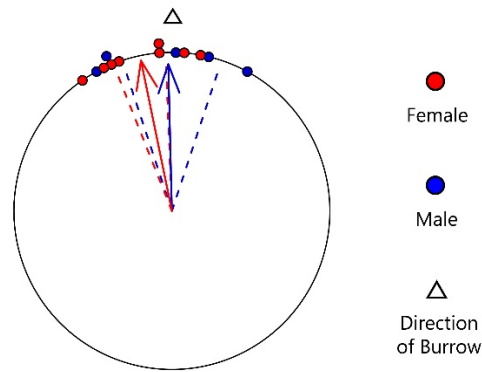
Extended Data Figure 2. Male and female *N. oerstedii* orient towards home equally well while foraging. Homeward orientations of male and female individuals during experiments in the greenhouse when animals were not manipulated. Each point along the circumference of the circular plot represents the orientation of the homeward path of one individual with respect to position of the burrow (empty triangle). Blue-filled circles represent males while red-filled circles represent females. Arrows represent mean vectors, where angles of the arrows represent the mean vector angles and arrow lengths represent the strength of orientation in the mean direction ($\bar{R}$). Dashed lines represent 95% confidence intervals. Males (n=5) and females (n=8) both exhibited significant orientations (p < 0.01 for both groups). No significant difference in orientation was observed between males and females (p>0.5). From Patel and Cronin (2020a) [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.

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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.

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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.

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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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