J Exp Biol Advance Online Articles. First posted online on 20 June 2013 as doi:10.1242/jeb.089649
Access the most recent version at http://jeb.biologists.org/lookup/doi/10.1242/jeb.089649

Homing abilities of the Australian intertidal ant, *Polyrhachis sokolova*

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Homing in an intertidal ant

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Abstract

The pressure of returning and locating the nest after a successful foraging trip is immense in ants. To find their way back home, ants use a number of different strategies (e.g., path integration, trail-following) and rely on a range of cues (e.g., pattern of polarised skylight, landmark panorama) available in their environment. How ants weigh different cues has been a question of great interest and has primarily been addressed in the desert ants from Africa and Australia. We here identify the navigational abilities of an intertidal ant, *Polyrhachis sokolova* that lives on mudflats where nests and foraging areas are frequently inundated with tidal water. We find that these solitary foraging ants rely heavily on visual landmark information for navigation but they are also capable of path integration. By displacing ants with and without vector information at different locations within the local familiar territory we created conflicts between information from the landmarks and the path integrator. The homing success of full-vector ants, compared to the zero-vector ants, when displaced 5 m behind the feeder indicate that vector information had to be coupled with landmark information for successful homing. To explain the differences in the homing abilities of ants from different locations we determined the navigational information content at each release station and compared it to that available at the feeder location. We report here the interaction of multiple navigation strategies in the context of the information content in the environment.

Keywords: navigation, path integration, landmark-panorama, cue-competition

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Introduction

At the end of a foraging trip ants return home typically using one of three navigation strategies: (a) following a pheromone trail, (b) taking the shortest path home, a strategy known as path integration (for reviews, see Collett and Collett, 2000b; Wehner and Srinivasan, 2003), or (c) returning by using familiar landmark information (Collett et al., 2007). In trail following, individuals who travel along a particular route produce a pheromone trail secreted by one of their abdominal glands. A follower who also travels on the same route, detects these pheromones from the chemoreceptors present on their antennae to follow the trail until they reach the destination (e.g., Hölldobler and Möglich, 1980). In path integration, an individual leaving the nest keeps track of the distance travelled and the angles steered on the outbound journey and upon finding food integrates this information to compute the shortest home vector (HV) (Collett and Collett, 2000a; Collett and Collett, 2000b; Müller and Wehner, 1988; Wehner and Srinivasan, 2003). Distance travelled is estimated by a stride integrator (Wittlinger et al., 2006; Wittlinger et al., 2007) and compass information is derived from the pattern of polarised skylight (Wehner, 2001; Wehner and Müller, 2006). For landmark guidance, visual landmark information first needs to be learnt. For this, ants carry out a systematic learning routine when leaving the nest and also when leaving newly discovered food sources (Müller and Wehner, 2010; Nicholson et al., 1999). These learning walks are most likely crucial in pinpointing goals using visual landmarks (Narendra et al., 2007; Wehner and Räber, 1979).

From the ants studied so far, it is clear that the above navigation strategies are not species specific. For instance, inexperienced foragers of a trail-following ant *Paraponera clavata,* use information from the pheromone trails, whereas experienced individuals switch to relying on visual landmark information (Harrison et al., 1989). Among solitary foraging ants, for instance in the Australian desert ant *Melophorus bagoti*, individual ants typically establish and adhere to routes that meander around specific bushes and tussocks, but when familiar landmarks are unavailable they switch to relying on a path integrator (Kohler and Wehner, 2005; Narendra, 2007a; Narendra, 2007b). The converse holds true for the African desert ant, *Cataglyphis fortis*, which typically relies on path integration, but switches to relying on landmark information when available (Collett and Collett, 2000a; Graham et al., 2003; Knaden and Wehner, 2005; Müller and Wehner, 1988; Müller and Wehner, 2010; Wehner et al., 1996). The ability to orient using the pattern of polarised skylight and visual landmarks is not restricted to ants active in bright light conditions only. The large eyed bull ant *Myrmecia pyriformis* is a case in point. These ants navigate to specific trees during the evening twilight and return to their nest in the morning twilight (Narendra et al., 2010), the periods of the day when the pattern of polarised skylight is most simple since the sun is at the horizon (Cronin et al., 2006). These ants derive compass information from both the pattern of polarised skylight and visual landmarks even in the dim light

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conditions at which they operate (Narendra et al., 2013; Reid et al., 2011). It is becoming increasingly evident that the information content available in the environment strongly influences the navigation strategies used by ants and the navigational decisions they make (Zeil, 2012). One of the most compelling pieces of evidence for this comes from the Australian desert ant, *M. bagoti,* in which ants that inhabit landmark-rich habitats relied on their path integrator to travel about 43% of their home vector and this increased to 70% in ants that inhabit landmark poor habitats (Cheng et al., 2012; Cheung et al., 2012; Narendra, 2007a).

Since animals can use more than one navigational strategy, it is of great interest to identify how animals resolve situations when a conflict occurs between multiple navigation strategies. Studies on cue conflict in ants can be categorised as follows: (a) conflict between HV and landmarks; (b) conflict between celestial and terrestrial cues, (c) conflict between celestial and idiothetic cues, and (d) conflict between food vector and vector derived from local landmarks. A conflict between HV and visual landmarks appears to be resolved in two distinct manners. In one, animals ignore information from the HV and directly home in to the nest (*Formica japonica*: Fukushi and Wehner, 2004; *Myrmecia croslandi*: Narendra et al., in review). In the other, animals resolve the conflict by following a compromise direction between the HV and the landmarks (*M. bagoti*: Narendra, 2007b; also see Wystrach et al., 2012). Cue conflict between the celestial and terrestrial cues on an outbound journey, is resolved by choosing a compromise direction indicated by the two cues (*Myrmecia pyriformis*: Reid et al., 2011). But, when a conflict is created between the compass information provided by celestial cues and idiothetic cues, ants solely rely on the celestial cues (*C. fortis*: Lebhardt et al., 2012). When conflicts occur between the food vector and a vector attached to a local landmark (e.g., end of a channel), ants followed a direction which is a compromise between the directional estimates of the two cues (*C. fortis*: Collett, 2012). We here aim to identify the navigational strategies used by the intertidal ant, *Polyrhachis sokolova* (Forel 1902) and determine how they resolve conflicts between HV and landmark information while returning to the nest. To the best of our knowledge, this is the first study that addresses navigational strategies in the Old World ant genus *Polyrhachis*, thus contributing towards a comparative analysis in the family Formicidae.

Methods

Study species

The intertidal ant, *Polyrhachis sokolova* (Forel, 1902) is unique among ants in nesting at the land and ocean interface of the mangrove zone (Robson, 2009; Robson and Kohout, 2007), where their nests are regularly inundated by tides. The mangrove trees provide a distinct panoramic skyline in the landscape with no other conspicuous landmark features on the ground. The ants construct

subterranean nests at the base of mangroves and when the tide water reaches the nest, loose soil particles surrounding the nest entrance collapse to form a plug to prevent water from entering the nest, thus keeping the interior chambers dry during high tides (Nielsen, 1997). These ants typically feed on bird droppings and dead seafood (e.g., crabs) that get washed in by the tides (pers. obs. A. Narendra). They mostly travel on dry land but when they encounter a body of water, remarkably, they swim. While swimming they use their first two pairs of legs as paddles and hold their hind legs on the water surface in line with the body (Fig. 1; Robson, 2009). Given the nature of the substrate on which they forage (mud and/or water) it is unlikely that these ants use pheromone trails for navigation. The ants are found along the Australian east coast from Torres Strait to Gladstone in Queensland and also in nearby tropical countries (Andersen et al., 2013; Kohout, 1988). Our study was carried out in the mangrove habitats of Pallarenda, Townsville, QLD, Australia (Fig. 1). The study was carried out during the day at low tides in the months of April and May, 2012.

Ant training

We trained ants to a feeder placed 7 m North of the nest. The typical food source used for ants such as 10% sugar or honey solution and cookie crumbs failed. After we noticed some ants feeding on dead crabs, we provided clams (*i.e.,* Pipis (*Plebidonax deltoides*), purchased from the local seafood stores) as a food source for these ants, which they drank from or tore and carried small pieces to the nest. Ants leaving from the feeder (full-vector ants) were captured individually in foam-stoppered Perspex tubes and transferred in the dark to one of seven release stations. Ants were released at (1) *the feeder*, (2) *1m lateral* to the home direction, (3) *1m lateral & 5m behind*, (4) *5m lateral*, (5) *5m lateral & 5m behind*, (6) *50m lateral* or (7) *>100m away* from the feeder. To test the navigation abilities in the absence of vector information, we captured ants returning from the feeder close to the nest (zero-vector ants) and released them at the same seven release stations. Zero-vector and full-vector ants were released at one of the randomly chosen release stations. Tested ants were marked with a single colour to ensure they were recorded only once.

Ant tracking

Ant paths were tracked by placing miniature flags at every 10 cm behind a walking ant, carefully avoiding disturbing the ants' progress. Ants were tracked between 0800-1100 hrs and 1500-1800 hrs. We avoided tracking when the sun was in the zenith, i.e., when the pattern of polarised skylight was strongest in the horizon, which makes it less reliable as a compass cue. The flag-marked path was later recorded using a Differential Global Positioning System (DGPS, NovAtel Inc., Canada). The set-up consists of a base station antenna (GPS-702-GG L1/L2, GPS plus GLONASS), a base station receiver (FLEXPAK-V2-L1L2-G GPS plus GLONASS RT-2), a rover antenna (ANT-A72GLA-

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TW-N (532-C) and a rover receiver (OEMV-2-RT2-G GPS plus GLONASS). In a DGPS, a stationary reference or base station calculates corrections for a mobile rover antenna, the position of which is determined with centimetre accuracy at least on a local scale, in our case an area of about 120 m radius. The stationary base station electronics and antenna were mounted on a tripod and set to integrate antenna position readings over 30 minutes. The rover receiver electronics was carried on a backpack and connected to the rover antenna that was mounted at the end of a long, hand-held stick, so that it could be moved close to the ground along a flag-marked path (Narendra et al., 2013). The base station and rover communicate through a radio link, allowing the exchange of corrections that provide position accuracy of the rover antennae of 1-2 cm. Northing, Easting and Height coordinates in metres, together with the standard deviations of position error estimates were recorded and monitored at 1 sec intervals with a laptop computer and extracted with a custom-written Matlab program (Matlab, Nattick, USA).

Ants displaced close to the familiar route were tracked until they reached the nest or for up to 20 minutes, which was well within the time required for ants to travel directly home from the largest displacement. When ants were displaced to unfamiliar locations, we tracked them until they began a search. To identify the start of search we measured the cumulative distance travelled from the release point. The location where this distance decreased for more than 4 consecutive points (equivalent to 15-20 cm) was identified as the start of search. Circular analyses of heading directions of ants from different release stations was carried out based on Batschelet (Batschelet, 1981) using Oriana (Kovach Computing Service, Anglesey, UK). We compared the distance travelled by full- and zero-vector ants that were released in unfamiliar locations, relative to their path length. For this, we used animals whose path length was ≤ 10 meters.

Analysis of the panoramic scene

We captured the panoramic scenes at each of the release locations on a single day between 1000-1015 hrs using a Sony Bloggie camera (MHS-PM5). The camera was leveled using a spirit level. During the gathering of these images, reference directions (e.g., Nest and/or Northing) were identified. The circular panoramic images were unwarped to rectangular panoramas measuring 1759 x 198 pixels which corresponded to 360° x 40.52° using a custom written Matlab program. Sun glare and reflection artefacts were removed using the colour replacement tool in Adobe Photoshop CS6 (Adobe Systems Inc.) to copy adjacent pixel values into the corrupted areas. The images were converted to grey scale, shifted (Matlab *circshift* function) to align the nest direction in the center of each image and low pass-filtered with a 18x18 pixel Gaussian filter with a resolution of 6 pixels/degree to match the interommatidial angle of the eye of *P. sokolova* (Narendra et al., in review). We compared view familiarity between different release sites by determining the rotational image difference function

The Journal of Experimental Biology – ACCEPTED AUTHOR MANUSCRIPT

(rotIDF) (for details, see Stürzl and Zeil, 2007; Zeil et al., 2003). We did this by calculating the pixel differences for a shift in each pixel between the image at the feeder and the image at each release station using Matlab *circshift* function. The values were then squared and averaged. For each image shift the root mean squared pixel differences was determined. The minimum derived by such a comparison (i.e., least difference between images) indicates home direction for each release location.

Results

a) Full-vector ants in local familiar area

The initial heading direction of ants released at the *feeder* location (θ=93.50°; Fig. 2a) was close to that indicated by the HV (θ=100.0°; indicated by a black arrow in circular plots in Fig. 2). All ants from this location returned to the nest directly without exhibiting any search (Fig. 2a). The initial heading direction of ants released *1m lateral* (θ=74.14°; Fig. 2b) was directed slightly away from both the true nest direction (θ=92.0°) and HV (θ=100.0°). All ants from this release location returned to the nest directly without exhibiting any search (Fig. 2b). Ants released *1m lateral & 5m behind* also exhibited an initial orientation (θ=65.69°, Fig. 2c) away from both the true nest direction (θ=91.0°) and the HV (θ=100.0°). Nearly 90% of the ants released at this location returned to the nest (Fig. 2c). Few ants (4 out of 10) engaged in a brief search (U-turns), before heading directly to the nest. The initial heading direction of ants released *5m laterally* (θ=65.69°, Fig. 2d) was directed between the true nest direction (θ=58.0°) and the HV (θ=100.0°). Only 50% of the individuals released at this location returned to the nest (Fig. 2d). The initial heading direction of ants released *5m lateral & 5m behind* (θ=94.58°, Fig. 2e) was also directed between the true nest direction (θ=73.0°) and the HV (θ=100.0°). Nearly 72.72% of ants released at this location returned to the nest (Fig. 2e). Most ants from this group travelled a distance greater than that indicated by their path-integrator and subsequently corrected their heading to travel towards their familiar foraging corridor, before reaching the nest.

At all release stations the initial heading directions of the full-vector ants were not significantly different from the directions predicted by the path integrator (P_s<0.001, V test) and by the true nest (P_s<0.001, V test, Figs. 2a - 2e).

b) Zero-vector ants in local familiar area

At all release stations the initial heading directions of the zero-vector ants were not significantly different from the directions predicted by the path integrator (P_s<0.001, V test) and by the true nest (P_s<0.001, V test, Figs. 2f – 2j).

All ants released at the *feeder* (Fig. 2f) and at the *1m lateral* location (one exception; Fig. 2g)

The Journal of Experimental Biology – ACCEPTED AUTHOR MANUSCRIPT

successfully returned to the nest. Among the ants released *1m lateral & 5m behind* (Fig. 2h), only one ant returned to the nest and the majority of them searched close to the release location. Among the ants released *5m laterally* (Fig. 2i), only 20% of the individuals successfully returned to the nest. Of the two successful ants, one was initially directed towards the fictive nest and corrected its heading to travel to the familiar corridor and subsequently to the nest. The second ant was initially directed towards the habitual route, but then corrected its heading to travel towards the fictive nest and then corrected its heading once more to travel directly to the familiar corridor and then the nest. The unsuccessful ants in this group drifted in the direction towards the fictive nest but turned back and began searching after travelling a maximum of 3 m (Fig. 2i). Among the ants released *5m lateral & 5m behind* (Fig. 2j), only two ants reached the nest. Both these ants walked towards the fictive nest and travelled a distance greater than the feeder-nest distance. Both ants corrected their heading direction at nearly the same spatial location, following which they headed to the habitual route and then reoriented to head to the nest. Most of the unsuccessful ants in this group (Fig. 2j) drifted towards the feeder location, but turned back after travelling a maximum distance of 5 m.

c) Homing in unfamiliar area

The initial heading direction of full-vector ants was directed towards the fictive nest at both *50m lateral* (nest = 90°; θ=88.42°, Fig. 3a) and at *>100m distant* location (nest = 90°; θ=90.88°, Fig. 3c). The initial heading direction of zero-vector ants was not directed towards the fictive nest at both *50m lateral* location (nest = 90°; θ=62.97°, Fig. 3b) and at *>100m distant* location (θ=57.49°, Fig. 3d), but occurred within ±90° of the fictive nest position relative to the release location. All full-vector ants, except two, travelled distances shorter than that indicated by their path integrator, before beginning a search (middle row in Fig. 3a, 3c). Zero-vector ants released at *50m lateral* and at *>100m distant* location began searching immediately upon release. This is evident when distance travelled from the release location was compared between zero- and full-vector ants with path lengths of ≤10 m. At the *50m lateral* location the full-vector ants travelled farther from the release point (3.98 ± 0.62 m; mean±s.e.) compared to the zero-vector ants (1.54 ± 0.24 m; mean±s.e; $P<0.01$, $t=3.066$, $df=23$, t-test; bottom panel in Fig. 3). At the *>100m distant* location also the full-vector ants travelled farther from the release point (3.90 ± 0.38 m; mean±s.e.) compared to the zero-vector ants (1.44 ± 0.25 m; mean±s.e; $P<0.001$, $t=4.621$, $df=24$, t-test; bottom panel in Fig. 3). The zero-vector also returned repeatedly either to or close to the release point (indicated by arrows in the bottom panel in Fig. 3).

d) Navigational information content in the environment

Panoramic views available at all release stations are shown (Fig. 4a, 4b). Images are aligned such that nest or the fictive nest position is in the centre of the image. We compared view familiarity of the

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feeder location with all release locations using the rotational image difference function (rotIDF). A comparison of the view from the feeder with itself produced a minimum, i.e., least image difference (black curve in Fig. 4c), which coincided with the South direction that indicated the nest direction. A detectable minima was present at all the local release locations (locations 2,3,4,5,6 in Fig. 4c). The depth of the minimum however decreased as the distance from the nest increased (blue, green, brown, red in Figs. 4c). Strangely, a detectable minimum was available at even the two distant release locations (light blue and yellow in Fig. 4c). To investigate this, we compared views from the *feeder* with the *50m lateral* location (Fig. 5a) and views from the *feeder* with the *distant* location (Fig. 5b) at different elevations. A comparison of views with elevation between 10-40° (upper part of the panorama), which was predominantly information from the sky (red box and red curves) produced a strong minimum. In contrast, comparison of views with elevation between 0-10° (lower part of the panorama), which has landmark information (brown box and brown curves) did not provide a distinguishable minimum, at least for the distant site.

Discussion

The intertidal ant, *P. sokolova* is a solitary foraging ant that nests at the base of mangroves and forages along the mudflats during low tide. Ants that arrive at a feeder when displaced to a distant location travelled following their home vector providing evidence for path integration. Zero-vector ants when displaced either at or near to the feeder location headed directly to nest, providing evidence that *P. sokolova* ants can home in using landmark information. When a conflict between the direction indicated by the HV and landmark information was created, as was the case at release locations of *5m lateral* and at *5m lateral and 5m behind*, ants initially head in a direction which is a compromise between that indicated by the HV and landmark information. When zero-vector ants were displaced to local release stations, only a small proportion of animals returned to the nest. This suggests that at these local release locations, vector information coupled with landmark information is required for most ants to home in to their nest.

At the *1m lateral* location (Fig. 2b), there was little discrepancy between the directions indicated by the home vector (HV) and the landmarks indicating the true nest position. The initial orientation of these ants appeared to be directed towards the familiar route between the feeder and the nest and was not directed to the nest or followed the HV. Once animals were in the familiar corridor they headed directly to the nest. It was, however, difficult to pinpoint whether ants were guided by HV or by landmark information. Hence releasing zero-vector ants at the same location (Fig. 2g) demonstrated with certainty that *P. sokolova* can return home using landmark information alone and without vector information. Their ability to path integrate was evident when full-vector ants were displaced to

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unfamiliar locations, where ants walked in the direction towards the fictive nest (Figs. 3a, 3c). The rotIDF indicate that the view similarity between the feeder location and distant location was primarily driven by information from the sky and not from the landmarks (Fig. 5). It is perhaps due to this dominant sky information that animals released at the distant location rely on their path integrator (Fig. 3c). For path integration, these ants most likely derive compass information from the pattern of polarised skylight (Labhart and Meyer, 1999; Wehner and Labhart, 2006), which draws support from the specialised photoreceptors in the dorsal rim area of their eyes (Narendra et. al., in review).

Another release location where there was little discrepancy between the directions indicated by the HV and landmarks was at the *1m lateral & 5m behind* location (Figs. 2c, 2h). At this release station, most of the full-vector ants (90%) returned to the nest, exhibiting individualistic paths. Full-vector ants, however, had HV information only for 7 m and hence should have started searching at 7 m or earlier (Cheung et al., 2012), which they did not. In most cases animals continued to travel in a well-directed path to the nest. Some ants carried out a short U-turn following which they headed directly to the nest. Thus the second half of their journey was most likely visually guided. As indicated from the IDFs (Fig. 4b), the similarity in the views increases as one gets closer to the nest, thus providing animals a reliable visual cue to locate home (Stürzl and Zeil, 2007; Zeil et al., 2003). But few zero-vector animals returned to the nest (Fig. 2h) indicating that this release location was too far away for ants to return home using landmark information alone. Most ants continued searching for the 20-minute recorded duration. This is despite there being a detectable minimum when comparing the views from *feeder* and the *1m lateral & 5m behind* (brown curve in Fig. 4b). Similarity in views appears insufficient to trigger homing in majority of the zero-vector ants, suggesting that perhaps vector information is required to some extent even to rely on visual landmark information.

The maximum discrepancy between the compass directions of the HV and landmark information is at the *5m lateral* site (Fig 2d, 2i) and at the *5m lateral & 5m behind* site (Figs. 2e, 2j). Full-vector ants released at both these locations could have again traveled their HV partially or completely, before beginning a search (Cheung et al., 2012), but they did not. We noticed three distinct phases in the homing trajectories of these ants. Phase I: paths immediately after release; phase II: search and reorientation; phase III: final approach. In Phase I, animals travelled in a direction intermediate between that indicated by the HV and landmark information. Here, ants traveled in a straight line until they were about 2.6 m from the nest position, indicating that ants released at *5m lateral & 5m behind* site (Fig. 2e) travelled a distance greater than their HV. Phase II began at nearly the same spatial location for ants from both the groups. Here, ants began to search and in most cases reoriented to head towards the familiar foraging corridor. Some ants (especially in Fig. 2d) searched extensively and did not find the familiar corridor within the recording duration and were considered ‘lost’. In Phase

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III, ants reoriented as soon as they reached the familiar corridor (~1.3 m from the nest) and headed directly to the nest. In the case of zero-vector ants released at these two locations (Figs. 2i, 2j), majority of the ants were considered to be lost after 20 minutes of recording. However, the initial heading direction of these ants also was directed towards the fictive nest. Few zero-vector ants from these two release stations were successful in finding the nest (red lines in Fig. 2i, 2j). Interestingly, these successful ants again displayed a three-phase homing behavior similar to the full-vector ants, with the reorientation at the second phase starting at the same spatial location. The view similarity of the *5m lateral* and *5m lateral and 5m behind* release stations with the views at the feeder appear to be sufficient for a few zero-vector ants to return to the nest (green and red curves in Fig. 4b).

The initial heading direction of zero-vector ants towards the fictive nest at the local release stations (*5m lateral* and *5m lateral & 5m behind*; Figs. 2i, 2j) is quite puzzling. It is unlikely that a residual vector caused this behaviour. This is because, zero-vector ants were captured 5-10 cm from the nest entrance while returning from the feeder and this residual vector is less than the distance where the initial heading direction (50 cm from release) of ants was noted. If ants could recall their recent home vector when faced with unfamiliarity, this could explain their behaviour. The initial heading direction of zero-vector ants in the unfamiliar location (*50m lateral* and *distant*; Figs. 3b, 3d) occurred only in the southern hemicycle, i.e., ±90° of the fictive nest position. Perhaps, even the little landmark information that was available in the southern half of the panorama (see bottom panel in Fig. 4c) resulted in animals heading only in the southern half.

Foragers of *P. sokolova* rely on both visual landmarks and on vector information for homing to their nest. When a conflict occurs between the HV and landmark information, ants initially head in a direction that is a compromise between the two and then correct to head towards the nest. In some cases, landmark information alone appears to be insufficient for homing and vector information coupled with landmark information is necessary for homing. We are currently identifying the navigational tactics used by these ants while swimming.

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Acknowledgements

We are grateful to Jochen Zeil for his support and advise in all stages of this project. We thank the Defence Science and Technology Organization, Australia for the initial loan of the DGPS system and Javaan Chahl, Matt Garratt and Mark Snowball for designing, constructing and maintaining DGPS electronics and Janelle Evans and Mahenddra Raj for field support. We are grateful to Jan Hemmi and Wolfgang Stürzl for their advice and help with Matlab programming and camera calibration.

Funding

We acknowledge funding support from the Australian Research Council's (ARC) Centres of Excellence Scheme (CEO561903), an ARC Discovery Early Career Award (DE120100019) and ARC Discovery Grant (DP1093553).

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Legends

Figure 1. Study species and location. Top: The intertidal ant *Polyrhachis sokolova* swims during high tides in its mangrove habitat. The ants use their first two pair of legs to power the swim. Bottom left panel show the study location. Inset shows study site in Australia (red circle). Foraging corridor from nest (N) to feeder (F) is indicated in grey; *50m lateral* location (50mL) and *>100m distant* location (D). Bottom right panel shows foragers of *P. sokolova* feeding on a dead crab washed in by the tide. Photo credits: Ajay Narendra.

Figure 2. Homing behavior of *Polyrhachis sokolova* in the local familiar environment. Ants were trained to travel from the nest (N, blue circle) to a feeder (F, yellow circle). Trained ants that arrived at the feeder were captured individually and released as full-vector ants (top panel) or ants were followed back close to the nest and captured close to the nest and released as zero-vector ants (bottom panel). Captured ants were released either at the (a,f) *feeder*, (b,g) *1m lateral*, (c,h) *1m lateral & 5m behind*, (d,i) *5m lateral*, and (e,j) *5m lateral & 5m behind*. Circular plots indicate heading direction of ants at 0.5 m from release location. Black arrow: nest direction predicted by path integrator; Blue arrow: true nest direction. Red: successful ants; Black: ants unsuccessful after 20 minutes of recording. Mean heading direction (θ) and length of the home vector (r) are shown.

Figure 3. Homing behavior of *Polyrhachis sokolova* in distant unfamiliar environments. Ants trained to travel between nest and feeder were captured either leaving at the feeder (full-vector) or returning close to the nest (zero-vector) and released at either (a,b) *50 m lateral* to the nest-feeder line or (c,d) at *>100m* away at a distant location. Top panel: Circular plots indicate heading direction of ants at 0.5 m from release location. Mean heading direction (θ) and length of the home vector (r) are shown. Middle panel: Trajectories of ants with the release location (R) and fictive nest position (N*) are shown. Bottom panel: Relationship between path-length and distance from release location. Full-vector ants travel farther from release location whereas zero-vector ants remain close to release. Arrows indicate positions where ants return to the start of release location.

Figure 4. Determining the rotational image difference function (rotIDF) by comparing views from the feeder looking at the nest with views from all release stations. (a) Illustrates the schematic of the nest, feeder and all release locations. (b) Panoramic views from all release locations with the nest in the center are shown. Images are low-pass filtered (5.93°) to match the interommatidial angle of a worker of *P. sokolova*. (c) Comparison of views from *feeder* with view from the *feeder* (2-Black), *1m lateral* (3-Dark Blue), *1m lateral & 5m behind* (4-Brown); *5m lateral* (5-Green); *5m behind & 5m lateral* (6-Red); *50m lateral* (7-Light Blue); *>100m distant* (8-Yellow). The depth of the minima is maximum when views of feeder are compared to itself (black). The depth of the minima decreases as one moves away from

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383 the feeder and the nest. Symbols in the schematic and the boxes around panoramic images are colour
384 coded to match the curves from rotIDF.

385 Figure 5. Navigational information content in the environment at different elevations. Panoramic views
386 and rotational image difference analysis of (a) comparison of feeder view and 50m lateral view and (b)
387 comparison of feeder view and distant view. Top row: panoramic images with an elevation of 0°-40°
388 (blue box and blue curves); Middle row: panoramic view with an elevation of 10°-40° (red box and red
389 curves); Bottom row: panoramic views with an elevation of 0°-10° (brown box and brown curves).
390 Within each elevation top image is the view from feeder and bottom image is view from (a) *50m lateral*
391 location or (b) >*100m distant* location.

392

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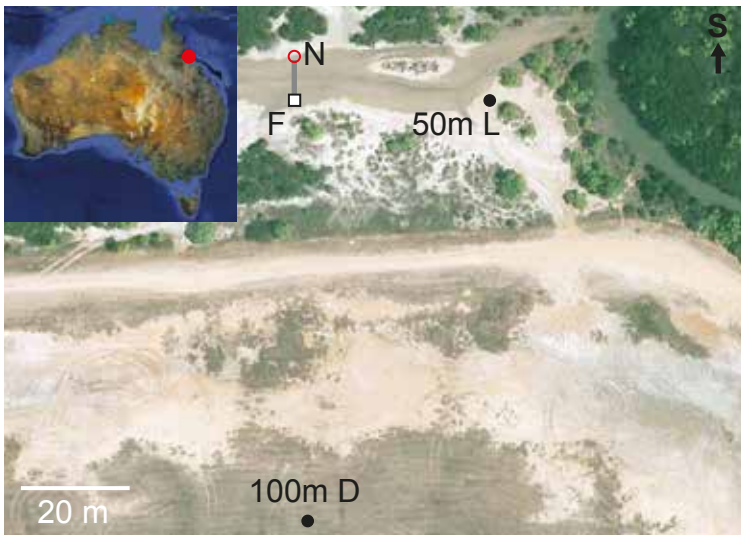
Figure 1



Homing abilites of an intertidal ant

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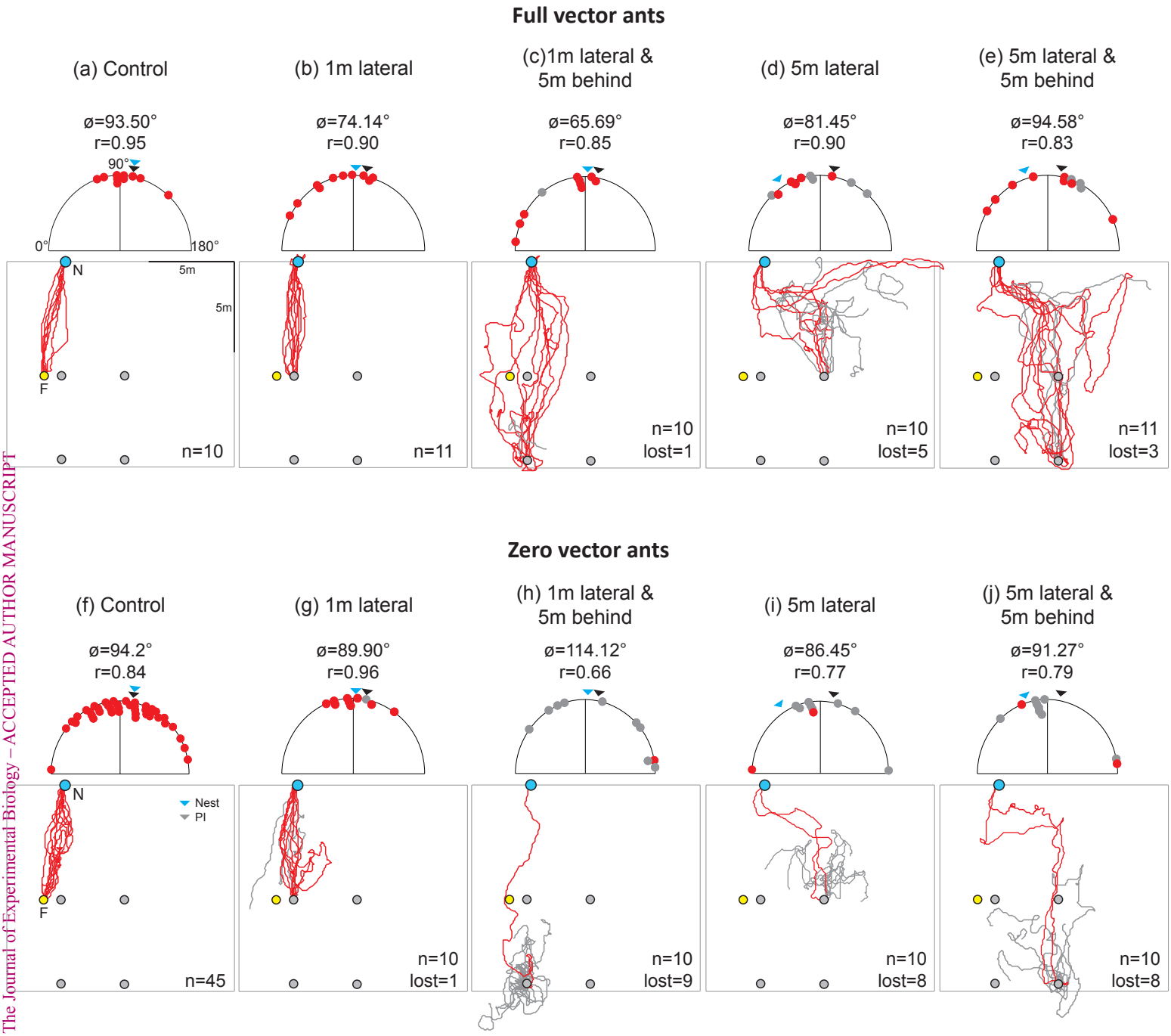
Figure 2



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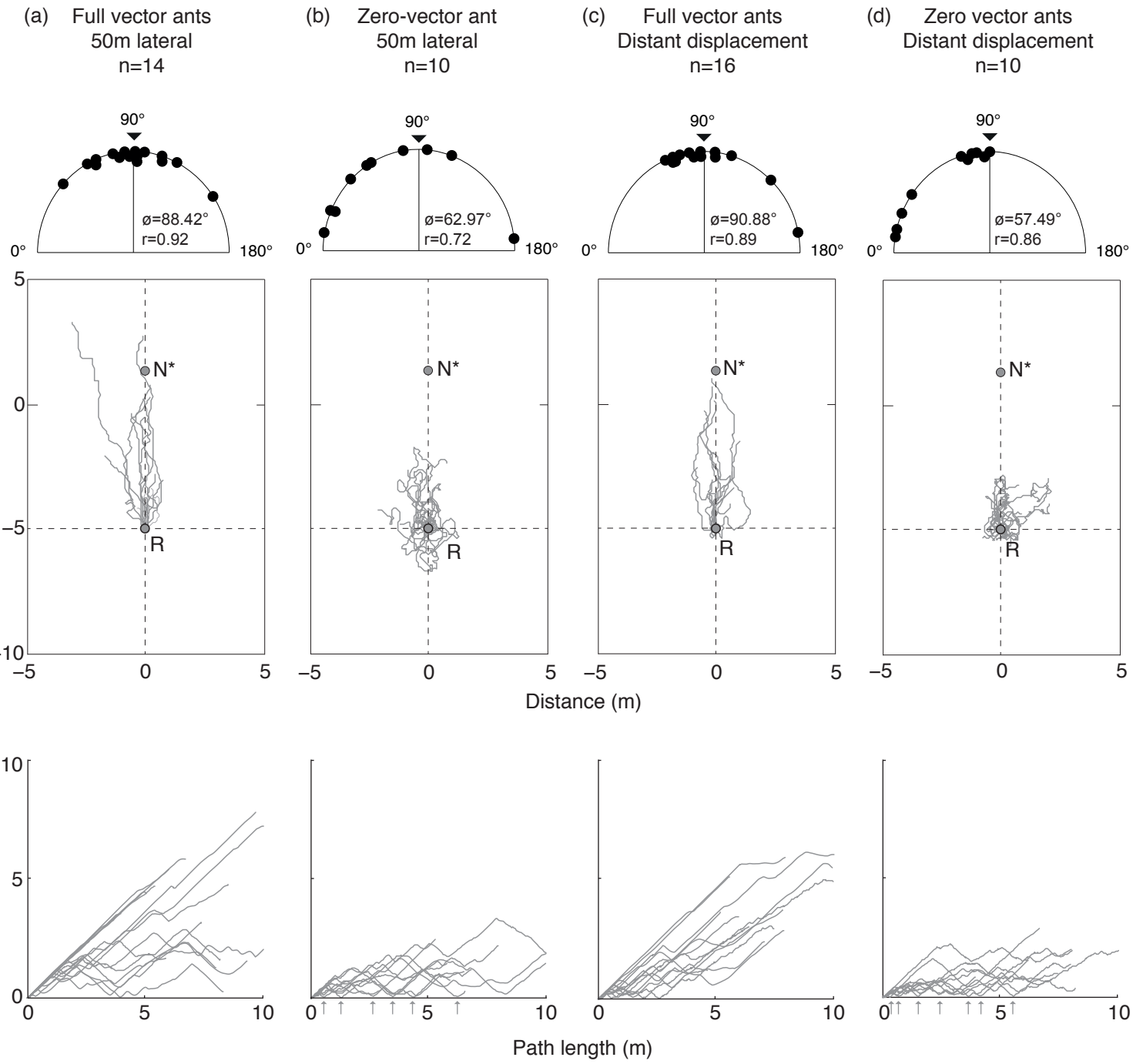

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Figure 4

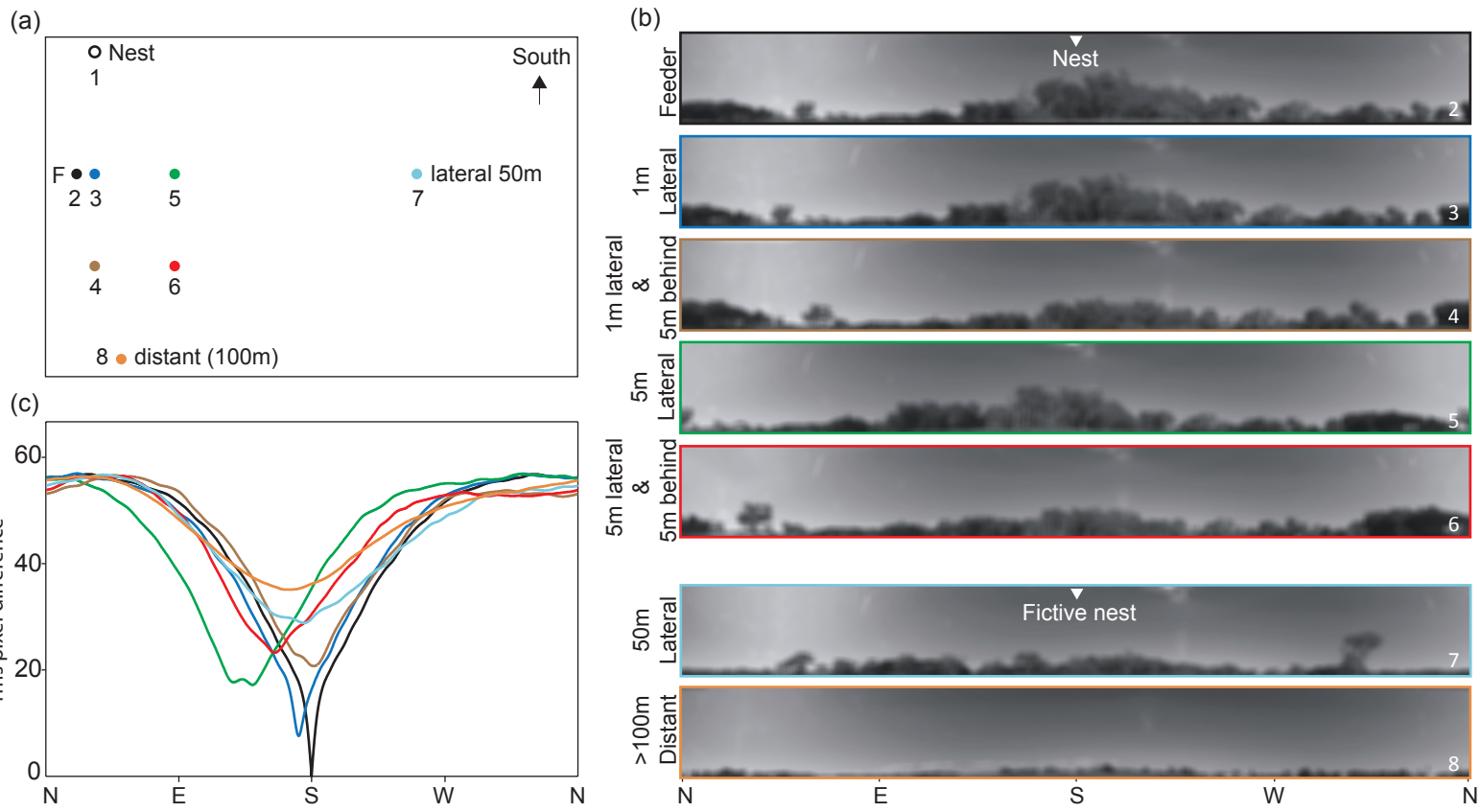

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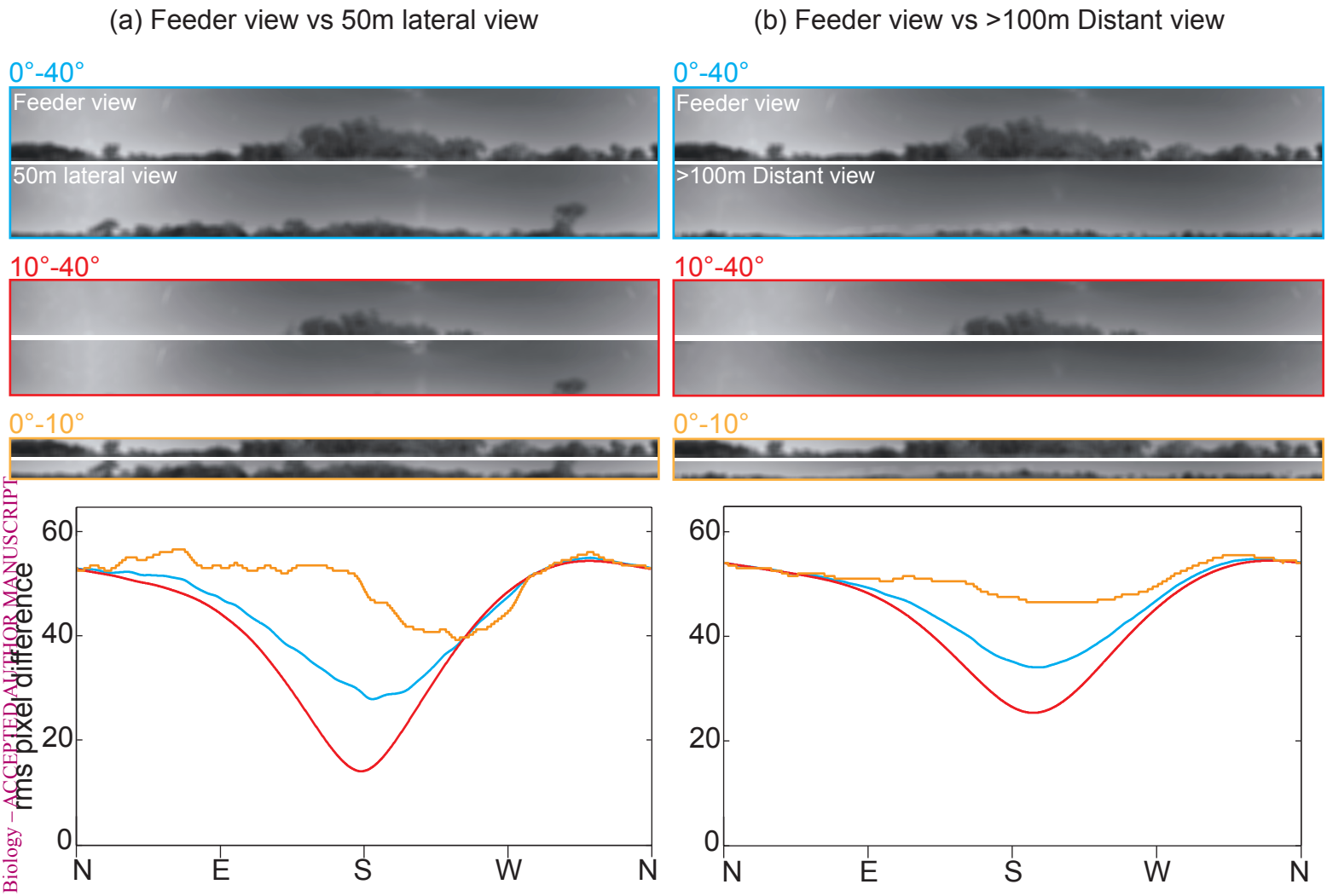
Figure 5



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