1 **Traveling through light clutter: Path integration and panorama guided**
2 **navigation in the Sonoran Desert ant, *Novomessor cockerelli***
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Abstract

Foraging ants use multiple navigational strategies, including path integration and visual panorama cues, which are used simultaneously and weighted based upon context, the environment and the species' sensory ecology. In particular, the amount of visual clutter in the habitat predicts the weighting given to the forager's path integrator and surrounding panorama cues. Here, we characterize the individual cue use and cue weighting of the Sonoran Desert ant, *Novomessor cockerelli*, by testing foragers after local and distant displacement. Foragers attend to both a path-integration-based vector and the surrounding panorama to navigate, on and off foraging routes. When both cues were present, foragers initially oriented to their path integrator alone, yet weighting was dynamic, with foragers abandoning the vector and switching to panorama-based navigation after a few meters. If displaced to unfamiliar locations, experienced foragers travelled almost their full homeward vector (~85%) before the onset of search. Through panorama analysis, we show views acquired on-route provide sufficient information for orientation over only short distances, with rapid parallel decreases in panorama similarity and navigational performance after even small local displacements. These findings are consistent with heavy path integrator weighting over the panorama when the local habitat contains few prominent terrestrial cues.

Keywords: Celestial compass; Cue weighting; Panorama similarity; Solitarily foraging; Vector length

1. Introduction

Over the past few decades, several species of ant have been extensively studied for their navigational abilities (Wehner, 2003; Cheng et al., 2009). This research has revealed that foraging ants dynamically use multiple strategies to navigate, often switching between strategies at different stages of the journey or based on the availability of cues (Cheng et al., 2014; Bühlmann et al., 2020). Multiple strategies may also operate simultaneously, with information from different sources being integrated in a weighted fashion (Czaczkes et al., 2011; Wehner et al., 2016). Comparisons across species have revealed both commonalities and differences, with the dominance of particular strategies depending on foraging ecology and the local environment (Bühlmann et al., 2011; Cheng et al., 2014). Specifically, chemical cues appear to play a role in navigation for socially foraging ants (Czaczkes et al., 2011, 2015; Freas et al., 2020) but less so for ants that forage individually. The amount of visual clutter in the local environment determines both the distance at which visual panorama-based guidance is usable (Zeil et al., 2014), as well as the weighting experienced foragers give to visual terrestrial cues over the path integrator (Bühlmann et al., 2011; Cheng et al., 2012; Schwarz et al., 2017). This makes ant navigation an ideal system to study how the environment shapes the use of behavioral systems.

Ant foragers are adept at visual navigation, deriving compass information from multiple visual cue sets including learned panorama cues through view-based matching (Baddeley et al., 2012; Zeil et al., 2014) and celestial cues via a path integrator (Wehner and Srinivasan, 2003) with a back-up mechanism of systematic search to pinpoint the nest entrance (Schultheiss et al., 2015). Path integration (PI), informed by the coupling of a celestial compass and pedometer, allows foragers to keep an estimate, or vector, of its current position in relation to its starting point (Wehner and Srinivasan, 2003; Wittlinger et al., 2006). When an environment contains terrestrial cues, in addition to accumulating a vector, many species rapidly learn and retain visual landmark information through acquiring views of the panorama to reach goal locations (Wystrach et al., 2011; Zeil and Fleischmann, 2019). The nest panorama is acquired during pre-foraging learning walks (Zeil and Fleischmann, 2019) while views along the foraging route are learned during the first few foraging trips (Freas et al., 2019a).

View-based navigation models in ants involve the comparison of current views with retained view memories to guide movement (Zeil et al., 2003; Baddeley et al., 2012). Retained panorama views can direct foragers back to the nest or route within a certain distance or

‘catchment area’ around the learned panorama site (Zeil et al., 2014). This area is dependent on the environment’s clutter, as similarity between panoramas is dependent on prominent distant landmarks, which are stable as a navigator moves through the environment when such visual cues are unobstructed by local clutter (Stürzl and Zeil, 2007; Murray and Zeil, 2017). In open environments, ant species such as *Melophorus bagoti* and *Myrmecia croslandi* can successfully return to the nest after local displacements via panorama cues over distances up to 10m away (Wystrach et al., 2012; Narendra et al., 2013), while in the heavy clutter of forested habitats, the Australian bull ant *Myrmecia midas*, is unable to navigate when displaced 5m from known sites (Freas et al., 2017; Freas and Cheng, 2019).

Navigational systems are active concurrently, with behavior dictated by different cue weightings that change dynamically en route (Wystrach et al., 2019) based on the current navigational context and each species’ sensory ecology (Büehlmann et al., 2020; Wehner et al., 2016). When views and the PI directionally conflict, foragers will often choose an intermediate heading direction (Collett, 2012; Legge et al., 2014; Narendra et al., 2007; Wehner et al., 2016). Alternatively, one cue set can dominate the navigator’s behavior while the conflicting cue is ignored (Collett et al., 1998; Freas and Cheng, 2017; Narendra et al., 2007).

The degree of habitat clutter also influences the weighting ant navigators assign to cue sets, particularly the PI. Increases in visual landmark clutter correspond negatively to PI weighting across multiple ant species, with ants living in visually cluttered environments relying less on their PI. Ant species in heavily cluttered forested environments, such as *Gigantiops destructor* and *Myrmecia midas* follow their PI for only short distances or immediately engage in search behavior when the visual panorama is unfamiliar (Beugnon et al., 2005; Freas et al., 2017), while species inhabiting featureless environments (*Cataglyphis fortis* and *Melophorus oblongiceps*) run off their full PI-based vector even when unfamiliar landmarks are experimentally added (Wehner and Srinivasan, 1981; Büehlmann et al., 2011; Schultheiss et al., 2016). In intermediate clutter, *Melophorus bagoti* typically completes under half of its accumulated PI before the onset of search, with this proportion based both on the local environment and individual forager experience (Narendra, 2007; Cheng et al., 2012; Schwarz et al., 2017). Behavioural differences across ant species appear influenced by the local visual cues at each nest/route (Cheng et al., 2012), with the panorama mismatch between views learned

122 along an established route and the novel panoramas of distant locations dictating the portion of
123 the PI run off (Schwarz et al., 2017).

124 In the current study, we explore the individual navigational strategies and cue weighting
125 of the Sonoran Desert ant, *Novomessor cockerelli*, a species that largely forages individually
126 (Whitford, 1976; Davidson, 1977), yet is able to secrete short lasting pheromone cues for
127 recruitment to large food pieces (Hölldobler et al., 1978) which they transport cooperatively back
128 to the nest (Buffin and Pratt, 2016; Buffin et al., 2018). We find that *N. cockerelli* relies on both
129 a PI-based vector as well as surrounding panorama cues to navigate, both on and off its foraging
130 route. Despite the presence of visual terrestrial cues present at the field site, this species shows a
131 heavy reliance on its PI. Experienced foragers exposed to unfamiliar scenes run off almost the
132 full proportion of their homeward PI (85%) before beginning to search for the nest entrance.
133 When the PI and panorama cues directionally conflict, the PI initially dominates orientation
134 behavior, yet over the course of the homeward journey cue weighting changes with foragers
135 switching to panorama-based navigation mid-journey. Given the presence of multiple landmark
136 cues, including trees and distant mountains, visible at both the nests and along each route, the
137 observed heavy weighting of the PI might seem counterintuitive. Nevertheless, image analysis
138 along the foraging route at Nest 3 shows rapid drops in panorama similarity even over small
139 distances, suggesting these scattered terrestrial cues may be inconspicuous to ant navigators.

141 2. General Methods

142 2.1 Field site and study species

143 Tests were conducted on three *Novomessor cockerelli* nests in October and November 2019. All
144 nests were located at the South Mountain Municipal Park in Phoenix, Arizona, USA
145 (33°19'43.10" N, 112°01'02.60" W). Nest 1 was located ~100m from Nests 2 and 3 which were
146 30m apart. *N. cockerelli* nests are common across the southwestern USA, inhabiting open desert
147 environments with scattered ground cover consisting of trees, cacti and distant mountains
148 (~1.5km at the South Mountain site). In all conditions, each tested forager was marked with
149 enamel paint to prevent future testing.

151 2.2 General Data Analysis

In all three experiments, path data was collected initially on graph paper and then digitized (GraphClick, Arizona Software). Orientation data was analyzed using circular statistics (Batschelet, 1981). For forager paths, angular headings were recorded as a forager path first crossed 50cm and 2m distance from the release site. In two testing conditions, the 2m testing distance was reduced due to the constraints of the condition. In Experiment 1's Zero-Vector Cluttered condition, forager headings were recorded at 50cm and 1m as most foragers left the testing area opposite the vector/nest direction and travelled into an area of dense brush that could not be cleared to extend the testing area. In all subsequent testing, the testing grids were expanded to at least 2m on each side. Additionally, in Experiment 2's 90° Off-route 1.5m condition, headings were recorded at 50cm and 1.5m given the nest entrance was 1.5m from the release site. In all conditions, if headings at both distances did not differ, only the more distant headings were reported (all 50cm heading data is compiled in Supplemental Table 1 and 2).

Rayleigh tests were conducted to determine if headings were non-uniform, indicative of oriented behavior. If data was non-uniform, V-tests, which test if headings are significantly grouped in a particular direction, were used to determine if headings were oriented to a predicted direction (i.e. the nest or vector directions). However, V-tests are statistically weak, often showing significant orientation to multiple close directions. We confirmed orientation to a predicted direction by calculating if the predicted direction was also within the 95% CI of observed headings.

Mean heading directions between conditions were compared using Watson-Williams F-tests. Differences in heading variance between non-uniform conditions were analysed using Var Tests (Wystrach et al., 2014). In Var Tests, absolute differences from the mean vector were calculated for each condition and then compared using non-parametric Wilcoxon tests. Path straightness was analysed using the ratio between the straight-line distance from the released site to the grid exit location with the forager's recorded path length. These path straightness values ranged between zero to one, with one being a straight path. Between condition path straightness comparisons were analysed using Mann-Whitney U-tests with Holm-Bonferroni corrections for multiple comparisons. The single Path straightness comparison within a condition in Experiment 2 (between the 1st and 2nd half of the Full-Vector 10m condition) was analysed using a Wilcoxon Signed-Rank Test.

3. Experiment 1 - Panorama availability experiments

3.1 Methods - Panorama blocked tests

At Nest 1, an 18m foraging route was established for two days from the nest entrance to a feeder site daily stocked with crushed cookie pieces (LotusTM). During this period foragers were allowed to freely forage at the feeder site and return to the nest with food. During testing, a 60cm × 60cm wooden board was placed at the mid-point (9m) of this route and levelled ~5cm above the ground, resting on four flat top stakes (Figure 1A,B). Upon this board was painted a goniometer consisting of a 30cm radius circle surrounding a center release point, consisting of 24 wedges of 15° each.

Foragers were tested with or without a homeward vector. Full-Vector (FV) individuals were collected from the feeder with an accumulated PI-based vector estimate of the distance and direction to the nest, while Zero-Vector (ZV) foragers were collected after running off this vector and collected just before they entered the nest, when PI cues would be directionally uninformative. Foragers were transported to the mid-point test site (Figure 1B). In the Unblocked conditions, foragers (FV foragers n = 21; ZV foragers n = 21) were released onto the goniometer with the surrounding terrestrial cues visible (Figure 1A), while in the Blocked conditions foragers (FV foragers n = 20; ZV foragers n = 20) were released onto the goniometer with the surrounding cues blocked using a 50cm uniform high (110cm diameter) black circular arena that was erected around the goniometer (Figure 1A,B). This arena blocked all visual cues of the terrestrial panorama while still allowing foragers to view the celestial cues in the overhead sky (Figure 1A). Additionally, this arena was raised ~5cm off the ground to allow for the presence of potential olfactory cues. After release, foragers' initial headings were recorded as they crossed the goniometer line at 30cm.

3.2 Results - Panorama blocked tests

Results at Nest 1 indicate that *N. cockerelli* can attend to either (when available) the visual panorama and celestial-based PI for orientation while on-route. Both ZV and FV foragers released at the midpoint with access to both panorama and sky cues exhibited headings at 30cm that were non-uniform and oriented in the nest direction at 0° (Table 1; Figure 1B). When the surrounding panorama cues were blocked, orientation to the nest direction was maintained only in FV foragers (Table 1; Figure 1B). In ZV foragers, which were without directional PI

information, access to visual panorama cues were critical to orientation, which ceased when released within the blocking arena. Instead these ZV foragers exhibited uniform headings, indicative of search behavior (Table 1; Figure 1B). These results suggest that while either cue set can be used, at least one must be available for successful on-route orientation.

3.3 Methods - Cluttered/Clear tests

Nest 2 was uncharacteristic for the area as it was located at the edge of a dry stream bed and the area around this nest was partially covered with new growth of grass tussocks (Figure 2A,B, Cluttered Side). Here, a plastic feeder (15cm × 15cm × 10cm) was sunken into the ground 5m from the nest entrance. During pre-testing training, foragers were allowed to freely visit the feeder for two days before testing began. Along this established foraging route between the nest and the feeder, a 6m × 6m grid of 1m squares was constructed using pegs and string. Vegetation, both in a ~10cm width along the route (in order to clearly observe returning foragers) as well as the 6m × 3m area to the right of the route (feeder to nest) was largely naturally clear of brush and was more representative of the degree of clutter in the general habitat (Clear Side). We removed the few small patches of grass and rocks from the Clear Side to allow for an unobstructed view of the surrounding distant panorama cues while the heavy local clutter vegetation to the left of the route remained intact (Figure 2A,B).

FV foragers and ZV foragers were collected at the feeder or nest identical to procedures at Nest 1 (Figure 2C). Foragers (n = 15 all conditions) were released either just outside the feeder, or displaced 2m laterally to the left or right of the feeder into the cluttered or clear landscape respectively (Figure 2C). The Cluttered side displacement site panorama consisted of many local landmarks that largely blocked any distant landmark cues (Figure 2B). In contrast, these distant landmarks, including mountains and bushes, were clearly visible in the panorama at the Clear Side release site (Figure 2B). After release, foragers' homeward paths were recorded using pencil and graph paper until they reached the nest or left the testing area.

3.4 Results - Cluttered/clear tests

Foragers, with or without a remaining homeward vector, released on-route successfully oriented and returned to the nest. Headings were non-uniform and oriented to the nest (Table 1; Figure 2D) and mean headings were not significantly different between the ZV and FV On-route

conditions (Watson-Williams F-test; $F_{(1,28)} = 0.14$; $p = 0.715$). Initial navigational uncertainty at release, measured through increased heading variance 2m from release, also did not differ between ZV and FV On-route conditions (Var test; $Z = 0.29$; $p = 0.772$). Yet after orientation, navigational uncertainty rose in ZV foragers as they returned along the homeward route to the nest, with these foragers exhibiting significantly lower path straightness compared to FV foragers (Mann Whitney U-test; $U = 34$; $p < 0.001$; Figure 2D). In On-route testing, initial heading performance reinforces the findings at Nest 1, indicating that foragers can rely on either PI or the visual scene to orient. Additionally, the observed decreases in path straightness in ZV foragers suggests both PI and visual homing are active concurrently along the route. The observed paths are consistent with ZV foragers accumulating a conflicting vector that is in 180° conflict with the visual route during the inbound trip. The PI is always active and does not update after displacement, meaning that as ZF foragers navigate from the release site using visual panorama cues, an accumulating PI directs them back to the release point. This directional conflict increases navigational uncertainty, despite the forager traveling along a well-known route.

When displaced laterally (2m) onto the Cluttered Side, ZV foragers did not orient to the nest direction successfully, suggesting that with many local terrestrial cues blocking the familiar distant scene, foragers could not orient successfully. Initial headings were uniform, indicative of search behavior (Table 1; Figure 2D), yet a majority of foragers, 53% (8 of 15), re-entered the foraging route and successfully returned to the nest after a prolonged search. These observed paths are consistent with foragers engaging in search behavior until returning close to a familiar visual route (~ 1 m) and subsequently using these visual cues to navigate to the nest. In contrast, FV foragers released onto the Cluttered Side were initially guided solely by their PI system, exhibiting non-uniform headings that were grouped in both the nest (0°) and vector (338° ; V-test at 338° ; $\mu = 0.983$; $p < 0.001$) directions according to V-tests, yet only the vector direction was within the 95% CI of headings (Table 1; Figure 2D). After following the PI for the first 2m, forager paths curved away from the PI and towards the nest direction, suggesting a switch to navigation via the panorama along the route with 80% (12 of 15) of foragers returning to the nest entrance (Figure 2D).

When displaced laterally (2m) onto the Clear Side, both ZV and FV Foragers immediately oriented, exhibiting non-uniform headings (Table 1; Figure 2D). According to V-

tests, ZV and FV forager headings were grouped in both the nest (0° ; Table 1) and vector (22° ; ZV Foragers, V-test at 22° ; $\mu = 0.855$; $p < 0.001$; FV Foragers, V-test at 22° ; $\mu = 0.986$; $p < 0.001$) directions, however, only the nest direction was within the 95% CI of ZV forager headings, while only the vector direction was within the 95% CI of FV forager headings (Table 1; Figure 2D). Additionally, mean headings were significantly different between ZV and FV foragers (Watson-Williams F-test; $F_{(1,28)} = 17.92$; $p < 0.001$). The headings suggest that foragers without PI information relied on the panorama to navigate to the nest while foragers with both PI and the panorama (with a 22° directional conflict) predominately attended to their PI for at least the first 2m. Heading variance did not differ between ZV and FV foragers displaced onto the Clear Side (Var test; $Z = 0.954$; $p = 0.342$).

In fact, in FV foragers mean headings at 2m did not significantly differ between the Clear and Cluttered conditions (Watson-Williams F-test; $F_{(1,27)} = 0.03$; $p = 0.864$), suggesting foragers would predominately attend to their PI regardless of the presence of a familiar panorama, at least initially. Additionally, just as in Cluttered Side FV foragers, Clear Side FV foragers did not follow their vector for its complete length. After 2m, paths began to curve in the nest direction with 93% (14 of 15) of foragers returning to the nest entrance (Figure 2D).

4. Experiment 2 Off-route displacements

4.1 Methods - behavioral testing

Next, we tested navigational strategy use and performance as foragers were displaced locally off their known foraging route with increasing distances from known sites. This behavioural data was coupled with analysis of panorama similarity between these sites. At Nest 3, a feeder set-up identical to Nest 2 was constructed 5m from the nest entrance and foragers were allowed to train along the route collecting food for two days before testing. Six release sites were designated: one on-route site just outside the feeder (5m), three sites past the feeder at 6.5m, 8m and 10m from the nest entrance respectively, and two release sites 90° off the foraging route (clockwise) at 1.5m and 5m from the nest (Figure 3A). Two grids comprised of 1m squares were constructed using pegs and string. For Past Feeder conditions, a 4m wide grid was constructed from the nest entrance to the release site with 2m on each side. For each testing site, the grid extended 2m past the release site to include forager paths as they picked a heading. In the 90° Off-route conditions, an $8\text{m} \times 8\text{m}$ grid was erected. This grid was off-set by two meters in the vector direction (2m to

the left of the nest and 6m to the right) to allow foragers tested with a remaining 5m vector to fully run off their vector before leaving the testing area (see Figure 6B,D).

ZV foragers were collected just as they returned to the nest entrance, and released at one of the six release sites. FV foragers were collected from the feeder and tested at four of the release sites; 5m, 10m, 90° 1.5m and 90° 5m. As FV foragers released past the feeder could rely solely on their remaining vector to return to the known route (5m), we initially only tested FV foragers at 10m and as all these foragers successfully oriented and returned to the known route, FV foragers were not tested at the 6.5m and 8m sites. In all conditions, paths were recorded until the individual either reached the nest or left the testing grid.

4.2 Methods - panorama analysis and navigational performance

Image analysis comparisons between the closest known site panoramas and release sites allowed us to determine if sufficient visual similarity exists to orient by visual panorama cues. 360° nest-centered reference images of known panoramas were collected along the known foraging route (Theta 360° camera, Ricoh™). For each image analysis, the reference panorama was chosen as the closest known panorama to the testing site (the feeder panorama for the Past Feeder displacements and the nest panorama for the 90° Off-route displacements; Figure 3B). To compare displacement site panoramas to those of these known sites, 360° panoramic images were also collected from each release site (Figure 3B). Rotational image mismatches were calculated between the reference panorama and each release site panorama. For each image, the sky was converted to a single blue color to remove the sun, the image was converted to greyscale (blue color channel only) and downsized to 360p width × 80p height (~60p above and ~20p below the horizon). The sums of the absolute pixel intensity difference between release sites and reference panoramas for all orientations in 1° steps were calculated using rotational image difference functions (rotIDF) in MATLAB (Zeil et al., 2014; Stürzl and Zeil, 2007).

We compared foragers' navigational performance at each release site to the depth of the valley of mismatch in the panorama (Freas and Cheng, 2019). First, rotIDF minimum depth was calculated by subtracting the minimum pixel difference value (best match direction) from the 95th percentile of values for each release site comparison with the reference panorama. For Past Feeder conditions, the rotIDF minimum depth from each release site panorama to the feeder panorama was used, while in the 90° Off-route conditions, the nest panorama was used. A

Pearson's correlation coefficient was used to test the association between these rotIDF minimum depths and each forager's heading error. Heading error was calculated as the angular difference between each forager's heading at 2m and the rotIDF minimum or best match direction.

4.3 Results - behavioral testing

At Nest 3, when comparing the reference panorama at the feeder site, with the 5m release site (same location), the rotIDF shows a distinct best match direction in the nest direction at 0° (Figure 3B; rotIDF minimum depth: 0.992×10^6). Behavioral data at this known site mirrored our on-route results at Nests 1 and 2. ZV foragers released just outside the feeder at 5m, exhibited paths that were non-uniform and oriented to the nest (Table 1; Figure 4B). Additionally, 16 of 20 (80%) foragers travelled the full homeward route and successfully returned to the nest entrance.

When the 6.5m site panorama was compared to the reference panorama, rotIDFs showed a distinct valley of mismatch indicating the best match direction was 47° to the left of the nest at 313° (Figure 3B; rotIDF minimum depth: 0.495×10^6). Behavioral data mirrored this panorama similarity as well as the shift in the best matching direction to the left of the nest direction with ZV foragers released at this site (6.5m) exhibiting paths that were non-uniform and oriented to the nest. These headings were biased to the left of the true nest direction with mean headings at 335.8° but both the nest (0°) and best match (313°) directions were within the 95% CI of forager headings (Table 1). Additionally, 8 of 12 (66.7%) of these foragers successfully returned to the nest (Figure 4C). Despite nest-ward orientation in both the 5m and 6.5m conditions, circular variance of headings was significantly higher in the 6.5m group (Var test; $Z = -2.394$; $p = 0.008$) which corresponded with decreased panorama similarity between the known panorama and the 6.5m release site panorama despite the relatively small 1.5m distance from a known panorama.

Release site panorama similarity between the feeder site and release sites continued to degrade as displacement distance increased. Analysis of the 8m site panorama compared to the reference panorama showed a less distinct best match direction 67° to the left of the nest direction at 293° (Figure 3B; rotIDF minimum depth: 0.343×10^6). Behavioral data at 8m in ZV foragers suggests there was insufficient panorama similarity to successfully orient, as paths were uniform and only 25% (3 of 12) of foragers returned to the nest (Table 1; Figure 4D). Similarity continued to degrade at the 10m site, which showed no distinct valley of mismatch with the best

match direction 64° to the right of the nest direction (Figure 3B; rotIDF minimum depth: 0.193×10^6). ZV foragers released at the 10m site exhibited paths that were non-uniform, indicating oriented behavior, but these headings were not oriented in either the nest direction (Table 1; Figure 4E) or the direction of best match (V-test at 64° ; $V = -0.358$; $p = 0.960$). Instead these foragers were oriented in the direction opposite the nest and recently run off vector (V-test at 180° ; $V = 0.552$; $p = 0.003$) and this direction was within the 95% CI of headings (Table 1). Orientation in this direction is consistent with backtracking behavior, a behavior that occurs when ZF ant foragers are exposed to unfamiliar panoramas.

FV foragers that were released with a 5m vector, either at the feeder site or at 10m, oriented to the nest direction, exhibiting non-uniform headings that were grouped in the nest direction (Table 1, Figure 4A,F). In the 5m FV condition, all (15 of 15) foragers successfully returned to the nest, while in the 10m FV condition all foragers reached the known route and 90% (9 of 10) of foragers successfully returned to the nest.

Just as with on-route foragers at Nest 1, FV and ZV foragers released at the feeder (5m) initially showed no difference in navigational uncertainty as heading variance between groups was not significantly different (Var test; $Z = 1.183$; $p = 0.238$), however ZV foragers did exhibit significant decreases in path straightness compared to FV foragers (Mann-Whitney U test; $Z = -4.45$; $p < 0.001$; Figure 5A). Additionally, initial navigational uncertainty through heading variance did not significantly differ when comparing FV foragers released at 5m or 10m (Var test; $Z = -0.416$; $p = 0.674$). However, 10m FV forager paths showed significantly lower path straightness compared to 5m FV foragers (Mann-Whitney U test; $Z = 3.58$; $p < 0.001$; Figure 5A). When 10m FV forager paths were split into the first and second 5m halves of their homeward path, path straightness only significantly decreased in the second half (when foragers had run off their homeward vector but had returned to the known visual route) compared to both 5m FV foragers (Mann-Whitney U-test; $Z = 3.91$; $p < 0.001$) and the first half of their own path from the 10m release site (Wilcoxon Signed-Rank Test; $Z = -2.80$; $p = 0.004$; Figure 5A). Path straightness did not significantly differ between 5m FV foragers and the first half of 10m FV forager paths (Mann-Whitney U test; $Z = 0.47$; $p = 0.319$). Additionally, path straightness of the second half of the 10m FV condition was not significantly different from ZV foragers released at the same 5m site (5m ZV condition; Mann-Whitney U-test; $Z = -0.73$; $p = 0.234$; Figure 4A). These path straightness differences were indicative of increasing navigational uncertainty due to

an accumulating vector in 180° conflict of the panorama cues on the route in both ZV foragers released at 5m as well as in the second half of the homeward journey in foragers released at 10m with a 5m remaining vector.

At Nest 3, when comparing the nest reference panorama, with the 90° 1.5m release site, the rotIDF shows a distinct best match 7° to the left of the nest direction at 353° (Figure 3C; rotIDF minimum depth: 0.450×10^6). Behavioral data aligned with orientation via visual homing as ZV foragers released 90° 1.5m Off-route exhibited non-uniform headings that were oriented in both the true nest direction (0°) and the best match direction (353°) at 1.5m from the release site and 93.3% (14 of 15) of foragers successfully returned to the nest (Table 2; Figure 6A).

Just as in Past Feeder conditions, the rotIDF best match with the reference panorama degraded as release site distance from the known panorama increased. Analysis of the 90° 5m site panorama compared to the nest reference panorama showed a less distinct best match direction just 5° to the left of the nest direction at 355° (Figure 3B; rotIDF minimum depth: 0.284×10^6). Forager behavior corresponded with this decrease in panorama similarity with ZV foragers released 5m 90° Off-route not orienting to either the nest or the best match direction. These foragers were not initially oriented (uniform) at 50cm (Supplemental Table 2), yet by 2m headings were non-uniform (Figure 6B). At both distances, forager headings were not grouped in the true nest or the best match direction (Table 2) but were grouped in the compass direction opposite their recently run off vector, orientation behavior consistent with backtracking (Table 2; 50cm V test at 90°; $\mu = 0.395$; $p = 0.038$; 2m V test at 90°; $\mu = 0.723$; $p < 0.001$). Only 12.5% (2 of 16) of foragers successfully returned to the nest (Figure 6B).

FV foragers released at the 1.5m site exhibited non-uniform headings that were initially grouped only in the path integrator direction at 50cm (Supplemental Table 2; Figure 6C). However, most foragers quickly abandoned the vector direction at ~1m and turned toward the nest. By 1.5m, headings were still non-uniform but headings were now in a compromise direction between the vector and nest, with many foragers completely abandoning the vector (Figure 6C). According to the V-tests, headings were grouped in both the nest and vector directions, as well as the best panorama match direction, yet all three directions (vector, nest and panorama) were outside the 95% CI of headings (Table 2). FV foragers collected with a 5m vector and released 5m 90° Off-route, oriented solely to the path integrator. Initial orientations were non-uniform and grouped in the vector direction at 270° and not the true nest direction at 0°

(Table 2; Figure 6D). 50% (5 of 10) of foragers released at this location successfully returned to the nest.

Finally, we conducted a single between condition comparison between the Past Feeder and 90° Off-route testing conditions. We compared navigational performance of foragers released at the same 1.5m distance from the closest known panorama, the 6.5m Past Feeder and the 90° 1.5m conditions. (In this comparison, given the 90° 1.5m condition's close proximity to the nest entrance, measurements of circular variance were collected at a distance of 1.5m from the release site in both conditions). These release sites had comparable degrees of panorama similarity with each's closest known panorama (rotIDF minimum depth at 0.495×10^6 and 0.450×10^6 respectively). However, navigational performance was significantly better in foragers released at the 90° 1.5m site. These foragers exhibited significantly lower heading variance (Var test; $Z = 3.60$; $p < 0.001$) and significantly higher path straightness on their homeward journey (Mann-Whitney U test; $Z = 2.76$; $p = 0.003$) compared to foragers released at 6.5m (1.5m past the feeder).

4.4 Results - panorama analysis and navigational performance

RotIDF minimum depth size significantly correlated with angular error in ZV foragers in the Past Feeder and 90° displacement conditions. As rotIDF minimum depth increased, the angular error between foragers' individual headings and the rotIDF minimum direction decreased (Figure 5B). As panorama similarity between known sites and the release site decreased, forager's ability to successfully orient at these sites suffered.

5. Experiment 3 - Path integration in an unfamiliar panorama

5.1 Methods

Finally, we tested the proportion of the homeward vector that experienced foragers completed when exposed to an unfamiliar panorama at a distant testing site. Feeder sites from the previous testing conditions at Nests 1 and 3, at 16m and 5m from their respective nests, were kept stocked with crushed cookies and foragers from both nests were allowed to continue to freely forage at the feeder sites before testing. At Nest 1, FV foragers were collected from the feeder with an accumulated vector of 16m. These foragers were transported in an opaque phial to a distant (~140m) unfamiliar clearing where a 20m × 5m testing grid (1m squares) was erected in line

with the homeward vector compass direction. This distant displacement testing was replicated at Nest 3 with FV (5m vector) foragers collected from the feeder site on a 5m route. These foragers were released at a distant site ~115m away with a 10m × 5m grid. After release, foragers' paths were recorded until the forager left the testing area. These paths were split into pre-search paths with foragers homing via the path integrator and search paths. The onset of search was identified as the first sharp > 50° turn with the forager continuing for the new direction for at least 20cm. Any sharp turns that occurred in the first meter were excluded to allow foragers to choose a heading after release. For each forager, the direction and distance from the release point at the onset of search was recorded.

Given the South Mountain field site has distant mountains (both in the north and south compass directions) that could act as potential terrestrial cues across long distances, we conducted both behavioral control testing at Nest 1 and panorama analysis comparisons between each nest site panorama and the corresponding distant release site. As a behavioral control condition, ZV foragers at Nest 1 were collected as they reached the nest, after running off their 16m vector, and displaced to the distant site. Around this release site, a 5m × 5m testing grid (1m squares) was erected and the foragers' paths were recorded. With ZV foragers, we analyzed forager path headings as they first reached 2m from the release site. Image analysis comparisons between the nest panoramas (reference image) and distant release sites were conducted using rotIDFs for both nests (see above for rotIDF procedure).

5.2 Results

FV foragers displaced distantly with either a 16m or 5m vector followed their accumulated vector, exhibiting homing paths that were non-uniform and grouped in the vector direction at the onset of search (Table 1; Figure 7A,B). These foragers followed their homeward vector almost the entire vector distance, running off (mean ± s.d.) 13.65±2.35m (85.34%) of the 16m vector distance or 4.26±1.58m (85.12%) of the 5m vector distance before the onset of search. Both vector distance percentage traveled (Mann Whitney U-test; $p = 0.72$) and mean heading direction (Watson-Williams F-test; $p = 0.48$) did not significantly differ between Nests 1 and 3. In contrast, ZV foragers collected after running off their 16m vector at Nest 1, immediately engaged in search behavior (uniform headings) around the release point when displaced to the same distant site (Table 1; Figure 7C). Image analysis of the panoramas at each nest site and their

corresponding distant release sites showed no distinct valley of mismatch in any direction (Supplemental Figure 1A; Nest 1 rotIDF minimum depth: 0.152×10^6 ; Nest 3 rotIDF minimum depth: 0.090×10^6).

6. Discussion

6.1 Individual cue use

Novomessor cockerelli foragers employ two of the major individual strategies commonly used by individually foraging ants, a path integration system based on celestial cues and an odometer as well as the use of learned panorama views. Both on and off the foraging route, foragers could attend to either strategy to orient when these cues were available. In Experiments 1 and 2, when the panorama was unobscured by local clutter (or the blocking arena) and panorama similarity between current and known sites existed, foragers could orient to these visual cues to return straight to the nest both on or off the foraging route. When panorama cues were unavailable or contained little to no similarity with known sites, foragers without PI information could no longer orient successfully, engaging in search behavior, even when tested just above the established foraging route.

In contrast, foragers with a PI-based vector relied heavily on this system. Across experiments, when the surrounding panorama was unfamiliar or obscured, foragers with a remaining PI would orient and travel in the vector direction regardless of this heading's alignment with the nest's true direction. In Experiments 1 and 2, when the route panorama and PI cues directionally agreed, foragers oriented correctly and travelled straight to the nest area. Yet under directional conflicts between the panorama and the PI, foragers would initially ignore panorama information and attended solely to the PI, regardless of panorama similarity. In Experiment 1 when foragers were released on the clear side with a 22° conflicting vector and panorama directions, FV foragers initially oriented to the PI alone for the first 2m before shifting toward the true nest direction. In Experiment 2 at 1.5m from the nest, panorama cues were ignored by foragers with a directionally conflicting PI, which travelled exclusively in the vector direction (90° to the left). Regardless of whether sufficient panorama similarity existed to successfully navigate in the true nest direction at both of these release sites (ZV conditions), foragers initially ignored these cues in favor of the PI.

Despite heavy PI weighting, visual guidance via the panorama and the PI systems were concurrently active in both FV and ZV ants based on homeward paths. In Experiments 1 and 2, ZV foragers placed back on the route, as well as the 2nd half of paths for FV foragers released double the route distance at 10m, showed evidence that they were accumulating PI information after displacement consistent with a 180° conflicting vector as foragers travelled to the nest. Off-route, even after only small displacements where panorama similarity sufficient to orient existed (Nest 2, Clear side and Nest 3, 90° 1.5m) the PI system initially dominated but weighting later shifted mid-journey with forager paths curving toward the true nest direction. These curved paths indicate cue weighting between strategies was dynamic during the homeward journey with foragers switching from PI dominated navigation to panorama dominated navigation after running off part of their vector. Two weighting changes are likely occurring during these homeward journeys leading to the observed curved homeward paths. First, PI weighting decreases along with vector length (Wystrach et al., 2015), meaning that the PI cue becomes weaker as the forager runs off the PI distance. Additionally, as a forager following its PI nears the nest area (i.e. Clear Side FV foragers), its current panorama views increases in similarity with its memorized panorama views at the nest, likely increasing navigational weighing given to these cues.

6.2 Panorama similarity

Navigational performance via panorama cues (angular error) corresponded with the degree of similarity between the panorama at the displacement site and known panoramas (rotIDF minimum depth). Foragers were shown to successfully orient to the nest when displaced to the known route as well as sites 1.5m from the closest known panorama. Beyond this distance, navigational performance rapidly decreased with foragers displaced 3m and 5m from known panoramas being largely unable to orient to the nest. These decreases in performance correlated with decreases in rotIDF minimum depth. Analysis of the panorama similarity over short distances suggests that the terrestrial cues present in the environment, at least locally around Nest 3, are insufficient to provide navigational information to these foragers over distances above 1.5m. Findings suggest that the Sonoran Desert habitat at the South Mountain site contains few prominent terrestrial cues that could aid orientation through view-based matching over displacements above 1.5-2m given forager orientation at Nests 2 and 3. Even the presence of

mountain ranges, prominent to the human eye and unobscured by local clutter at ground level (Figure 3B) showed no evidence of improving forager orientation over this distance. These findings suggest that foraging ants in this ‘lightly cluttered’ habitat may heavily rely on their path integration system, at least partially due of the lack of prominent terrestrial cue information leading to a habitat with small panorama catchment areas between sites (Stürzl and Zeil, 2007; Murray and Zeil, 2017).

Catchment areas of natural scenes rely both on the presence of prominent distant landmarks as well as the landmark density, or clutter, in the environment (Zeil et al., 2014; Murray and Zeil, 2017). In ant navigation studies, small catchment areas are typified by highly cluttered forest environments where local landmarks block more distant cues (Zeil et al., 2014; Murray and Zeil, 2017; Freas and Cheng, 2019). The visibility of these prominent distant cues is critical for maintaining panorama similarity between sites (Zeil et al., 2003). Species inhabiting highly cluttered habitats, such as the forest nesting bull ant *Myrmecia midas* (Supplemental Figure 2), can only successfully orient via the panorama over distances <5m from known sites (Freas and Cheng, 2019). This pattern of high local clutter is present in the current study with foragers released into high clutter (Figure 2B), only 2m from a known site, being unable to successfully navigate via the panorama. As habitats become more open, distant prominent landmarks remain visible over longer distances. In the open clutter of the Australian outback (Supplemental Figure 2), *Melophorus bagoti* can orient to the nest from displacements up to 8-10m away with only memories of the nest panorama (Wystrach et al., 2012; Deeti et al., 2020). However, large catchment areas also require open environments to contain these prominent landmarks. In lightly cluttered environments where terrestrial cues are scattered and near the horizon (Supplemental Figure 2), such as around Nests 1 and 3, the lack of prominent terrestrial cues appears to result in small catchment areas around known locations and rapid drops in panorama similarity measured through rotIDF minimum depth. *N. cockerelli* navigational performance suffers in line with these panorama changes with foragers unable to successfully orient using panorama cues at distances above 1.5-2m from known sites.

Interestingly, at Nest 3 there were distinct differences in forager navigational performance (circular heading variance and path straightness) between the two release sites 1.5m from a known panorama (the 6.5m and 90° off-route 1.5m sites) despite the same displacement distance and similar rotIDF minimum depths. The superior navigational performance observed in

the 90° off-route 1.5m condition at Nest 3 is likely influenced by foragers' learning walks. During these walks, foragers learn multiple views around the nest in looping paths that often extend multiple meters from the nest entrance (Zeil and Fleishmann, 2019). While no study has explored learning walks in *N. cockerelli*, given work in multiple other species, these foragers likely have view memories acquired during these walks that extend close to or beyond 1.5m from the nest, meaning the true panorama similarity between this release site and foragers' closest known panorama is almost certainly higher than our analysis would suggest. Given we are estimating foragers' experiences, the rotIDF minimum depth comparisons at Nest 3 should be seen as general proxy for foragers' panorama memories beyond the foraging route rather than as the single nest-oriented panorama memory in use.

6.3 Navigation at distant sites

N. cockerelli foragers at two nests with a remaining PI-based vector and exposed to an unfamiliar panorama oriented to their vector direction and travelled almost the complete homeward vector distance, running off ~85% of their vector before the onset of search. This vector run off is markedly larger than other ant species inhabiting environments with terrestrial cues, and is consistent with a lightly cluttered environment where differentiating familiar and unfamiliar views may be difficult. The habitat in which ants forage is predictive of their navigational behaviour, with cue weighting changing along a scale of clutter density. The density of clutter in an environment correlates with both the distance at which panorama similarity is sufficient for navigation (discussed above) as well as the weighting foragers give to the PI and panorama cues. In heavily cluttered environments, foragers follow their vector less than a meter before beginning search (Beugnon et al., 2005; Freas et al., 2017) while in species inhabiting intermediate clutter, foragers complete under half of their vector before the onset of search (Narendra, 2007; Bühlmann et al., 2011). In featureless environments foragers will run off their full vector when displaced distantly (Bühlmann et al., 2011; Schultheiss et al., 2016). The behavioural evidence of PI cue weighting in this habitat, at least the local environments around Nest 1 and Nest 3, corresponds with a midpoint between the full vector distance seen in barren habitat species (*C. fortis* and *M. oblongiceps*) and the ~45% vector completion seen in intermediate clutter habitats (*M. bagoti*).

These weighting differences across habitats appear shaped by the local terrestrial cues present around each nest and each individual's foraging experience rather than species specific behavioural adaptations. The degree of panorama mismatch between known panorama cues acquired along the foraging route and the unfamiliar panoramas of distant sites dictate vector runoff distance. *M. bagoti*, which forage at sites that, (uncharacteristically for that area) lack terrestrial cues, complete almost their full vector distance when exposed to unfamiliar panorama cues compared to nests located in areas surrounded by clutter (Cheng et al., 2012). To distinguish unfamiliar panorama cues from familiar ones, foragers need to learn the familiar environment along the foraging route. *M. bagoti* foragers trained along a foraging route for multiple days complete significantly less of their homeward vector in unfamiliar panoramas compared to naïve foragers (Schwarz et al., 2017). While training foragers along routes involves allowing multiple days (typically two) of training, foragers form robust panorama memories of these routes rapidly after only a few trips (Freas and Cheng, 2018; Freas and Spetch, 2019). In the current study, we did not categorize route experience on the level of the individual, yet foraging routes to the feeder sites were well established with the feeders stocked for over a week before the start of distant site testing. Consequently, we expect tested foragers at Nest 1 and Nest 3 to be experienced with the established feeder route, with the observed vector proportion run off reflective of the low clutter density of the local habitat. Comparisons of local habitat clutter across multiple *N. cockerelli* nests, namely between the uncharacteristically heavy clutter at Nest 2 and the other nests, would be of interest. Unfortunately, Nest 2 failed toward the end of Experiment 1 and all other nests discovered at the South Mountain field site were located in lightly cluttered areas.

6.4 Potential presence of trail pheromone

Though *Novomessor cockerelli* is thought to largely forage alone, foragers are known to use pheromones to recruit nest mates to large food pieces that can only be transported cooperatively (Hölldobler et al., 1978; Buffin and Pratt, 2016). It is possible that during our experiments a pheromone trail along the foraging route was deposited. For multiple reasons, we believe this was unlikely to result in the observed navigational behaviors, with our results clearly implicating use of both a PI and panorama guidance strategies. First, pheromone cues are unlikely to influence behaviour that occurs off the established foraging route. Additionally, cookie pieces

were purposefully crushed to allow foragers to collect and transport pieces back to the nest alone, while pheromone deposits in *N. cockerelli* are only associated with large food pieces that require multiple individuals to transport. Additionally, there is currently no evidence in ants of straight-line pheromone trails providing polarity information of their inbound or outbound directions (Czaczkes et al., 2015). This would necessitate the use of other directional cues to resolve this ambiguity. Even socially foraging species rely on individual cue sets such as visual landmarks to guide navigation (Czaczkes et al., 2011, 2015). *V. pergandei*, another Sonoran Desert species that is also present at the South Mountain site, forages both socially and individually and its PI system provides directionality while the trail pheromone acts as a context cue dictating the weighting ascribed to the PI system over search (Freas and Spetch, In Review). This species will only follow their vector for a few meters without the presence of the pheromone cue. *N. cockerelli* will complete a larger proportion of their path integrator at an unfamiliar location than ant species that do not use pheromone trails at all, suggesting that pheromone cues are not typically used when foraging individually.

6.5 Backtracking behavior

As a final interesting finding, in some conditions at Nest 3 (90° off-route 5m and ZV 10m) where ZV foragers did not orient to the nest, we found that foragers instead oriented in the direction opposite the recently run off vector direction. This orientation behaviour is consistent with a backup strategy termed backtracking (Wystrach et al., 2013). In individually foraging species, foragers with a near zero vector state that have recently been exposed to the nest panorama and then displaced to an unfamiliar location will travel opposite their recent vector direction. It is theorized that this behaviour aids foragers that have returned to the nest area but overshot the entrance traveling into unfamiliar panoramas. This behaviour has been shown in multiple ant species as well as in honeybees (Collett et al., 1993; Collett and Collett, 2009; Plowes et al., 2019; Wystrach et al., 2013) though the underlying mechanisms modulating backtracking behavior can vary based on a species' foraging ecology (Freas et al., 2019b). In the current study, we only see evidence of backtracking in two conditions, both of which meet the criteria laid out in Wystrach et al. (2013). In contrast, foragers in the ZV Cluttered Side condition at Nest 1, the Panorama Blocked condition and the ZV (16m vector) distant displacement at Nest 2, showed uniform headings indicative of non-directed search. Yet, in the ZV Cluttered Side

condition many of the foragers that did not rediscover the foraging route did exit the testing site in the direction predicted by backtracking. Additionally, the high arena walls of the Panorama Blocking experiment may have influenced search behaviour with foragers avoiding unfamiliar landmarks. Further study is needed to fully explore both the prevalence and underlying mechanisms of backtracking in *N. cockerelli*.

7. Conclusions

Novomessor cockerelli foragers attend to both a homeward vector informed by path integration and the surrounding panorama to navigate both on and off their foraging routes. Foragers heavily weight their path integrator, with foragers completing almost their full (~85%) homeward vector at an unfamiliar site. Additionally, the path integration dictated direction initially dominates orientation behavior under cue conflicts with the panorama, yet this weighting is dynamic with foragers switching to panorama-based orientation after a few meters. Path integration reliance and poor panorama homing after local displacement is consistent with this species' habitat in which visual terrestrial cues are highly scattered and low to the horizon, resulting in small catchment areas of panorama similarity. Finally, *N. cockerelli* foragers show some evidence of backtracking behavior, travelling opposite a recently run off vector when presented an unfamiliar panorama after recently experiencing the nest panorama.

Author contributions

Conceptualization and methods: CAF and MLS; Data collection: CAF, Formal analysis, CAF Funding acquisition, MLS, Roles/Writing - original draft: CAF Writing – review/editing: CAF, NJP and MLS.

Conflict of interest

Authors declare that they have no conflict of interest.

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional

guidelines for the care and use of animals were followed. Additionally,
all testing conditions were non-invasive and all individuals
were returned to the nest after testing.

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Tables

Table 1. Circular statistics for forager headings in Experiments 1, 2 & 3.

		Mean Vector	95% CI		Rayleigh Test		V-Test Nest at 0°	
Condition	<i>n</i>		Minus	Plus	<i>Z</i>	<i>p</i>	<i>V</i>	<i>p</i>
Experiment 1 - Panorama Blocked tests								
Unblocked ZV	21	1.9°	352°	12°	17.9	<0.001	0.924	<0.001
Unblocked FV	21	6.1°	339°	33°	6.9	<0.001	0.571	<0.001
Blocked ZV	20	147.3°	-	-	0.5	0.559	-	-
Blocked FV	20	17.4°	351°	44°	7.0	<0.001	0.564	<0.001
Experiment 1 -Cluttered/Clear tests								
On Route ZV	15	0.7°	353°	8°	14.1	<0.001	0.971	<0.001
On Route FV	15	2.4°	357°	8°	14.6	<0.001	0.985	<0.001
Cluttered ZV (at 1m)	15	50.3°	-	-	0.3	0.767	-	-
Cluttered FV	14	334.9°	329°	341°	13.6	<0.001	0.892	<0.001
Cleared ZV	15	356.2°	346°	7°	13.5	<0.001	0.948	<0.001
Cleared FV	15	19.5°	14°	25°	14.6	<0.001	0.930	<0.001
Experiment 2 – Off-route displacements – past feeder								
5m ZV	20	352.6°	335°	10°	12.3	<0.001	0.777	<0.001
6.5m ZV	12	335.8°	296°	16°	3.6	0.023	0.501	0.006
8m ZV	12	189.7°	-	-	0.2	0.825	-0.127	0.730
10m ZV	12	193.2°	155°	231°	3.9	0.018	-0.552	0.997
5m FV	15	355.9°	352°	0°	14.7	<0.001	0.989	<0.001
10m FV	10	355.0°	349°	1°	9.8	0.648	0.986	<0.001
Experiment 3 – Distant displacements								
							V-Test Vector at 0°	
16m FV (Search Onset)	14	2.6°	359°	6°	13.8	<0.001	0.993	<0.001
16m ZV	11	204.9°	-	-	0.5	0.648	-	-
5m FV (Search Onset)	13	0.0°	353°	7°	12.5	<0.001	0.978	<0.001

Table 2. Circular statistics for forager headings in the Experiment 2 90° off-route displacements.

Condition	n	Mean Vector	95% CI		Rayleigh Test		V-Test Nest at 0°		V-Test Vector at 270°	
			Minus	Plus	Z	V	V	p	V	p
Experiment 2 - 90° off-route Displacements										
1.5m Displacement ZV (at 1.5m)	16	2.6°	349°	17°	12.4	<0.001	0.881	<0.001	-0.040	0.589
1.5m Displacement FV (at 1.5m)	15	326.3°	305°	348°	9.5	<0.001	0.664	<0.001	0.442	0.007
5m Displacement ZV	10	81.8°	49°	115°	5.3	0.003	0.465	0.324	-0.723	1.000
5m Displacement FV	10	270.2°	265	276°	9.8°	<0.001	0.003	0.494	0.992	<0.001

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853 **Figure 1.** Testing diagrams and forager headings in Panorama Blocked Tests at Nest 1. (A)

854 Panoramas of Nest 1 taken at the nest site, feeder site and mid-point testing site with the

855 panorama either available or blocked. (B) Diagrams of the testing conditions and circular

856 histograms of initial forager headings at 30cm at Nest 1. Zero-Vector or Full-Vector Foragers

857 were tested with the panorama along the route either available or blocked using a circular arena

858 (50cm height). In each circular histogram, the nest/vector direction was set at 0°. Forager

859 headings are grouped in 15° bins. The arrow denotes the length of the mean vector and the mean

860 heading direction. n, number of individuals; $\bar{\theta}$, mean vector; r, length of mean vector.

Figure 2. Diagrams and forager paths in Clutter/Clear Tests at Nest 2 (**A**) Image of the testing set-up at Nest 2. Any ground clutter at Nest 2 was removed along the 5m foraging route and to the right side creating a ‘Clear Side’ where distant terrestrial cues were visible while the left ‘Cluttered Side’ was left intact. (**B**) Panoramas along the foraging route and at the 2m lateral displacements on the Clear and Cluttered sides. (**C**) Diagrams of collection and displacement conditions at Nest 2. Foragers were either collected at the feeder (Full-Vector) or after returning to the nest entrance (Zero-Vector) and displaced On-Route or 2m laterally onto the Cluttered (grey area) or Clear Side (white area). (**D**) Forager paths after displacements. On-Route displacements released foragers just outside the feeder and followed foragers until they returned to the nest. Foragers’ paths after 2m lateral displacements to the Cluttered (black paths) or Clear sides (grey paths).

Figure 3. Testing diagrams and Rotational Image Difference Functions (rotIDFs) for testing at Nest 3. (A) Full-Vector (black arrows) and Zero-Vector (grey arrows) foragers were displaced and tested at one of six release sites. Release sites were designated in a straight-line past the 5m foraging route at 5m feeder (control), 6.5m, 8m and 10m from the nest (Past Nest conditions) or 90° clockwise off-route, at 1.5m or 5m. RotIDFs were created by rotating the panorama at each release site in 1° steps and comparing the pixel difference to the reference image. Reference images on the top row were chosen as the closest of the two known panoramas (feeder or nest) to the release sites of either the (B) Past Feeder conditions or the (C) 90° Off-route conditions. RotIDFs compare the pixel difference between the reference panorama with the panorama at each release site. In each panel, the solid black line represents the rotIDF comparison. For each panorama, nest direction is centered at 0°.

Figure 4. Forager paths after displacement at Nest 3 in the Past Feeder conditions. Foragers were released just outside the feeder with either a (A) Full-Vector or (B) Zero-Vector. Zero-Vector foragers were also released past the feeder at (C) 6.5m, (D) 8m and (E) 10m. (F) Full-Vector foragers were released past the feeder at 10m. *n*, number of individuals.

Figure 5. Navigational performance at Nest 3. **(A)** Box plots of path straightness in the FV Past Feeder conditions at Nest 3. Each full condition is indicated as a grey box plot while the 10m Full-Vector condition was also split into its two 5m halves (white plots), with the first half occurring on an unfamiliar route with a 5m vector and the second half occurring on the known foraging route, but with an accumulating vector in 180° opposition to the direction of the nest. The measure of path straightness was defined as the ratio between observed path length and the straight-line distance to the forager's exit location. Each box plot shows the median (middle line) and 25th and 75th percentile while the whiskers extend to min and max values. **(B)** Angular heading error plotted with rotIDF minimum depths at each local release point in both the Past Nest and 90° Off-route conditions. RotIDF minimum depth for each release site panorama was calculated as the difference between the minimum-pixel-difference and the 95th percentile value. As rotIDF minimum depth increased, the angular error between individual forager headings at 2m and the rotIDF minimum direction significantly decreased ($r_{(80)} = -0.438$; $p < 0.001$).

Figure 6. Forager paths after displacement at Nest 3 in the 90° Off-route displacement conditions. Zero-Vector foragers were collected after returning to the nest and released at (A) 1.5m or (B) 5m. Full-Vector foragers were collected from the feeder with a 5m vector and displaced 90° and either (C) 1.5m or (D) 5m from the nest. The grey circle indicates the release site. n , number of individuals.

Figure 7. Forager paths after distant displacement at Nests 1 and 3. Foragers from (A) Nest 1 with a 16m vector or (B) Nest 3 with a 5m vector were released at an unfamiliar site. Pre-search paths are black while search paths are grey. The open circle marks the ‘fictive nest’, defined as the nest location based on the forager’s vector state upon release. (C) Foragers from Nest 1 collected after running off a 16m vector and released at the distant site. In the ZV condition, as foragers did not orient, foragers’ full paths are shown in black. The black triangle denotes the direction of the recently run off vector. The grey circle indicates the release point. *n*, number of individuals.