

**Visual homing in field crickets and desert ants:
a comparative behavioural and modelling study**

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Abstract

Visually guided navigation represents a long standing goal in robotics. Insights may be drawn from various insect species for which visual information has been shown sufficient for navigation in complex environments, however the generality of visual homing abilities across insect species remains unclear. Furthermore various models have been proposed as strategies employed by navigating insects yet comparative studies across models and species are lacking. This work addresses these questions in two insect species not previously studied: the field cricket *Gryllus bimaculatus* for which almost no navigational data is available; and the European desert ant *Cataglyphis velox*, a relation of the African desert ant *Cataglyphis bicolor* which has become a model species for insect navigation studies.

The ability of crickets to return to a hidden target using surrounding visual cues was tested using an analogue of the Morris water-maze, a standard paradigm for spatial memory testing in rodents. Crickets learned to re-locate the hidden target using the provided visual cues, with the best performance recorded when a natural image was provided as stimulus rather than clearly identifiable landmarks.

The role of vision in navigation was also observed for desert ants within their natural habitat. Foraging ants formed individual, idiosyncratic, visually guided routes through their cluttered surroundings as has been reported in other ant species inhabiting similar environments. In the absence of other cues ants recalled their route even when displaced along their path indicating that ants recall previously visited places rather than a sequence of manoeuvres.

Image databases were collected within the environments experienced by the insects using custom panoramic cameras that approximated the insect eye view of the world. Six biologically plausible visual homing models were implemented and their performance assessed across experimental conditions.

The models were first assessed on their ability to replicate the relative performance across the various visual surrounds in which crickets were tested. That is, best performance was sought with the natural scene, followed by blank walls and then the distinct landmarks. Only two models were able to reproduce the pattern of results observed in crickets: pixel-wise image difference with RunDown and the centre of mass average landmark vector.

The efficacy of models was then assessed across locations in the ant habitat. A 3D world was generated from the captured images providing noise free and high spatial resolution images as model input. Best performance was found for optic flow

and image difference based models. However in many locations the centre of mass average landmark vector failed to provide reliable guidance. This work shows that two previously unstudied insect species can navigate using surrounding visual cues alone. Moreover six biologically plausible models of visual navigation were assessed in the same environments as the insects and only an image difference based model succeeded in all experimental conditions.

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Declaration

I declare that this thesis was composed by myself, that the work contained herein is my own except where explicitly stated otherwise in the text, and that this work has not been submitted for any other degree or professional qualification except as specified.

(Michael Mangan)

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Chapter 1

Introduction

Many insects construct nests, hives or burrows that provide shelter from the climate and protection from predators. Foragers are tasked with venturing from these havens and exploring their local habitat in search of food. This time spent in open terrain can be extremely costly for individuals as they are exposed to predatory and environmental dangers. Many insect species have evolved efficient search strategies to limit the time spent seeking food resources (for a review see (Bell, 1990)). Yet this exploration phase represents only the first stage of the forager's journey: after locating food the animal must return with its bounty to the safety of the nest as quickly as possible.

The same task must also be addressed in a variety of robot applications. For example domestic robots must relocate their charging station after completion of their circuitous cleaning routine. Or when deployed in the aftermath of a disaster, search and rescue robots must return to the command or medical centre after locating trapped or wounded persons.

In both cases, when homing commences the agent (insect forager or robot) is armed with a multitude of sensory data amassed whilst travelling to its current location. Insects have been shown to integrate this multi-modal sensory stream to generate an estimate of the location of the nest relative to the current location (discussed in detail in chapter 2). However, where strategies are reliant upon idiothetic cues, such as distance measurement by step counting, cumulative errors increasingly corrupt the homing signal. Many insects instead navigate predominantly by visual means, which offers a more robust (allothetic) signal and can provide long-lasting guidance once learned.

Diurnal insects sample their visual environment through a pair of apposition

compound eyes (Land, 1997; Land and Nilsson, 2002). Thus evolution has converged upon a dominant sensory modality and sensor design sufficient for insects to robustly navigate their complex worlds. Such findings raise the following questions:

1. Are visual navigation abilities conserved across diurnal insects?
2. If so, do all insects navigate by a general visual homing mechanism?

It should be noted that a number of models have been proposed as candidate algorithms employed by insects, yet compelling evidence for the use of one or other scheme by insects has not been forthcoming.

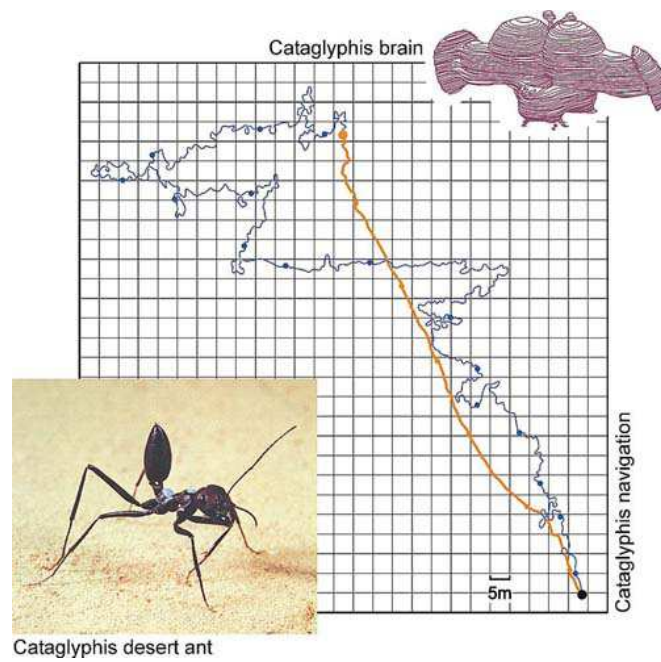
This thesis addresses these issues directly through a combined behavioural and modelling study performed in two insect species: the field cricket *Gryllus bimaculatus* and the desert ant *Cataglyphis velox*. The remainder of this chapter presents the methodological procedure followed throughout this study, the reasoning behind the choice of model systems, the key contributions that result from this work, and finally the structure of the remaining thesis.

1.1 Methodology

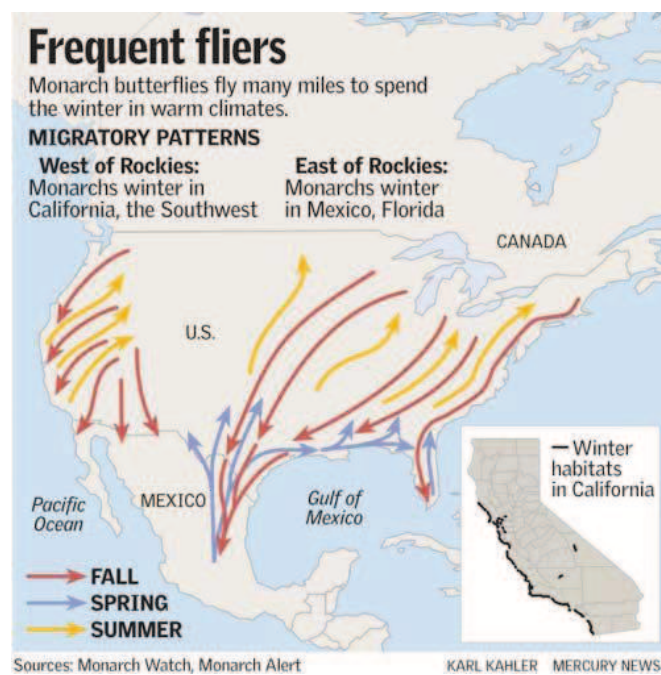
1.1.1 Insects as Model Systems

The repertoire of complex behaviours expressed by insects has fascinated scientists for centuries. Such behaviours include nest building, mate finding, courtship, predation and predator avoidance, and communication. The inspiration behind this work however is motivated by the incredible journeys insects complete in search of food, mates and shelter (see figure 1.1). These navigational feats are made all the more impressive when one considers that the insect brain contains less than one million neurons (note that the human brain is estimated to contain between 10 and 100 billion neurons).

Thus in insects we find an ideal synthesis of demonstrable complex behaviours that are of interest to biologists and engineers, and a limited nervous system that offers a more tractable medium for the study of these complex behaviours than that of higher order animals. Furthermore, contrary to intuition, recent evidence suggests that reduced neural density does not result in a proportional limit on the complexity of tasks solved by insects (Chittka and Niven, 2009). Rather that increased brain size



(a)



(b)

Figure 1.1: **Insect Navigators.** (a) Desert ants inhabiting featureless salt-pans of northern Africa search for food morsels under the baking midday sun (black line). After locating food they are able to return to their nest by the direct path. Figure from Wehner (2010) (b) Monarch butterflies perform annual cross-continental migrations often over thousands of miles. Figure from Krieger and Kahler (2007).

may simply offer further refinement of sensory input and increased memory capacity. In such a circumstance, developing an understanding of the neural processes mediating behaviour in these parsimonious brains may unravel the fundamental mechanisms necessary for complex behaviour. This in turn may inform studies into the functioning of higher order animals including humans.

In this thesis two insect species are studied: the field cricket *Gryllus bimaculatus* and the desert ant *Cataglyphis velox*. The following sections discuss the specific factors leading to use of these species in this work.

1.1.1.1 The Field Cricket *Gryllus bimaculatus*

Gryllus bimaculatus is found across tropical and subtropical regions of Africa and the Mediterranean basin. They are solitary, burrow dwelling animals probably most noted for their robust phonotaxis behaviour; the ability to home to a sound source in order to locate a mate. The abundant availability of animals and ease of housing means that crickets are ideally suited to laboratory studies. As such they have become a popular organism for neuroethological and biorobotic studies into a variety of behaviours from phonotaxis (Huber et al., 1989; Schildberger, 1988; Webb, 1995), to multi-modal cue integration (Webb and Harrison, 2000; Payne et al., 2010), and predator avoidance (Camhi, 1980; Chapman, 2001).

In contrast relatively little is known of the visual navigation abilities of the cricket. One remarkable study revealed that the presence of surrounding visual cues aids male crickets to steer a course back to shore after leaping into a pond to avoid a predator (Beugnon, 1986). However, it is not clear from this work that crickets are not using a simpler strategy such as beacon aiming, or associated orientation cues.

While little is known of the role vision plays in cricket navigation, the structure and function of the cricket visual system has been described in detail by (Labhart et al., 1984) and is shown to be anatomically similar to ants and bees.

In summary *Gryllus bimaculatus* presents an opportunity to ask whether visual homing abilities are conserved across insect species by targeted experimentation in an organism whose visual sensing is similar to expert navigators but for which little, if any, homing data exists.

1.1.1.2 The Desert Ant *Cataglyphis velox*

Cataglyphis velox are thermophilic central place foragers that scavenge for arthropod corpses during the hottest hours of the day. These exploratory paths can extend over one hundred metres in length, yet when a food morsel is located the forager will reliably relocate to the inconspicuous nest (the mechanisms underlying this behaviour are discussed in detail on chapter 2). The surface temperature during these foraging trips typically ranges between 40° and 70°. Thus the use of pheromone trails is not possible as any substance deposited on the desert surface evaporate almost instantly. Consequently individual foragers must possess the full suite of tools required for navigation, and can therefore be treated as fully autonomous agents.

The searing temperatures to which foragers are exposed results in life threatening stresses on the ant body. This has led to a number of physical adaptations to alleviate some of the stress induced during foraging excursions (Cerdeira and Retana, 2000). *Cataglyphid* foragers possess extremely long legs compared to other ant species. The initial benefit is obvious in that the body mass of the forager is raised from the desert surface. Moreover, longer legs enable foragers to move very quickly, limiting the time spent on the desert surface. Indeed, they have been termed the "race horses of the insect world" (Wehner, 2008). In addition to increased leg length, the overall body size of foragers is markedly larger than that of workers confined to the nest. It has been suggested that the distinction in body size to caste can be attributed to larger bodies offering more heat tolerance. Given that the desert ant has evolved several physical adaptations to limit the stresses induced in the extreme heat, it seems reasonable to suggest that the ant may have also evolved efficient, if not optimal, navigational strategies.

Desert ants rank amongst the most fascinating and well studied of the insect navigators. However most studies to date have taken place in northern Africa or Australia, in *Cataglyphid* and *Melophorus* genera respectively. *Cataglyphis velox* are indigenous to the shrub-like habitat of southern Spain. This environment is visually similar to that of central Australian ant *Melophorus bagoti*, and offers an opportunity for a novel comparative study: do distinct insect species exploiting a similar ecological niche navigate by similar methods?

The choice to study ants in the field rather than in the laboratory was driven by two factors. Firstly, desert ant colonies are particularly difficult to maintain in the laboratory. Or more specifically, it is prohibitively hard to keep the proportion of

brood to workers high enough such that the foragers are motivated to feed consistently (personal experience, and personal communication with Markus Knaden). When studying desert ants in the field in the spring and summer, strong nests can be sought and selected for use providing large numbers of subjects motivated to feed, and usually a corresponding increased data yield. It should be noted however that such studies are thus constrained by seasonal and environmental factors. The second factor influencing the choice to perform field studies in desert ants was the opportunity to sample the ant habitat as viewed by the insects. To the best of the authors knowledge no image database sampled within the ant habitat and from a camera simulating the ant-eye existed prior to this work.

1.1.2 The Role of Modelling in Insect Navigation

Webb and Consi (2001) define biorobotics as a "multidisciplinary field that encompasses the dual uses of biorobots as tools for studying animal behaviour and as testbeds for the study and evaluation of biological algorithms for potential application to engineering."

It is the former definition that is the primary aim of this thesis. Indeed, the field of insect navigation has long benefited from complementary behavioural and modelling studies. For example, the classic snapshot model was developed in a computer simulation specifically to replicate honey bee search patterns observed in landmark manipulation studies (Cartwright and Collett, 1983).

Model instantiation requires that hypotheses be formalised, and where possible quantified, allowing the model to be implemented as a computer simulation or on a physical robot. This process is not only essential but can provide vital feedback to biologists about crucial knowledge gaps (within both the target organism and the proposed hypothesis), which can inspire further experimentation.

Yet the major benefit of biorobotic studies comes through closing the sensory-motor loop. Insects are not passive observers of their environment but actively influence their sensory input through their own movement. It is difficult, if not impossible, to accurately predict *a priori* the sensory stimuli that an insect will experience as it engages its environment. However by building biorobots it is possible to embed models within a system capable of moving and thus interacting with its environment in a manner similar to the target organism. Note that embedding the robot system within the animal habitat can in itself provide inspiration to modellers.

For example (Zeil et al., 2003) used a gantry robot with a panoramic camera attachment to sample the natural visual environment in which insects navigate. Further analysis of the image data revealed that insects could home using a simple pixel matching algorithm without any need for complex feature extraction (discussed in detail in Chapter 2.1).

1.1.3 Constraints

Webb (2001) defines a series of dimensions along which biorobotics models can be characterised, and by which they can be constrained. That is, by addressing where biorobotic models reside on certain dimensions, authors can place their model in context of other studies and inform the reader of the conclusions that should be drawn from their results. For example, ant colony optimisation theory applied to communication takes inspiration from biology but insights drawn from such work are unlikely to inform myrmecologists. These dimensions are discussed in the following sections with specific relation to the modelling performed in this study.

1.1.3.1 Biological relevance

The modelling work undertaken in this thesis is intended to have high biological relevance. Only biologically plausible models are considered and their performance is assessed by their ability to replicate the behavioural data when exposed to similar experimental paradigms rather than absolute performance.

Constraining computational and sensory capabilities to the limited resources of the insect compels modellers to seek the simplest mechanism by which the behaviour can be produced. Indeed, recent studies show that insects tested in similar laboratory paradigms as mammals can produce similar data. For example, rats trained to locate an inconspicuous exit found in one corner of a rectangular arena will regularly confuse the correct location with the geometrically opposing corner (Cheng, 1986). Errors persist even when disambiguating visual cues are provided which has led to the proposal of a geometric module in the mammalian brain which competes with spatial learning systems. Wystrach and Beugnon (2009) showed that ants placed at the centre of a rectangular arena will display the same rotational errors. Furthermore, earlier modelling, constrained to be biologically plausible in insects, has shown the behavioural data can be explained by a simple homing mechanism rather than a more involved geometric module (Stürzl et al., 2008).

1.1.3.2 Match

As the overarching aim of this thesis is to investigate the mechanisms by which insects navigate, matching the biological data is sought throughout by assessment of model performance by direct comparison to real biological data. That is, models are exposed to the same experimental manipulations as the animals and the relative performance in each condition reported rather than absolute performance *per se*. Moreover, care is also taken to match the experimental procedure. For example, models and insect data are reported given the same numbers of trials, model homing trials are started from the same locations from which animals started, etc.

1.1.3.3 Accuracy

The modelling undertaken in this thesis only aims to accurately replicate the insect visual sensing abilities. The structure and function of the insect compound eye is well understood (see Land (1997) and Land and Nilsson (2002), chapters 7 and 8 for reviews) and the cameras used in this work seek to accurately replicate this view of the world. Furthermore, image pre-processing parameters are derived from the biological data.

1.1.3.4 Medium

Where possible, models are supplied with sensory input sampled from the same environment in which animals are tested. Sensory input sampled from simulated worlds risks the introduction of biases and assumptions which may, or may not be present in the real world. Thus, in both modelling studies image databases are gathered within the same environment in which the insect data was recorded.

Whilst image databases sampled at discrete locations in the environment, the sensory-motor coupling can be considered the same as that if models were implemented on a real robot: movement within the image database is driven by model output which in turn affects the resulting sensory input. Image databases were chosen as the medium rather than implementation of a fully autonomous robot for practical reasons. To not bias performance in favour of any particular model various image processing parameters are optimised across models. Such computational explorations are completely unfeasible and unsuitable for implementation on a robot platform.

Furthermore, an assumption of all the current visual homing models is that images are correctly aligned with the stored reference image. This assumption would be violated by an unconstrained autonomous robot. It should be noted that various authors have offered solutions to this problem but is outwith the scope of this study.

1.1.3.5 Abstraction

The image database methodology outlined above offers significant advantages over a robot implementation in terms of off-line processing and model testing capabilities. However, the movement of agents within the databases approximates a grid world solution and therefore all motor systems relevant to insect locomotion movement have been abstracted from this work. Moreover, the stepped path that models tread towards the target location cannot be compared directly to the route traversed by freely moving insects.

Moreover, image databases should offer *idealised* visual sensing. That is, without the need to correct for yaw, pitch and roll, that the animal must compensate for.

1.1.3.6 Level

All models discussed in the thesis are implemented at the algorithmic level. Thus, the work presented cannot claim to offer insights into the exact neural processes governing visual homing in insects or indeed offer any hint as to the location of such functionality in the insect brain. However, such an approach offers insights into the information that insects derive from their visual surroundings, and how they manipulate this data for guidance.

1.1.3.7 Generality

In this study we ask explicitly if any of the current suite of biologically plausible models visual homing can generalise across the visual homing behaviours of different insect species. It should be noted that model parameters (both at the image pre-processing stage and within the model processes) are intentionally optimised rather than predefined. This may elicit differing solutions, and where appropriate such results shall be highlighted and discussed.

1.2 Thesis Outline

The following thesis is divided into five main chapters:

Chapter 2 surveys the growing evidence for a general mechanism of visual guidance across insect species. This is presented as an insect navigational tool-kit with discussion of the sensory and neural mechanisms underlying behaviour. Studies involving crickets and ants are given precedence as they are the species used in this work, however where appropriate reference is made to works in other species.

In chapter 3 a novel laboratory paradigm is outlined in which the visual homing ability of the field crickets is assessed.

In chapter 4 a suite of biologically plausible visual homing models are assessed in the same visual conditions in which crickets were trained. Models are ranked not on their absolute performance but rather their ability to replicate the performance of the crickets.

Chapter 5 describes a field study in which the natural foraging patterns of the European ant *Cataglyphis velox* were observed.

Chapter 6 compliments this field study by assessing the efficacy of the same suite of visual homing models but within the natural habitat of the ant.

Chapter 7 concludes the thesis by bringing together the various results presented, highlights their implications, and closes with a discussion of future research possibilities facilitated by this work.

Chapter 2

Literature Review

2.1 Introduction

Increasing evidence suggests that despite navigating through vastly different environments whilst using diverse methods of locomotion and sensing, different insects make use of similar environmental cues for guidance. Moreover, central place foraging insects process and combine these cues in similar ways resulting in comparable navigational behaviours. Taken together, this repertoire of behaviours can be thought of as a navigational tool-kit. Wehner (2008) proposed such a tool-kit for the desert ant which is here extended to a general navigational tool-kit for insects (figure 2.1).

It should be noted that we do not consider long distance navigational feats observed in insects such as migration, or any swarm based strategies such as trail following. Instead this work focuses on the ability of individual animals to navigate their local environment. This generally serves one of two purposes: to return an animal to the safety of the nest after foraging and to guide the animal to a previously visited feeding site.

The study of insect navigation has been active for more than a century generating a vast literature. As this work investigates the homing behaviours of ants and crickets this literature review shall focus primarily on studies involving these insects. Nevertheless, care is taken to highlight examples where similar behaviours have been observed in other species. In this review the various navigational strategies shown in figure 2.1 shall be briefly discussed, but the focus for the remainder will be on visual homing strategies.

The ability of insects to navigate their complex habitats despite their limited

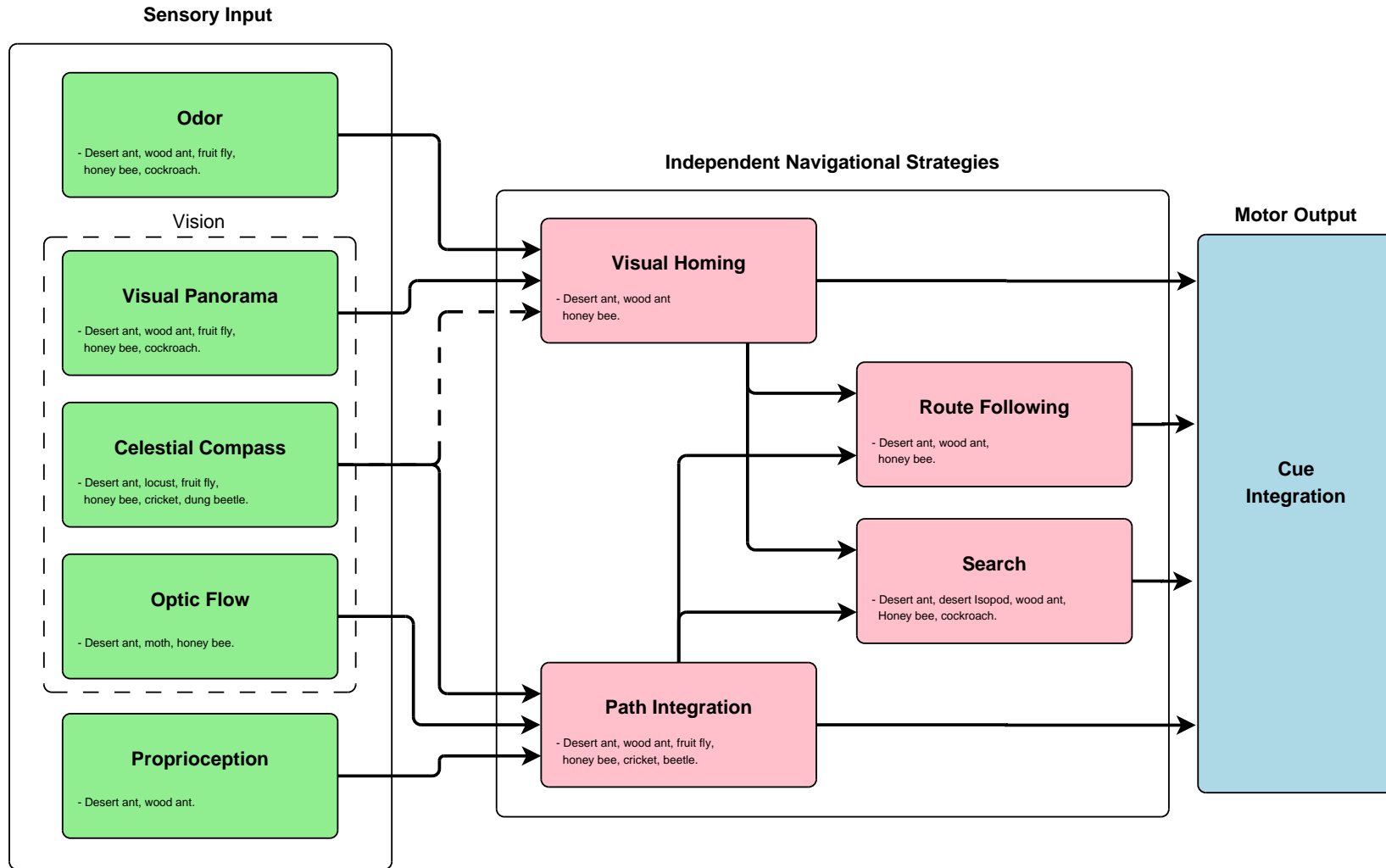


Figure 2.1: **Insect Navigational Toolkit.** The sensory input block shows the most commonly used sensory cues that generalise across insects with a list of the species for which they have been observed. The independent navigational strategies block shows the distinct guidance strategies employed by insects exposed through natural observation and experimental manipulation. Competing output from the distinct strategies are then integrated leading to the common navigational behaviours observed in central place foraging insects.

neural hardware and low resolution visual system has drawn interest from computer science and engineering as well as biological fields. The second section of this literature review introduces a series of biologically plausible models of visual homing that shall later be tested in the same conditions as insect data is recorded. The homing scheme underlying each model is described in detail and previous model testing discussed, particularly where model performance has been compared to behavioural data.

2.2 Insect Navigation

2.2.1 Systematic Search

The rudimentary navigational behaviour displayed by insects is the systematic search; a strategy called upon when the all other guidance systems fail, or more succinctly when an animal is lost. Search is clearly distinguished by the characteristic looping path centred where the animal believes the target (nest or feeder) to be located (Wehner and Srinivasan, 1981). The specific search pattern displayed differs according to the insect species: desert ant (*Cataglyphis fortis*), desert isopod and cockroach fit a probability density function (Müller and Wehner (1994); Hoffmann (1983); Durier and Rivault (1999) respectively); desert ant (*Melophorus bagoti*) follows a composite Brownian walk (Narendra et al., 2008); ant (*Temnothorax albipennis*) fits a super diffusive pattern (Franks et al., 2010); and honey bee (*Apis mellifera*) performs a systematic search before switching to a Lévy flight (Reynolds et al., 2007). Despite the variety of exploratory patterns, the presence of the search behaviour as a "navigational safety net" appears fundamental across insects.

The search is not a rigidly pre-programmed routine but instead an adaptive strategy. Desert ants have been shown to adapt the spread of the search in relation to the length of the homing trip (Merkle and Wehner, 2010) and familiarity of surrounding visual cues (Merkle and Wehner, 2009). Additionally honey bees have been shown to switch from a systematic search to a Lévy flight if the nest is not located quickly (Reynolds et al., 2007).

The adaptive nature of the search provides a powerful tool for inferring an animal's confidence in its navigational system and remains an active research field. However as the search is always submissive to other guidance strategies and the focus of this study is on visual navigation, the systematic search shall not be discussed

further in this review.

2.2.2 Path Integration

Insects maintain a virtual life-line (known as the home vector) linking the animal's current position with the nest throughout every foraging journey. When food is encountered the home vector is engaged and guides the animal home by the direct path. This strategy of navigation is known as path integration and has been observed in numerous insect species: desert ant ((Pièron, 1904) as cited by (Collett and Collett, 2002)); honey bee (Von Frisch, 1967); cricket (Beugnon and Campan, 1989); fruit fly (Neuser et al., 2008); beetle (Rasa, 1990); woodlouse (Hoffmann, 1978). The path integrator remains active throughout the homeward journey allowing for enforced diversions from the "bee-line" before homing recommences along the updated direct path (Wehner, 2003).

Vector navigation is not limited to guiding an insect home but can be inverted to guide insects to previously visited feeding sites as shown in desert ants by Collett et al. (1999). This recycling of the information content of the home vector is demonstrated by the waggle dance of honeybees. Returning foragers that have found a profitable feeding site pass on the direction and distance of the food site to nest mates through a series of waggles and runs (Von Frisch, 1967; Dyer, 2002).

In visually barren environments path integration has been shown sufficient for accurate navigation (for reviews see Wehner and Srinivasan (2003), Collett and Collett (2000)). Less is known about this form of navigation in crickets. Beugnon and Campan (1989) showed field crickets to use path integration when returning to their burrow, although data was only sampled for foraging distances up to 1m. Crickets were also shown to use celestial cues to swim by the direct path back to the shore after a predator-avoidance leap into a lake (Beugnon, 1986).

Path integration requires two sources of information: a compass heading and a measure of distance travelled. By continuously integrating these two streams of information insects maintain an accurate home vector. The pattern of polarised light and solar gradient expressed in the celestial hemisphere provides insects with an allothetic compass cue defining the direction of travel (desert ant (Vowles, 1950; Labhart, 1986); honeybee (Wehner and Strasser, 1985); fruit fly (Wolf et al., 1980); cricket (Brunner and Labhart, 1987); desert locust (Eggers and Gewecke, 1993)). Odometric information is generated through a combination of idiothetic (step-counting) and

allothetic (optic flow) cues in walking insects (desert ant (Wittlinger and Wolf, 2010); ladybird (Zanker and Collett, 1985); fruit fly (Götz and Wenking, 1973)), whereas flying insects rely on allothetic cues alone (honey bee (Esch and Burns, 1996; Srinivasan et al., 1996), moth (Kennedy and Marsh, 1974)).

As path integration is an iterative process it is prone to corruption by cumulative errors (Merkle et al., 2006). Ants compensate for such errors by extending the spread of their systematic search in proportion to the length of foraging journey and hence cumulative error (Merkle et al., 2006; Merkle and Wehner, 2010). Furthermore Müller and Wehner (1988) report a systematic error in the home vector of ants biasing the direct homeward path towards the area covered on the ant's outward journey. The benefit of crossing the outward path is clear in that the animal may recall the familiar terrain and then pinpoint its nest using visual means.

Path integration is always dominant to search. However when in conflict with familiar visual cues the home vector is not expressed with visual homing strategies proving dominant (Andel and Wehner, 2004; Kohler and Wehner, 2005; Narendra, 2007b; Bregy et al., 2008). Despite the output of the path integrator being suppressed in such environments, insects continue to compute their home vector throughout their foraging excursions. In situations where visual cues fail entirely the home vector can be expressed to provide an alternative guidance strategy. It should be noted that the visual surroundings influence the extent to which the home vector is expressed. Narendra (2007a) displaced desert ants from their natural foraging ground to a new location in the habitat such that visual cues were unfamiliar to the foragers. Yet, in the same study removal of all visual cues through the use of channels during both learning and testing induced ants to run off their entire home vector. More extreme instances of this behaviour are observed in wood (Fukushi, 2001) and tropical ants (Beugnon et al., 2005) that both remain faithful to their home vector for less than 40cm after a displacement to an unfamiliar location before search is engaged.

2.2.3 Visual Homing

Most insects inhabit environments rich in visual information rather than the barren landscapes in which path integration is so vital. Prominent visual features are largely stable for insects that forage at consistent times of the day over the course of their short lives. That is, one would not expect local vegetation to change drasti-

cally over the short life span of an individual forager (desert ants have a foraging life expectancy of one week (Ziegler and Wehner, 1997)).

The simplest use of visual information observed in insects is beacon aiming, where prominent visual features act as attractors. This strategy can guide animals over large distances to familiar locales and can be used to pin-point the nest entrance if marked by a conspicuous visual landmark (for reviews see (Collett and Rees, 1997; Collett and Collett, 2002)).

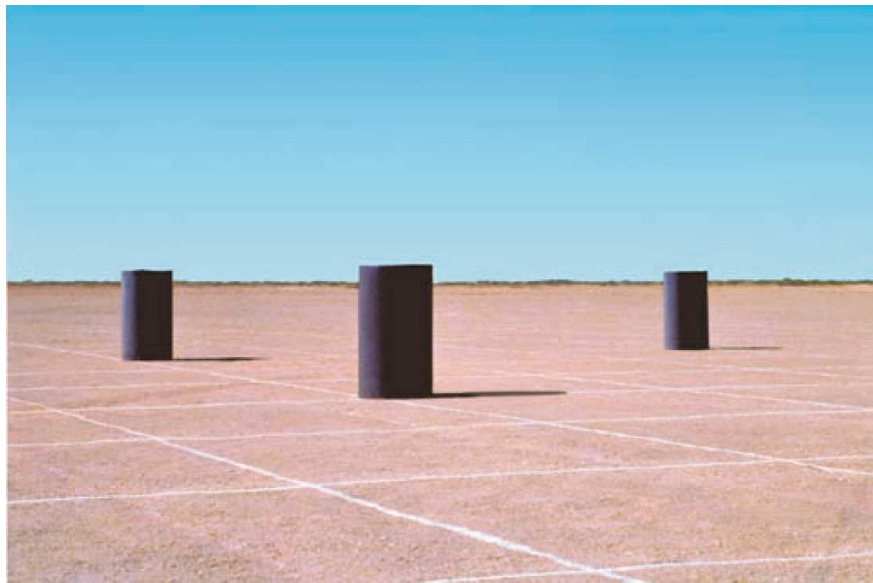
A far more impressive and robust use of visual information is observed in a behaviour known as visual homing. Using information present in the surrounding visual panorama numerous insect species can pin-point inconspicuous nesting (or feeding) sites (desert ant (Wehner and R aber, 1979); wood ant (Durier et al., 2003); honeybee ((Anderson, 1977) who also cites an earlier study by (Lauer and Lindauer, 1971)); hoverfly (Collett and Land, 1975); cockroach (Mizunami et al., 1993, 1998b); wasp (Tinbergen and Kruyt, 1938)). This form of navigation is sufficient for guidance even in the absence of the other navigational mechanisms.

2.2.3.1 Homing Using Visual Snapshots

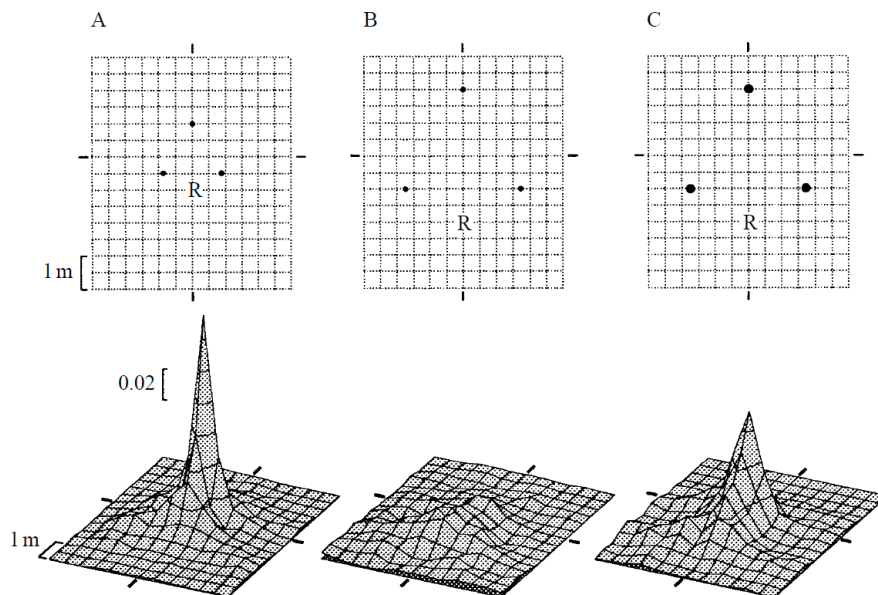
Visual homing has traditionally been studied through landmark manipulation experiments (Tinbergen and Kruyt, 1938; Anderson, 1977; Cartwright and Collett, 1982). Wehner et al. (1996) used this methodology to expose the homing strategies of desert ants (*Cataglyphis bicolor*) when returning to their nest. Ants were trained to shuttle to and from a feeding site with three large black cylinders placed in a triangular arrangement around the nest (see figure 2.2). Post learning ants that had returned to the nest and thus expired their home vector were captured and transferred to a test site configured in one of three arrangements;

1. Landmarks of the same size and position as in training.
2. Landmarks of the same size but placed at double the distance as in training.
3. Landmarks of double the size and placed at double the distance as in training.

In tests (1) and (3) ants searched consistently at the centre of the test site where the landmarks edges subtended the same retinal position as experienced during training (see figure 2.2 (b)). In test (2) however, a more diffuse search pattern was evident as the retinal position of all landmarks could not be completely matched to that experienced in training at any one position.



(a)



(b)

Figure 2.2: **Visual homing in desert ants.** (a) Virtual reconstruction of training site in which *C. fortis* ants foraged naturally whilst three landmarks surrounded their nest. (b) Search distributions of ants captured on return to the nest and released at a test site in one of three conditions: (A) Landmarks as in the training situation. (B) Landmarks of identical size but twice as distant. (C) Landmarks twice the size and distance. Figures from Wehner et al. (1996)

Similar experimentation has been carried out in the Australian desert ant *Melophorus bagoti* (Narendra et al., 2007). When tested in the landmark manipulation tests (1) and (3) ants searched repeatedly at the same location as in the former study. However during test (2) it is reported that ants searched close to individual landmarks where the closest landmark subtended the retinal position and size as in training.

The contrasting results observed may be a consequence of slight differences in the data recording procedure. Wehner et al. (1996) recorded for five minutes whereas Narendra et al. (2007) recorded the ant search patterns for only two minutes. It seems possible that in the former study desert ants may have initially attempted to match the retinal position of frontally fixated landmarks. Indeed, Åkesson and Wehner (2002) showed that *C. fortis* ants (as in Wehner et al. (1996)) initially focus their search where they first encounter a visual match with their nest-based memory. Only after this initial bout of searching do they move to align other cues such as celestial orientation. It may also be possible that ants entered a more general searching behaviour given a longer search period. More data analysis may be required to verify if the search patterns of the species are indeed distinct, with specific regard to the early search patterns of *Cataglyphis*.

Visual homing is not limited to nest locating but can be generalised to guide insects to other important locations in their habitat. A similar experiment to those outlined above was undertaken in wood ants by Durier et al. (2003) who surrounded an inconspicuous feeder with a similar array of landmarks in an otherwise barren environment. After a training period the feeder was removed and wood ants searched consistently at the feeder location as indicated by the landmarks. Thus reproducing the behaviour observed in desert ants when returning to their nest in test (1) above. Additional manipulations of the landmark array showed ants to centre their search at the location where the retinal position (and thus size) of the prominent landmarks most closely matched that as experienced in training.

Similar behaviours have also been observed in other central place foraging insect species including bees (Anderson, 1977; Cartwright and Collett, 1982, 1983), and wasps (Tinbergen and Kruyt, 1938; Zeil, 1993). To date however little is known about the visual homing ability of crickets. In a field study, Beugnon and Campan (1989) displaced crickets from their burrow to various locations in their habitat and observed their paths after release. Crickets were unable to return to the burrow except at distances less than 20cm from where the burrow entrance may have been

visible. There is some evidence that crickets use visual landmarks to stabilise their swimming direction after a predator-avoidance leap into a lake (Beugnon, 1986). However in this study the landmark cue was a large black cardboard screen. Such cues are known to act as attractors to insects and the observed paths may be explained by this simpler strategy. More recently juvenile bush crickets have been shown able to learn the orientation of their nest in a maze scenario using visual cues (Hale and Bailey, 2004). While these studies indicate a role for visual cues in cricket navigation there is as yet no clear evidence of visual homing as described in other insect species.

2.2.3.2 Information Content of Snapshots

Landmark manipulation studies have shown that insects store a two-dimensional "snapshot" of the visual scene as viewed from the target location. When homing the insect moves to align the current view of the world with the stored snapshot. Experimenters have sought to reveal the visual features encoded in the snapshot memory and thus key to the visual homing procedure. In order to frame these studies correctly it is first necessary to understand what insects perceive from their visual environments.

Most diurnal insects sense their visual surroundings through a pair of fixed apposition compound eyes and a number of simpler eyes known as ocelli. The ocelli are simple camera-like intensity detectors found on the dorsal area of the insect head. The ocelli have large fields of view, a fast sample rate and have been found to play a role in various behaviours including light level detection, flight control, and even navigation (for a review see Mizunami (1995)). However the majority of visual input is perceived by the apposition compound eyes. Each eye is comprised of an array of facets complete with its own lens, cornea and photosensitive rhabdom. Each facet samples light from a relatively large acceptance angle (typically between 1° and 7° depending on species and eye region) providing insects with a very low resolution view of the world. The facets abut one another in a hexagonal layer that is warped into two convex eye structures that protrude laterally from the insect head. Insects therefore perceive the entire upper hemisphere centred on the head of the animal.

Recent studies have shown that the skyline vector generated by the contrast between sky and terrain provides sufficient and necessary information for guidance in both wood and desert ants ((Fourcassié, 1991; Fukushi, 2001) and (Graham and

Cheng, 2009a,b) respectively). Wood ants maintain homing precision when all but the most prominent skyline peaks are removed. Desert ants in contrast require that larger portions of the skyline panorama are visible for accurate homing. Intriguingly Graham and Cheng (2009a) have also shown that desert ants derive orientation cues directly from the panoramic skyline. These directional cues have been shown to dominate celestial compass cues when the competing modes of information are put in conflict. Evidence for the use of the skyline panorama as a directional cue has also been shown for the honey bee (Towne and Moscrip, 2008).

The physiology of the facets in the compound eye offers indirect support to the theory that the panoramic skyline is the dominant visual cue used for homing. Individual facets in the desert ant *Cataglyphis bicolor* possess two photo-receptors types sensitive to either green or ultra violet light wavelengths (Mote and Wehner, 1980; Labhart, 1986). Sensitivity to green light is maximal in ventral parts of the eye and minimal in more dorsal areas. The opposite is true for UV sensitivity which is maximal in the dorsal regions and decreases through to the ventral areas. Thus in facets sampling from lateral visual space where the majority of skyline cues exist, both UV and green sensitivity are present. Möller (2002) demonstrated that the visible skyline can be robustly extracted using such a UV-green opponent channel. Similar UV and green sensitivity has also been reported in the honey bee (Menzel and Blakers, 1976).

Whilst the panoramic skyline provides a salient and robust cue in many environments, many insects successfully navigate through visually dense environments such as forests where there is no obvious UV/green skyline cue. Moreover insects can learn to home to target locations under laboratory conditions in the absence of such skyline information.

Wood ants and honeybees perform similarly in similar landmark manipulation conducted in the laboratory to the field studies outlined above ((Durier et al., 2003) and (Cartwright and Collett, 1983) respectively). In such laboratory conditions ants have been shown to encode the desired retinal positions of the vertical edges of prominent local landmarks (Judd and Collett, 1998) and therefore implicitly remember the angular width of prominent landmarks (Harris et al., 2007). Ants are thus thought to home by fixating and approaching prominent goal based landmarks until the retinal position of the landmark edges matches those in the corresponding snapshot memory (Judd and Collett, 1998; Nicholson et al., 1999). When there are numerous prominent landmarks, ants fixate and approach each landmark for a

small period. Thus when ants approach landmarks their paths are sinusoidal at the local level but direct to the goal site when viewed across the entire approach (Durier et al., 2003).

Although the approach wood ants make to a target is dominated by frontally fixated visual features, care is also taken to correctly align peripheral landmarks (Durier et al., 2003) and other contextual information (Graham et al., 2004). Such contextual information is sourced from over 120° of the ants peripheral field of vision (Durier et al., 2003). Interestingly, in the absence or relocation of the prominent landmark, contextual cues are sufficient to guide the ant to the snapshot location (Graham et al., 2003).

2.2.3.3 Mechanisms Supporting Snapshot Learning

It is thought foraging insects aid the learning of important locations through stereotypical learning flights or walks. Bees and wasps leaving the nest for the first time will fly in arcs of increasing radius while fixating the nest location (bees (von Frisch and Lindauer, 1954; Dyer and Gould, 1983; Lehrer, 1993; de Ibarra et al., 2009); wasps (Tinbergen, 1932; Zeil, 1993)). Ants cannot move obliquely and instead perform looping exploration runs around the nest interspersed with pauses and slow on the spot rotations at various locations (Wehner et al., 2004). Müller and Wehner (2010) recently observed the Namibian desert ant *Ocymyrmex robustior* to initiate new learning walks following any alteration of the visual panorama by the experimenter. The authors report that foragers fixate their nest site directly during such pauses. Wood ants will also fixate the exact feeder location during nest-based learning walks (Judd and Collett, 1998) but intriguingly fixate conspicuous landmarks during feeder-based learning walks (Nicholson et al., 1999). It remains unclear if this represents a completely different strategy.

Despite variation in their exact structure, the use of a stereotypical learning procedure when leaving a location of importance for the first time seems common across central place foragers. It is thought this provides foragers with an opportunity to store the salient and robust cues visible close to the goal that are later used for homing. Baddeley et al. (2009) recently showed that the learning flights of bumblebees are not structured to optimally extract information about the distance of prominent landmarks around the nest. An alternative hypothesis is that the learning walks provide insects with opportunities to store multiple visual snapshots at various locations around the nest. Conclusive evidence supporting either hypothe-

sis is yet to be presented.

2.2.4 Visually Guided Routes

Many insects develop visually guided routes allowing fast, reliable and safe passage to and from profitable feeding sites (desert ant (Wehner et al., 1983; Collett et al., 1992); wood ant (Rosengren, 1971; Graham et al., 2003); ponerine ant (Fresneau, 1985); tropical ant (Macquart et al., 2005); bees (Janzen, 1971); wasps (Baerends, 1947) as cited by (Collett et al., 1992)). Even in species that normally traverse pheromone labelled routes, foragers learn the visual cues present along their routes. Moreover when the visual and pheromone cues are placed in conflict visual cues are shown to be dominant (Klotz, 1987; Harrison et al., 1989). Ants store visual route memories in long-term memory lasting the entire lifetime of the forager (Ziegler and Wehner, 1997). Indeed it has been shown that wood ants recall their visually guided routes after even over-wintering (Rosengren, 1971; Fourcassié, 1991).

2.2.4.1 Idiosyncrasy of Routes

Desert ants in both Africa and Australia have been shown to establish fixed routes to profitable feeders when visual cues are available ((Wehner et al., 1996) and (Wehner, 2003) respectively). A detailed account of route fidelity and its reliance on visual cues was recently described by Kohler and Wehner (2005) for the central Australian desert ant *Melophorus bagoti*. Foraging ants were allowed to scavenge without interference and locate an experimentally placed feeding site in their natural habitat of grass scrub. Foragers developed individual, idiosyncratic routes by which they travelled repeatedly to and from the feeding site. That is, every forager developed a route by which it travelled to the feeder and a second distinct route by which it returned to the nest. An example of the repeated outward and inward routes followed by an individual ant is shown in figure 2.3.

Analysis of the routes showed that the outbound and inbound routes of an individual ant are statistically independent. Furthermore, the routes of individual foragers are statistically independent of the routes of other foragers travelling to and from the same feeding site. That is, each ant develops its own unique path leading to and from profitable food sources.

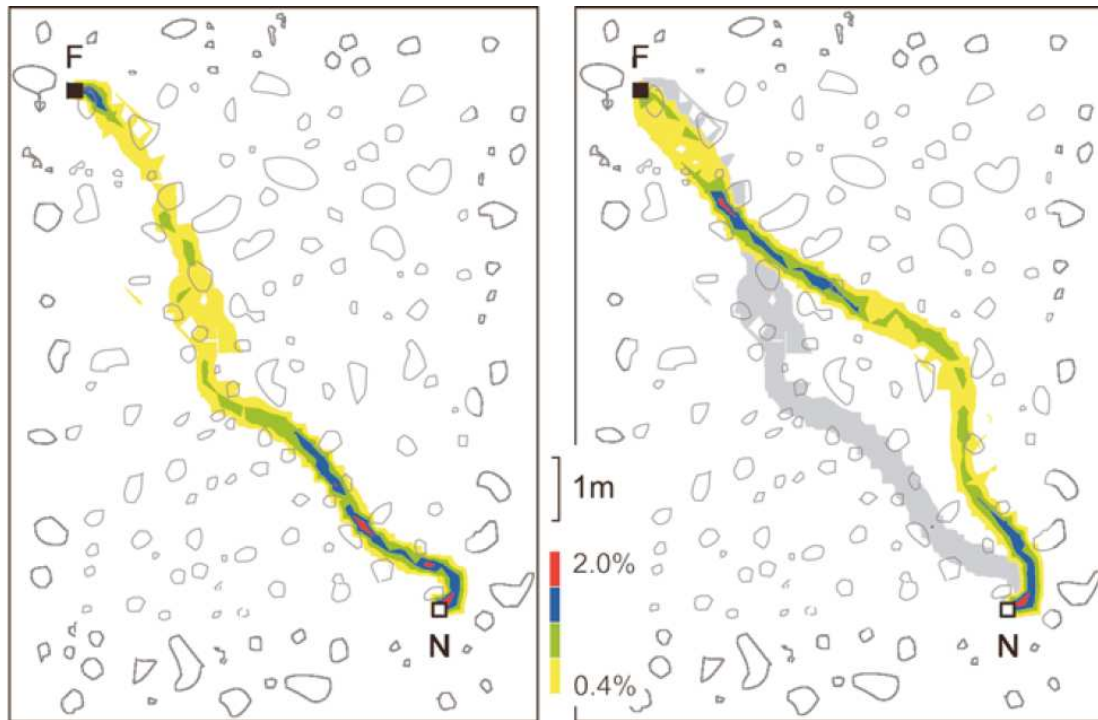


Figure 2.3: **Idiosyncratic Routes of desert ants (*M. bagoti*)**. Ants were allowed to forage without aid and locate a hidden feeder in their natural habitat populated by grass tussocks. The subsequent 5 paths of the ant to and from the feeding site were recorded and the path densities plotted (left: outward paths, right: inward paths with outward paths shown as grey shadow for comparison). The feeder location is marked by F, the nest as N, and the grass tussocks through which the ants must weave as grey polygons. (Figure from (Wehner, 2003)).

2.2.4.2 Mechanisms of Route Guidance

Kohler and Wehner (2005) showed that visual route memories can be completely decoupled from the global path integrator. After formation of idiosyncratic routes as outlined above ants were subjected to a series of displacements trials. Ants were either displaced from the nest where they should have expired their home vector and thus termed zero vector ants. Or from the feeder where they would have access to a complete home vector and hence termed full vector ants. The three displacements trials undertaken were:

1. Zero vector ants returned to the feeder.
2. Zero vector ants displaced halfway along their inward route.
3. Full vector ants displaced halfway along their inward route.

If visual route memories are coupled to a particular global path integrator reading then the routes should not be recalled after displacement. In contrast ants returned to the nest via the previously observed route in all cases (see figure 2.4).

Successful route recall is however reliant on motivational context. Wehner et al. (2006) forced *M. bagoti* foragers to travel to and from an experimental feeder through distinct regions of their natural habitat. As in previous studies individual ants learned idiosyncratic outward and inward routes but the experimental manipulation ensured that visual surroundings on both legs was markedly different. Homing ants were then displaced from a location halfway along their inward path to a location halfway along their outward route. Instead of recalling and following the outward route, ants followed the home vector orientation. When displaced just prior to entering the nest to the same location systematic search was engaged. These behaviours mimic those of an ant displaced to a completely novel visual setting indicating that ants did not recognise their route at all.

Although not expressed when familiar visual cues are present the path integrator remains active throughout route following excursions and is engaged when visual navigation fails. Kohler and Wehner (2005) displaced ants from the feeder to unfamiliar locations in their environments and reported that they immediately set off in the heading as indicated by the home vector rather than towards the nest or the learned route. Wehner et al. (2006) also reports that ants displaced from halfway along their inward path to a location in their outward path engage and followed their remaining home vector.

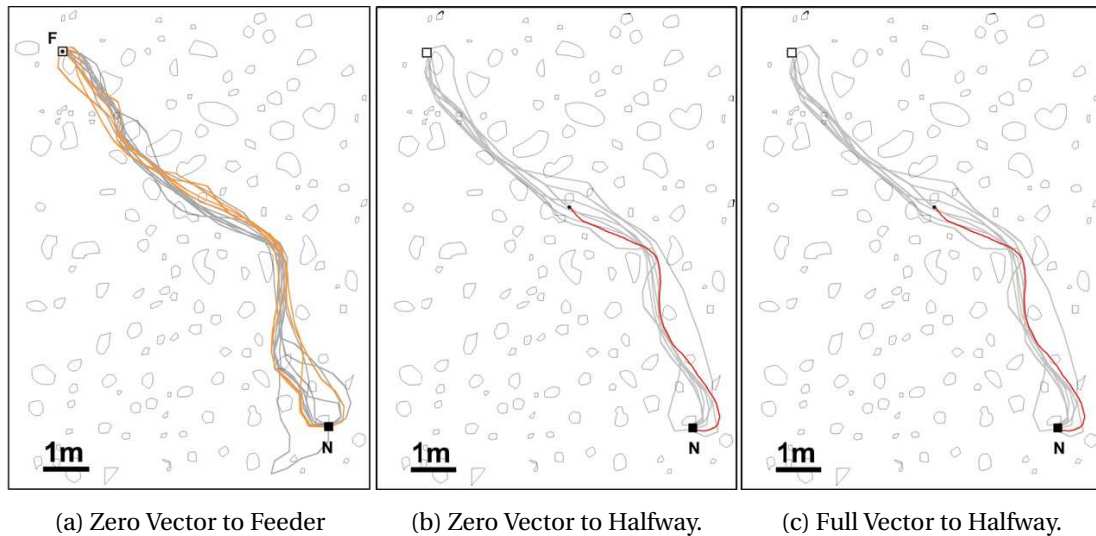


Figure 2.4: **Decoupling visual route memories from the global path integrator in desert ant *M. bagoti*.** The observed repeatable homeward route of a single foraging ant is shown in grey. (a) Paths of the ant when captured after a homing trip at the nest and released at the feeder site are shown in orange. (b) Paths of the ant when captured at the nest and released approximately halfway along its idiosyncratic route are shown in red. (c) Paths of the ant when captured at the feeder and released approximately halfway along its idiosyncratic path are shown in red. (Figures adapted from Kohler and Wehner (2005))

Ants have been shown capable of learning multiple routes leading back to the nest. Sommer et al. (2008) forced *M. bagoti* foragers to return from a regular feeding through one region of their habitat after their first eight visits to a feeder by placing a channel leading ants from the feeder to a specific region of the habitat. The channel was then moved forcing animals to return to the nest through a different region of the habitat. Ants formed distinct routes through the distinct regions. Moreover the memories of each route were retained in long term memory rather than being overwritten by newly acquired memories. Animals displaced back to the original route region were able to recall and traverse their earlier routes. Moreover the authors report that some ants were able to store three distinct routes leading foragers back to the nest.

2.2.4.3 Constituent Components of Route Guidance

The use of routes to navigate cluttered environments is a common strategy employed by numerous insect species (Rosengren, 1971; Collett et al., 1992; Wehner et al., 1996; Kohler and Wehner, 2005). The recall of a previously traversed route has been shown dependent on visual input and motivational state of the animal. However as yet little is known about the underlying guidance mechanisms leading the insect along their learned paths.

Conspicuous landmarks are known to act as beacons which can guide insects over large distances. Additionally, distal visual features are also known to provide stable cues over large distances guiding foragers to the vicinity of a target location. Once within the general area of the target visual homing provides a means for accurate relocation of even largely inconspicuous locations.

In the studies discussed previously the target location represented the final destination of the forager; either a feeding site or the nest. However for continuation of a route, encountering a previously visited location may trigger an associated navigational cue. Indeed desert ants have been shown to learn associations between local vectors and a visual scene as shown in figure 2.5. Moreover when the global home vector is placed in conflict with the local vector through experimental manipulation the local vector is found dominant (Collett et al., 1998). Control trials (data not shown here) ruled out the association of motor commands confirming a reliance on celestial compass cues. Similar associations of local vectors to visual scenes have been found in other species of desert ant and also honey bees (desert ant: *M. bagoti* (Legge et al., 2010); honey bee (Srinivasan et al., 1997)). Furthermore

Collett and Collett (2009) have shown that local vectors can be utilised for guidance on outward as well as when homeward journeys suggesting the common use of this strategy.

Tropical and wood ants which cannot rely on celestial compass cues have been shown to associate motor commands with a visual stimulus (tropical ant (Macquart et al., 2005); wood ant (Lent et al., 2009)). Indeed in the later study idiothetic motor input was sufficient for route maintenance when visual cues were temporarily removed.

Combining visual place memories with local guidance cues in a successive manner has been hypothesised as the route strategy employed by many insects.

"... they (desert ants) can associate familiar landmark scenes with local vectors (Collett et al., 1998) and motor commands (Collett et al., 2001; Bisch-Knaden and Wehner, 2001), which enable them to proceed directly from one place to the visual catchment area of the next. In this way, they can follow fixed routes by learning landmarks distributed along the "visual corridors" defined by these routes." (Wehner, 2003)

Note that route navigation in ants can be explained using strictly procedural mechanisms (Knaden et al., 2006) and does not require that insects build a metric map of their habitat. The argument of whether ants *could* translate their procedural memories into such a metric map has been freshly opened by Müller and Wehner (2010) and Graham et al. (2010). However, as conclusive evidence that insects link procedural memories into a global representation is yet lacking, this work assumes that insects utilise the more parsimonious procedural methodology.

2.2.5 Summary of Insect Navigation

Various insect species utilise common cues for navigation through similar mechanisms generating comparative navigational behaviours.

When no terrestrial cues are present insects navigate via path integration. Compass information is provided by either a celestial compass or proprioception, and optic flow and proprioception provide odometry readings. Integrating both data readings provides the forager with a home vector at all times linking its current position to the nest. However, the procedural nature of the process renders path integration susceptible to cumulative errors.

Insects therefore rely upon terrestrial cues when available. Visual homing provides a means of locating even the most hidden of nest entrances using the visual

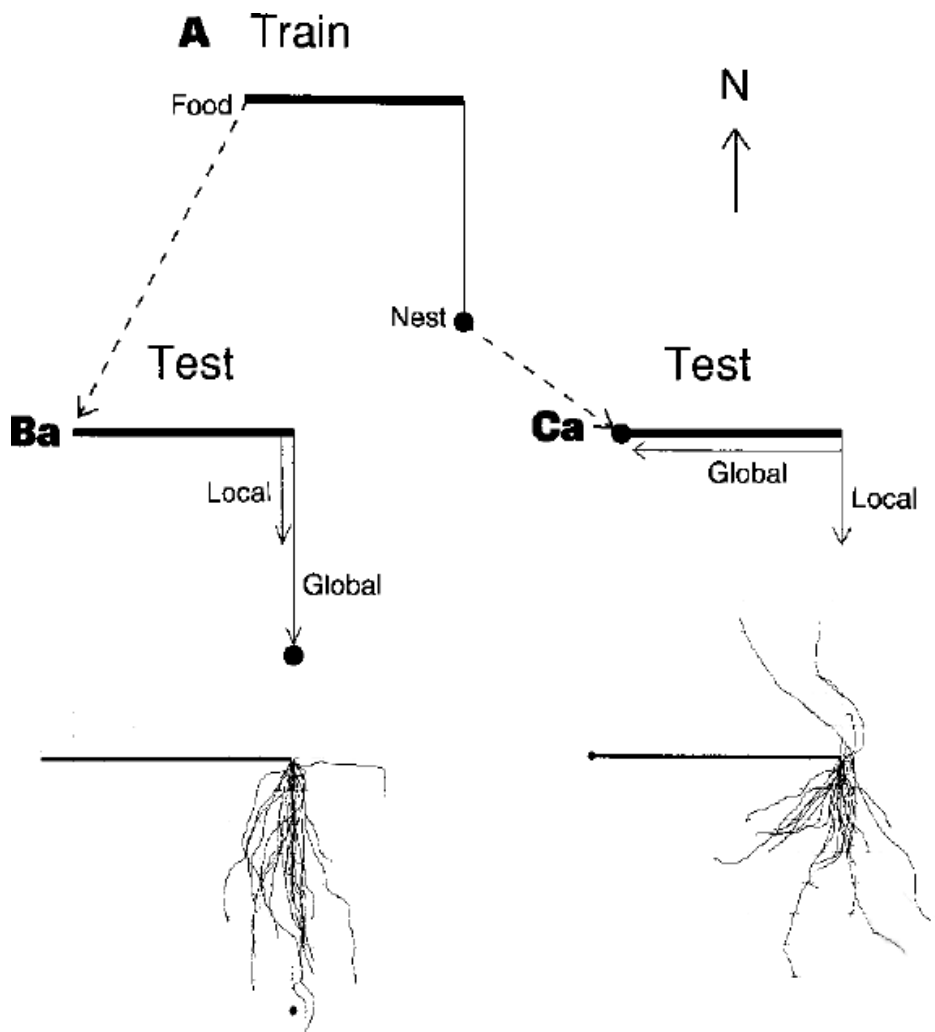


Figure 2.5: **Navigating by local vectors (*C. fortis*)**. (A) Ants were allowed to forage over 8m of open terrain before following a 8m trench west to a feeder. Thus to return to the nest the ants must travel south from the trench exit. Ants were captured at either the feeder or nest and released at a test site with a similar channel (B and C respectively). In both test conditions ants generally head south from the trench exit for the first 2m. For full vector ants they then start to bias their approach using the global path integrator whereas zero-vector ants initiate search behaviours. (Figure adapted from Collett et al. (1998)).

panorama. The exact mechanism and cues utilised by insects during visual homing remains open to question.

Visual cues are also dominant in the common routes following behaviour of insects navigating cluttered environments. Routes are generally considered to consist of associations of visual memories with local navigational cues such as motor commands or vectors. By chaining such associations, insects are thought to navigate via a series of procedural instructions and not through a geometric mapping of their habitat.

2.3 Modelling Insect Visual Navigation

The robustness of the navigational behaviours of insects has drawn interest from researchers in engineering as well as biological fields. This has led to various models being proposed to explain the different navigational strategies outlined in the previous section (for example for path integration see Mittelstaedt and Mittelstaedt (1973); Müller and Wehner (1988); Wittmann and Schwegeler (1995); Hartmann and Wehner (1995); Vickerstaff and Paolo (2005); Merkle et al. (2006); Haferlach et al. (2007). As the emphasis of this study is on visual modes of navigation other behavioural capabilities are not discussed further. Instead the following section provides a brief overview of the background of visual homing models before a comprehensive review of the models implemented in this work.

In their seminal paper Cartwright and Collett (1983) proposed a visual homing algorithm capable of reproducing the search behaviour of bees observed in landmark manipulation studies. This model has since become known as the snapshot model. The algorithm first stores the panoramic image as viewed at the nest location i.e. the snapshot. When homing the model moves to reduce the mismatch in angular position and size of corresponding landmarks in the current world view with those in the snapshot.

The snapshot model provides a conceptually simple model that reproduces the behaviour of bees and ants in many of the landmark manipulation studies outlined previously. The snapshot model has been superseded by more robust and biologically plausible variants (see section 2.3.1), however the iterative matching of current world view to a goal-based snapshot remains the de facto algorithm for visual homing models.

2.3.1 Visual Homing Models

The various visual homing models proposed as possible strategies employed by insects can be broadly split into two classes: feature-based models and view-based models. Feature-based models, for example the snapshot model of Cartwright and Collett (1983), extract features from the visual surround such as angular size and bearing of prominent landmarks. Comparison of the features extracted at the home location with the corresponding features extracted from an image taken at a displaced location allows a homing vector to be calculated. View-based models, by contrast, use comparison of the raw images as seen from the home and the displaced location. For example, Zeil et al. (2003) show that the pixel-wise root mean square (RMS) difference between a panoramic reference image and image viewed from a displaced location increases monotonically with distance. Homing can then be achieved through some form of gradient descent where either agent movements allow the home direction to be inferred (Zeil et al., 2003) or where simulated agent movements allow a home vector to be estimated (Franz et al., 1998; Binding and Labrosse, 2006; Möller and Vardy, 2006; Möller et al., 2007).

As the explicit aim of this study is to investigate the visual piloting strategies employed by insects, only visual homing models that can be considered “*biologically plausible*” are considered. A criterion for the selection of such models was outlined by Vardy (2005):

1. As the insect brain has limited neural capacity, models must not be so computationally complex that no convincing argument can be made for their implementation in the neural hardware of an insect.
2. As the retinotopic mapping is maintained throughout sensory pathways from the insect eye through the optic lobes then all calculations required by the model must be theoretically possible using local retinotopic calculations rather than global searches in the image space.

Applying the above criterion, the following five models were selected for use in this study:

1. Average Landmark Vector Model.
2. Centre-of-Mass Average Landmark Vector Model.
3. Differential Optic Flow Models:

- (a) First Order
- (b) Second Order

4. Image Difference Functions.

It should be noted that the Average Landmark Vector Model is the only feature-based model to adhere to the biological plausibility constraints. This is due to the need of feature-based models to solve the correspondence problem; which feature in the snapshot image corresponds to which feature in the current view. Solving the correspondence problem requires a global search across the entire image to be robust and thus violates criteria 2.

Additionally no models that require the agent to internally simulate all possible movements prior to home vector computation (e.g. image warping (Franz et al., 1998)) are considered either as they are unlikely to be computed by the insect brain and thus violate criteria 1.

For each model a description of the specific algorithm is provided with a discussion of any comparative data to that of insects.

2.3.2 Average Landmark Vector Model

The Average Landmark Vector (ALV) model is a derivative of the classic snapshot model (Cartwright and Collett, 1983) offering an extremely parsimonious system which also bypasses the correspondence problem (Lambrinos et al., 2000). Rather than storing the complete two dimensional image at the home location only the average landmark vector is computed and stored. The average landmark vector is computed by firstly reducing the input image to a one dimensional black and white strip. Various thresholding methods can be implemented to increase robustness of the image conversion process and shall be discussed in more detail in later sections. Unit vectors are then drawn towards each of the vertical edges present in the 1D strip. Taking the mean of the vectors across the entire image provides the home location average landmark vector (ALV_H). When the agent is moved to a distant location (C) the current average landmark vector (ALV_C) is calculated in the same manner. The home vector can then be calculated through a simple vector subtraction ($h = ALV_C - ALV_H$) as shown in figure 2.6.

The ALV model has been shown to home successfully in simulated environments consisting of distinct landmarks within an infinite horizon background (Lambrinos

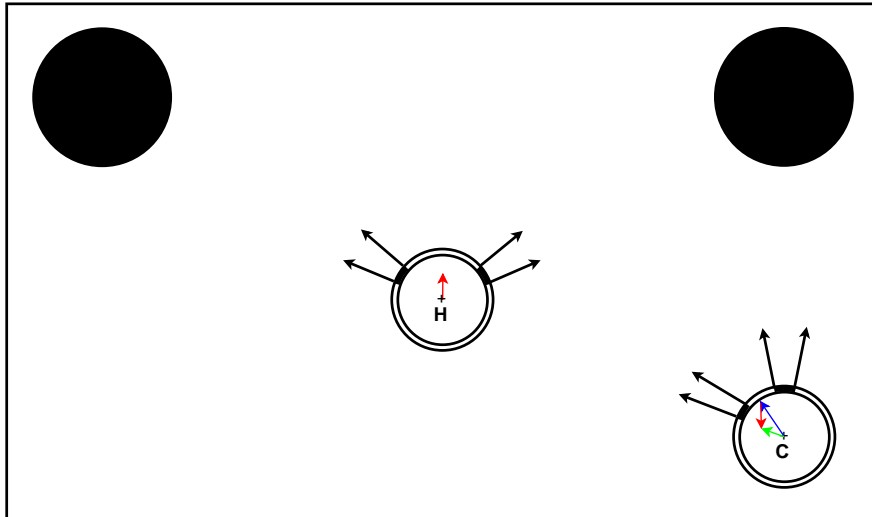


Figure 2.6: **Average-Landmark-Vector Model.** Aerial view of theoretical homing area. Black cylindrical landmarks as used in the behavioural homing studies described previously are shown as filled circles. The home location is marked by H and the current position by C. The ring surrounding each of the locations shows the 1-D input image as sampled from that location. The (ALV_H) is calculated at the home location H by taking the mean of the unit vectors projected to each visible edge in the snapshot image (red arrow). The (ALV_C) is also generated at the current location C in the same manner (blue arrow). Through a simple vector ($h = ALV_C - ALV_H$) subtraction the home vector is calculated (green arrow).

et al., 2000). Homing has also been successfully achieved on a mobile robot in a university lobby (Möller et al., 2001). The parsimony of the ALV model has allowed a completely analogue implementation to be realised on a mobile robot base (Möller, 1999). Inside a small arena marked with black card on an otherwise white background the analogue system was successfully able to relocate a previously visited target location.

Lambrinos et al. (2000) implemented and tested variants of the classic snapshot model on a mobile robot in the same desert habitat in Africa where landmark manipulation experiments were conducted in *Cataglyphid* ants. Modified versions of the snapshot model were shown to return successfully to the home location after a displacement. It should be noted however that models were never assessed under landmark manipulations as experienced by animals. Moreover the ALV model was not explicitly tested on the robot as the authors claim its similarity to the snapshot model and use of the same image cues would produce the same results.

2.3.3 Centre-of-Mass Average Landmark Vector Model

The Centre-of-Mass Average Landmark Vector (COMALV) Model (Hafner, 2001) as its name suggests is conceptually similar to the ALV model. Vectors are again derived at both the home and current locations and the home vector calculated by the same vector subtraction. However rather than using identified edges to calculate these vectors, the COMALV model stores the vector projecting to the "centre of mass" in each image:

$$\text{COMALV} = \sum \left(I(\theta) \begin{pmatrix} \cos(\theta) \\ \sin(\theta) \end{pmatrix} \right) \quad (2.1)$$

where $I(\theta)$ is the image intensity value at the bearing indicated by θ in the one-dimensional input image.

The input image is again reduced to a one dimensional vector through a vertical averaging of grayscale values. Use of the grayscale input directly bypasses the image thresholding required by the ALV model.

The COMALV Model was originally derived through the use of a learning procedure on an artificial neural network, but in this work we only consider the mathematical derivation described by the above equations. The COMALV model has performed successfully in homing trials in simulation and also on a mobile robot

within an office environment (Hafner, 2001). An equivilant COMALV Model was also shown to generate long-range homing cues (up to 2m) when tested in a simulation of the habitat in which ant routes were recorded (Basten and Mallot, 2010). Furthermore the algorithm is computationally cheap and bypasses both correspondence and feature extraction issues. The model however required re-tuning of parameters to home successfully in differing image databases (Vardy, 2005).

2.3.4 Differential Optic Flow Models

Building upon the finding that successful block-matching models of visual homing are dependent upon low frequency rather than high frequency components of images, Vardy and Möller (2005) derived two homing models based on classic differential optic flow techniques. The differential models perform only local searches for image correspondences and therefore fulfill biological plausibility constraints failed by block-matching methods.

The First Order (FO) model rests on the assumption that pixel intensities are maintained across images such that:

$$H(x, y) = C(x + u, y + v) \quad (2.2)$$

where H is the intensity of the pixel at image position (x, y) in the home image and C is the intensity of the same pixel at its new location in the current image given by summing the previous pixel location with the translation vector (u, v) caused by agent movement.

The Second Order (SO) model assumes that intensity gradients rather than pixel intensities are maintained across images such that:

$$H_x(x, y) = C_x(x + u, y + v) \quad (2.3)$$

$$H_y(x, y) = C_y(x + u, y + v) \quad (2.4)$$

where H_x and H_y are the partial derivatives of the pixel intensity at image position (x, y) in the home image and C_x and C_y are the partial derivatives of the intensity of the same pixel at its new location in the current image given by summing the previous pixel location with the translation vector (u, v) caused by agent movement.

Differential models seek to calculate the translation vector (u, v) of each pixel by calculating the intensity gradients (FO model), or the second derivative of the

intensity gradient (SO model), surrounding the pixel in question. This allows the translation vector orientation to be calculated locally, which is then converted into a home vector through an approximate vector mapping technique. That is, knowledge of the robot hardware allows the translation vector existing in image space to be transformed into a home vector in robot space. As differential models derive home vectors at all pixels in the image, the overall home vector is computed by taking the mean of all home vectors across pixel locations.

Differential methods have classically been applied to optic flow problems where pixel translation is small between successive images. In such cases intensity gradients are robust ensuring good translation vector calculation across pixels. The success of these models in homing tasks is therefore somewhat counter-intuitive as the scale of agent translation between image captures causes large pixel translations between home and current image. Such image shifts are shown to have catastrophic effects on the accuracy of the translation vector calculations. However, Vardy (2005) demonstrated that incorrect home vectors are uncorrelated and therefore when averaged they generally cancel each other out. Moreover in the focus of expansion (the portion of the image that the robot is heading directly towards) and contraction (the portion of the image that the robot is receding from) in the image, pixel movement remains small. Thus in these regions of the image the small image translation assumption is valid, resulting in blocks of accurate translation vectors. These correct and correlated home vectors dominate when averaged across pixel locations (known as the democracy effect) producing an accurate overall home vector.

Although the procedure outlined above may sound computationally complex, differential optic flow models remain biologically plausible. The majority of the model calculations are local and are ideally suited to parallel computation as could be performed retinotopically by insects. The differential visual homing models have been shown to home successfully within a number of indoor image databases such as an office environment, and a university hall-way (Vardy and Möller, 2005). However to the best of this authors knowledge neither variant of optic flow model has been tested in environments where the homing behaviour of insects is known.

2.3.5 Image Difference Function Model

The image difference function (IDF) model of visual homing has its roots in the finding that the pixel-wise intensity difference between aligned images taken from dif-

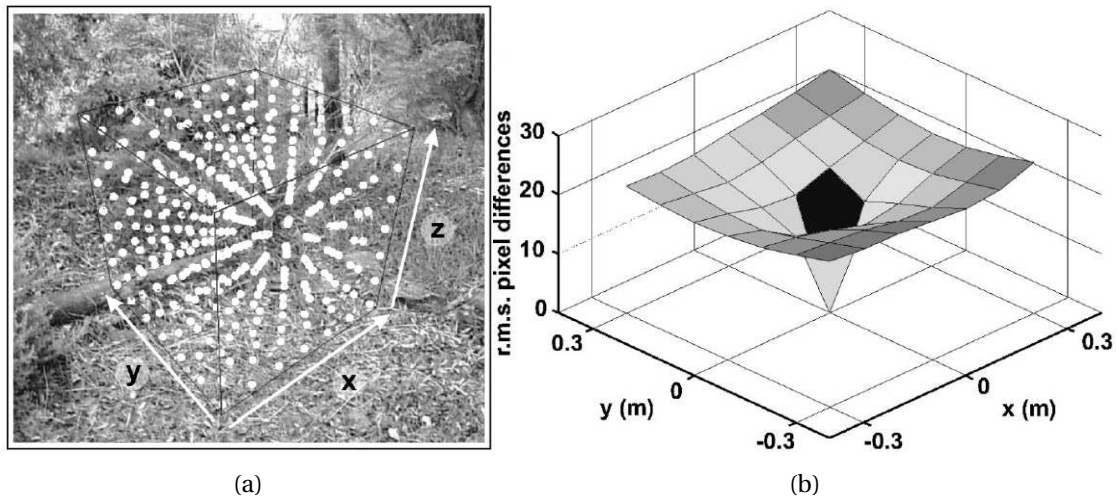


Figure 2.7: **RMS Image Difference Function in outdoor environment.** Images taken using panoramic camera mounted on a robot gantry. (a) Images were sampled at 10cm intervals in 1m cube as indicated by the white dots. (b) The RMS difference between the central image and the remaining images sampled in the plain are shown as an image difference function. (Figures adapted from (Zeil et al., 2003))

ferent locations tends to increase smoothly and monotonically with distance (Zeil et al., 2003). Plotting the difference between images across locations therefore reveals a sloped surface where the minimum corresponds to the home location (see figure 2.7).

By sampling the image differences at a number of locations in the environment (by either simulated or actual agent movement), simple gradient descent (or ascent) algorithms can utilise the difference slope to return to the home.

Gradient descent models have been shown capable of homing in natural outdoor scenes (Zeil et al., 2003; Stürzl and Zeil, 2007), in indoor environments using image databases (Zampoglou et al., 2006), (Vardy, 2005), and also on a mobile robot in a laboratory environment (Zampoglou et al., 2006).

Recently gradient descent models were shown able to reproduce the data observed in ants when trained to home via a single corner of rectangular arena. In the recent laboratory study, ants were found to regularly confuse directly opposite corners of an unmarked rectangular arena (Wystrach and Beugnon, 2009). Note that the arena corners housed exit tubes leading the ant back to its nest. When corners were labelled with prominent visual cues entry into the wrong exit tube ceased however it should be noted that ants still confused the corners initially. Stürzl et al.

(2008) have demonstrated that the data observed can be reproduced using the image difference function model.

2.3.6 Survey of Homing Models in a Virtual Ant Habitat

Basten and Mallot (2010) recently assessed the performance of two biologically plausible visual homing models within a virtual reality simulation. The 3D world in which the models were tested was a replica of the habitat in which Kohler and Wehner (2005) recorded idiosyncratic routes of *M. bagoti*. As Kohler and Wehner (2005) only presented an aerial mapping of the ant habitat the virtual world consisted of green coloured grass tussocks (all 25cm tall) in all locations outlined as landmarks in the original mapping. The remainder of the world consisted of flat regions of open ground, and a blue sky background augmented with solar lighting cues. Model testing was performed off-line using an image database with images sampled every 10cm across virtual world using an variable resolution ant eye model approximated for *M. bagoti*.

The study assessed the homing ability of models when provided with two distinct visual cues from the environment. In the first case models were provided with grayscale panoramic images such that intensity was the salient cue. Alternatively, models were provided with only the skyline cue using a blue/green opponent channel mechanism as outlined by Möller (2002). The skyline cue therefore is more parsimonious as it is represented by a 1-dimensional vector indicating terrain elevation at all azimuthal angles.

The first model assessed was termed an "adapted ALV model" by the authors but is equivalent to the COMALV model outlined previously. The second model implemented was an IDF model. The authors chose an uncentred correlation coefficient as their metric and therefore used a gradient ascent scheme for homing.

Both models were assessed on the extent of the area from which an agent could successfully return to a target location. This region is commonly known as the catchment area. Target locations comprised 86 sites along a real ant route as recorded by Kohler and Wehner (2005). The COMALV model produced the largest catchment areas of approximately 1m² and 2m² when supplied with intensity and skyline input cues respectively. The IDF model could only produce mean catchment areas of approximately 0.6m² and 0.5m² when supplied with intensity and skyline input respectively.

2.3.7 Modelling Visually Guided Routes

To date there have been few attempts to create biologically plausible route following models.

Vardy (2006) developed a novel route learning procedure that proved successful when tested in a simulated art gallery. Snapshot memories were chained together by local vectors resulting in a sparse topological map of the route. When homing the model expired 80% of the local vector before switching to visual homing by matched-filter descent in IDF.

Smith et al. (2007) developed an extremely parsimonious route guidance system based on the ALV Model. When exploring the environment new snapshots were generated every time the number of identifiable landmarks in the panoramic image changed. When homing the model used the ALV Model to home to each snapshot memory in the defined sequence that they were stored. The model was tested on a robot gantry in an indoor environment interspersed with black cylinders. Testing showed that the model enhanced robustness of the ALV Model specifically with regards to aliasing. Furthermore, some simple routes were traversed in the artificial environment.

Both models however require route memories to be recalled in sequence which does not reflect the insect data. As discussed in section 2.2.4.2 ants displaced along their route can recognise the familiar terrain and follow the route home. The sparse model proposed by Vardy (2006) is particularly susceptible as the visual memories are spaced widely apart and linked with local vectors. This leaves large regions of route that would appear unfamiliar when compared to any of the route memories. It should be noted that neither author claims that their model is an accurate account of how insects navigate, but instead focus on the ability to extend visual homing capabilities to more realistic tasks. With this in mind neither model is compared to insect data in a quantitative manner. Indeed there is no model of route following in the current literature that the author is aware of that has been tested in situations where route following has been observed in animals.

2.3.8 Summary of Insect Visual Navigation Models

A number of models of visual homing have been proposed that adhere to the snapshot methodology but function through distinct mechanisms and using different visual cues. One class of model extracts specific features from the environment

and by moving to decrease the discrepancy of the feature locations between current view and snapshot can return home. Whilst conceptually simple, correct matching of features between images (the correspondence problem) requires a global search in the image space and thus rules many models biologically implausible. The ALV Model represents the only feature-based model that fulfills the biologically plausible constraints defined by Vardy (2005).

View-based methods do not extract features and instead use look for image discrepancy at the pixel level or use the entire image directly. Four view based models successfully adhere to the biological constraints including an intensity summing model, two optic flow based methods and a gradient descent on image difference algorithm.

Only the ALV and IDF models have been tested in real world environments where the homing ability of insects is known. An equivalent model of the COMALV and an IDF were also recently tested within a simulated environment where ant routes were tested. All of the above models successfully returned to the target location in the specific test.

2.4 Summary

Insects navigate their complex habitats with amazing accuracy despite their small brains and low resolution vision. Such feats are achieved using a suite of distinct navigational strategies combined in what has been termed the "*navigational tool-kit*". The complimentary strategies making up the tool-kit include systematic search, path integration and visual homing. Other strategies such as trail following may also be employed but are known to be dominated by vision based techniques. By some cue integration procedure, that is not yet fully understood, insects are equipped with a robust guidance system sufficient for piloting vastly different habitats; from the barren desert salt pans of northern Africa to the deep undergrowth in the tropical forests of South America. Moreover, growing evidence suggests that various insects utilise common sensory cues and techniques to guide them through their specific ecological niche leading towards a common underlying guidance system; that is, a "*general navigational tool-kit*".

The prevalent strategy by which insects pin-point often inconspicuous locations in their habitat is visual homing. Visual homing is sufficient for guidance when other strategies including path integration are absent and is dominant when these

strategies are present. Visual homing requires that insects store information about the world viewed from the location to which they later wish to return. To relocate the target animals move as to increase the match between their current view of the world and the stored memory of the target location. Landmark manipulation studies have shown that insects seek to retinotopically align relatively unprocessed visual features directly rather than matching other features of the environment such as the distance to prominent landmarks.

Visual homing allows foragers to pin-point journey start and end-points with precision using local visual cues. However, many insects forage over large distances. For such foragers visual cues sampled at a single location are unlikely to be stable over a sufficient range to provide guidance over the insect entire journey. A common strategy for insects navigating such distances is the development of visually guided routes. Experimental manipulation has shown that ants associate local vectors and motor commands with visual scenes sampled along their repeated paths. Such findings have led to the hypothesis that routes may be the product of a series of visual memories stored along the paths traversed by foragers. Visual homing similar to that outlined above could guide insects to visual waypoints where an associated vector or motor command would be triggered leading towards the next visual memory.

It should be noted that such a strategy does not require the construction of a geometric map of the environment inhabited by the insect, and is therefore likely to be a more parsimonious use of memory and computation resources limited by the small brain of insects.

A series of models have been developed, both in simulation and on real robots with the explicit aim of reproducing visual homing behaviours given the constraints imposed on insects by their sensory and nervous systems. These models adhere to the snapshot matching algorithm whereby they move as to minimise the discrepancy between the current view of the world and that of a memory of the target location. However, models vary in the information from the visual surround that is extracted, stored and manipulated to generate the motor commands.

Models can be broadly split into two classes: feature-based and view-based. Feature-based models extract features of the visual surround at both the target and current locations. When homing the disparity of features in image space allows a home vector to be generated in robot space. Feature-based models can be computationally cheap as they only store the location of features in the goal image. How-

ever, they generally require a global search in image space to locate corresponding features which is thought to be biologically implausible in insects. View-based models do not extract any features from the visual scene and instead use the entire image directly. This class of model often requires that the entire image be stored in memory increasing the memory load. However image comparison is generally resolved in a parallel computation across pixel locations which is well-suited to early visual processing neuropils of insects. It should be noted that the view-based models also differ in terms of the visual input that is compared at the pixel level for example local optic flow fields versus image intensity. Furthermore the differing homing schemes employed by the models can produce distinct homing performance.

The remaining chapters of this thesis seek to address two key hypothesis raised in this literature review:

- *Are visual homing capabilities conserved across diurnal insects indicating a general navigational ability across species?*
- *If so, is there a method of visual homing that can account for such behaviours across insect species?*

To address the first hypothesis two behavioural studies are undertaken in insect species for which little or no visual navigation data exists. Chapter 3 assesses the visual homing ability of the field cricket *Gryllus bimaculatus* in an assay commonly used to test for place memory in mammals. And chapter 5 presents a field study in which the route forming behaviour of the European ant *Cataglyphis velox* is assessed. Where possible direct comparison is made to data already published for other insect species, specifically those occupying in similar ecological niches.

Both behavioural studies are designed with model verification in mind. In the laboratory study homing performance of crickets is assessed with various visual surrounds that are well suited to particular homing models such as distinct artificial landmarks favoured by feature-based models and a natural scene suited to view-based models. Chapter 4 presents a modelling study where all biologically plausible models of visual homing are tested in the same paradigm as the animals. To the best of the authors knowledge this is the first time that all of the biologically plausible models of insect visual homing have been tested and compared directly to insects homing data.

If routes are constructed by chaining together visual memories, then the same models should provide robust guidance cues in the ant habitat. In chapter 6 an

image database is collected within the same environment that the natural routes of ants were observed. To the best of the authors knowledge this is also the first large scale image database collected in the ant habitat. Models are again assessed for their efficacy and robustness in guiding insects through this more natural surrounding.

Studies of this type are very timely. The natural homing behaviours of insects are well documented for an array of species. Moreover, experimental manipulation studies have revealed some of the general mechanisms underpinning navigation. However, for proposed models of insect navigation to be properly verified, testing must be carried out using the same sensory input as experienced by animals. Indeed it is not entirely clear what information is available in the natural world viewed by the insect. Recently leaders in the field of insect navigation have encouraged such studies, and it this thesis adopts the same ethos:

"a crucial task, though not easy to accomplish, would be to get more detailed information about the visual inputs actually experienced and acquired by the insects as they negotiate their ways through their foraging grounds, at best starting with the time at which the animals commence foraging. Reconstructing the optic flow experienced by the insect as it moves through its environment - either by computer simulations (after having recorded the 3D structure of the surrounding landscape) or, better yet, by moving a camera along the insect's path - would be a first step in analysing what navigationally relevant information the insect might extract from the visual scenes" Wehner (2008)

"In order to understand the intimate relationship between vision and behaviour, an effort needs to be made to reconstruct vision from the view-point of behaving animals in their natural environment. The future of visual neuroscience thus lies in going natural;" Zeil et al. (2008)

Chapter 3

Visual Homing in the Field Cricket

Note that data presented in this chapter also appears in Wessnitzer et al. (2008).

3.1 Introduction

Mizunami et al. (1993, 1998b) devised a test for place memory in the cockroach *Periplaneta americana* based on the classic water maze paradigm used for rodents (Morris, 1981). The animal is placed in an unpleasant environment (for rats, a pool of water; for cockroaches, a heated metal arena) and is thus motivated to move until it locates a safe position (an underwater platform; or a cool spot, respectively). Several lines of evidence are used to argue that the animal locates the (invisible) safe position using surrounding visual landmarks (outside the pool or on the sides of the arena), i.e. that it has formed a 'place memory'. The animal is able to relocate the target location from novel starting points in subsequent trials, and searches preferentially in that location on trials when the platform (or cool spot) is removed. Animals are less successful in learning the task when no visual cues are provided. Moreover, when the visual cues are rotated, the animal will search in the vicinity of the 'fictive' target indicated by those cues.

Scotto-Lomassese et al. (2003) report that they attempted to test the ability of the house cricket *Acheta domesticus* using the Mizunami *et al.* approach (which has been dubbed the Tennessee Williams paradigm) but found that "*the first motivation of crickets was to escape from the closed arena*". It should also be noted that the data presented by Mizunami et al. (1998b) is suggestive rather than conclusive: due to substantial variability in behaviour, no statistical significance of the apparent improvement in locating the target over ten trials is reported, and searching in the



Figure 3.1: Female field cricket of the species *Gryllus bimaculatus*

fictive location after cue rotation is reported only for two individuals. However the main point of their report is the demonstration that ablation of the mushroom body neuropils in the cockroach significantly affects performance on this task, but does not change performance when the target itself is visible.

In this chapter the ability of the field cricket *Gryllus bimaculatus* to learn and subsequently relocate an invisible target position using surrounding visual cues is assessed using the same "Tennessee Williams" paradigm. Specifically, the following research questions are posed:

- *Can field crickets learn to relocate a hidden target using surrounding visual cues alone?*
- *If so, is performance better when supplied with distinct visual cues or a more cluttered visual panorama?*

3.2 Methodology

3.2.1 Animals

Adult female *Gryllus bimaculatus* crickets (figure 3.1) were isolated after their final moult and maintained individually in small plastic cages under a 12/12 hour light/dark cycle. The animals were kept at 21 ± 1 degrees and were fed water and dog food.

3.2.2 General Procedure

Cricket are placed in a circular arena with a metal floor on top of a water tank. The water tank maintains a temperature of about 50 °C which in turn heats the metal floor surface of the arena, and to some extent, the surrounding the metal wall. A single circular cool spot on the arena floor is created by continuously circulating cool

water through a separate, insulated compartment of the water tank (Figure 3.2a.). This target is visually and texturally indistinguishable from the surrounding area.

Trials are initiated by placing the cricket at a random location in the arena. The animal is then allowed to move and explore the arena freely. The trial ends if the cricket finds and remains at the cool spot for 30 seconds. Trials lasting longer than 5 minutes without the cricket finding the target are halted to prevent heat-shock to the animal. In such cases the individual cricket is placed on the cool spot by the experimenter. By covering the cricket with a glass it is forced to remain on the cool spot for 30 seconds. Crickets are rested for two minutes between trials in an opaque beaker. Between trials, the arena is wiped clean to remove any olfactory cues left by the animal.

3.2.3 Experiments

3.2.3.1 30cm Arena

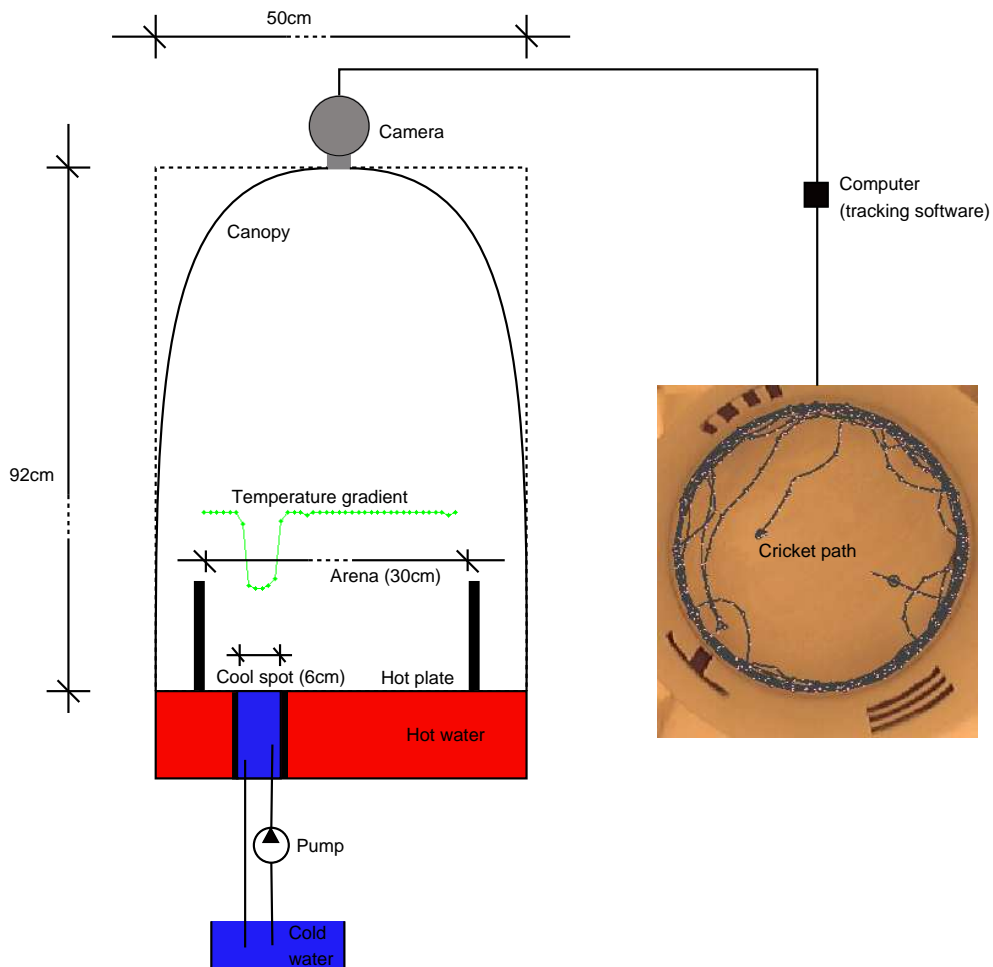
The first experiment aimed to replicate, using crickets, the tests performed on cockroaches by Mizunami *et al.* (Mizunami et al., 1998b). The arena diameter was 30cm and the target cool spot diameter approximately 6cm. Animals were tested under three conditions:

1. With the visible target (a metal plate of distinct colour compared to the hot-plate surface). No other visual cues were provided.
2. With an invisible target and artificial visual cues mounted on the arena the walls. The artificial cues were a black T shape, black and white horizontal stripes and black and white vertical stripes as shown in figure 3.2a.
3. With an invisible target and no visual cues provided.

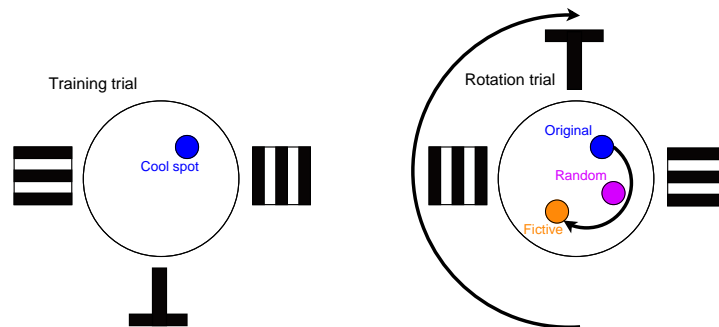
In all conditions, the arena was covered by a white canopy to reduce the possibility of the animals using external visual cues, such as laboratory furniture or lighting. In each condition, each cricket was tested on ten successive trials, and the time taken to locate the cool spot recorded.

3.2.3.2 40cm Arena

In the second experiment the arena diameter was increased to 40cm, thus approximately doubling the ratio of arena to target area, reducing the likelihood that the



(a)



(b)

Figure 3.2: **Place memory experimental setup.** (a) The hot water tank heats the arena floor and lower regions of the arena wall to approximately 50°C. A cool spot is maintained at a moderate temperature by a cold water pump. External cues are removed by a canopy and crickets are tracked by an overhead webcam. (b) For the rotation trials, the wall of the arena is rotated by 180°, changing the position of the visual cues, and creating a fictive target location relative to those cues.



Figure 3.3: **Natural scene stimulus.** The natural scene wallpaper was wrapped around the inside of the arena wall providing the cricket with a more noisy and cluttered visual reference.

cricket could find the cool spot using some random search strategy. The target was always invisible, and crickets were tested in one of four visual cue conditions:

1. With 3 simple black and white shapes on the arena wall as in experiment 1 condition 2.
2. With a more natural scene stimulus provided as shown in figure 3.3.
3. With no visual cues provided i.e. with blank arena walls.
4. With all visual stimulus removed by testing in the dark. (control)

For each of these conditions the original white canopy was replaced by a dark canopy to try to further reduce any external visual stimuli. As for the experiments within the 30cm arena, there were ten learning trials, for each condition.

After the tenth trial crickets were also tested with the arena wall, and thus the visual cues for the first two conditions, rotated (c.f., figure 3.2b). During this test the cool spot was removed and thus the entire hotplate surface evenly heated. If the animal was using the provided visual cues to determine the target location, this manipulation should create a fictive target location, relative to the cues. If the crickets are not using these cues, the fictive position should be no more attractive than the original target position or any other random point in the arena at a similar distance from the walls.

3.2.4 Data Analysis

An overhead web-camera (Logitech) was used to record the behaviour of the animals directly on the computer at 5 frames per second. For the dark control experiments the infrared filter on the camera was removed. Cricket positions were

extracted from the video recordings with customised tracking software developed by Rosano and Webb (2007). The data is then further analysed with scripts written in or provided by MATLAB. We extracted the following measures from the captured data: time to reach certain areas in the arena, path length, velocity, time spent in vicinity of the wall. Non-parametric pair-wise comparisons are made to establish significant differences between conditions and trials.

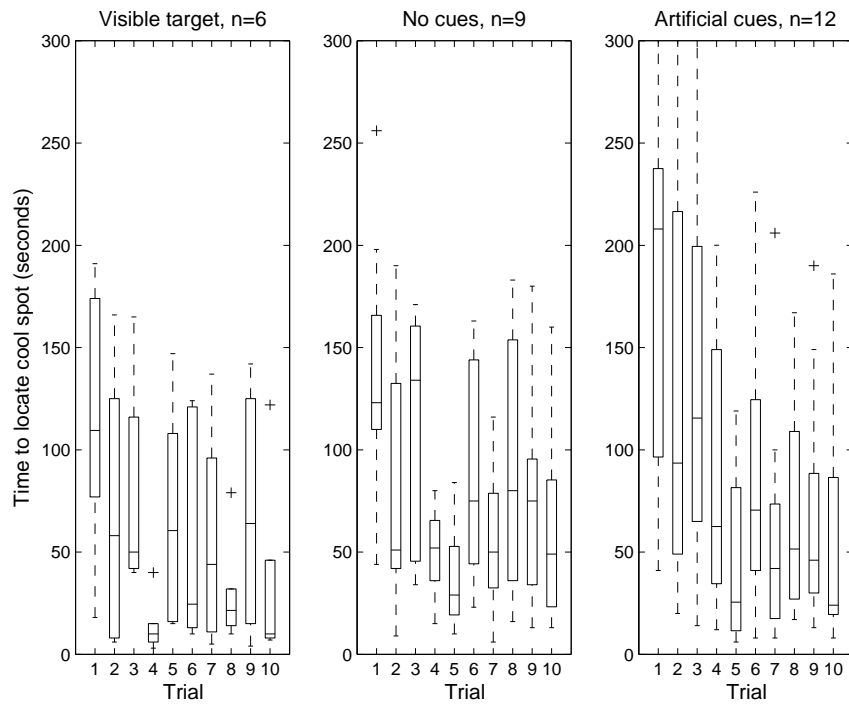
3.3 Results

3.3.1 30cm Arena

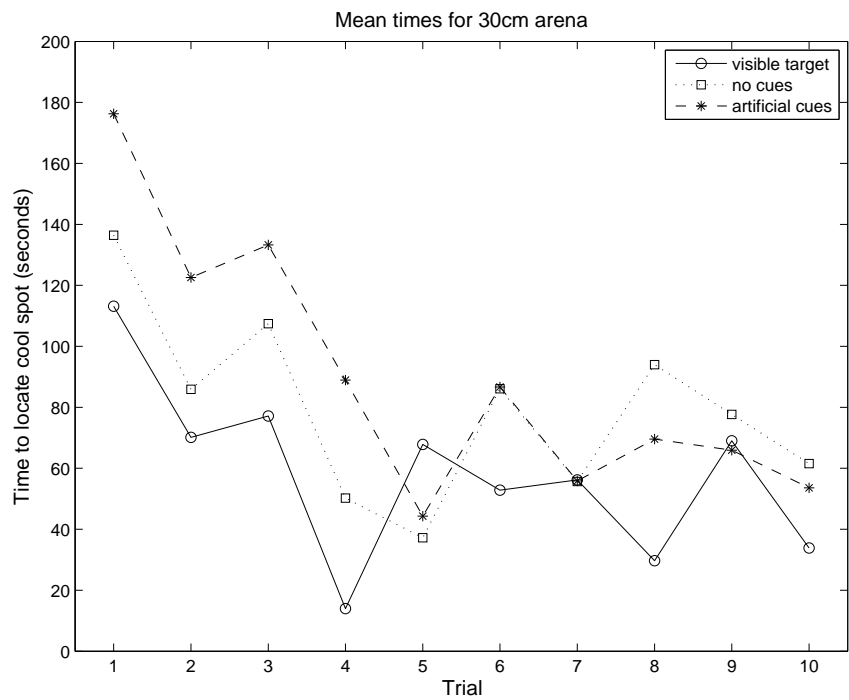
The time taken to locate the cool spot over the ten trials for each condition are shown in figure 3.4a as a series of box plots. The mean times taken to locate the cool spot for the three conditions plotted against trial numbers are also shown in figure 3.4b.

It is apparent that the time taken to locate the target decreases over the first five trials. Comparing trial one and trial ten showed a significant improvement in all conditions (Wilcoxon signed rank test: visible target $p=0.06$; no cues $p<0.005$; artificial cues $p<0.001$). While this suggests that crickets are indeed learning to locate the cool spot, the similarity of behaviour with and without cues suggests either that the 'no cues' condition does in fact contain some cues, such as visual cues above the arena walls caused by shadows on the canopy from the structure supporting the camera; or that the insect is using some strategy other than visual memory to locate the target more quickly on successive trials.

A closer examination of the recorded paths on individual crickets provided some insight (see figure 3.5). It should be noted that the tracks of the animal shown are a good representation of the general behaviour of the crickets across conditions. The first thing to note is that the cricket approaches the target position from a variety of directions. This rules out the use of some stereotyped motor response associated with a particular location in the arena to locate the cool spot. Most crickets on being introduced to the arena did show a strong tendency to run towards and along the walls, presumably trying to escape the arena. These wall-following bouts would often recur in later trials, even after the animal had several times previously moved directly to the target (and even when the target was visible). It is therefore possible that the observed improvement in homing times could be explained by crick-



(a)



(b)

Figure 3.4: **30cm Arena Results.** (a) Box-plots of time taken to find the cool spot over 10 trials with a with a visible target (left), no visual cues (middle), or artificial visual cues mounted on the arena wall (right). (b) Comparison of mean times to locate the cool spot for the three conditions over the ten learning trials.

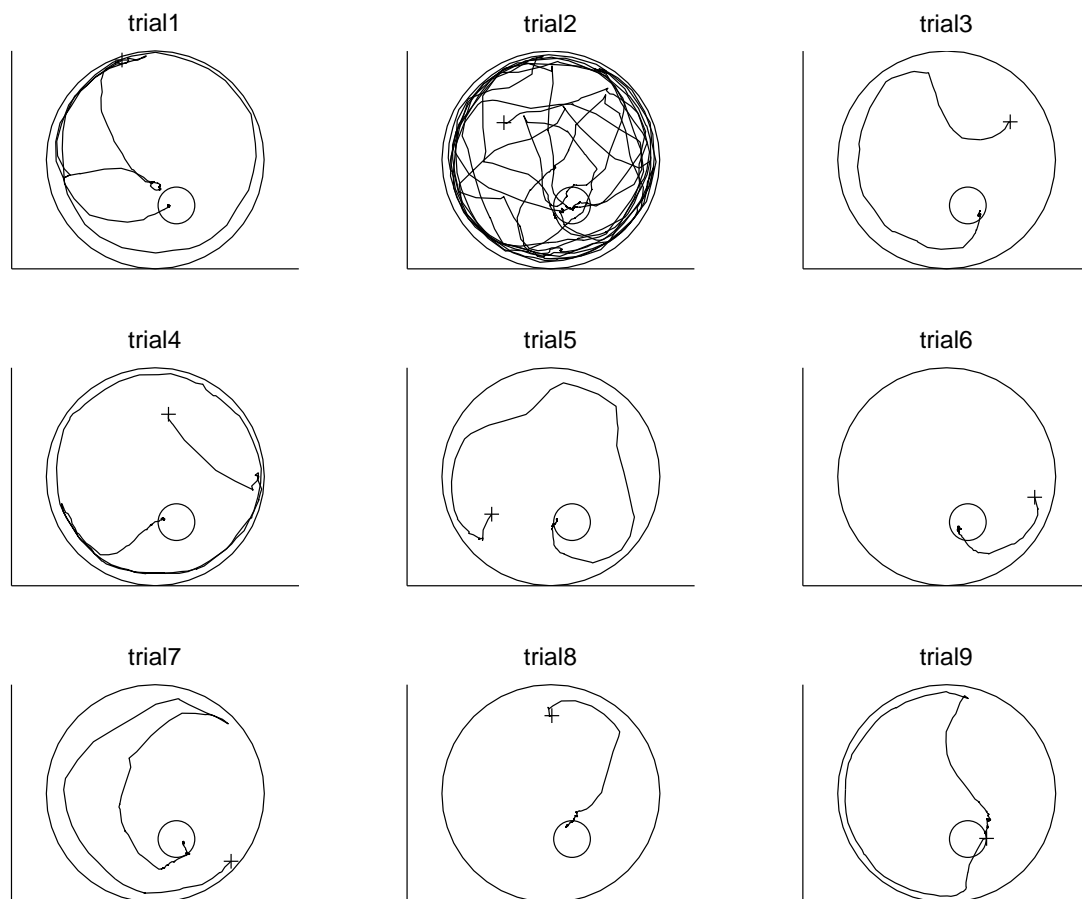


Figure 3.5: **Paths of an individual cricket during learning trials.** Paths from first nine trials for one cricket within the artificial visual cues condition. The cross marks the start of the path and the small circle the hidden target location.

ets merely learning to resist wall-following. Figure 3.6 plots the percentage of time spent wall-following for the trials with artificial visual cues, and also the residual durations of the tracks excluding the wall-following. Note that wall following was defined as the time spent by the cricket within 4cm of the arena walls. After correction of the homing times by removal of wall following some variability is removed but the learning trend over successive trials remains. Thus it does not appear that increased performance can be explained simply by the animal reducing the time spent wall-following, i.e., wall-following explains some of the pattern but not the overall trend towards faster times. We also note that the faster time to locate the target is not simply due to faster movement by the animal, as the average velocity tended to decrease over the 10 trials.

There was also some evidence that crickets found the visual cues themselves attractive (initial use of a solid black square target had to be abandoned as this proved

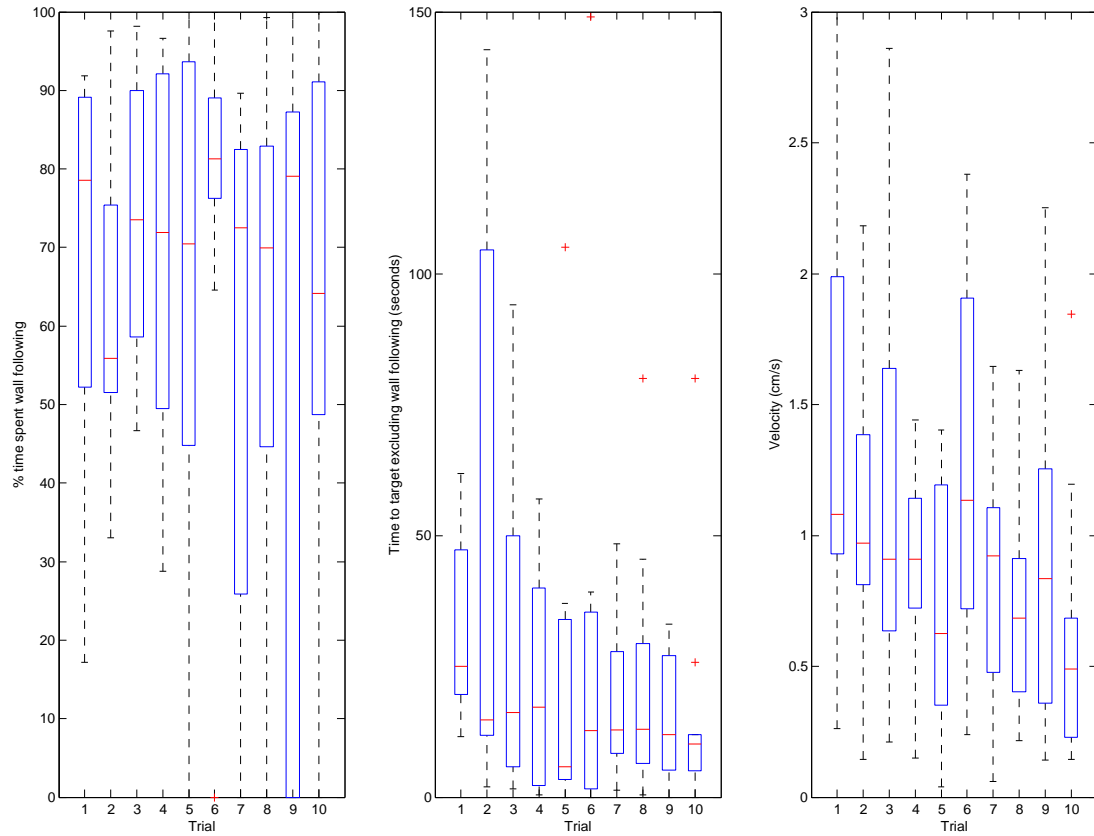


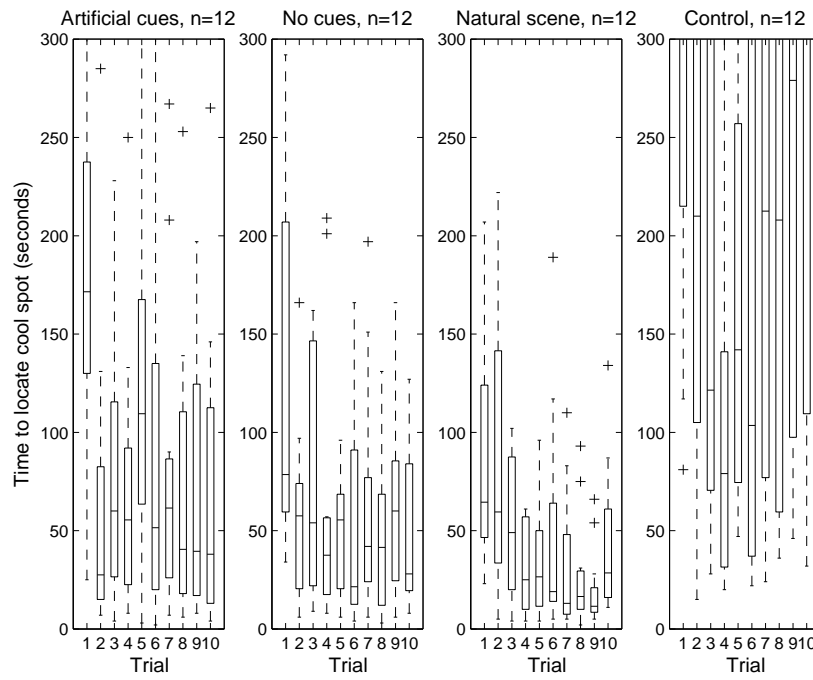
Figure 3.6: **Influence of wall-following and average velocity on performance.** Data taken from crickets subjected to the artificial visual cues condition ($n=12$). (left) The percentage of time during the learning trials spent wall following; (middle) The residual of times to locate the target after exclusion of the time spent wall following; (right) The mean and standard deviation of the crickets' velocity against trial numbers (the green line represents the median).

strongly attractive). However, on at least some trials with visual cues, the cricket would stop at some point in the arena, fixate each of the visual cues and then move quite directly to the target location, suggesting that visual memory of the relation of distant cues to the target could be employed. Moreover, on other trials, both with and without cues, it was observed that some crickets would circle the walls but make repeated deviations away from them, which was also a moderately successful strategy for encountering the target. In the 30cm arena the chance of finding the target once away from the wall is quite high.

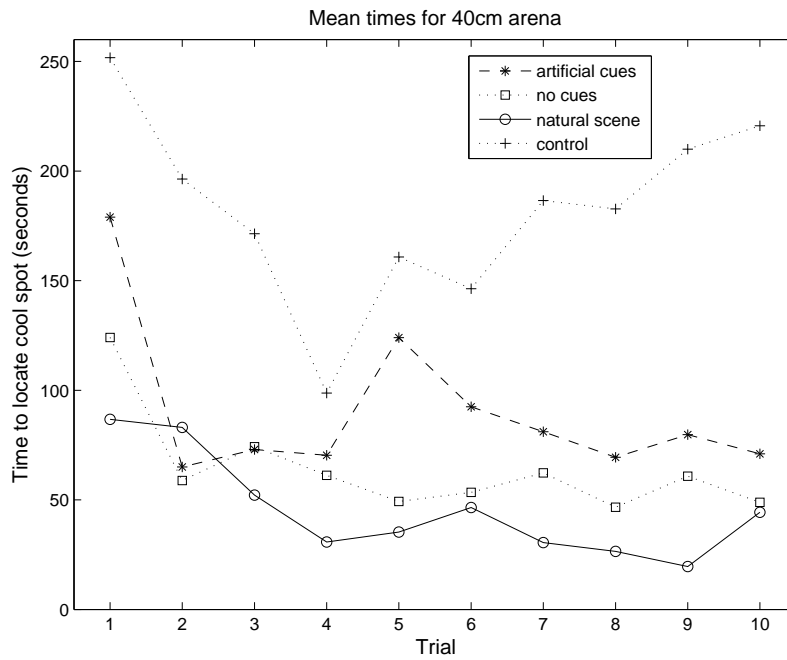
Trials conducted within the 30cm arena showed that crickets increase their homing performance over ten learning trials. However, the performance under the various test conditions was similar. Whilst some qualitative analysis suggests that visual cues were being used, and other strategies such as increasing average speed or decreasing wall-following tendency have been ruled out, it cannot be concluded without question that crickets are homing by visual means. With this in mind, the experimental setup was altered to aid disambiguation of the strategy in use.

3.3.2 40cm Arena

Using an increased arena diameter of 40cm the ratio of open arena to cool spot area was approximately doubled. Learning performance was compared in the four conditions outlined previously: with artificial cues; with a natural scene; with no cues; and in the dark. Crickets showed improved performance when comparing trials 1 and 10 in all conditions except for the dark control condition (Wilcoxon signed rank test: for artificial cues $p < 0.01$, no cues $p < 0.01$, natural scene $p = 0.06$, dark $p > 0.4$), see boxplots in figure 3.7a. For the artificial cues there seemed to be a sharp improvement on the second trial but no further improvement; performance from trials 4-10 is slightly worse than it was in the 30cm arena (comparing the average times across these trials, 84s vs. 61s, Wilcoxon rank sum test: $p < 0.05$). Comparing the means for the three conditions in the 40cm arena (figure 3.7b) it is clear that the improvement is greatest for the 'natural scene' condition, but also, perhaps surprisingly, that the artificial cues on the walls produce worse results than 'no cues' (comparing averages across trials 4-10 using Wilcoxon rank sum test, natural vs. artificial cues, 33s vs. 84s, $p < 0.001$, natural vs. no cues, 33s vs. 55s, $p < 0.05$, artificial vs. no cues, 84s vs 55s, $p < 0.05$). All three conditions are significantly different from the control dark condition (average 172s).



(a)



(b)

Figure 3.7: **40cm arena results.** Time taken to find the hidden cool spot over 10 trials in the 40cm arena (a) from left to right, with artificial visual cues on the arena wall, no cues, a natural scene on the arena wall, control experiment in the dark; (b) comparison of mean times for all conditions.

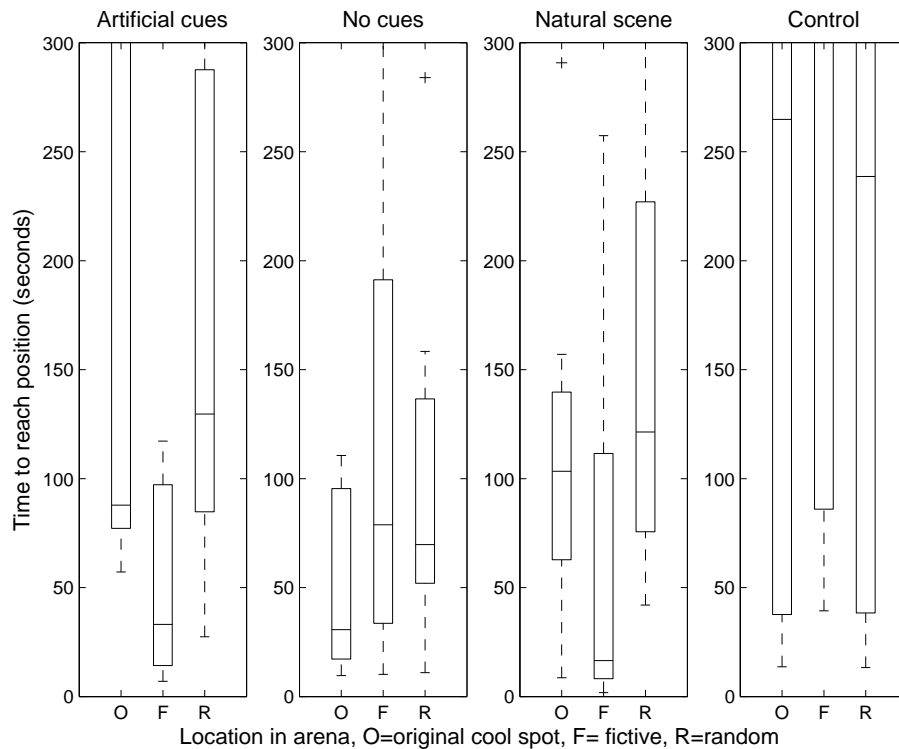


Figure 3.8: **Rotation trials in 40cm arena.** For artificial cues and the natural scene the fictive position of the cool spot indicated by the rotated cues or panorama is approached more quickly than the original location, or a random position. For ‘no cues on arena wall’ the original position is approached more quickly than the fictive or random locations. In the control experiment, no spot, original, fictive or random, is approached significantly faster.

Figure 3.8 shows the results for the rotation tests with artificial, natural, no cues on the arena, and in the dark. The time from the beginning of the trial until the cricket’s track crosses the original location of the cool spot, the fictive location indicated by the cues or panorama, or a random location of an equal size and equal distance from the walls is shown in the boxplots. Each location is defined as a 2cm radius circle. For natural cues, the time to reach the fictive location is significantly faster than the time to reach the original location or a random position (sign test, original vs. fictive $p=0.0386$). For artificial cues, the same pattern was observed but the results were of marginal significance (original vs. fictive $p=0.11$). For ‘no cues’ crickets seem to reach the original location more quickly suggesting that they may be able to use other information (that has not been rotated) than the wall cues for locating the hidden target location. For the control condition, crickets show no preference and no attraction to any of the test locations.

3.3.3 Post Analysis

The unexpected observation of significantly improved performance in the “no cues” condition suggests that visual cues other than those explicitly provided were present in the experimental set-up. This hypothesis is also supported by results from the rotation test in which crickets trained in the blank walls condition return to the original cool spot location preferentially.

To test for such cues images were sampled within the arena provided configured as in the blank walls trials. Firstly a webcam was placed at the centre of the arena and pointed towards the arena ceiling. The recorded image is shown in figure 3.9 (a) clearly showing the lighting imbalance in the overhead canopy caused by the overhead lamps. The grey-scale rotational intensity variation in the canopy is plotted in figure 3.9 (b). To assess the presence of lighting cues at lower levels a panoramic camera was placed at the arena centre. This allowed the light intensity levels across the entire arena wall to be sampled in one image. The recorded image, and azimuthal grey-scale variance are shown in figure 3.9 (c) and (d) respectively.

It is clear that the experimental paradigm did not completely remove all external visual cues with light intensity gradients present in both the ceiling and the arena walls. Such cues may have provided subtle but sufficient rotational information to guide crickets trained in the “no cues” condition.

3.4 Conclusions

The posed research questions investigated in this chapter are answered directly:

- *Can field crickets learn to relocate a hidden target using surrounding visual cues alone?*

The results presented demonstrate that the field cricket *Gryllus bimaculatus* is capable of using surrounding visual cues to relocate a hidden target position, in an arbitrary task setting. This is suggested by the observed performance improvement over trials, and the ability to relocate the cool spot from different starting positions, but is most strongly supported by the results of the rotation trials. In these trials, only the visual cues on the arena walls were changed, controlling for all other possible sensory cues that might potentially have contributed to the observed learning, and a corresponding change in the crickets preferred location was observed. Hence, memory of the surrounding visual cues is sufficient for homing in this task.

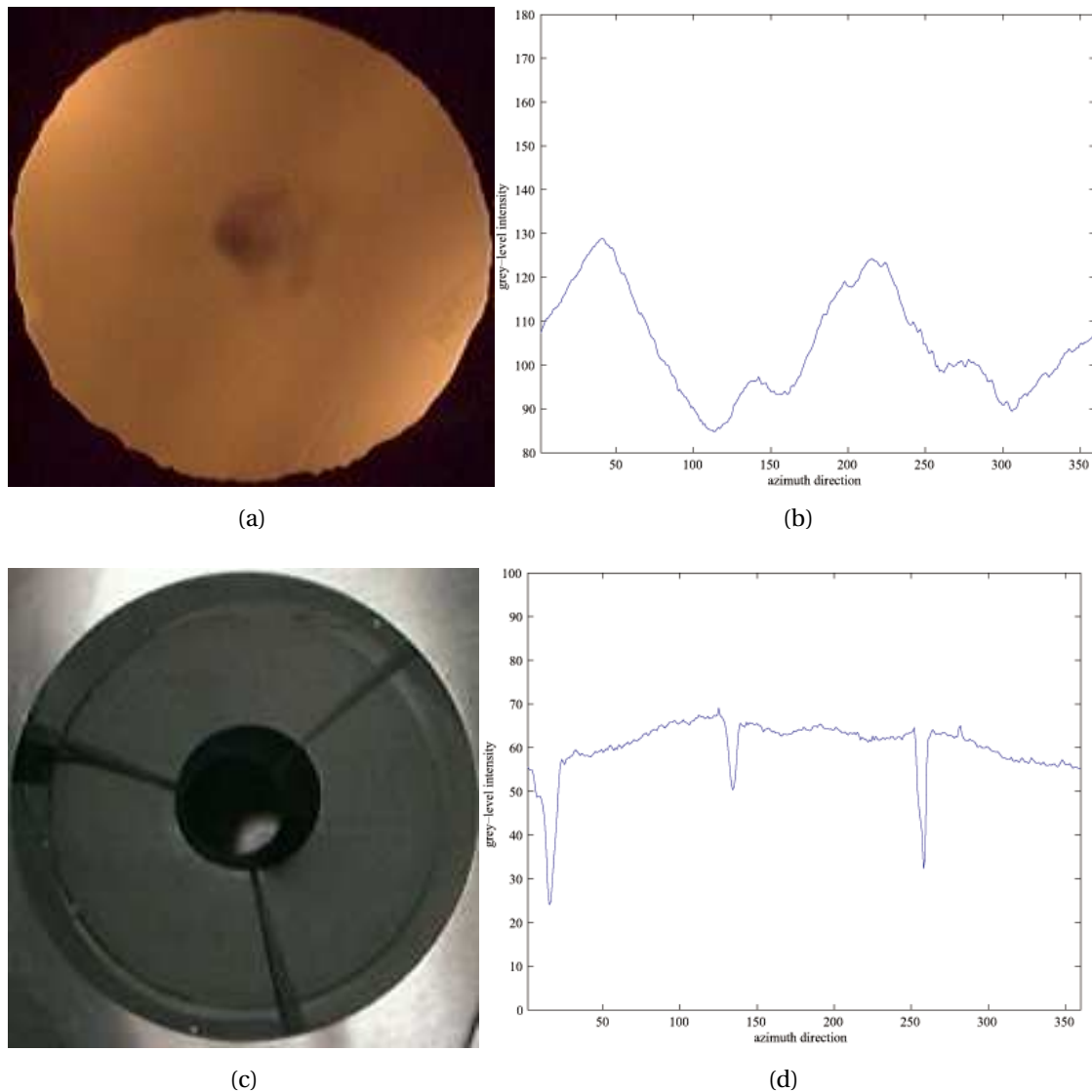


Figure 3.9: **Post Analysis of external visual cues.** (a) Image of the arena ceiling taken using a standard webcam from the centre of the arena floor. (b) Grey-scale intensity against azimuth is plotted depicting the rotational intensity gradient present in the arena canopy. (c) Image of the blank arena wall taken using a panoramic camera. The field of view of the includes the the entire 360° azimuthal range and extends in elevation to just below the arena wall top. (d) Grey-scale intensity against azimuth is showing a single peaked intensity grain intensity are caused by the camera mounts.

- *If so, is performance better when supplied with distinct visual cues or a more cluttered visual panorama?*

Within the smaller (30cm diameter) arena the performance of cricket in the various test conditions could not be distinguished. However, by increasing the arena diameter to 40cm the ratio of arena to cool spot area was doubled and the performance gap between conditions increased. Best performance was observed when a natural scene was supplied as visual stimulus followed by no cues and finally distinct landmarks. Analysis of the experimental paradigm revealed residual visual cues which may have been used by crickets in the no cues paradigm. This is indirectly supported by the fact that crickets trained in the "no cues" condition return to the original cool spot location after rotation of the arena wall. No improvement was observed when crickets were trained in the dark indicating that visual input was necessary for successful homing.

3.5 Discussion

The findings presented in this chapter clearly demonstrate that female crickets are able to relocate a target location using surrounding visual cues in an arbitrary task setting. This result corresponds to results reported in cockroaches assessed in a similar experimental paradigm (Mizunami et al., 1998b). Furthermore, in a recent study Ofstad et al. (2010) replicated the place learning findings reported here in the fruit fly *Drosophila melanogaster*. The particular experimental set-up used an array of LEDs to provide visual input and an adverse arena floor made up of heated tiles. Fruit flies learned to relocate the cool spot when both the target location itself and the corresponding visual cues were rotated in synchrony.

In the Mizunami et al. (1998b) study in cockroaches, they found that an ablation of the Mushroom Bodies neuropils significantly affects performance with the surrounding visual cues, but does not change performance when the target itself is visible. A large body of evidence supports a role for learning and memory of the Mushroom Bodies (e.g. summarized in Heisenberg (2003)). However, Ofstad et al. (2010) investigated the role of the Central Complex in homing using the *Drosophila* genetic toolkit and found that specific regions of the central complex were crucial to performance.

The Tennessee Williams paradigm may help in elucidating the strategies of the

visual homing behaviour of insects and in determining the involvement of the Mushroom Bodies and Central Complex in visual homing. This paradigm may allow for the unique possibility to investigate the neural basis of visual homing in insects by recording from neurons in freely moving animals (e.g. Mizunami et al. (1998a)).

Chapter 4

Modelling Visual Homing in the Field Cricket

Note that data presented in this chapter also appears in Mangan and Webb (2009).

4.1 Introduction

It has been shown that crickets can learn to return to a target location in experiments analogous to the Morris water-maze used to assess place memory in mammals (Morris et al., 1982). Insects are placed in a hostile environment (a hotplate maintained above 40°C) from which they would seek an escape. An invisible cool spot, maintained at a moderate temperature represented the only refuge. Over successive trials the time taken by the insects to re-locate the cool spot decreased significantly. Removal of all visual cues (trials performed in the dark) resulted in no improvement in re-location times, and the search is affected by rotation of the visual surroundings.

If insects are using a feature-based technique to return to locations of importance then it might be expected that performance would be best when distinct landmarks, easily segmented from the background, are presented. In contrast, a view-based algorithm will perform more successfully when a complex scene is presented, as it uses information from each pixel directly. In the hotplate experiments described in chapter 3, crickets were tested with both distinct landmarks and a natural scene stimulus. Learning was observed in both cases but the natural scene elicited greater improvement in homing times and more consistent learning. Figure 4.1 shows box plots of time taken to locate the cool spot by crickets during the final

four out of ten learning trials, when their homing times had stabilised. It is clear that crickets locate the cool spot fastest in the Natural Scene surround followed by Blank Walls (previously described as "no cues"), Distinct Landmarks and then the Dark Control. Statistical comparisons (Table 4.1) show that the Natural Scene surround elicits significantly better results than all other paradigms, and performance in the Dark Control is significantly worse than all conditions providing any visual stimulus.

Surprisingly, results in the Blank Walls surround and Distinct Landmarks are not significantly different, but as discussed previously (see section 3.3.3) the Blank Walls environment did not eliminate all visual cues, as a combination of shadows in the canopy and light gradients across the arena wall remained. It may also be noted that as the Natural Scene was provided by a poster wrapped around the arena wall, no natural depth information is provided. Observations from other insects would suggest that homing might be even better with a truly 3-D environment. However, the poster offers a much more natural stimulus than the classic landmarks as it contains many spatial frequencies, contrasts, and contours.

The data presented in the cricket behavioural study offers an unprecedented opportunity for model validation. To the best of the authors knowledge the ALV and IDF models are the only schemes included in this work to have been tested in a similar task setting to homing insects. An equilant ALV model was shown to successfully return to a snapshot taken at the centre of an array of large, black and therefore easily identifiable landmarks (Lambrinos et al., 2000). Unfortunately the authors did not present data after landmark manipulations. The IDF model has recently been shown to account for the homing errors observed in ants when released at the centre of an angular arena (Stürzl et al., 2008). All models presented have been shown to successfully home in office surroundings, or natural habitats, and in some cases even continue to perform well under dynamic changes in lighting and scenery. However, in such cases there is no direct comparison to insect performance and thus models cannot be validated as possible strategies employed by the animals.

In this chapter all biologically plausible models outlined in section 2.3.1, and therefore both view-based and feature-based model types, are implemented and tested in the same visual environments that were presented to the crickets. Thus the specific research question investigated in this chapter can be summarised as the following:

- *Can any of the biologically plausible models of insect visual homing proposed to date (including both view-based and feature-based model types) reproduce the pattern of performance shown in figure 4.1 and table 4.1 when tested in the same suite of visual conditions as the animal?*

4.2 Methodology

4.2.1 Image Databases

Three image databases were collected from within the cricket experimental arena on a 2cm*2cm grid using a Khepera II mobile robot mounted with a custom built wireless panoramic camera turret (see figure 4.2). Images were collected with the arena configured as for the cricket trials giving three sets of 208 images: Natural Scene (NS), Distinct Landmarks (DL), and Blank Walls (BW). All images were captured with the camera in the same orientation. Similar image databases have been used to model the homing behaviour of rats in a rectangular arena (Stürzl et al., 2008). It is worth noting that the Blank Walls database images are not uniform, as might be expected. Instead, imbalances in the arena lighting cause a clear intensity gradient to form on the arena walls culminating in a bright region (not visible the naked eye) located NNW of the cool spot position. This seems to have been sufficient for homing in the cricket, and as we shall demonstrate, also suffices for homing in some of the tested models.

4.2.2 Homing process

Visual homing models, as described in the literature, frequently differ not only in how the home vector is determined but also in how it is used to generate motion. Here consistency is maintained across the implementations so that only the relative efficacy of each model's method of determining the home direction will contribute to the results. A block diagram of the homing process for one time step is shown in figure 4.3.

Visual Input is received from the image database in the form of an unprocessed image (Figure 4.2 (c), (d), and (e)) as would be supplied by a robot positioned at the corresponding grid position. The Cricket Eye Model then unwraps and unwarps a ring corresponding to 20° above and below the image horizon. Note that as the

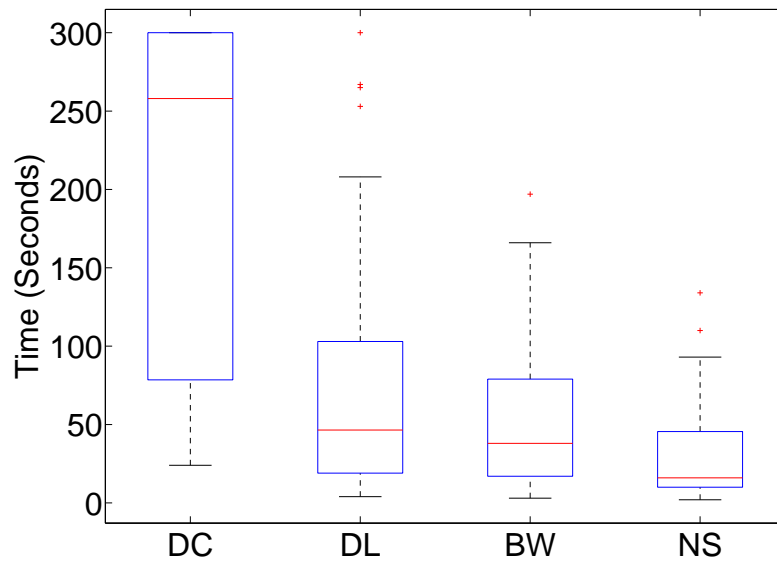


Figure 4.1: **Cricket homing times.** Box plots showing times taken to locate the cool spot for crickets across trials 7-10 (i.e. after learning) in the different visual surroundings ($n=12$). Boxes show lines at the lower quartile, median, and upper quartile values. Whiskers indicate the most extreme values within 1.5 times the interquartile range from the ends of the box. Outliers are shown as + signs. Testing within the Natural Scene (NS) produces fastest homing times, followed by Blank Walls (BW), Distinct Landmarks (DL) and the Dark Control (DC) respectively.

	NS	BW	DL	DC
NS	X	<0.01	<0.01	<0.01
BW	<0.01	X	0.54	<0.01
DL	<0.01	0.54	X	<0.01
DC	<0.01	<0.01	<0.01	X

Table 4.1: **Cricket homing times statistical analysis.** P-values calculated using Wilcoxon rank-sum test when comparing homing times across trials 7 - 10 within the four experimental paradigms.

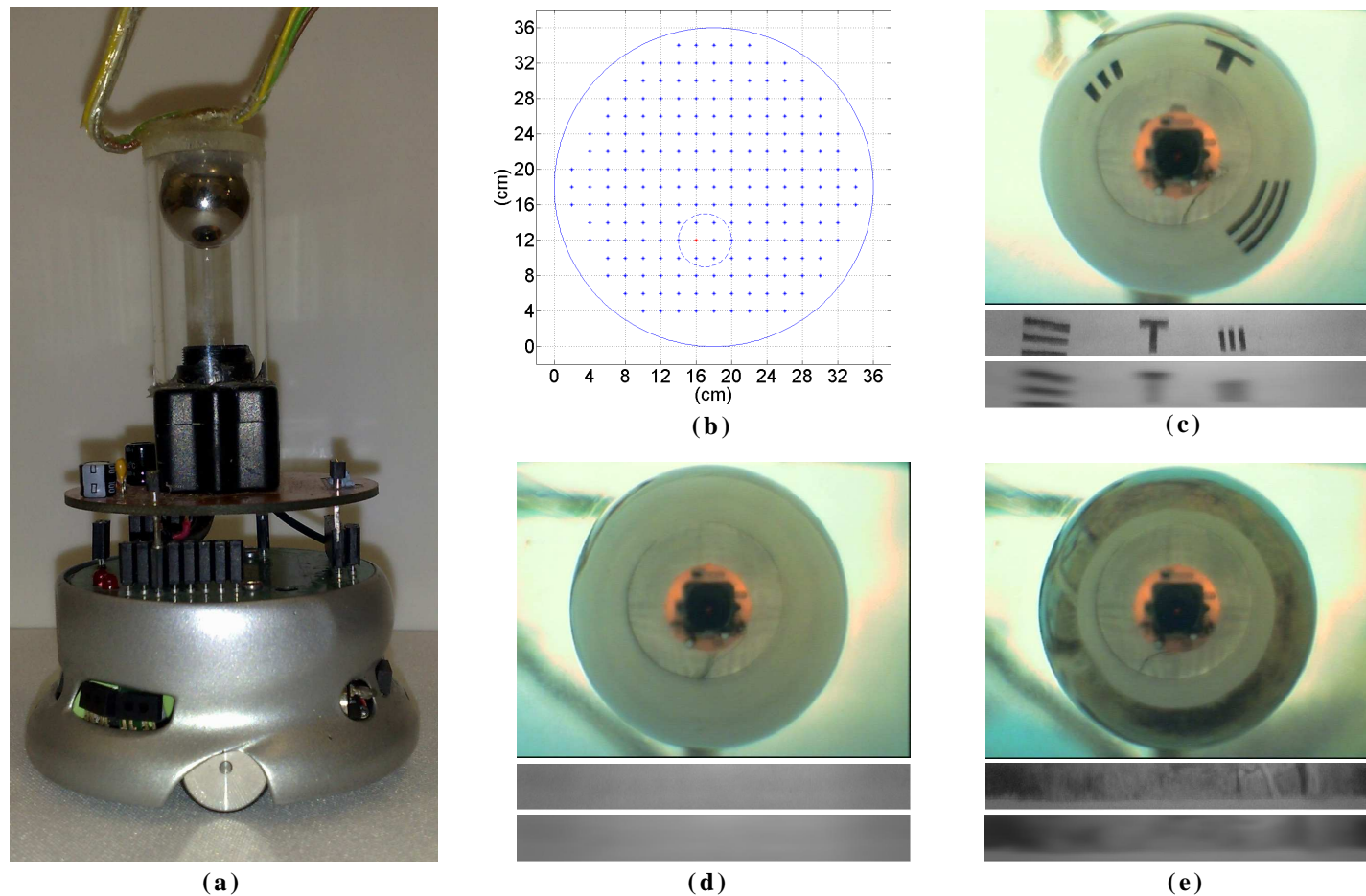


Figure 4.2: **Image databases used to simulate insect movement.** (a) Khepera II robot base with custom wireless panoramic camera turret used to record image database. (b) Cricket arena diagram showing 2cm*2cm grid where images were sampled. The cool spot perimeter is shown by the inner circle and the home position used in the modelling study is located at grid location (16,12). (c), (d) and (e) Sample images from the DL, BW, and NS image-sets respectively at the home location. Below is shown the images' unwrapped at 1° resolution to the maximum image size of $\pm 20^\circ$ around the horizon prior to smoothing, and also the same sample images post smoothing.

camera turret is mounted above the robot base unit and with the mirror located above the camera to prevent image interference from cables, the image horizon is approximately 10cm above the arena floor. Images are initially unwrapped at 1° resolution in both azimuth and elevation. A precise estimate for the visual acuity of the ventral areas of the cricket species *Gryllus bimaculatus* eye could not be found, but interommitidial angles of 1° have been observed in the dorsal rim area (Labhart et al., 2001). Note that the models are also tested with lower resolutions (see Section 4.2.5). Images are then blurred using a first order Butterworth filter where the cut-off frequency is defined using the acceptance angle of 6° as observed in *Gryllus campestris* (Labhart et al., 1984). The Cricket Eye Model images sampled at the home positions within each of the test environments are shown in figure 4.2 under the corresponding original images.

Grid position 16,12 was chosen as the home location and images taken at this location in the various environments act as the reference images during homing. The specific Homing Model under test is then used to calculate the home vector at the current location. The Motor Output then selects the cardinal direction most closely matching the home vector and updates the agent position to the nearest grid location in the defined direction. As described below, different levels of noise can be added to the home vector direction after it has been calculated and before the movement is determined. A similar motor output routine has been used to simulate the paths of homing rats in a virtual image database (Cheung et al., 2008). Note however that the Run Down model (section 4.3.4.2) is an exception as it does not calculate an explicit home vector but instead moves first and then evaluates, on the basis of image difference, whether to continue in the same direction or randomly try a new direction. If the agent attempts to move to a location outwith the image-database (equivalent to the cricket encountering the arena wall) then the agent is forced to move to the closest available location to the right. This procedure keeps the agent within the image-database and simulates a simple wall following response when the wall is encountered.

The process described above iterates until either the home location is found or the path-length exceeds 300 steps. This stop condition was selected as cricket trials were ended after 300 seconds if the cool spot had not been located. The ability of the homing models to replicate the cricket behaviour is assessed by recording the homing path lengths produced within each of the three environments. We then compare directly the path lengths produced by each model with the homing times

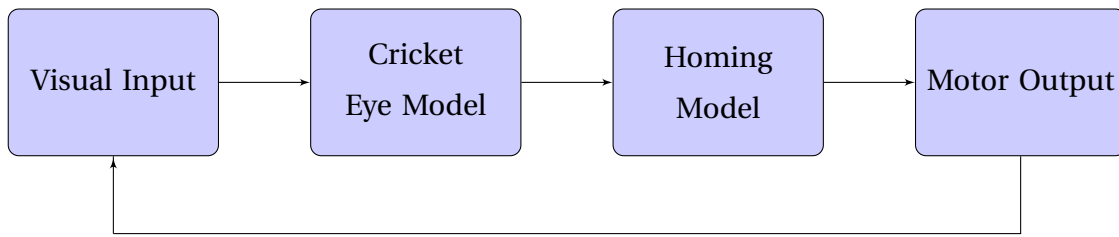


Figure 4.3: **Homing Procedure used for all modelling trials.** Visual input for the current location is passed through an eye model defined for the cricket as shown previously. The model in use then compares this current world view with the snapshot image and generates a home vector. The model then moves to the grid location closest to the home vector. All processing steps are kept consistent throughout except the method used to determine the homing direction.

of crickets in the same environments. Homing trials are initiated from the same 48 positions (and where appropriate, orientations) from which cricket trials were initiated. It should be noted that as cricket start locations were chosen at random in the behavioural study this leads to somewhat different start positions and orientations within each environment. The start locations and orientations used within each environment are shown in figure 4.4. We also calculate the home vector from every grid position so as to visualise the overall effectiveness of the homing method. Home vector plots are shown with the average angular error (AAE) which is calculated by taking the mean error between home vector calculated at each location and the known ideal home vector and provides a simple measure of model accuracy.

4.2.3 Control trials

In the original experiments a completely dark arena acted as the control. This would produce a uniformly black image set, making any visual homing process ineffective. To generate comparable control data for the simulation, random search paths were generated from the same 48 start positions as crickets tested in the Dark Control (see figure 4.4). At each time step the agent moves randomly in one of the four possible directions with equal probability, until either the home is encountered or the path-length exceeds 300 steps. This process produces path lengths with comparable median (289) and upper and lower quartiles (300 and 125) as the observed path durations of crickets in the dark (median 258, quartiles 300 and 79).

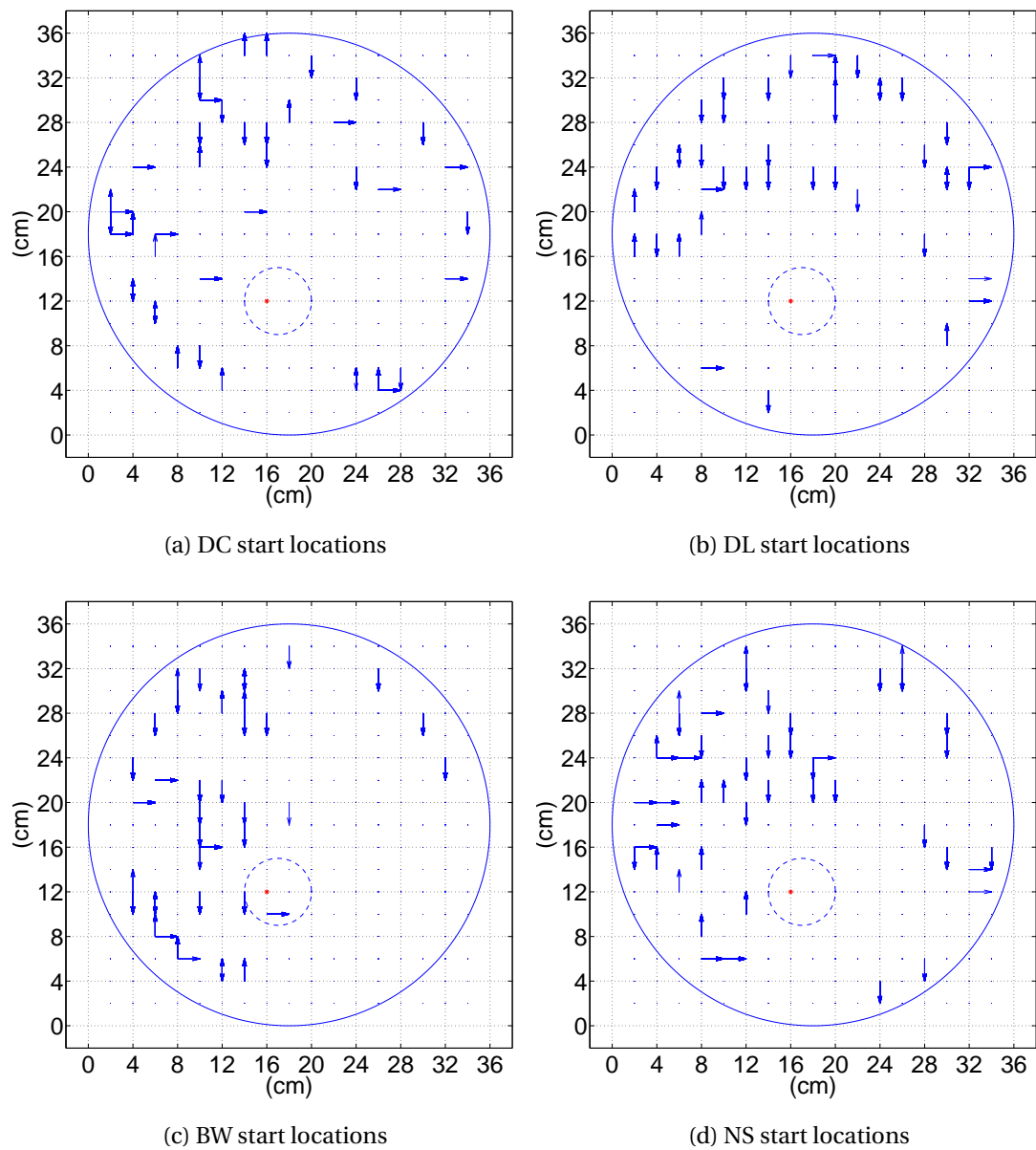


Figure 4.4: **Start positions from which crickets and model trials are initiated.** The start positions and approximate heading direction of the crickets as in the final four trials are shown by the blue arrows. This gives 48 start positions and orientations for each test environment from which trials are also initiated in all subsequent model testing.

4.2.4 Models of Visual Homing

As the explicit aim of this study is to investigate the strategies employed by crickets when returning to the cool spot, only visual homing models that can be considered “biologically plausible” are implemented. A criterion for the selection of such models was outlined by Vardy (2005): as was outlined in section 2.3.1. Applying the above criterion, the following six models were selected for use in this study:

1. Average Landmark Vector Model.
2. Centre-of-Mass Average Landmark Vector Model.
3. Differential Optic Flow Models:
 - (a) First Order
 - (b) Second Order
4. Image Difference Function Models using:
 - (a) GradDescent
 - (b) RunDown

It should be noted that the Average Landmark Vector Model is the only feature-based model to adhere to the biological plausibility constraints. All other models are view-based. For each model the results for the optimised model after parameter tuning are presented followed by a brief discussion of why the homing behaviour succeeds or fails in the different environments.

4.2.5 Parameter Tuning

In their original forms, the different visual homing models implemented in this study utilise various further pre-processing steps such as image smoothing, or using only a certain area of the image, to improve performance. Rather than make any assumptions about such image processing in crickets, which might bias the results towards one or other homing model, an optimisation procedure is used to tune the pre-processing parameters individually for each model. That is, optimisation is done by exhaustively searching through all possible parameter combinations and determining which parameters (if any) produce the same performance trend across the different visual environments as we observed for the crickets. Parameters are optimised according to two successive criteria:

1. Median path-lengths in all visual environments must statistically outperform the Dark Control.
2. Median path-lengths in the Natural Scene environment must statistically outperform homing within both the Distinct Landmarks and Blank Walls environments.

Statistical comparison of the homing performance is performed using the Wilcoxon rank-sum test. For each model, the outcome from the parameter setting that produces the closest match of medians and interquartile differences to the cricket data will be presented in the results, and the pattern of parameter settings that pass or fail the criteria discussed.

This search through parameter space also allows an analysis of the relative robustness of the the different models. More specifically the effect on performance of changing the various parameters is assessed for all models. The free parameters optimised by the models are:

Image Smoothing: In many studies, visual homing is performed on images that have been highly low-pass filtered; a processing step easily performed in neural hardware. Vardy (2005) outlines a Gaussian low-pass filtering scheme where images are convolved with the kernel:

$$G = [0.005 \quad 0.061 \quad 0.242 \quad 0.383 \quad 0.242 \quad 0.061 \quad 0.005] \quad (4.1)$$

in the x and then the y direction. It is shown that successive applications of this filter is comparable to convolving with a single larger Gaussian. Thus smoothing the cricket eye images using Gaussians of various sizes is achieved by optimising for 0, 1, 3 or 5 applications of this Gaussian Filter.

Down-sampling rate: As the cricket eye model unwraps the raw image at a resolution of 1° , down-sampling can be thought of as resetting the visual acuity to 1° , 2° , or 4° . This is achieved by sampling every 1, 2 or 4 pixels both horizontally and vertically from those images supplied by the cricket eye model. It is worth noting that these values are closely matched to the visual acuity of *Gryllus campestris* (1°), the honeybee eye *Apis meliphora* (1.7°), and desert ant *Cataglyphis bicolor* (4°) (Land, 1997). Although it should also be noted that

the acceptance angle of the honeybee and ant eye are 2.6° and 3° degrees respectively compared with the cricket eye acceptance angle of 6° which would result in less initial smoothing.

Image area used: Each model also optimises for the portion of the input image used to calculate the home vector. The input image from the Cricket Eye Model consists of $\pm 20^\circ$ of elevation around the horizon sampled at 1° azimuth giving a maximum image size of 360×41 pixels. Each model then selects whether to use:

1. 10° above the horizon.
2. 10° below the horizon.
3. Horizon pixels only
4. $\pm 5^\circ$ around the horizon.
5. $\pm 10^\circ$ around the horizon.
6. $\pm 20^\circ$ around the horizon.

Note the optic flow models cannot use the horizon pixels only as this does not allow vertical image gradients to be calculated.

Addition of noise to home vectors: The addition of noise to the homing signal aids certain models that otherwise become trapped in deterministic loops in the grid leading to high failure rates despite good general approximation of the home direction. At each homing iteration, noise is generated through the addition of an offset to the derived home vector. The offset is randomly selected from a circular normal distribution with a mean of zero and variable standard deviation. Models optimise for the noise standard deviation (noise SD) which ranges from 0 (no noise) to 90° in increments of 10° . The maximum noise SD setting of 90° results in a 62% chance that additional noise corrupts the home vector by more than 90° , resulting in movement in a random orientation with respect to the generated home vector.

Image Type: Some models can operate with black and white, rather than greyscale, images. The COMALV and IDF models are optimised for either image type, where black and white images are generated by thresholding the output of

	DC	DL	BW	NS
DC	X	<0.01	0.12	<0.01
DL	<0.01	X	<0.01	<0.01
BW	0.12	<0.01	X	<0.01
NS	<0.01	<0.01	<0.01	X

Table 4.2: **ALV statistical analysis.** P-values calculated for comparisons between path-lengths in the various image databases using the ALV model. Note the significant difference of NS and control is in the wrong direction (NS worse than control).

the cricket eye model at the median greyscale value. The ALV model inherently converts images to black and white to define landmarks and thus only optimises for greyscale images. The differential optic flow models can only operate on greyscale images.

4.3 Results

4.3.1 Average Landmark Vector Model

Figure 4.5 shows the homing path lengths produced by the ALV model in the various image databases, and the home vectors generated in each environment. Table 4.2 shows the p-values of the statistical comparisons of homing path lengths.

It is clear that the ALV Model does not reproduce the same performance trend as observed in crickets. Indeed no parameter setting produced shorter path lengths in all visual environments when compared to the control; the first performance criterion. This failure is caused by inaccurate home vector generation within the Natural Scene due to the difficulty in consistently defining edges within such an environment. It should be noted that the simple edge detection techniques employed by Lambrinos et al. (2000) were found inadequate for homing within the cricket surrounds, specifically within the Natural Scene. Therefore, the more robust edge detection procedure implemented by Möller et al. (2001) to achieve successful homing in the university lobby was adopted but resulted in similar failures. The slightly improved path lengths produced within Blank Walls are attributable to the background intensity gradient outlined previously which the ALV Model defines as a single landmark that is generally detected across arena positions allowing some-

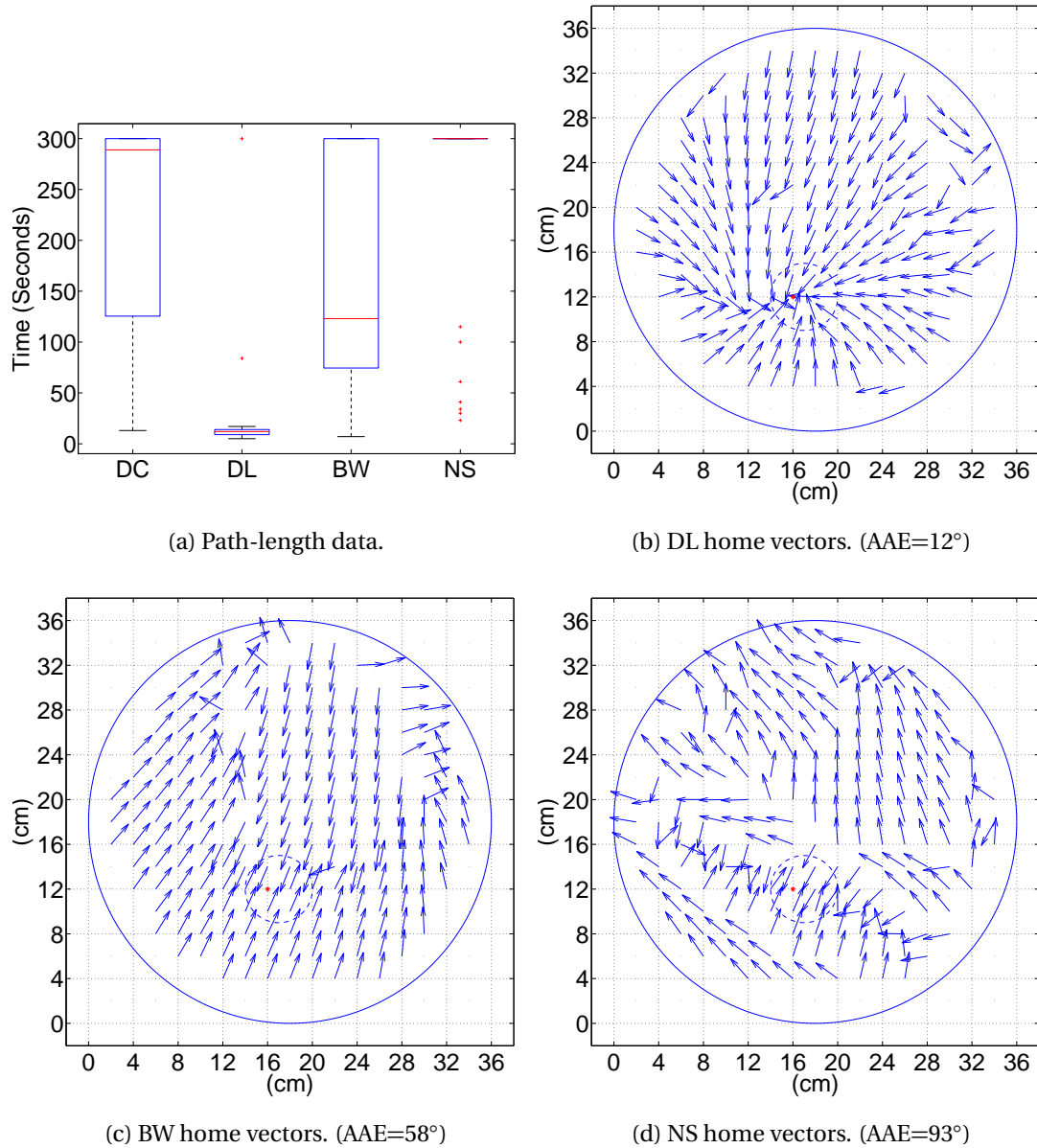


Figure 4.5: **ALV model results.** (a) ALV Model path lengths within the three image databases and control condition. Optimal parameter settings: downsampling rate = 1, No. of Gaussians=1, image region used = horizon pixels only, and noise SD=10° using greyscale images. Boxes show lines at the lower quartile, median, and upper quartile values. Whiskers indicate the most extreme values within 1.5 times the interquartile range from the ends of the box. Outliers are shown as + signs. (b), (c), (d) Home vectors generated using the optimal parameter settings in the DL, BW and NS surrounds respectively. Note that the single bar at 300 for the NS results indicates that all homing trials save outliers reached the stop condition.

	Edges identified in home image	Mean edges identified across image locations	Variance in edges identified across image locations
DL	6	5.9320	0.8897
BW	2	1.9612	0.3922
NS	4	4.4951	1.8401

Table 4.3: **Edge detection robustness of the ALV model.** Comparison of the number of edges identified in the home image compared to the mean and standard deviation found at all subsequent image positions in each environment.

what accurate home vector generation. In contrast, within the distinct landmarks surround, where edges are easily identified, home vectors are accurate from most regions of the arena, resulting in short path lengths.

Table 4.3 shows the mean number of edges detected across image positions within each of the image databases compared with the number of edges found in the home image of those image-sets. Within the Natural Scene the high degree of variance in detected edges catastrophically affects correct home-vector calculation. Despite a higher degree of edge detection accuracy within Blank Walls, the small number of detectable edges also results in inaccurate home vector calculation when edges are incorrectly defined. Furthermore, the reduced intensity range within Blank Walls images renders the model susceptible to noise and makes accurate ALV computation difficult resulting in a high Average Angular Error. In contrast, within Distinct Landmarks six edges are detected in the home image. The larger number of distinguished edges in this environment increases the robustness of the ALV when edges are incorrectly identified, or missed, resulting in the improved performance displayed. It may be possible to improve the performance of the ALV Model in the Natural Scene using a more sophisticated feature extraction algorithm. However as homing is close to optimal in Distinct Landmarks it seems unlikely that any such enhancement would produce statistically superior homing in the Natural Scene surround, as is observed in crickets.

4.3.2 Centre-of-Mass Average Landmark Vector Model

Figure 4.6 shows the homing path lengths produced by the COMALV model in the various image databases, and the home vectors generated in each environment. Ta-

	DC	DL	BW	NS
DC	X	<0.01	<0.01	<0.01
DL	<0.01	X	0.28	<0.01
BW	<0.01	0.28	X	0.01
NS	<0.01	<0.01	0.01	X

Table 4.4: **COMALV statistical analysis.** P-values calculated for comparisons between path-lengths in the various image databases using the COMALV model.

ble 4.4 shows the p-values of the statistical comparisons of homing path lengths.

Parameter optimisation of the COMALV model found 80 parameter combinations that pass both performance criteria and thus match the performance trend of the cricket data. These settings include every possible smoothing and acuity variant at least once indicating a robustness to these pre-processing procedures. In contrast, the only successful image region is $\pm 20^\circ$ around the horizon, and the image type is restricted to black and white images. All parameter settings require some level of noise for successful homing.

The selection of only the maximum image region setting is due the interaction of the landmarks and the background intensity gradient within the Distinct Landmarks surround. COMALVs obtained within both Blank Walls and Natural Scene generally orient towards an attractor in the environment when sampled across image locations. For example within Blank Walls, COMALVs are oriented towards the peak of the background intensity gradient outlined previously. An attractor is necessary such that when the home COMALV is subtracted from the current COMALV an appropriate angular offset is present resulting in correct home vector computation. However within Distinct Landmarks, for smaller image region settings, no such attractor exists as the T shaped landmark and background intensity peak coincide. This flattens the intensity gradient and removes the presence of a prominent COMALV. However, when $\pm 20^\circ$ images are presented, the proportion of blank arena wall to landmarks is increased, introducing a prominent attractor to which COMALVs orient and resulting in the improved homing observed.

It was found that the use of greyscale images had a catastrophic effect in the Blank Walls environment. This failure is caused by a subset of home vectors located near the home position which are inverted with respect to the true home direction across many parameter settings. Thus agents homing from certain arena

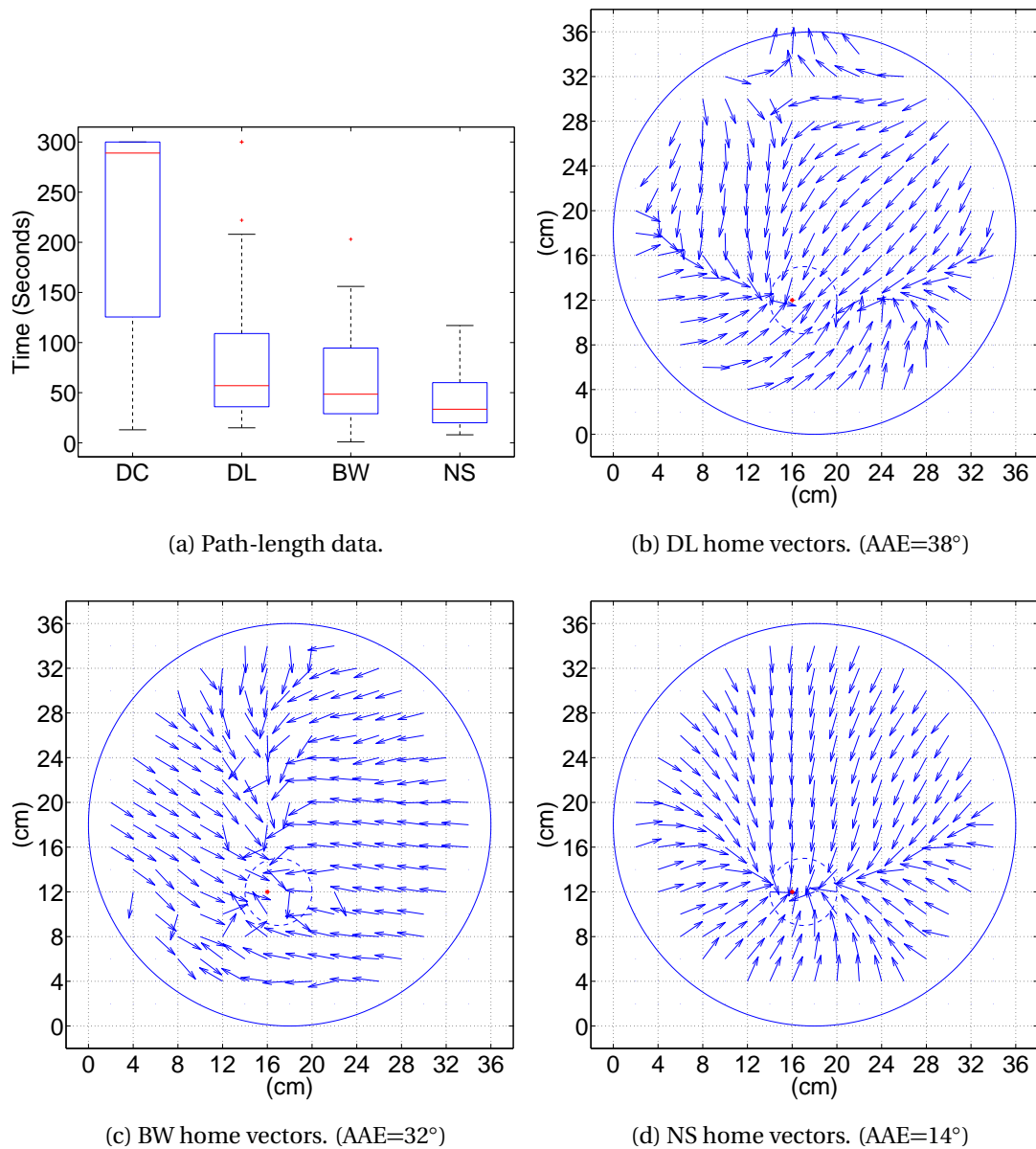


Figure 4.6: **COMALV model results.** (a) COMALV Model path lengths within the three image databases and control condition. Optimal parameter settings: downsampling rate = 2, No. of Gaussians=0, image region used = $\pm 20^\circ$ around the horizon, noise SD=80°, using black and white images. Boxes show lines at the lower quartile, median, and upper quartile values. Whiskers indicate the most extreme values within 1.5 times the interquartile range from the ends of the box. Outliers are shown as + signs. (b), (c), (d) Home vectors generated using the optimal parameter settings in the DL, BW and NS surrounds respectively.

areas would be deflected from the home position. The incorrect home vector direction was a result of the magnitude of the current COMALVs at these locations exceeding that of home COMALV; often only by a small amount but this is sufficient to produce a small but incorrectly oriented home vector. This problem is partially circumvented when sufficient noise is added such that agents near the home would sometimes reach it instead of being deflected. However the addition of such high noise levels degraded performance in the Distinct Landmarks surround to chance levels. No parameter combination using greyscale images could be found where path lengths within both Distinct Landmarks and Blank Walls are statistically superior to the control.

The impact of these anomalous home vectors within the Blank Walls surround is probably magnified by the use of an image-database rather than a fully autonomous robot study where images would be generated repeatedly across trials. There are also a number of simple modifications to the COMALV Model that may help overcome such deficiencies such as defining a minimum threshold between magnitudes that should be reached before home vectors are computed, weighing trust in home vector relative to magnitude, image normalisation prior to COMALV calculation, or the use of a momentum component that would push agents past erroneous home vectors. However none of these model extensions were implemented in this study, given that the use of blank and white images was sufficient to produce cricket-like results.

4.3.3 Differential Optic Flow Models

4.3.3.1 First Order Differential Model

Figure 4.7 shows the homing path lengths produced by the FO model in the various image databases, and the home vectors generated in each environment. Table 4.5 shows the p-values of the statistical comparisons of homing path lengths.

Parameter optimisation of the FO Model found no parameter settings that passed the first performance criterion where improved path-lengths are sought in all visual environments when compared with the control. Despite performing excellently within both Natural Scene and Distinct Landmarks, the FO Model fails to generate accurate home vectors within Blank Walls, where it never outperforms the control. This is because the lack of significant intensity variations within the Blank Walls environment does not allow a sufficient number of correct pixel-wise home-vectors

	DC	DL	BW	NS
DC	X	<0.01	<0.01	<0.01
DL	<0.01	X	<0.01	<0.01
BW	<0.01	<0.01	X	<0.01
NS	<0.01	<0.01	<0.01	X

Table 4.5: **First Order Differential model statistical analysis.** P-values calculated for comparisons between path-lengths in the various image databases using the FO model. Note the significant difference of BW and control is in the wrong direction (BW worse than control).

to be calculated such that when pixel-wise home vectors are averaged, the correct home vector prevails.

4.3.3.2 Second Order Differential Model

Figure 4.8 shows the homing path lengths produced by the SO model in the various image databases, and the home vectors generated in each environment. Table 4.6 shows the p-values of the statistical comparisons of homing paths.

Parameter tuning of the SO Model found five parameter settings that passed both performance criteria. These are comprised of two distinct settings buoyed by the addition of large noise terms. The first setting applies one Gaussian filter, to maximally sampled $\pm 20^\circ$ images with noise SD= 70° , 80° , and 90° . The second setting applies no smoothing to $\pm 20^\circ$ images downsampled at 2° with noise SD= 70° and 80° . The SO Model was tuned for only greyscale image type as explained in the methods.

As with the FO Model, homing within Blank Walls rarely outperforms the control when using the SO Model. This is again due to the absence of robust intensity gradients required by differential optic flow models to accurately compute home vectors. The increased accuracy of the home vectors generated by the SO Model within Blank Walls may have been expected as some image gradients are likely to be maintained even where individual pixel intensities are not. The use of minimal levels of downsampling and image smoothing increases the robustness of such gradients where they exist. Moreover, the use of the largest image region increases the influence of correct and correlated home vectors where they can be generated. How-

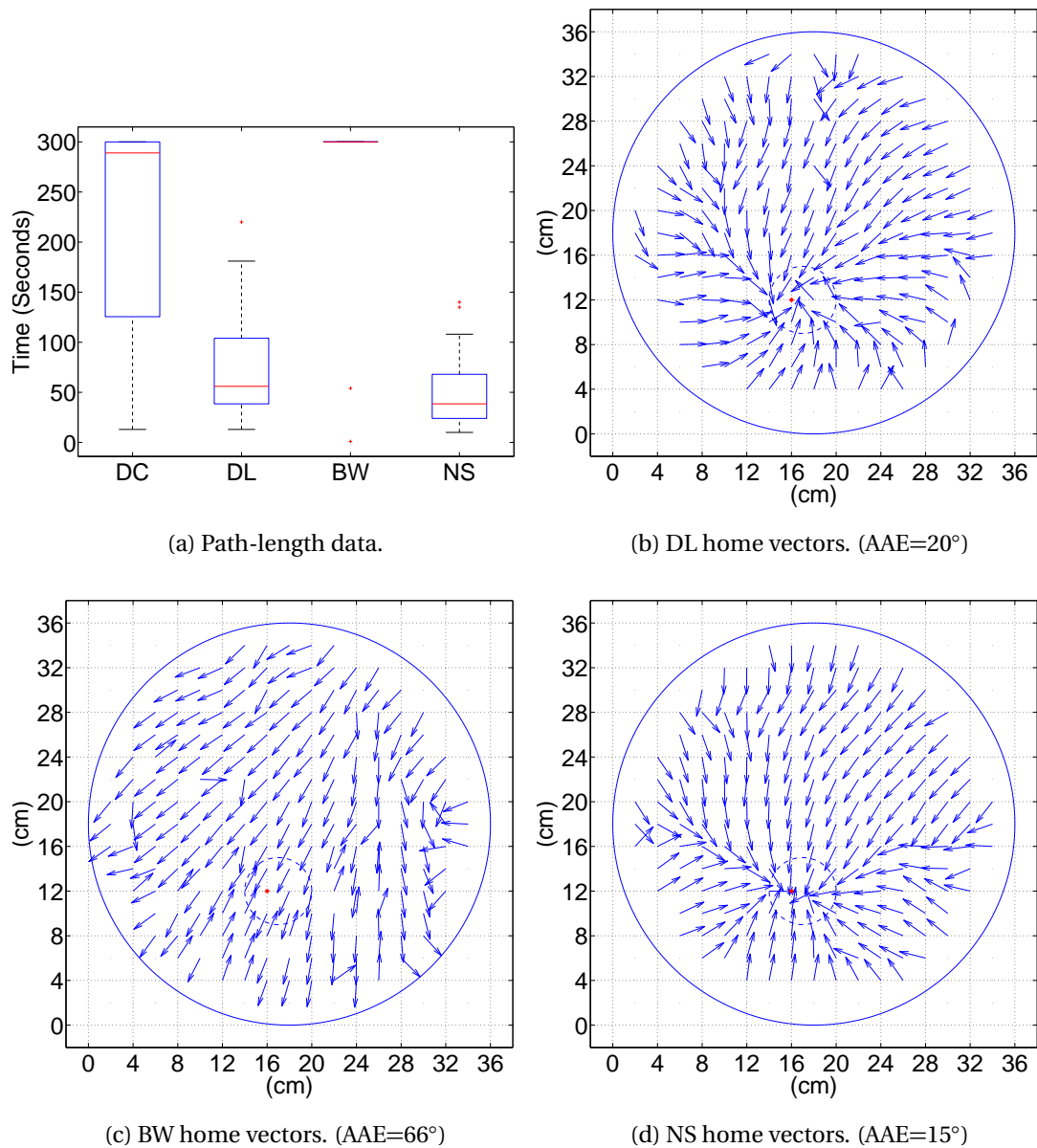


Figure 4.7: First Order Differential model results. (a) FO Model path lengths within the three image databases and control condition. Optimal parameter settings: downsampling rate = 2, No. of Gaussians=1, image region used = $\pm 10^\circ$ around the horizon, and noise SD= 90° using greyscale images. Boxes show lines at the lower quartile, median, and upper quartile values. Whiskers indicate the most extreme values within 1.5 times the interquartile range from the ends of the box. Outliers are shown as + signs. (b), (c), (d) Home vectors generated using the optimal parameter settings in the DL, BW and NS surrounds respectively.

	DC	DL	BW	NS
DC	X	<0.01	0.01	<0.01
DL	<0.01	X	<0.01	<0.01
BW	0.01	<0.01	X	<0.01
NS	<0.01	<0.01	<0.01	X

Table 4.6: **Second Order Differential model statistical analysis.** P-values calculated for comparisons between path-lengths in the various image databases using the SO model.

ever, despite this improvement the resultant path-lengths still fail to out-perform the control without the addition of a substantial noise term.

4.3.4 Image Difference Function Models

Figure 4.9 shows the image difference functions calculated within the various image databases using the RMS metric. It is clear that image difference functions are present in the cricket arena visual conditions and the following sections present the performance of two gradient descent algorithms previously used to home on similar difference manifolds.

4.3.4.1 GradDescent Homing Method

Figure 4.10 shows the homing path lengths produced by the GradDescent algorithm in the various image-sets, and the home vectors generated in each environment. Table 4.7 shows the p-values of the statistical comparisons of homing paths.

Parameter tuning of the GradDescent method found six parameter settings that passed both performance criteria. The image region used is limited to $\pm 20^\circ$ around the horizon, and the downsampling rate to 2 or 4. However the model seems robust to smoothing with all settings except no smoothing being used. The image type used is fixed as black and white. All six parameter settings require a small amount of additive noise (max noise $SD=30^\circ$, $\mu=16.67^\circ$, $\sigma=8.16^\circ$ across the parameter set). When greyscale images are used homing paths within Blank Walls fail to statistically outperform the control. This failure is caused by the image difference function generated within Blank Walls (Figure 4.9(b)) which appears noisy and littered with local minima. The rugged nature of the image difference function is likely due to the high degree of similarity in the BW greyscale images coupled with some noise

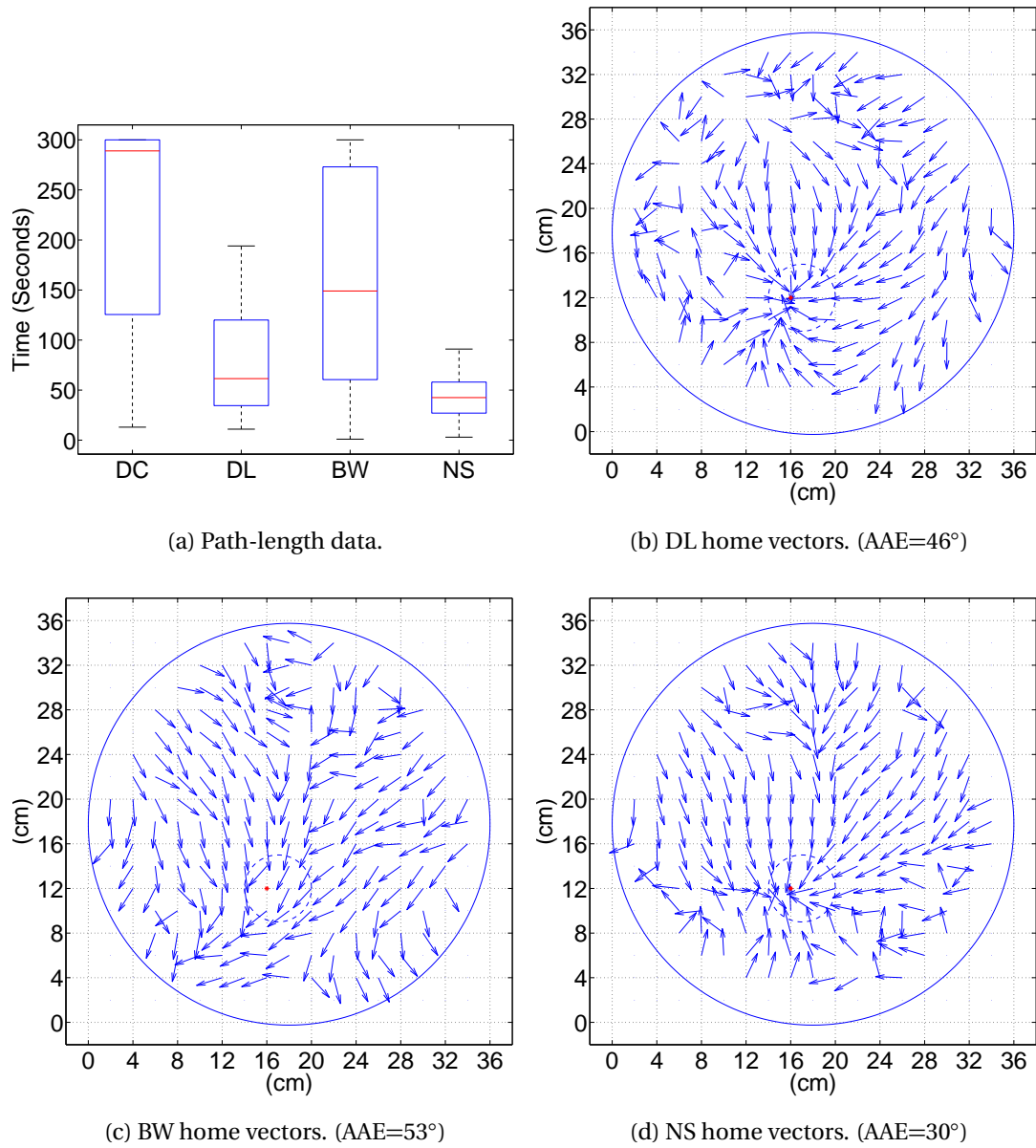


Figure 4.8: **Second Order Differential model results.** (a) SO Model path lengths within the three image databases and control condition. Optimal parameter settings: downsampling rate = 1, No. of Gaussians=1 and image region used = +/- 20° around the horizon, and noise SD=80° using greyscale images. Boxes show lines at the lower quartile, median, and upper quartile values. Whiskers indicate the most extreme values within 1.5 times the interquartile range from the ends of the box. Outliers are shown as + signs. (b), (c), (d) Home vectors generated using the optimal parameter settings in the DL, BW and NS surrounds respectively.

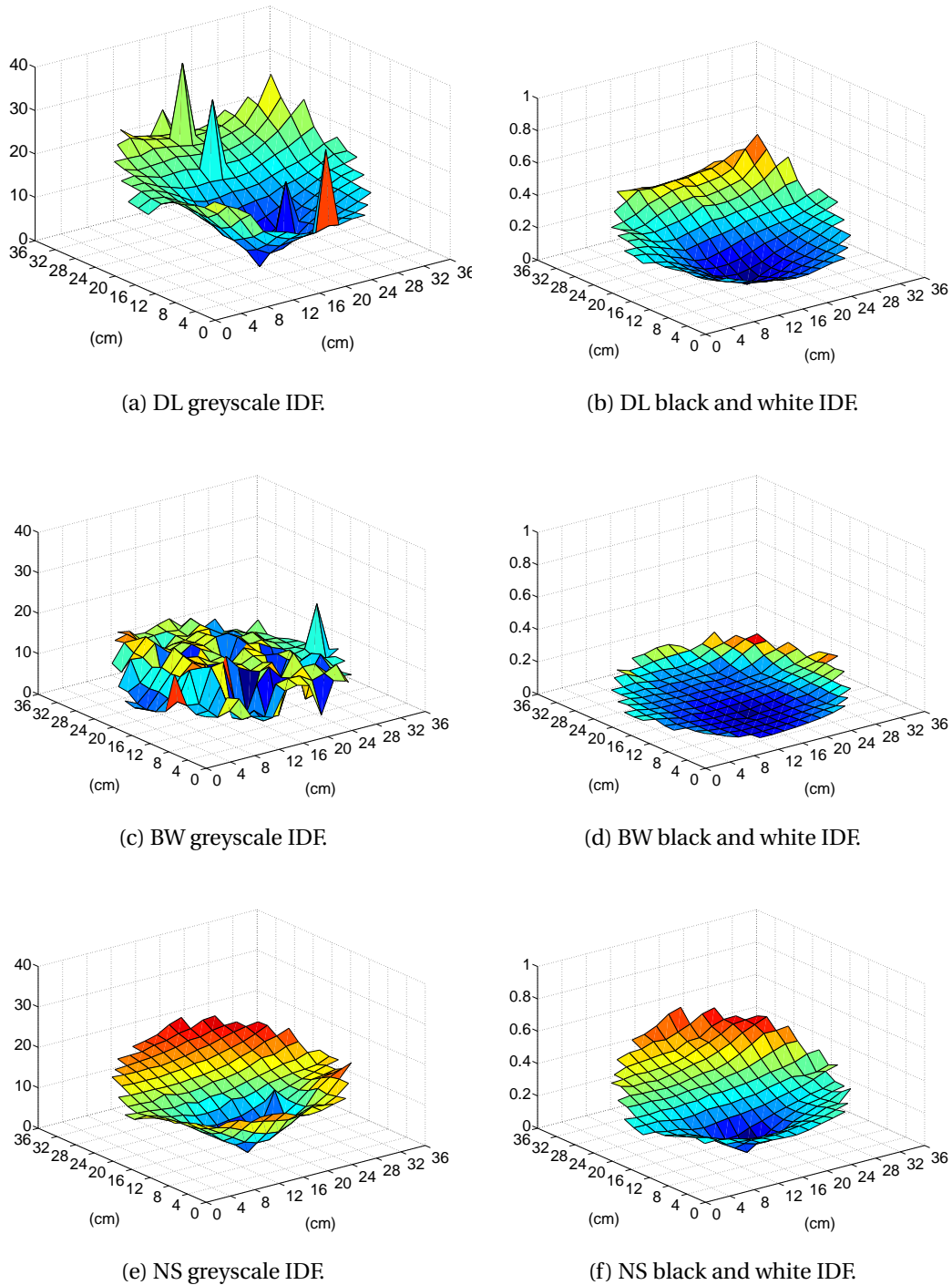


Figure 4.9: **RMS image difference functions (IDF) within the three image databases.** Note that the parameter settings are constant for both image types used: Number of Gaussians=0, downsampling rate=1, image regions= $\pm 20^\circ$ around the horizon. (a), (c) and (e) IDFs generated using greyscale images in the DL, BW and NS surrounds respectively. (b), (d) and (f) IDFs generated using black and white images in the DL, BW and NS surrounds respectively.

	DC	DL	BW	NS
DC	X	<0.01	<0.01	<0.01
DL	<0.01	X	0.3	<0.01
BW	<0.01	0.3	X	0.03
NS	<0.01	<0.01	0.03	X

Table 4.7: **GradDescent model statistical analysis.** P-values calculated for comparisons between path-lengths in the various image databases using the GradDescent model.

possibly introduced by the wireless camera. This makes successful and repeatable homing almost impossible using greyscale images regardless of other parameter settings. Conversion of the input images to black and white removes a dimensionality of the data producing smoothed image difference functions across image-sets, but with particularly profound effect on the Blank Walls image difference function (Figure 4.9(e)). The use of black and white images in preference to greyscale, improves homing across image-sets to the extent that statistically separating the performance between paths generated within the Natural Scene and those generated within the other surrounds becomes the main cause of model failure. The use of the largest image type in conjunction with downsampling increases the proportion of blank arena wall in comparison to landmarks and thus degrades the image difference function in Distinct Landmarks, without overly affecting the image difference function in Natural Scene. With the further addition of noise statistical separation can be achieved, at the expense of a much higher variance in the Distinct Landmarks paths than was found in the cricket data.

4.3.4.2 RunDown Homing Method

The path-lengths, and statistical comparisons for the RunDown algorithm are shown in figure 4.11 and table 4.8 respectively. Optimisation of parameters for the RunDown algorithm found six parameter settings successfully passing the performance criteria. The RunDown method seems robust to most parameter settings with all possible smoothing, downsampling and image regions (excluding horizon pixels only) being used. However, as with the GradDescent method, if greyscale images are used, path-lengths in Blank Walls are never significantly better than the control. With black and white images, many parameter settings pass the first criteria

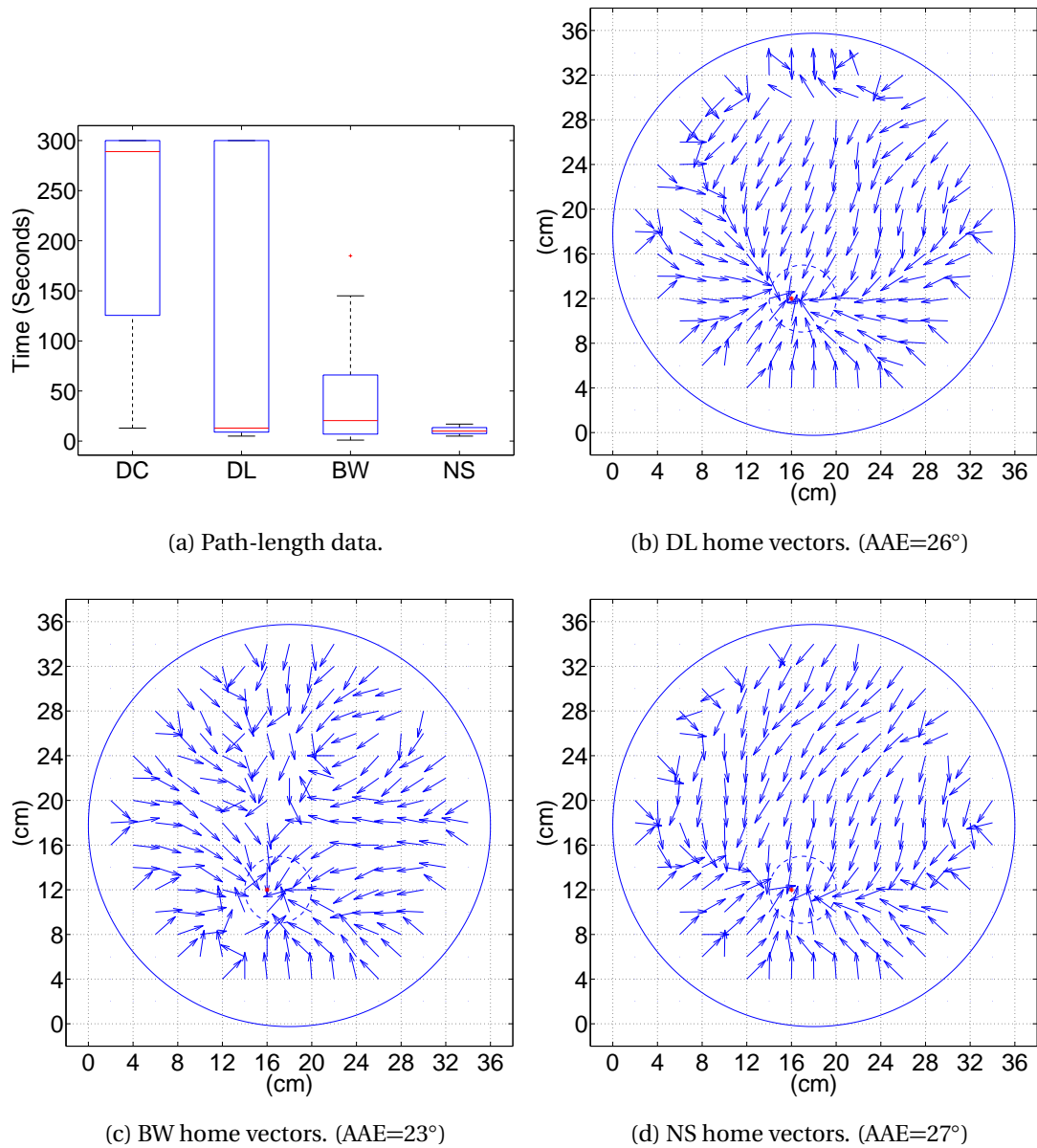


Figure 4.10: **GradDescent model results.** (a) Path lengths within the three image databases and control condition. Optimal parameter settings: acuity = 4° , No. of Gaussians=1, image region= $\pm 20^\circ$ around the horizon, noise SD= 10° and using black and white image type. Boxes show lines at the lower quartile, median, and upper quartile values. Whiskers indicate the most extreme values within 1.5 times the interquartile range from the ends of the box. Outliers are shown as + signs. (b), (c), (d) Home vectors generated using the optimal parameter settings in the DL, BW and NS surrounds respectively.

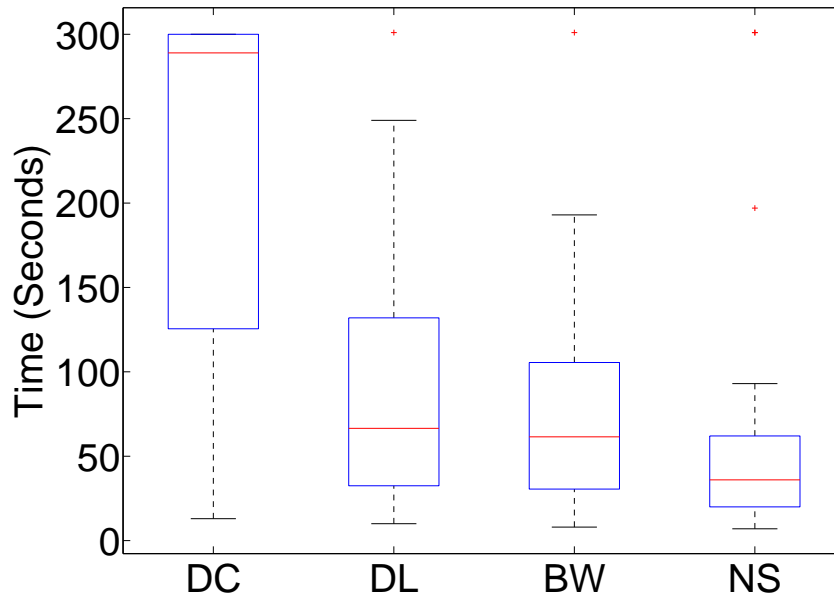


Figure 4.11: **RunDown results.** Box plots showing path-lengths obtained using the Run-Down model within the three image databases and control condition. Optimal parameter settings: downsampling rate = 1, No. of Gaussians=3 and image region used = $\pm 20^\circ$ around the horizon using black and white images. Boxes show lines at the lower quartile, median, and upper quartile values. Whiskers indicate the most extreme values within 1.5 times the interquartile range from the ends of the box. Outliers are shown as + signs.

of significantly shorter paths in all visual surrounds than the control, but although most combinations also show the trend of shorter paths for Natural Scene, this is not statistically significant except for the six settings mentioned.

4.4 Conclusions

Six biologically plausible models of visual homing have been implemented and tested using image data-sets taken directly from the visual environments in which cricket experiments were conducted. Each model was assessed for its ability to replicate the performance trends observed for crickets homing with different visual surrounds. That is: that homing was better with any visual surround than in the Dark Control and that homing was better with a Natural Scene than with Distinct Landmarks and Blank Walls. Homing paths were initiated from the same start-points, and where ap-

	DC	DL	BW	NS
DC	X	<0.01	<0.01	<0.01
DL	<0.01	X	0.02	<0.01
BW	<0.01	0.02	X	<0.01
NS	<0.01	<0.01	<0.01	X

Table 4.8: **RunDown model statistical analysis.** P-values calculated for comparisons between path-lengths in the various image databases using RunDown Model.

Homing model	Total parameter permutations tested	All visual surrounds outperform control	NS outperforms DL and BW
ALV	720	0	0
COMALV	1440	102	80
FO	600	0	0
SO	600	5	5
GradDescent	1440	426	6
RunDown	144	41	6

Table 4.9: **Summary of the model parameter tuning results.** The total parameter permutations are shown for each model. The values in the subsequent columns indicate the number of parameter permutations that successfully passed the performance indicated by the column title.

appropriate start directions, as the crickets. Additionally, across the model implementations, aspects of visual pre-processing and movement control were either held constant or optimised for each model by an exhaustive parameter search.

Table 4.9 summarises the results of the parameter search, indicating the number of possible parameter permutations (which, as explained in the methods, could vary for different models) and the number of permutations that met the performance criteria for each model.

It is therefore possible to answer the posed research question directly:

- *Can any of the biologically plausible models of insect visual homing proposed to date (including both view-based and feature-based model types) reproduce the pattern of performance shown in figure 4.1 and table 4.1 when tested in the same suite of visual conditions as the animal?*

The Average Landmark Vector and First Order Differential models were found to be incapable of reproducing the performance trends of crickets. The Average Landmark Vector model was unable to home in the Natural Scene, and always produced the best homing with Distinct Landmarks. Similar results might be expected for any feature-based homing algorithm that relies on reliable extraction of landmark features. The First Order Differential model in contrast homes well within both the Distinct Landmarks and Natural Scene but performance within the Blank Walls surround is statistically worse than the control condition. This can be explained by the fact that the useful homing information for this model is contained largely in the focus of expansion and contraction. In the Blank Walls environment, the foci generally coincide with regions of bare arena wall where intensity values are broadly similar and thus correspondences are difficult to accurately assess. The Average Landmark Vector and First Order Differential models are therefore dismissed as homing strategies employed by crickets.

The increased robustness of image gradients compared with absolute pixel intensities within the Blank Walls surround enabled the Second Order Differential Model to produce some parameter combinations that passed the performance criteria. However this is dependent on large levels of additive noise which are not only required to improve homing within Blank Walls but also to increase the performance gap between the Natural Scene and Distinct Landmarks. As a result, even with the optimal parameter settings, which minimised for both the difference in medians and inter-quartile range between cricket and model data, the median and variance generated within Blank Walls are substantially greater than the cricket homing times when tested in the same environment. Moreover unlike the cricket data, performance was significantly worse in Blank Walls than for Distinct Landmarks. Thus this algorithm does not match the cricket data as well as some others.

Gradient descent based models of visual homing were found capable of reproducing the performance trend of crickets. However the noisy image difference function produced within the Blank Walls surround when greyscale images were used prevented statistical improvement on the control condition. Through the use of black and white images rather than greyscale the image difference functions are smoothed such that homing is successful in all environments. Indeed this smoothing makes performance within Natural Scene and the other tests environments difficult to statistically separate. The GradDescent homing method successfully achieved statistical significance between Natural Scene and both Distinct Landmarks and

Blank Walls by downsampling the image at the maximum rate, which reduced the robustness of the image difference function within Distinct Landmarks, in combination with a small noise term. However, even with the optimal parameter choice, this produces much higher variance in path lengths in Distinct Landmarks than observed for crickets. Given that this method also requires the sampling of image differences in all cardinal directions before moving in the home direction, it seems less plausible than the simple RunDown method.

The RunDown method could successfully reproduce the right pattern of statistical differences across the visual environments and also provided a reasonable match to the observed median and spread in the cricket data. The COMALV Model also accurately reproduced the performance of crickets. The performance criterion was reached for 6 out of 144 possible parameter combinations for RunDown and for 80 out of 1440 possibilities for COMALV. For both methods, the performance criteria were only met when black and white images were used as input. This reduction in information dimensionality reduces the effects of noise in the Blank Walls environment. Both models were successful for all possible levels of image smoothing and image resolution suggesting they may be robust for different insect eye models, such as bee or ant. COMALV required some noise to prevent it from being trapped in loops; RunDown is an inherently noisy procedure. The COMALV algorithm worked only with the largest image type ($\pm 20^\circ$ around the horizon), whereas RunDown was also successful with more restricted fields of view, excepting when only horizon pixels were used.

From these results it can be concluded that the 'place memory' observed in the cricket experiments of chapter 3 can be explained by visual homing (rather than requiring more explicit spatial representations); and that simple calculation of either the image 'centre of mass' or the image difference is not only sufficient, but produces results closer to those observed for the cricket than more complex algorithms requiring feature extraction or optic flow calculation. In passing it is worth noting that the initially unexpected cricket homing in the Blank Walls environment is accounted for by these models without including the canopy area in the images; the very slight light gradient that existed across the arena was sufficient for homing. This may be important for eliminating unintended cues in any visual orientation experiments on insects. Additionally the finding that crickets home faster when the visual surround is a noisy natural scene in comparison to easily identified landmarks (as used in many previous homing experiments) may be used to guide the

design of future homing experiments in insects.

4.5 Discussion

Both successful methods are computationally cheap. The COMALV method is also cheap in requiring only one vector, rather than a home image, to be stored: although parallel retinotopic processing in the insect brain may mean image storage is also relatively cheap. The reliance of the COMALV Model on the entire image region suggests a possible experimental design to separate the COMALV and RunDown models. If the field of the view of the insect could be limited, either through eye capping or physical barriers, and its impact on the homing ability of insects observed, then the likelihood that the COMALV Model is the homing strategy in use could be inferred. Such screening experiments have sought to infer the portion of the visual scene used by homing wood ants (Fukushi, 2001) and desert ants (Graham and Cheng, 2009b), and may offer a modelling environment able to distinguish the homing models.

Analysis of the homing paths may also offer clues to the homing mechanism guiding crickets. As gradient descent models require a local sampling to infer the home direction it may be possible to analyse for stop and search patterns in homing paths. As mentioned previously, this type of behaviour was not obvious in the cricket study. Alternatively if the crickets are using an active move and sample policy as in RunDown then it would be expected for the home path to arc towards the home location rather than being direct. This is in contrast to the COMALV which should generate accurate and direct home vectors from many locations.

Similar databases of panoramic images have been used to investigate the rotational errors observed in rats trained to locate a corner in a rectangular arena (Stürzl et al., 2008). As in this study, image difference functions were shown to exist in the test environment. Use of a simple gradient descent technique was sufficient to reproduce the animal behaviour indicating a role for view-based homing rather than a dedicated geometric module. Furthermore, the behavioural results have been replicated in ants (Wystrach and Beugnon, 2009), which offers further evidence for the use of a gradient descent based homing in insects. Unfortunately, other models of homing were not also investigated in the above modelling study and therefore cannot be dismissed at this time. Such testing of different models in various experimental situations where model output can be directly compared to biological data

may allow further insights into the exact strategy used by insects and other animals.

One limitation of all biologically plausible homing models described here is that the orientation of the image at the current location must be the same as that of the home image. Many authors address this restriction by assuming the insect or agent has a compass to provide rotation information. However within the cricket arena no compass cues (magnetic or polarised) are available. Another possible solution is presented through image difference functions where it has been shown that the image difference between images increases smoothly and monotonically with rotation as well translation (Zeil et al., 2003). Thus to align the current image with one stored previously the agent must rotate the current image, either physically or mentally, until the minimum image difference is found. While this technique has been used successfully in modelling studies it seems unlikely that an insect could perform such image rotations mentally and there is no clear evidence from the behavioural data of crickets rotating to align images.

A possible solution to the alignment problem, where compass information is not available, is that insects may store multiple images at the home location, while oriented in different directions. Thus when the insect is performing a subsequent homing run, the home memory most closely matching the current world view would be used as a reference for calculating the current image difference or home vector. In this way locations of importance, which are visited repeatedly would have multiple, strongly re-inforced memories and could be approached from many directions without the need for a compass at all. This type of gradual learning of a location may account for the learning curve observed in the cricket behavioural experiments in chapter 3 and will be the subject of further study.

Chapter 5

Visually Guided Routes of the European ant *Cataglyphis velox*

5.1 Introduction

Desert ants inhabiting cluttered environments develop and maintain idiosyncratic routes to and from a regular feeding site (*Melophorus bagoti*: Wehner (2003); Kohler and Wehner (2005); Wehner et al. (2006), *Cataglyphis bicolor*: Wehner et al. (1996)). The routes traversed are unique to individuals despite all ant paths converging on common start and end points. Furthermore the path of individual ants when travelling to the feeding site is distinct to the route of the same ant when returning to the nest.

Kohler and Wehner (2005) demonstrated that visual cues are sufficient for route following as ants successfully recalled and traversed their learned routes when contextual path integration cues were either removed completely or out of synchrony with those normally experienced. It should be noted that the authors also showed that ants maintain a global home vector during route following which is expressed when the ant is visually lost (usually following a displacement). Wood ants that initially learn routes by trail following strategies also learn the visual cues along their paths. Moreover the visual cues become dominant to pheromones when placed in conflict (Klotz, 1987; Harrison et al., 1989).

In this chapter the route following behaviour of the European ant *Cataglyphis velox* is assessed. Similarly to their African cousins *velox* are large, thermophilic, central place, solitary foragers. They are located in the southern Iberian peninsula where the climate is hot and their environment semi-arid. The navigational

capabilities and strategies of *C. velox* are to date unknown, however as they fill the same ecological niche as their Australian and African counterparts, then similar behaviours may be expected.

The specific research aims of this study can be summarised as:

- *Do Cataglyphis velox foragers navigate to and from a regular feeding site by idiosyncratic routes? If so,*
 - *Are visual cues the primary and dominant mode of route guidance?*
 - *Are rudimentary guidance mechanisms, such as path integration and systematic search, maintained and utilised when visual cues fail?*

Previous behavioural studies in other desert ant species have addressed many, if not all of the above points directly. Therefore, it is vital to ascertain if behaviours and strategies are generalised across species sharing an ecological niche. Furthermore, the real world data shall directly influence subsequent modelling work.

5.2 Methodology

5.2.1 Animals

Cataglyphis velox are thermophilic central place foraging ants that scavenge for arthropod corpses during the hottest period of the day (Cerde and Retana, 2000; Cerde, 2001). This thermophilic behaviour was confirmed by recording foraging activity of the experimental colony over a four day period (13th-16th July, 2009). The surface temperature was monitored throughout using a HOBO data logger. To distinguish foraging activity from nest-based activity only ant paths extending further than 1m from the nest qualified as foraging. Activity was monitored from 10am until 7pm each day and the accumulated foraging activity binned into 30 minute windows. Figure 5.2 confirms that *Cataglyphis velox* are most active when soil temperatures peak. This is in common with other desert ant species who forage when other less heat tolerant arthropods have retreated underground.

The morphology of *Cataglyphid* foragers indigenous to the Mediterranean basin (including *C. velox*) are characterised by their "long legs, slender alitrunks and high running speeds" (Wehner, 2008). These attributes are shared with ecologically equivalent ants in southern Africa (*Ocymyrmex velox*) and to a lesser degree those in central Australia (*Melophorus bagoti*). It should be noted that this comparison is by no



Figure 5.1: **Forager of the ant species *Gryllus bimaculatus* departing from its inconspicuous nest entrance.** Image courtesy of Fernando Amor.

means exhaustive and other species not listed may also possess similar morphologies. However the comparison is intended to highlight evidence of parallel evolution in different desert ant species.

5.2.2 Field Site

The field study was conducted outside the village of Torrequinto near Seville, Spain (37° 19' 34" N, 5° 54' 14" W) between 7th May and 16th July, 2009. The nest was located in a flat area surrounded by randomly dispersed grass tussocks. Larger landmarks such as trees and buildings were situated over 30m away and thus could not be viewed by the ants. Figure 5.3 (a) shows a distant view of the field site demonstrating the absence of large visual landmarks close to the nest site. Furthermore any distant cues such as trees were occluded from ants by the grass tussocks as shown by panoramic images sampled close to the nest (see figure 6.3).

A 10m*10m area surrounding the nest was partitioned into a 1m*1m grid using metal markers pushed into the soil. The use of metal markers allowed the grid to be easily viewed by the experimenter without introducing any visual features that the ants may have used for guidance. The grid and landmark distribution were then mapped onto squared paper which was used for recording routes. Figure 5.3 (b) shows a closer view of the specific area that was mapped.

5.2.3 Natural Routes Recording

A feeder was installed approximately 7.5m from the ant nest and sunk into the earth to hide it from view until ants were very close. Crushed biscuit and honey water

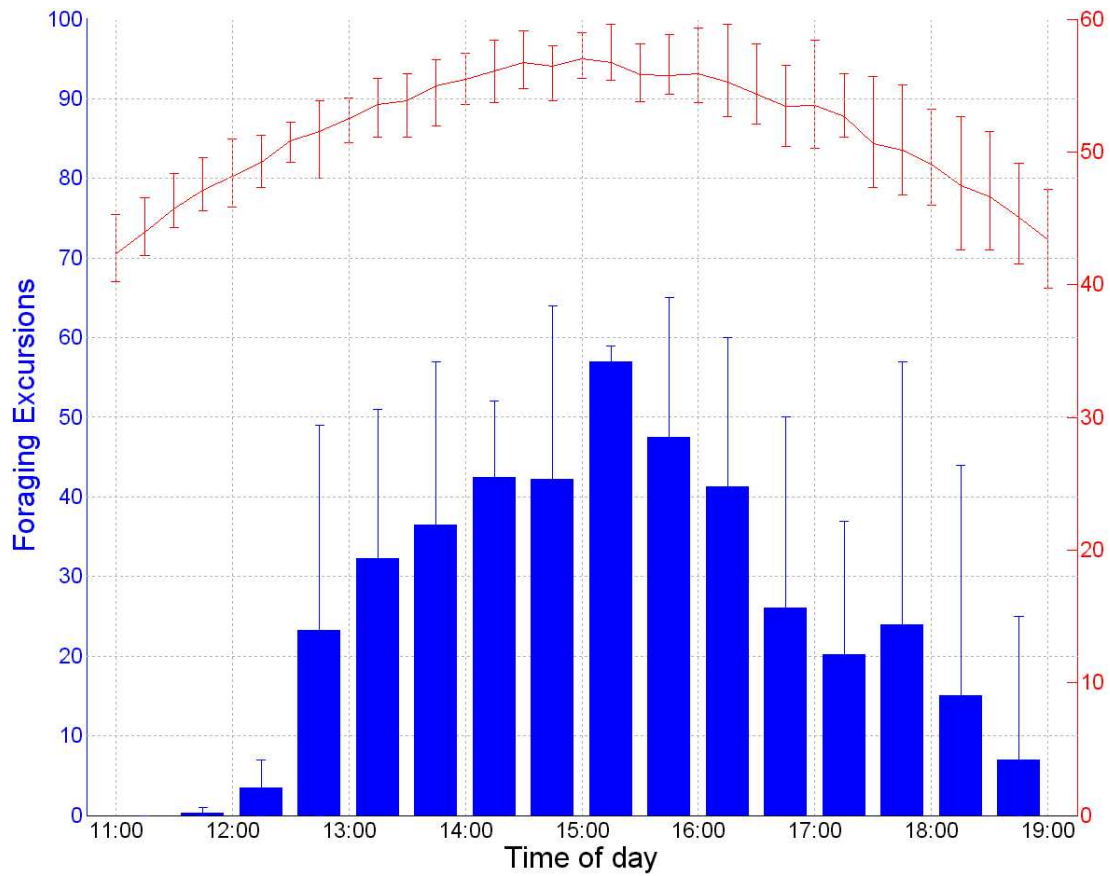


Figure 5.2: **Thermophilic behaviour of *Cataglyphis velox*.** Foraging activity of experimental nest averaged over a four day period. Activity is shown against both time of day and soil temperature.



(a) Distant view of field site.

(b) Local view field site.

Figure 5.3: **Field Site.** Experimental field site located near Seville, Spain showing the maze of grass tussocks that foraging ants must navigate to locate the hidden feeder.

acted as bait and ants were allowed to forage and discover the feeder without aid. Ants returning from the feeder were captured at the nest entrance and marked on the gaster with coloured paint. The four subsequent journeys of the marked ant to and from the feeder were then recorded without interference. These recordings of naturally occurring routes allow assessment of whether the ants followed repeatable, distinct routes to and from the feeding site.

It should be noted that ants were not captured at the feeder unless selected for observation and instead allowed to shuttle back and forth freely. Thus it cannot be concluded from the data presented how many journeys individuals may have been made to the feeder prior to recording.

5.2.4 Displacement Experiments

After completion of four undisturbed round trips ants were subjected to a succession of displacement trials as in Kohler and Wehner (2005). Ants were either captured at the nest or at the feeder prior to displacement. When captured at the feeder ants should have access to a complete home vector built up whilst traveling to the feeder and are thus termed full vector (FV). Conversely ants captured at the nest will have expended the home vector during the inward journey and are thus termed zero vector (ZV).

The first series of trials displaced ants to locations along their observed routes:

1. Zero Vector to Feeder (ZV to F)
2. Zero Vector to Half-Way (ZV to HW)
3. Full Vector to Half-Way (FV to HW)

These On-Route trials test whether the visual route memories can be recalled both in the absence of a global path integrator reading and also in the presence of an inappropriate home vector reading. If an ant follows a set path repeatedly then indexing visual memories using the global home vector could disambiguate closely matched visual scenes and also allow prediction of what visual scene *should* be currently viewed. The ZV to F trial returns ants from the nest to the feeder and therefore puts the home vector in direct conflict with the visual surround. That is, the visual memory expectation as cued by the home vector is that at the nest but the actual visual input corresponds to a feeder-based memory. By assessing whether

the ant can recall its previously observed inward route the interdependence of route memory recall on the global home vector can be inferred.

Displacing ants along their routes follows directly as a variant of the ZV to F trial as visual input and home vector output are again put in conflict. In the ZV to HW and FV to HW trials ants are displaced to a position halfway along their normal inward route from either the nest, or the feeder, respectively. It should be noted that as ants form independent routes, the location of the halfway point was specific to each ant. Figure 5.4 (b) illustrates the displacement procedure for the On-route trials.

Ants were also tested in a series of Off-Route trials:

1. Full Vector to Offset 1 (FV to O1)
2. Full Vector to Offset 2 (FV to O2)
3. Zero Vector to Offset 1 (ZV to O1)
4. Zero Vector to Offset 2 (ZV to O2)

In the Off-Route trials ants were displaced from either the feeder or nest, to two unfamiliar locations offset from their established inward route. FV ants should retain their global home vector when released, providing a guidance cue that should be expressed within the unfamiliar visual surround. In contrast ZV ants should have no navigational back-up system to guide them upon release as they will have expired the home vector on the homeward path. Ants are known to display systematic search patterns in the absence of other guidance cues characterised by concentric rings of increasing radius (Wehner and Srinivasan, 1981). Kohler and Wehner (2005) reported such search behaviours in displaced zero vector ants. After encountering the route however, ants immediately recognised the previously experienced location and followed their usual path back to the nest. Figure 5.4 (c) illustrates the displacement procedure for the Off-Route trials.

The On-Route trials were always performed prior to the Off-Route trials to avoid possible interference of new route memories gained by ants traveling in the novel areas offset from the observed routes. Within each series of experiments the trials were ordered randomly.

5.2.5 Additional Natural Routes Data

To perform a FV trial an ant must complete one undisturbed outward route prior to capture and displacement. Additionally ZV trials require a complete outward and

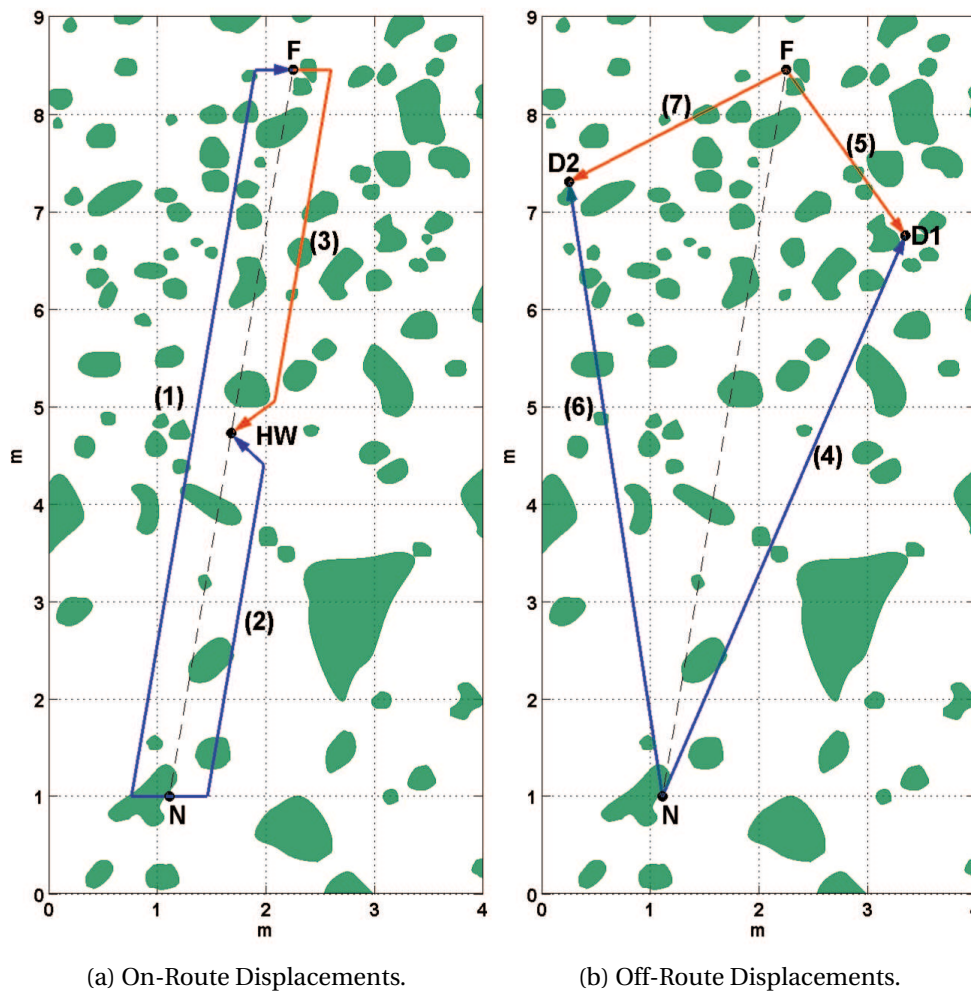


Figure 5.4: **Displacement trials experimental procedure.** The overhead mapping of the ant habitat is shown with the nest marked N and the feeder F. After 4 undisturbed journeys ants were subjected to a series of displacement trials. (a) Ants were transferred from the nest (zero-vector) back to the feeder (1) and also to a halfway point on their normal inward route (2). Ants were also taken from the feeder (full-vector) and released at the same halfway point (3). (b) Two displacement locations were chosen for Off-Route displacements each approximately 1.5m towards the nest by the direct path and then approximately 1.5m perpendicular to the direct path. Again ants were transferred from the nest (4 and 6) or from the feeder (3 and 5). Note that a grass tussock co-incident with the ideal location for displacement 2 and therefore it is slightly further from the direct path than 1.5m. It is also worth noting that both Off-Route release points are found amongst substantial vegetation reducing the likelihood that visual cues could guide ants in the immediate vicinity.

inward route to be completed. These control routes were recorded and added to the natural route data-set.

Furthermore ant recordings did not cease on completion of the displacement trials. Instead individuals were tracked for as long as possible with the longest duration being four days. Not only did this increase the number of undisturbed routes observed but offered an opportunity to conduct repeat displacement trials. The repeat trials conducted were chosen at random for each individual. It should be noted that no ants were subjected to more than two instances of any displacement trial and in no cases did any ant repeat all seven displacement trials.

5.2.6 Data Analysis

5.2.6.1 Route Similarity

To assess whether ants repeatedly follow set paths through their environment, and moreover to determine if these paths are distinct from those traversed by other ants, a route similarity metric is defined. The similarity metric is the area between individual routes and a median route calculated from all observed paths of a single ant. Thus a median route is generated for both the outward and inward routes of every ant. Note that the median route is calculated rather than the mean route such that where ants have traversed a landmark on both sides the most commonly passed side will prevail rather than a route segment passing through the centre of the landmark. The median route calculated for the outward paths of one ant is shown in figure 5.5(a) overlaid on the recorded natural foraging routes.

It follows that the area between the median route and the individual routes from which it was calculated should be small if a consistent route is followed (see figure 5.5 (b)). Conversely if ants do not adhere to consistent paths then larger area measures will prevail. The area metric also allows comparison of the routes followed by different ants. If multiple ants follow similar paths then the resultant areas metrics will be low however if distinct routes are traversed then larger area measures should be generated (see figure 5.5 (c)). The areas between all observed routes and medians are computed to assess whether ants follow idiosyncratic routes distinct from one another. Note that the the Wilcoxon Rank-Sum non-parametric test is used when comparing groups.

The same metric is also used to assess whether ants recall and traverse their routes in the displacement trials. When returned to the feeder the area between

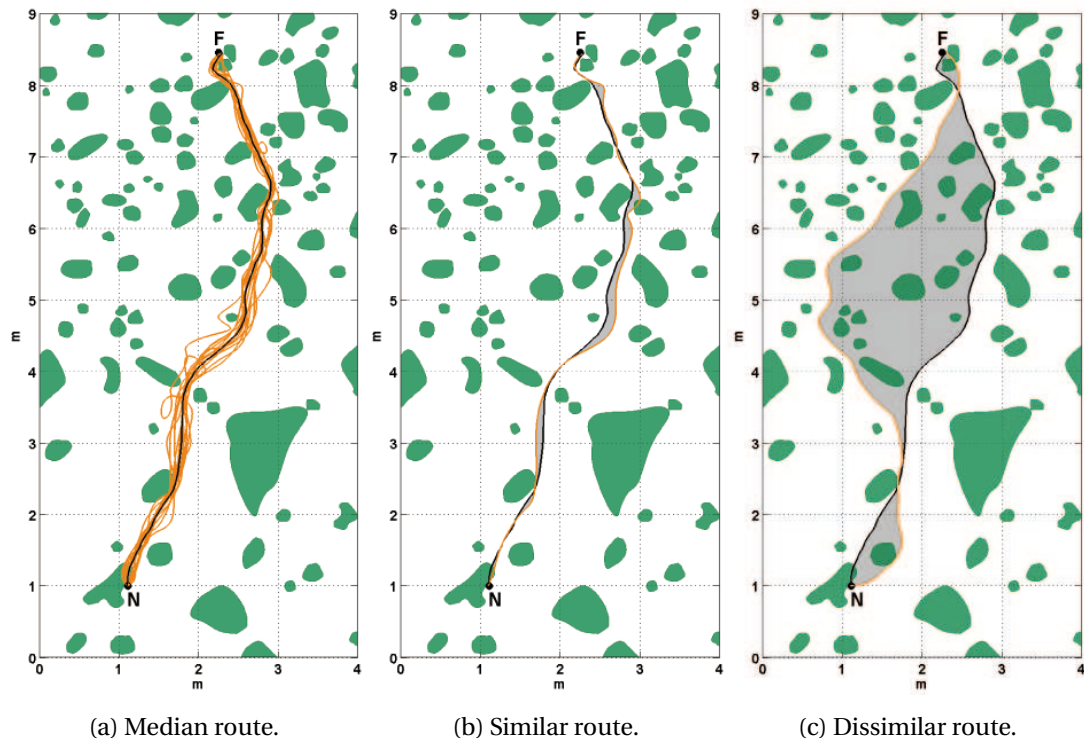


Figure 5.5: **Route similarity.** (a) The median outward route (black) calculated from the observed outward paths of one foraging ant (orange). (b) The shaded region shows the area between the median route and a later route of the same ant. The ant clearly follows the same path generating a low area reading of 0.35m^2 . (c) The shaded region shows the area between the same median route and a path of another ant. The routes are clearly distinct producing of much larger area value of 5.58m^2 .

the resultant path and the previously defined median route is measured. When displaced to a location along the route a partial area measure is used whereby only the area between release point and the nest is computed. This partial area measure is also used in the Off-Route displacement trials such that once an ant encounters its learned route it can be assessed whether it then recalls and follows the same path to the nest.

5.2.6.2 Displacement Trials

The displacement trials are intended to assess whether in the absence of familiar visual cues ants engage and follow their home vector orientation, or when visual and path integration cues are removed a systematic search is initiated. To assess the general path orientation after release the locations where paths intercept a series of concentric rings (radius 50cm, 100cm and 150cm) centred on the release point are extracted from the recorded paths. Figure 5.6 shows examples of the ring intercept data for ants released at both test sites.

Projecting from the release point to the ring intercepts allows a series of path orientation angles to be computed for each trial. The absolute angular error between the path orientation angles and projected home vector and direct nest orientation is then calculated providing an indication of fidelity to the home vector path or direct path to the nest. Statistical comparison between the zero-vector and full-vector groups is performed using the Wilcoxon Rank Sum test. Note that data for Off-Route trials is pooled from both release sites giving 19 data-points for the full-vector trials and 18 data-points for the zero-vector trials.

5.2.6.3 Route Corridors

To help visualise the variability in datasets a route corridor is defined for the outward and inward routes of every ant. To generate the previously outlined median routes the 50th percentile was computed across routes at a series of control across defining each path. These median control points are then splined together to generate the median route. The first route corridor is similarly defined by the 25th and 75th percentile measured at the same control points. This forms a tightly bound region around the median route and is therefore known as the inner route corridor. Additionally, an outer corridor is defined using the minimum datum still within 1.5 times the inter-quartile range (IQR) of the lower quartile, and the maximum datum

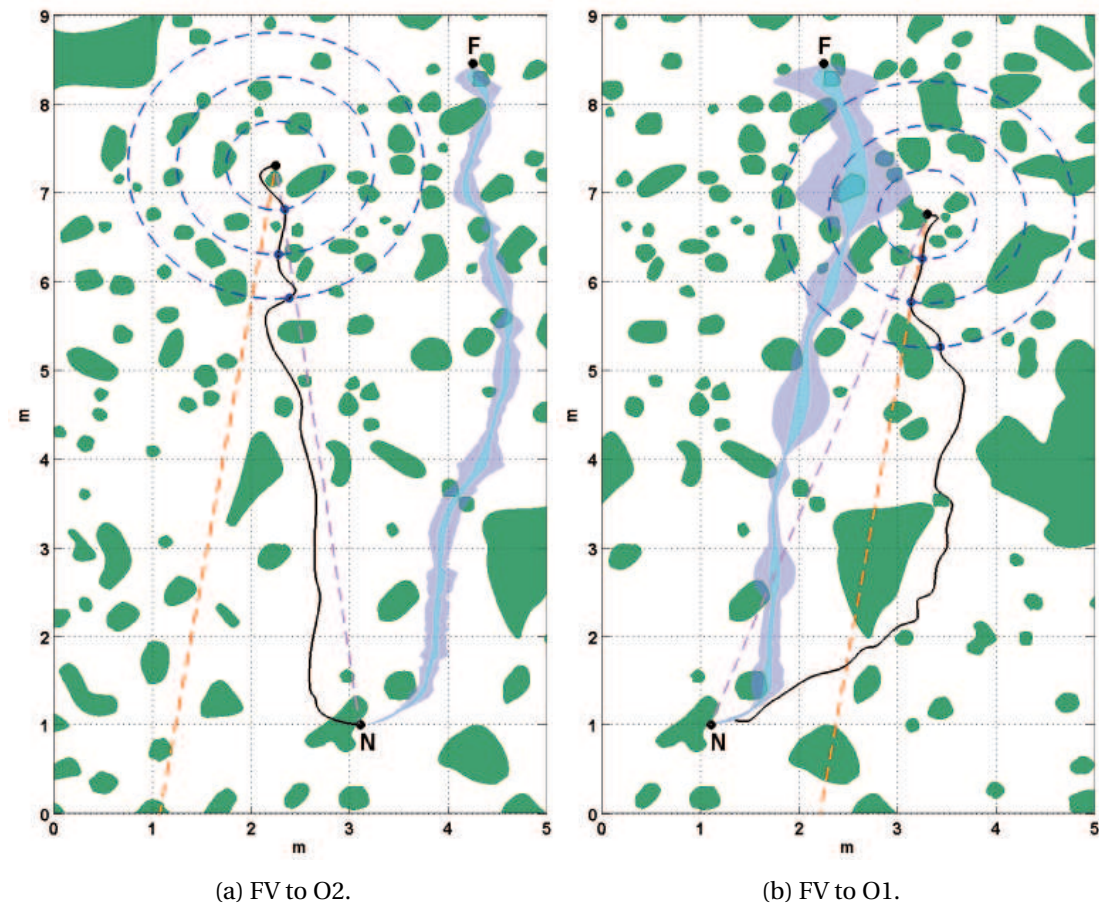


Figure 5.6: **Extraction of general path orientation in displacement trials.** The concentric rings (radius 50cm, 100cm and 150cm) are shown by the dashed lines. The direct path to the nest is shown by the dashed mauve line and the projected home vector from the release point by the dashed red line. The locations where the route first intercepts each ring is shown by a solid circle.

still within 1.5 times IQR of the upper quartile. These values are commonly used to show the variability of data in box-plots. Routes corridors are shown for the offset trials shown in figure 5.6 with the inner corridor shown in cyan and the outer corridor in dark blue.

Route corridors are also used to detect where displaced ants encounter their routes in analysis of the displacement trials. When the path of a displaced ant meets the outer route corridor the ant is assumed to have located its route and the area metric from that position to the nest calculated. If this metric falls within the area of the outer corridor (the whisker values on the boxplot) then it can be assumed that the ant has recalled and followed the route. Areas values larger than the whisker value indicates that the new path has larger variability than the observed paths and that the ant has not recovered its learned route.

5.2.6.4 Route Data Preprocessing

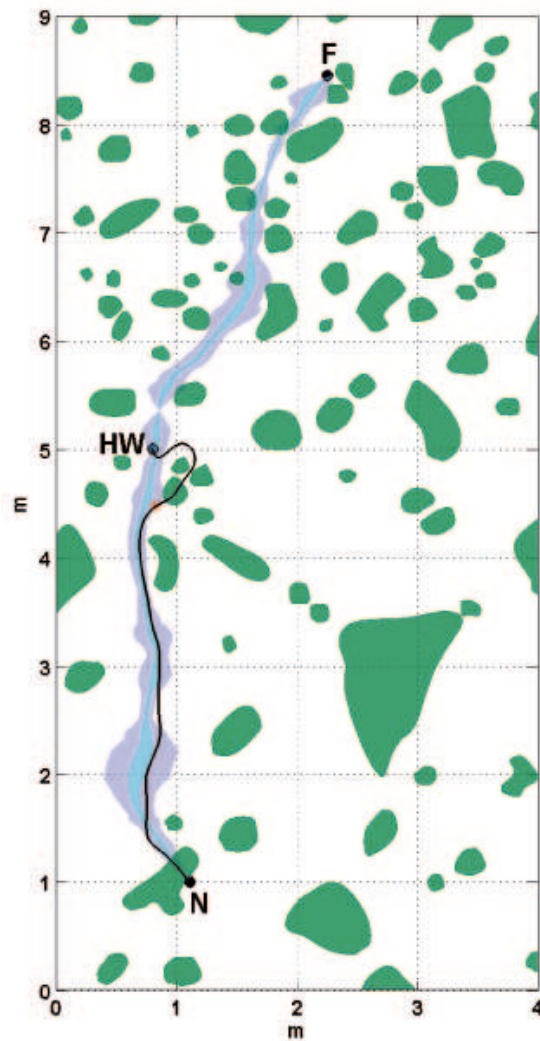
During the displacement trials some ants would dash at the moment of release in a random direction causing a deviation from the learned route (see figure 5.7). This seemed to be some form of reflexive escape behaviour. On most occasions the ant would stop with 0.5m from the release point, rotate and return to traverse its learned route back to the nest. For the analysis below the anomalous dash segments have been removed from the data by hand, and the area metric calculated from the point at which the ant recovers the route.

5.3 Results

5.3.1 Route Fidelity in *Cataglyphis velox*

Undisturbed routes were recorded for twelve ants. Seven ants developed a single repeatable route by which they travelled from the nest to the feeder, and also a single repeatable yet distinct route by which they travelled from the feeder to the nest (see figure 5.8 (a)). This data matches findings in other desert ant species inhabiting similar environments.

The remaining ants were observed to form multiple distinct routes on either the outward or inward leg of their journey. Three ants developed dual routes leading to the feeder, and two ants developed dual routes leading back to the nest (see figure 5.8 (b) and (c) respectively). It should be noted that all ants showing multiple



(a) Route corridors.

Figure 5.7: **Dash anomaly.** After release some ants dashed from the release site in a random direction often leading them away from the route. After this short lasting burst ants would stop, rotate and generally recover the previously traversed route. Shown in an example of this dash behaviour observed in after released during a ZV to HW trial. The portion of the path defined as dash behaviour (prior to the red star) is removed from the analysis of route recovery and fidelity.

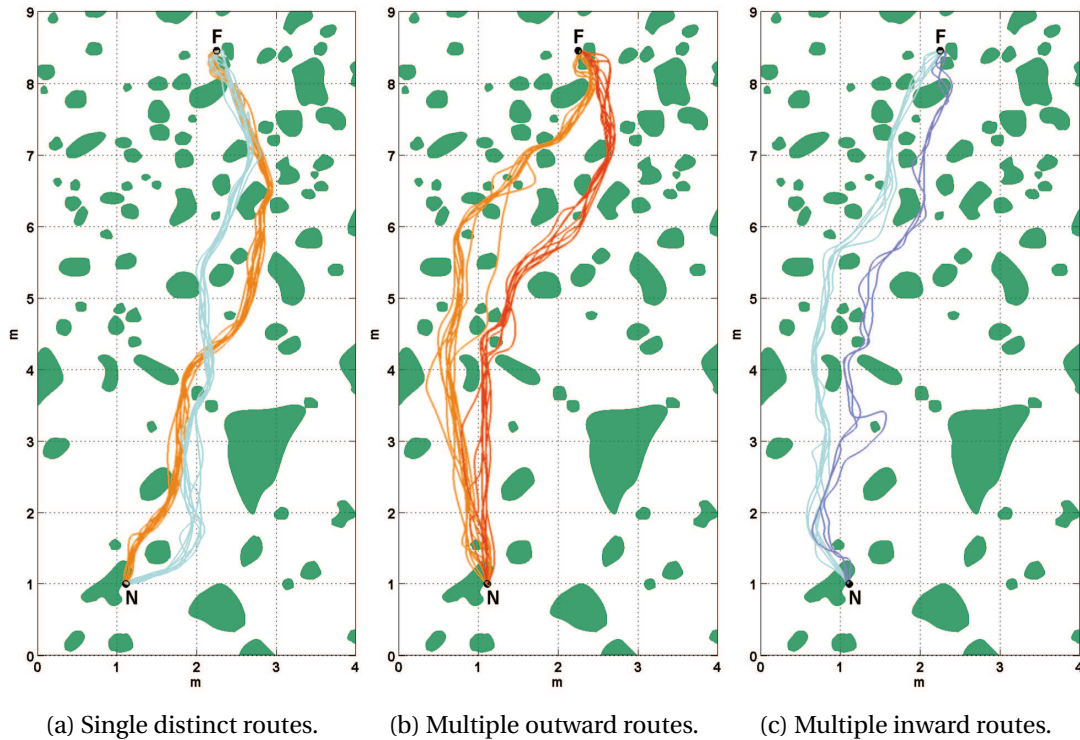


Figure 5.8: **Idiosyncratic routes of *Cataglyphis velox*.** (a) The recorded routes an ant forming single idiosyncratic routes to and from the feeder. Outward routes are shown in orange and inward routes are shown in cyan. (b) Recorded paths of an ant following dual outward routes. The most followed route is shown in orange and the less followed route is shown in red. (c) Recorded paths of an ant following dual inward routes. The most followed route is shown in cyan and the less followed route is shown in blue.

routes traversed the inverse journey by a single repeatable route. Experimental manipulations have shown that desert ants can learn multiple routes (Sommer et al., 2008) but to the best of the authors knowledge this is the first recording of naturally occurring multiple routes.

The partitioning of some routes data-sets into distinct sub-sets decreased sample size in some cases to the extent that they were too small to be included in the statistical analysis (less than 5 samples unsuitable for statistical tests). Table 5.1 shows the total number of routes recorded for each ant and where appropriate the break down into sub-routes.

Where possible every route combination is compared for statistical independence; that is for every ant its outward route(s) and inward route(s) are compared with the outward and inward routes of all other ants. 619 of 624 (>99%) route com-

Ant	Outward Routes	Inward Routes
1	17	14
2	9	5
3	11	8
4	19 (14 Left, 5 Right)	14
5	14	10
6	17	11 (8 Left, 3 Right)
7	8 (5 Left, 3 Right)	7
8	12	9 (6 Left, 3 Right)
9	12	11
10	11	9
11	17	13
12	17 (9 Left, 8 Right)	13

Table 5.1: **Breakdown of routes data recorded for each ant.** The routes scored out are those omitted from the statistical analysis due to low sample size.

parisons returned p-values < 0.02 indicating that routes are statistically distinct. Thus, in the vast majority of cases the routes followed by individual foragers to and from the feeder are independent of the paths taken by other ants travelling to and from the same locations. Furthermore, the outward and inward routes of individual ants are shown to be distinct in all cases. The independence of routes confirms that pheromone trails are not in use and furthermore closely matches route following behaviours of other ant species found in similar habitats.

5.3.2 On-Route Displacement Trials

5.3.2.1 Zero Vector to Feeder Trial

Twelve ants completed the ZV to F trial at least once giving a total sample size of fifteen. Thirteen of fifteen trials (87%) produced metric scores within the whisker boundaries computed for the natural routes. A typical ant path after displacement is shown in figure 5.9 (a).

In one case the large metric score is caused by a small loop in the path of the ant (see figure 5.9 (b)). However the area metric score remains small at 0.47m^2 and marginally out-width the defined boundary. Visual inspection of the path confirms

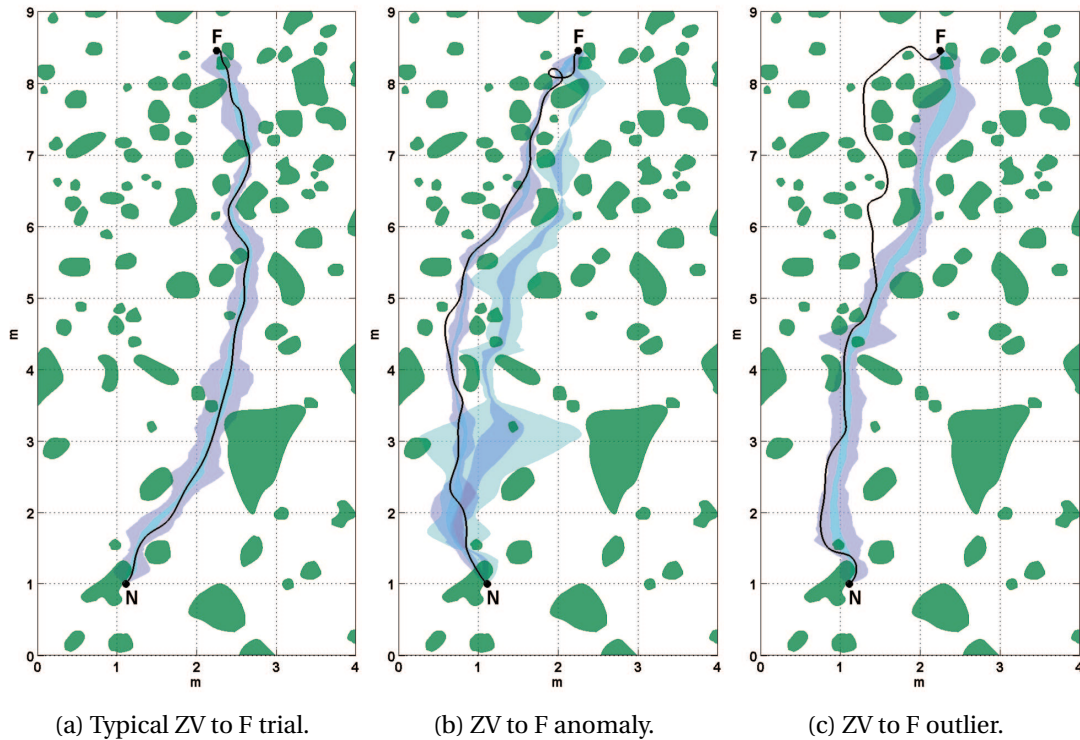


Figure 5.9: **Results of the ZV to F trials.** The black line indicates the path of the ant during the trial. (a) Example of ant following learned route home after displacement. (b) Route of ant whose area metric score is slightly out width the whisker boundary caused by the loop at the start of the trial. Note that this graphic has two route corridors as this ant displayed multiple route following behaviour. (c) Route of the single ant which did not follow the learned route home.

that the learned route was indeed maintained. Thus, in 14 of 15 trials (93%) ants successfully recalled and traversed the learned route back to the nest despite having run off their home vector.

The path followed in the remaining trial is shown in figure 5.9 (c). It is clear that the normal route is not followed, confirmed by a large area metric score of 2.43m^2 . When released the ant immediately dashed from the feeder taking it away from the normal route. The ant was observed to move slowly and rotate on the spot repeatedly whilst in the early portion of the path; behaviours generally expressed when foragers are lost. However, as the ant approached more familiar terrain close to its learned route an increase in speed was observed. It is clear that the learned route was then recognised and traversed to the nest.

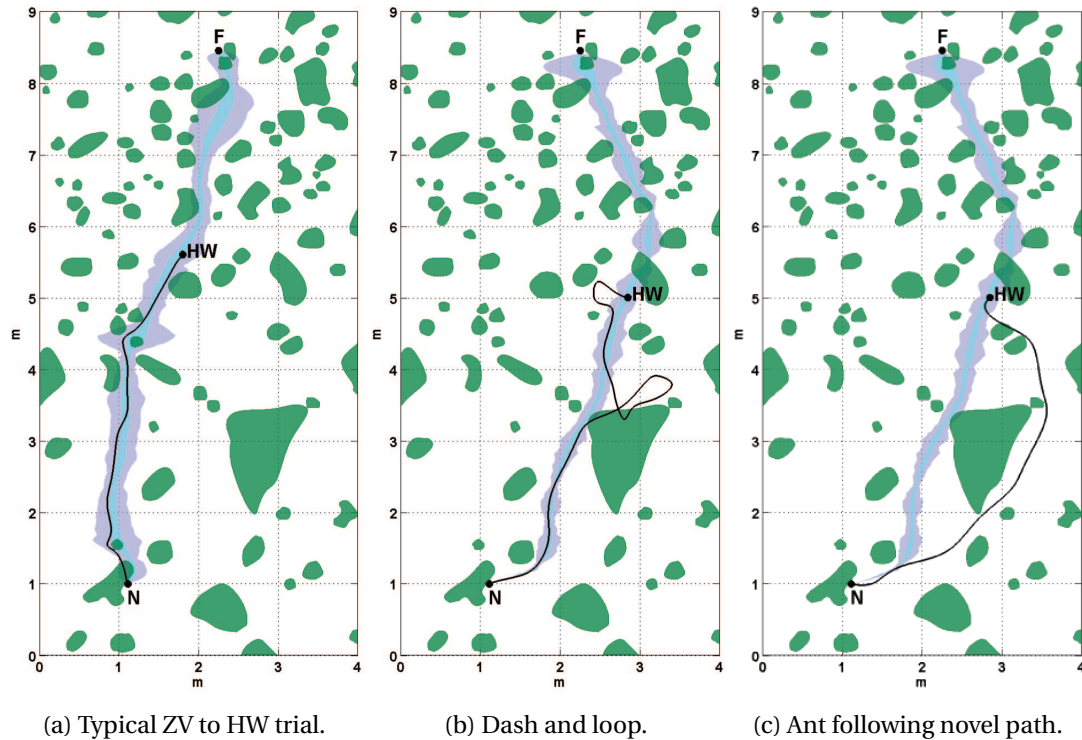


Figure 5.10: **Results of the ZV to HW trials.** (a) Example of ant that re-called the previously observed route immediately and followed it to the nest. (b) Path of an ant that dashed randomly after release before recovering route. (c) Remaining anomalous ZV to HW trial result.

5.3.2.2 Zero Vector to Halfway Trial

Eleven ants were subjected to at least one instance of the ZV to HW trial giving a total sample size of fourteen. Twelve of fourteen trials (86%) produced area metric scores within the whisker boundaries defined by the natural foraging paths. An example of such a trial is shown in figure 5.10 (a).

The remaining two trials (figure 5.10 (b) and (c)) occurred in the same ant. The first trial appears to roughly follow the previous route although is corrupted by a large loop which causes the metric score to be large. However visual inspection shows that the ant returns to the path and maintains the learned route to the nest.

In the second case the ant appears to follow a completely novel path back to the nest. However this ant had developed an alternate route leading to the nest, and instead returned to the nest via that path. Section 5.3.4.2 provides an in-depth analysis of the routes developed by this particular forager.

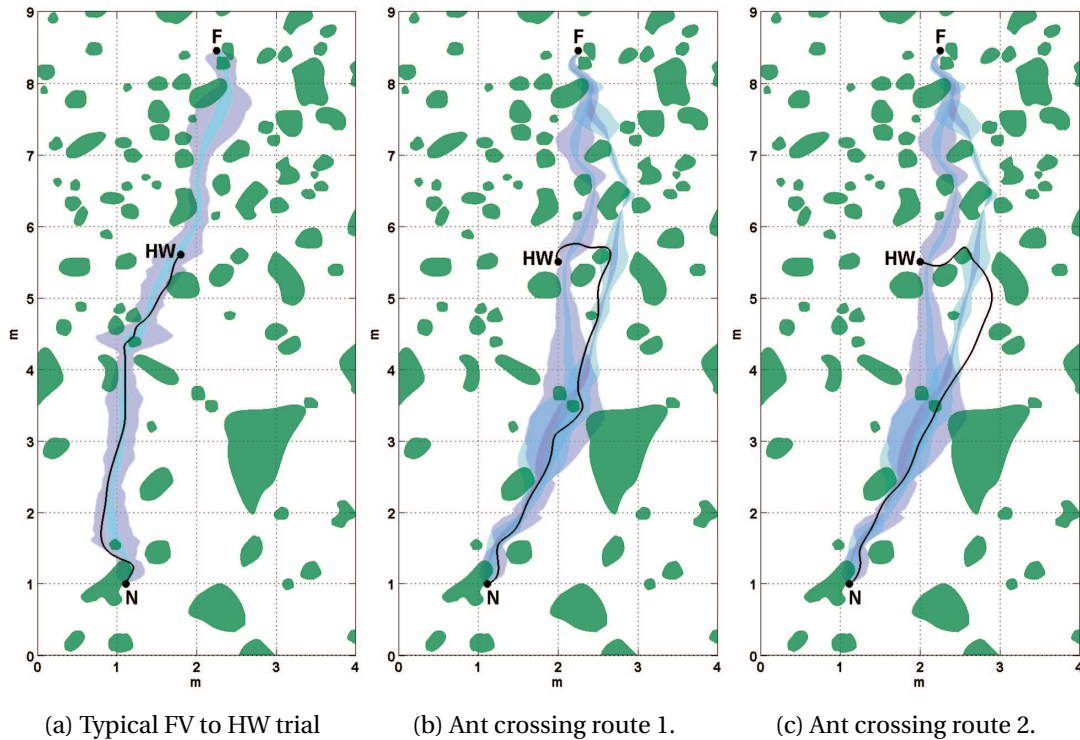


Figure 5.11: **Results of the FV to HW trials.** (a) Example of an ant that successfully recalled the route which it then followed to the nest. (b) and (c) Examples of dash on release leading the ant from one route to another after which the route was recovered and followed to the nest.

5.3.2.3 Full Vector to Halfway Trial

Eleven ants were subjected to at least one instance of the FV to HW trial giving a total sample size of thirteen. Eleven of thirteen trials (85%) generated area metrics within the whisker boundary indicating that the observed route successfully traversed. An example of successful route recall is shown in figure 5.11 (a).

The two remaining cases occurred in an individual ant and are shown in figure 5.11 (b) and (c). The ant clearly moves from the route on which it was released to the other inward route it had developed. This route is then recalled and traversed to the nest in both cases, although in the second case the route is shadowed somewhat.

Thus it is shown that *C. velox* foragers can recall and maintain their learned route at an arbitrary location despite the visual surround and global path integrator being completely out of context with that normally experienced. These results are in line with similar experiments conducted in other ant species in similar habitats.

5.3.3 Off-Route Displacement Trials

5.3.3.1 Data Preprocessing

In 23 of the 37 Off-Route displacement trials, ants encountered their previously learned inward route. At the moment of route encounter the current global home vector value would be vastly different from that expressed at the same location during normal route following. It should also be noted that during the Off-Route trials individuals encountered their learned routes across a continuum of locations as opposed to the single locations in the On-Route trials. This presents an opportunity to extend the analysis of the interdependence of the global path integrator with visual route memory.

Successful route recall is assessed using the same area metric initiated from the point at which the ant path first crossed the outer route corridor. It should be noted that only route encounters which occurred further than 1m from the nest were considered in this analysis to ensure that ants were recalling their route rather than nest-based cues.

In 15 of the 23 cases of route encounter the area metric score fell within the whisker boundary defined by the natural foraging routes. In a further four cases the area metric score was slightly larger than the defined whisker boundary. This was generally caused by a slight shadowing of the learned route as shown for an example case in figure 5.12 (a). Thus in 19 of 23 cases (83%) ants recalled and traversed their learned inward route when encountered regardless of the location of encounter and the home vector value.

The recall of familiar locations regardless of the path integrator context complements the previous analysis the On-Route trials. However the Off-Route displacement trials are intended to assess whether ants engage other navigational strategies when familiar visual cues are absent. Thus the paths of ants that encountered and recalled their learned route following an Off-Route displacement are segmented into two sections: non route following and route following. Only the path segments belonging to the non route following class (i.e. that prior to route encounter) are used during the following sections.

A number of trials were also omitted entirely from the subsequent analysis due to repeat trial effects. Figure 5.13 (a) shows one FV to O2 trial where the ant follows the approximate home vector heading before swerving to locate the nest. This was the first Off-Route trial performed by the ant and the resultant path is what would be

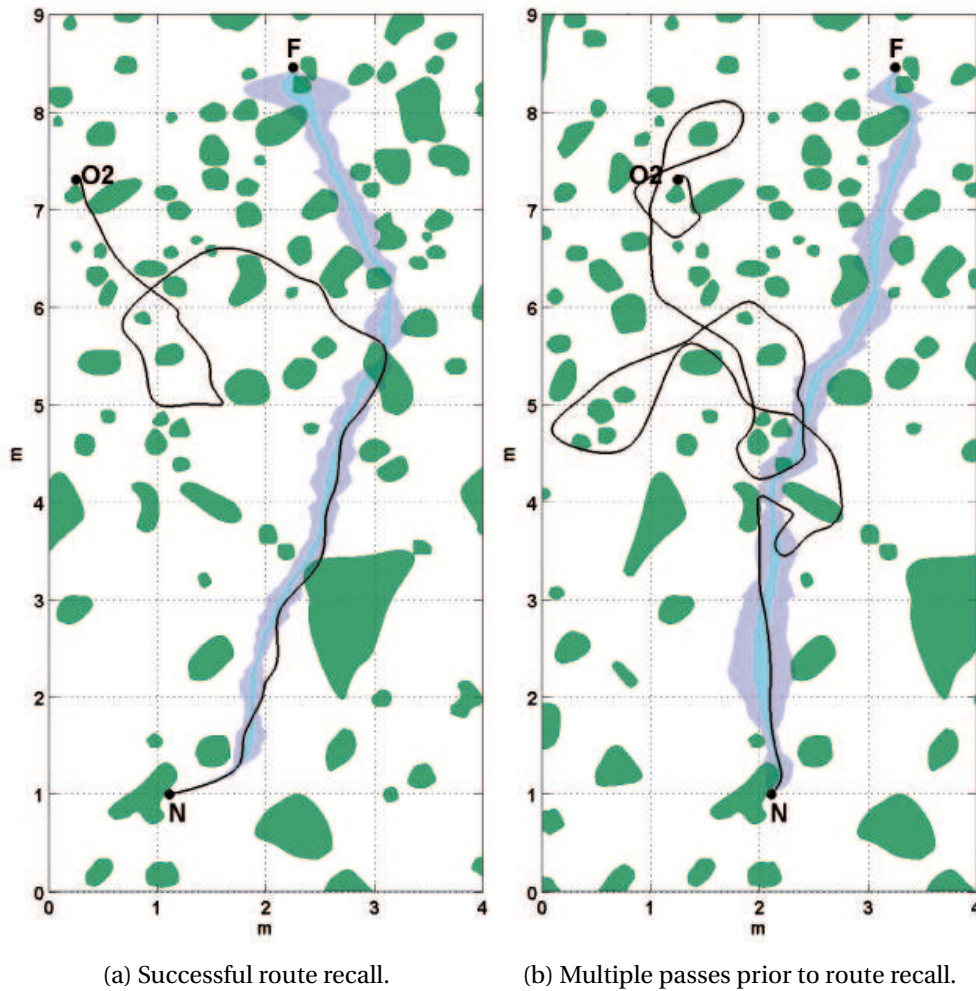


Figure 5.12: **Route recall following Off-Route Displacements.** (a) Example of ant for which the area metric score was marginally larger than during normal foraging. Visual inspection clearly shows that the learned route was recalled and traversed to the nest. (b) Example of ant that did not recall its learned route until the sixth encounter.

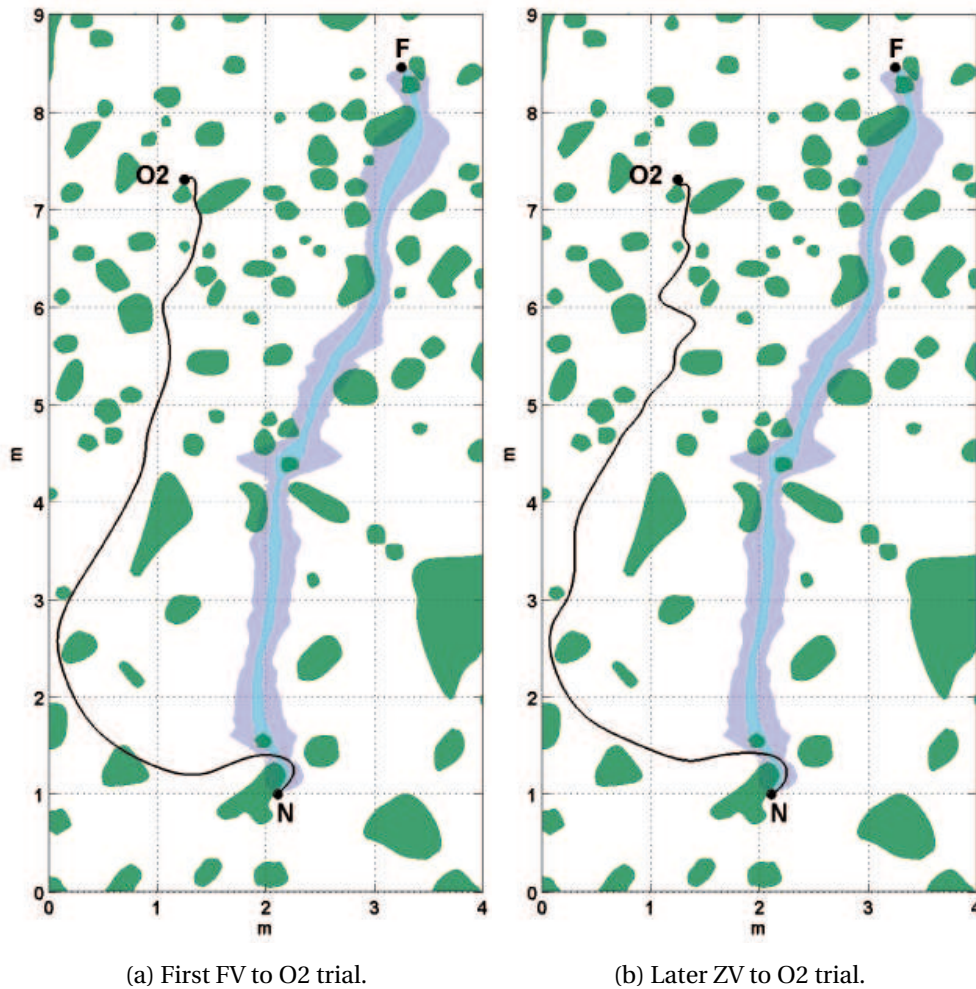


Figure 5.13: **Repeat trial effects.** Paths recorded for a single ant subjected to FV to O2, ZV to O2 and a repeat ZV to O2 trials showing the formation of a new route after the first displacement.

expected given previous studies; where the visual cues fail the ant is guided by the home vector. When later zero-vector displacements were performed the ant did not engage a systematic search instead following an identical path as in the earlier trial (see figure 5.13 (b)). It should be noted that this data suggests that ants are capable of learning routes from a single trial.

A total of eight trials are omitted from the statistical tests; two due to dropping biscuit and six due to new route formation. Table 5.2 shows the total Off-Route trials attempted, the number of trials compromised, and the remaining trials included in the statistical analysis. It should be noted that as the Off-Route trials were always performed after the On-Route trials factors such as predation, forager mortality and

Trial	ZV to O1	FV to O1	ZV to O2	FV to O2
Trials attempted	13	12	9	11
Trials compromised	1	1	3	3
Remaining trials	12	11	6	8

Table 5.2: **Ants subjected to various displacement trials.**

even bad weather contributed to a reduced n-number in the Off-Route group.

5.3.3.2 Full Vector Off-Route Displacements

Ants were displaced from the feeder to two locations offset from the direct path between nest and feeder. Previous studies have shown that when full vector ants are displaced to visually unfamiliar locations movement is guided by the path integration system. Figure 5.14 (a) and (b) shows the truncated paths of all ants subjected to full vector trials. It is clear that from both release points ants move in the general home vector direction. This is confirmed by small angular error between ant paths and the projected home vector as shown in table 5.3. Unfortunately due to the proximity of the offset locations to the direct nest-feeder path, the angle between projected home vector and the true nest direction is only 17°. Thus the paths of ants are statistically indistinguishable when measured against these two vector projections. A weak statistical separation is found showing the paths are closer to the home vector than the actual nest orientation by combining the data for both release points ($p=0.09$ for the 150cm ring). Figure 5.14 (c) displays the projection to the median intercept point for each of the concentric rings indicating the paths of ants directed between the home vector and true nest orientations.

Despite the difficulty in statistically separating the path orientations after displacement ants are shown to move in a consistent and directed direction on release. This direction is shown to correspond well with the direction that would be indicated by the home vector. If guidance cues are available from the environment then this directed movement should also be present in zero vector ants displaced to the same locations.

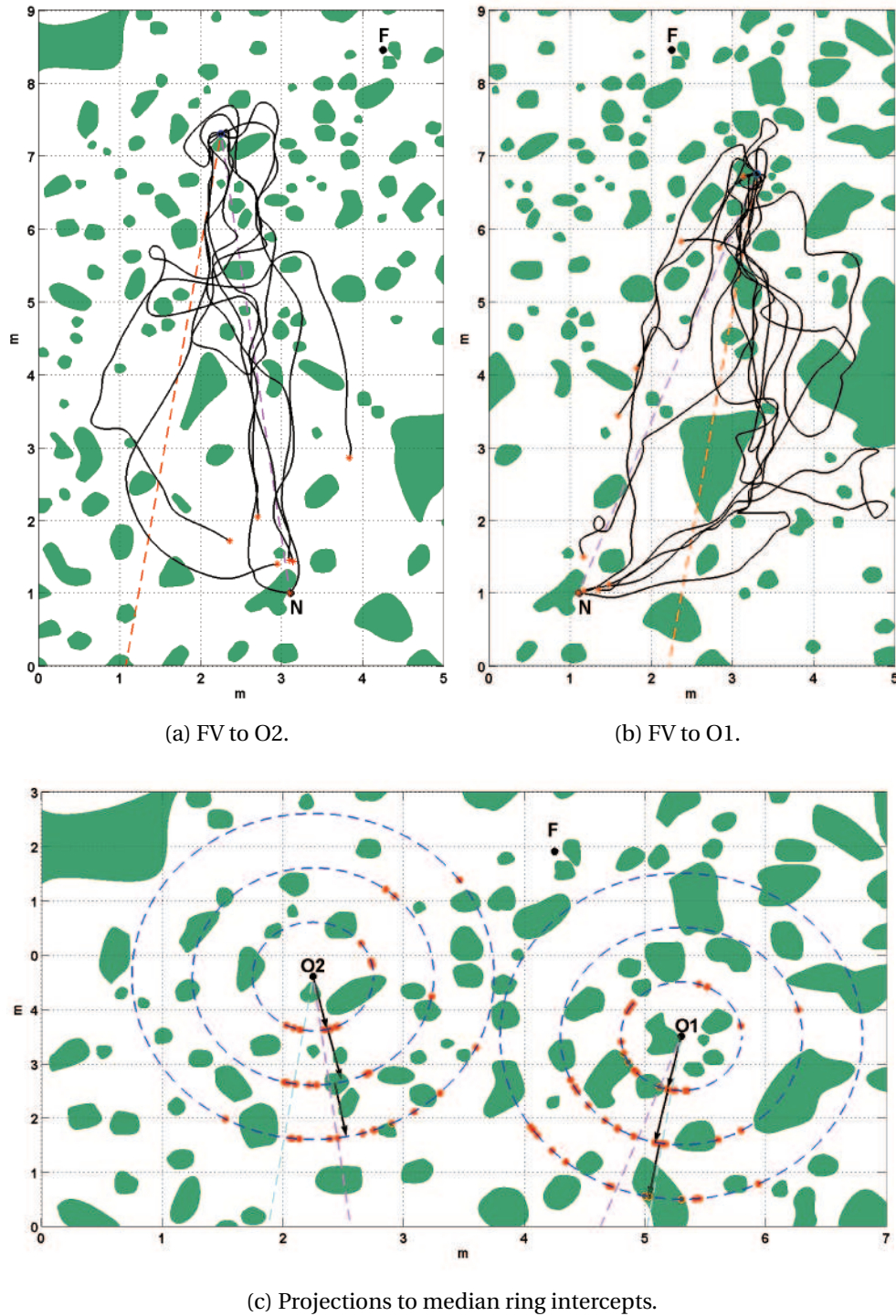


Figure 5.14: **Full-Vector Trials.** (a) and (b) show the paths of all ants after displaced to the predefined offset locations. (c) Projections to the median intercept points from the offset point for all displacement trials. The projected home vector from each offset location is shown by the dashed cyan line and the direct path from each offset to the nest by the dashed mauve line in all figures.

Trial	<i>n</i>	Concentric Ring	Home Vector	True Nest Vector
FV to O1	10	50cm	13°	20°
	10	100cm	3°	11°
	9	150cm	13°	21°
FV to O2	8	50cm	23°	34°
	8	100cm	23°	17°
	8	150cm	19°	12°
ZV to O1	12	50cm	46°	58°
	9	100cm	39°	41°
	7	150cm	32°	34°
ZV to O2	6	50cm	8°	16°
	6	100cm	19°	3°
	6	150cm	13°	18°

Table 5.3: **Median angular errors for Off-Route trials.**

5.3.3.3 Zero Vector Off-Route Displacements

The paths of all ants displaced from the nest to the offset locations are shown in figure 5.15 (a) and (b). The paths of zero vector ants are more circuitous than those observed in the full vector trials. Correspondingly the computed angular errors between the ant paths and the projected home vector and actual nest vector are larger than those for the full vector ants (see table 5.3). Figure 5.15 (c) plots the projected median ring intercept locations showing less fidelity to both the true nest direction and home vector orientation than the full vector paths.

There does however appear to be a bias towards the central area leading many ants to their learned inward route, and ultimately to the nest and safety. This is particularly prominent in the O1 trials as highlighted by the series of route encounters shown in 5.15(b). A similar bias in search was also reported by Kohler and Wehner (2005) when zero vector ants were displaced; they suggested ants were using long range visual cues to direct their search. The test site used in our study had no prominent landmarks such as trees visible to the ants which could have provided rough guidance cues. Ants were transported to the release point within a sealed container so no path-integration cues should have been present. It is possible that ants may have been able to recover the route by homing to local visual cues associated with

the route. Alternatively, some ants may have been guided by previous memories gathered on unseen journeys (see section 5.3.4.2).

5.3.4 Additional Analysis

Previous sections have presented the analysis required by the predefined research questions with particular emphasis in showing that *Cataglyphis velox* ants display similar foraging behaviours to other ants found in similar habitats and climates. However, the field study also revealed a number of novel findings that are reported in the subsequent sections.

5.3.4.1 The Role of Insect Heading on Route Recognition

Wehner et al. (2006) have shown that motivational state may govern the specific route memories that can be recalled; homing ants only recognise their inward route, completely ignoring their familiar outward path. Correspondingly in no circumstance did any homing ants (those with biscuit) recall and traverse their outward path to the feeder. Recall of the outward path only occurred in one forager that dropped its biscuit crumb when released after displacement. Upon release the forager initiated a systematic search before encountering its learned outward route which it traversed to the feeder, collected a new crumb and then returned to the nest via the normal inward path.

In the Off-Route trials outlined 15 of the 23 homing ants that encountered their learned inward route immediately recalled and traversed the learned path to the nest. In the remaining cases, ants either continued a classic search pattern, or in some cases moved towards the general nest area along a path distinct from the observed route. All foragers in this group were motivated to locate the nest and therefore others factors must also influence successful route recall.

Inspection of the route encounter data suggests a role for the current ant heading when the route is encountered. To test this hypothesis, the ant heading (approximated from the current direction of movement) is calculated for every entry of an ant into its route corridor. The headings are then categorised into those that result in successful route recall and those that do not. The difference between the ant heading at route corridor entry and the *ideal heading* i.e. the heading of the median route at the corresponding location provides the metric.

The Off-Route displacements provide 26 route encounters resulting in success-

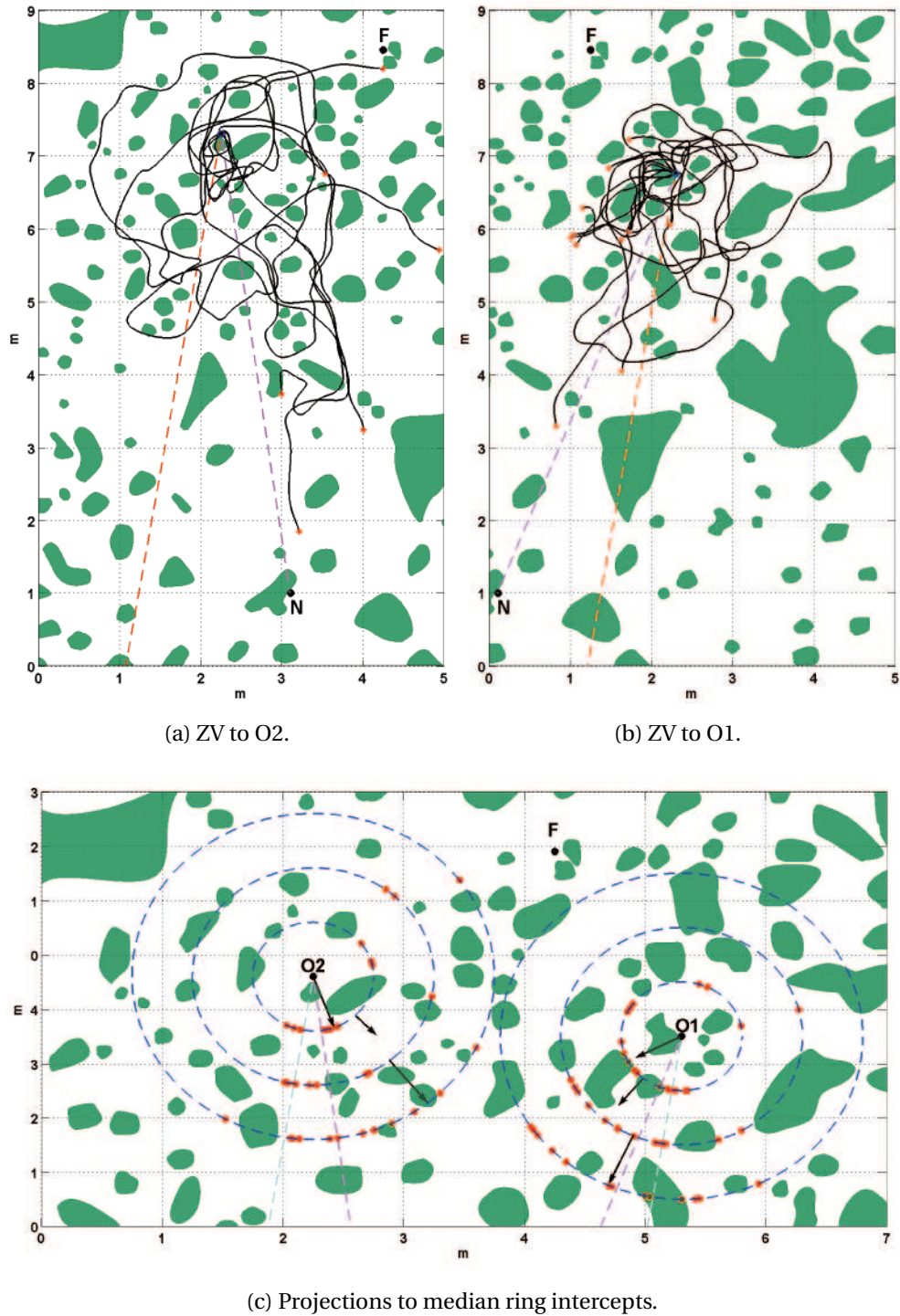


Figure 5.15: **Zero-Vector Trials.** (a) and (b) show the paths of all ants after displaced to the predefined offset locations. (c) Projections to the median intercept points from the offset point for all displacement trials. The projected home vector from each offset location is shown by the dashed cyan line and the direct path from each offset to the nest by the dashed mauve line in all figures.

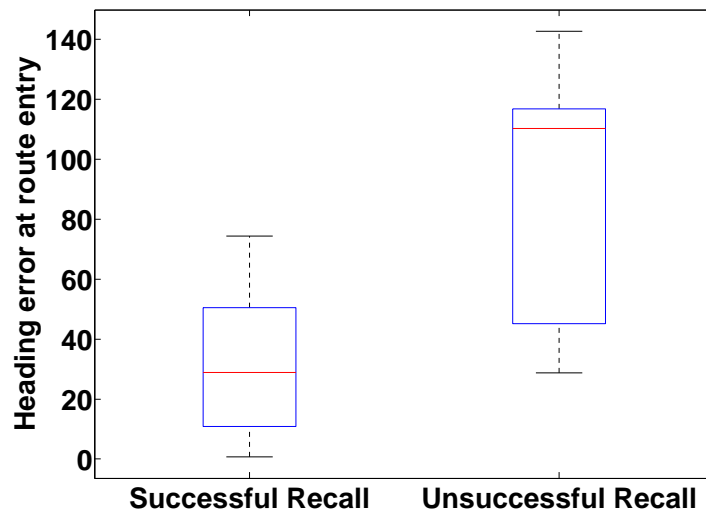


Figure 5.16: **Heading error influence on route recall.** Box-plots showing the heading error data calculated when the ant encounters its previously followed route separated for cases that resulted in a successful route recall and those that did not. Boxes show lines at the lower quartile, median, and upper quartile values. Whiskers indicate the most extreme values within 1.5 times the interquartile range from the ends of the box. Outliers are shown as + signs.

ful recall and 9 encounters for which the route was not recognised. For each category the heading errors (the difference between the ant heading at the moment of route encounter and the median route) are defined and the resultant boxplots shown in figure 5.16.

The ants that did not recognise their routes clearly approached the route at an increased angle than those ants that recalled their route (successful recall, median error=28°; unsuccessful recall, median error=110°). The difference between heading errors is also shown to be significant ($p < 0.01$) when the groups are compared using the Wilcoxon Rank-Sum test. We also note the maximum error resulting in successful recall was 74°.

Thus, it seems that memory recall may indeed be mediated by context as suggested by Wehner et al. (2006), but that correct alignment is required for robust identification of place.

5.3.4.2 C. *velox* Continuously Learn Novel Paths

As shown throughout the previous analysis, *C. velox* ants are capable of learning more than one route to and from the feeder location. In most cases the develop-

ment of such routes was not observed. However for one particular ant the gradual formation of an alternate route was fully recorded. Whilst traveling to the feeder by its normal outward route the ant encountered an insect corpse, which it gathered and returned to the nest by a direct (and thus novel) path. The ant could only carry part of the bounty on this journey and thus returned to collect the remnants of the same insect corpse, which was again transported to the nest by the novel path. Figure 5.17 (a) shows the normal route followed by the ant to the experimental feeder and (b) shows the two journeys to and from the novel prey site.

On a later outward journey the same ant again encountered prey whilst following its outward path. After collecting the prey the ant again returned to the nest by extending the novel path rather than using the established feeder to nest route (see figure 5.17 (c)). It is worth noting that the ant showed an expectation of prey on the subsequent outward path when arriving at the location where prey was previously plundered, identified by a series of search loops (see figure 5.17 (d)). On finding no prey the ant followed the remainder of the established route to the feeder.

A number of complete foraging excursions to the experimental feeder via the established routes were recorded prior to the ant encountering a third natural prey at P3 (see figure 5.17 (e)). As for the first prey the ant required two trips to gather all the available food. As shown in our data the ant followed the normal outward route to the all prey sites but returned by an alternate inward route.

It is worth noting that when returning from the experimental feeder the ant always used its previously established inward route. However, attention is drawn to the ZV to O1 trial of this ant as shown in figure 5.17 (f). The ant performed a classic spiral around the release point before arriving close to the prey site visited recently. The path of the ant then clearly follows the established alternative route to the nest. Furthermore, the previously anomalous data for the ZV to HW trial (see figure 5.10 (c)) can now be explained by the ant following the alternate route to the nest.

5.4 Conclusions

The primary aim of this study of *Cataglyphis velox* was to assess whether an ant species that inhabits similar environments to desert ants found in Australia and Africa navigates by similar means.

- *Do Cataglyphis velox foragers navigate to and from a regular feeding site by*

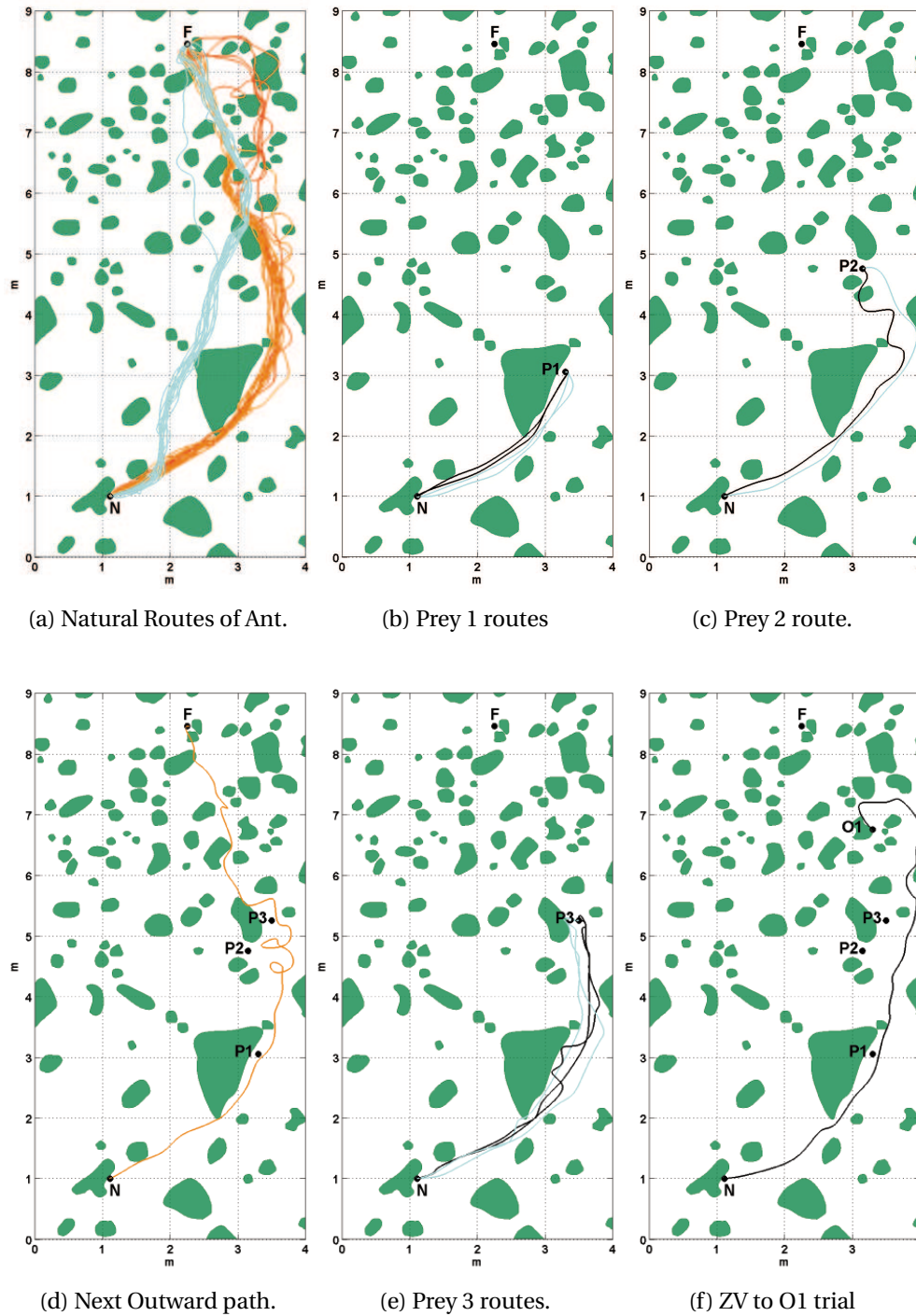


Figure 5.17: **The learning of a novel route by an ant.** (a) The natural routes of the ant (dual outward routes: orange and red; inward: cyan). (b) The routes of the ant to the first naturally occurring prey. (c) The routes to the second prey site. (d) The subsequent outward route showing loops where the last prey was discovered. (e) Routes to third prey site. (f) ZV to O1 trial where the ants returns to the nest via the alternate inward route.

idiosyncratic routes?

It has been demonstrated that *Cataglyphis velox* foragers learn and maintain idiosyncratic routes when traveling to and from a profitable feeding site. The outward and inward routes of individual ants are shown to be statistically distinct, and routes are unique to each individual. These routes are maintained throughout the life of the ant; route data was collected over successive days with the longest period being four days. The independence of routes despite travelling to and from the same locations further confirms that pheromones are not being used. These results are in line with previous studies in other desert ant species.

However, in contrast with previous observational studies some *C. velox* foragers formed multiple routes leading to, or from the feeding site. Memories of both routes are stored concurrently allowing either route to be recalled when appropriate. Indeed ants are shown to constantly update their route memory particularly when travelling through unfamiliar terrain for the first time. It should be noted that the ability of other ant species to learn and later recall multiple routes has been shown through experimental manipulation (Sommer et al., 2008) but this is the first demonstration of the use of multiple routes in a natural context.

- – *Are visual cues the primary and dominant mode of route guidance?*

To assess whether vision is the dominant route guidance cue ants were displaced to various locations along their route where the path integrator output was out of synchrony with that experienced during normal foraging. This had no influence on the ability of ants to recall and traverse their learned routes back to the nest indicating that visual cues are sufficient for route following. Furthermore, ants displaced to locations offset from their normal path were shown to recall their routes regardless of location of the route encounter or the home vector reading.

It should be noted that some ants did not recognise their route on the first encounter. Successful recognition of the learned path is shown to be highly dependent on the heading of the ant when the route is encountered. Indeed the largest heading error affording route recall was 74°; larger heading errors resulting in the route being ignored.

- – *Are rudimentary guidance mechanisms, such as path integration and systematic search, maintained and utilised when visual cues fail?*

Ants were displaced to novel locations in their habitat where the visual surrounding was unfamiliar. In similar circumstances other route following ant species are known to engage back-up navigational strategies. When displaced from the feeder ants should have access to a home vector generated during their journey to the feeding site. After displacement to both offset locations ants travelled in approximately the heading indicated by the home vector. Unfortunately the pre-defined displacement locations were not large enough to produce a large angular difference between the orientation as indicated by the home vector and the orientation towards the nest. Thus, the paths of full vector ants with reference to these two orientations cannot not be statistically distinguished.

Ants displaced from the nest in contrast will have expired the home vector on the inward leg of their foraging trip. Correspondingly after displacement the zero vector ant paths were less directed, and in some cases displayed looping paths normally expressed during systematic search. The analysis shows a larger spread of data however with a bias towards the central foraging area through which all learned routes passed. A similar bias in systematic search was observed in *Melophorus bagoti* when displaced to novel location. Kohler and Wehner (2005) suggest that the bias may have been caused by long-range contextual cues such as trees, however no such cues were present in the current field site. It seems possible that ants may have been able to perform some form of visual homing to local route memories which would have guided them towards the route rather than directly towards the nest.

A second possibility comes from evidence of ants quickly learning novel routes in their environment. This is particularly well documented in one ant that developed an alternate inward route, completely distinct from the route it would take when returning from the experimental feeder. Post-analysis of the displacement data of this particular forager shows that in two cases the ant recovered the alternate inward route rather than the main route from the feeding site. Had this route development not been witnessed then the data for both trials may have been mistakenly interpreted. It is plausible that other ants may have developed similar alternative route memories either during previous foraging trips or even when performing nest cleaning activities which lead the ants small distances from the nest. It is with this finding in mind that caution is used when drawing conclusions from the Off-Route displacement trials. As ants were not followed for their entire foraging lives it cannot be guaranteed that foragers have not learned alternate routes to the nest. To ensure no contamination by previously established memories ants would either have to

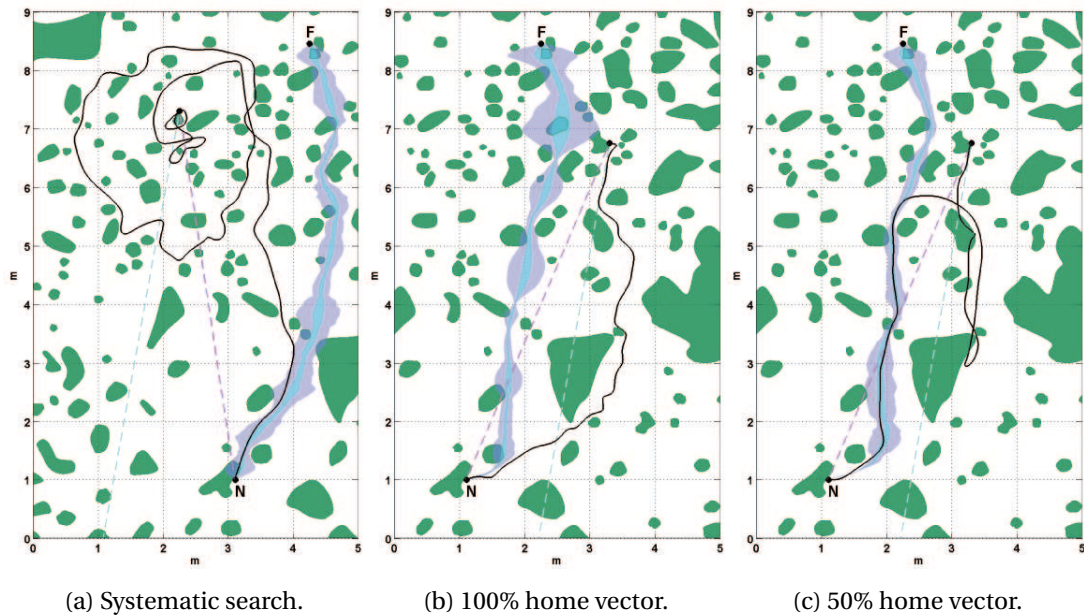


Figure 5.18: **Examples of ants displaying common behaviours when displaced to novel locations.** (a) Zero vector ant displaying the classic concentric loop pattern associated with the systematic search. (b) Full vector ant that completes almost 100% of its home vector before recovering the nest. (c) Full vector ant that completes only approximately 50% of its home vector before returning towards the release area prior to recovering its learned route.

be followed for their entire foraging life or displaced to a completely novel location where no visual cues could have been experienced before.

It should be noted however that individual Off-Route trials produced paths as reported in other studies. In figure 5.18 (a) a zero vector ant performs the classic looping search pattern characterizing a systematic search (Müller and Wehner, 1994) until its path approaches the route leading to the nest. Correspondingly, figure 5.18 (b) shows a full vector ant following the home vector as best it can whilst weaving through the grass tussocks. In this case the ant expires almost the full vector before approaching the nest directly. Recent studies (Narendra, 2007b) report that when visual cues are unfamiliar ants appear to lose confidence in their home vector. Thus they only express around 50% of the home vector before engaging a search as demonstrated by the ant path in figure 5.18 (c).

5.5 Discussion

The data presented clearly demonstrates that the European desert ant *Cataglyphis velox* adopts a similar foraging strategy to other ant species sharing the same ecological niche in other continents. Visually guided routes offer a robust form of navigation over large distances where cumulative errors erode the accuracy of the global home vector.

Visual input is shown sufficient for route following in *Cataglyphis velox* even when in conflict with path integration cues. Whilst the data presented cannot be conclusively interpreted, there is at least qualitative evidence that the path integrator remains active and guides foragers when visual cues fail. These results closely correlate with findings in the Australian ant *Melophorus bagoti* which inhabits a very similar environment, and hints towards a common strategy of navigation.

Schwarz and Cheng (2010) recently compared the visual learning performance of the African desert ant *C. fortis* which is generally found in barren open desert (Dillier and Wehner, 2004) to the Australian ant *M. bagoti* inhabiting shrub surround (Muser et al., 2005). Significant differences in performance were observed with *C. fortis* being outperformed by *M. bagoti* throughout. The authors hypothesise that this may be the result of an evolutionary bias towards visual learning in the *M. bagoti* ant that inhabits a visually cluttered environment whereas *C. fortis* existing in featureless regions may have optimised for path integration. *C. velox* offers an interesting middle ground for such studies, being evolutionary closer to *C. fortis* but

ecologically closer to *M. bagoti*. It may prove that the various species indeed share a common strategy and the results of Schwarz and Cheng (2010) are an indicative of an habitat specific fine tuning of cue integration. More comparative studies across species are required to resolve the subtleties of the various results observed in different species.

Chapter 6

Efficacy of Visual Homing Models in Natural Ant Habitat

6.1 Introduction

The time spent in the habitat of *Cataglyphis velox* offered a unique opportunity to sample the visual environment in which routes are formed. Such image databases sampled in natural environment through which insects pilot have become an increasingly powerful tool with which to study navigational behaviours. For example Zeil et al. (2003) used panoramic camera mounted on a gantry robot to sample an image database in a clearing near some woods. They were then able to show that a simple pixelwise difference measure increased with distance from the reference location and thus agents (model or animal) could home by simply following the error gradient. The realisation of this novel homing strategy was made possible by viewing the world from the insect perspective and analysing the data present in the visual surroundings.

More recently, individual panoramic images sampled under various experimental manipulations, in which insects were also observed, have allowed a systematic analysis of the visual cues necessary and sufficient for accurate homing to occur (Towne and Moscrip, 2008; Graham and Cheng, 2009b,a).

To the best of the authors knowledge no image database exists that maps the entire region in which ant routes are observed. However, it should be noted that a recent study (Basten and Mallot, 2010) tested two models of visual homing in a 3D simulation of the habitat in which routes of *Melophorus bagoti* were recorded (Kohler and Wehner, 2005). Unfortunately the authors only had the overhead map-

ping of the ant habitat to guide their simulated habitat design. Thus all grass tussock are set to a common height of 25cm with some local noise to produce an irregular finish.

Basten and Mallot (2010) focus their analysis on the efficacy of two models of visual homing when supplied with two distinct forms of visual input: an intensity image (as utilised in this work), and a 1-D vector encoding the panoramic skyline. The two models implemented were an IDF model and an adapted ALV model, which in essence is equivalent to the COMALV model of this work. The study optimised for the largest area surrounding an arbitrary goal location over which the model could provide accurate guidance cues. When supplied with intensity images ranges of approximately 1m^2 and 0.6m^2 were achieved for the adapted-ALV and IDF models respectively. Instead, when supplied with the skyline as stimulus model ranges of approximately 2m^2 and 0.5m^2 respectively were observed.

The 86 reference locations from which models were tested coincide with the recorded positions of a single ant travelling through along its repeated route. Thus, the efficacy of the models, and visual stimulus were only assessed relative to one ant and also in a limited region of the habitat. Indeed, there is no direct comparison between the modelling outcomes and observed desert ant routes.

In this chapter a modelling study is conducted using the principles outlined in chapter 4. An image database is presented that was collected within the same habitat in which ant routes were observed. The suite of biological models tested in the hot-plate paradigm are then tested within the ant habitat. Modelling using the raw images as input proved problematic and therefore a simulated ant habitat is constructed, allowing the models to be assessed with *ideal visual input*. That is, free from noise due to sun-glare, camera tilt, clouds, and sampled at high spatial resolution.

Specifically, the following research questions are posed:

- *Can any of the biologically plausible models of visual homing provide robust guidance in the ant habitat?*
- *If so, can a single visual memory provide guidance over the entirety of the observed routes - or are multiple memories required?*

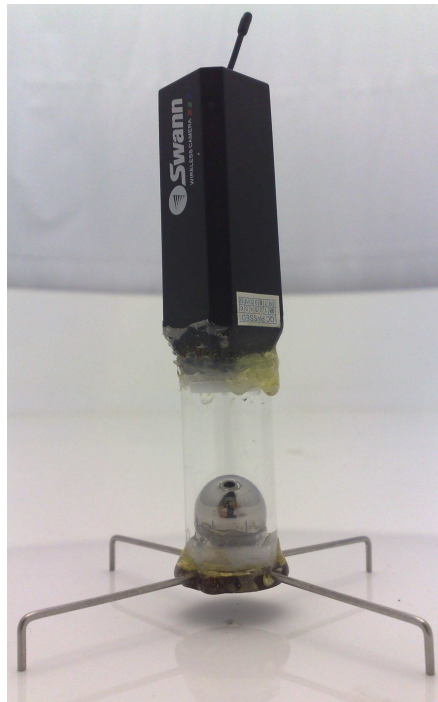


Figure 6.1: **Custom panoramic camera used to capture the image database in ant habitat.** Shown is the battery powered wireless camera above the polished ball-bearing acting as a mirror. The camera and base are linked by the acrylic tube which also protects the mirror from contaminants. The legs provided mechanical support and allowed the camera to be manually levelled in the uneven terrain.

6.2 Methodology

6.2.1 Image Database

An image database was collected using the custom panoramic camera system shown in figure 6.1. The camera is mounted above the mirror such that the image horizon closely matches that of an ant (ant head 1-2mm above surface, camera horizon approximately 15mm above surface). Images were sampled at 50cm intervals within the 10m*10m test area in which ants were observed. This produced an image database of 424 images as shown in figure 6.2. It should be noted all images are captured with the camera at a constant orientation.

Images are unwrapped using the OCamCalib Toolbox for MATLAB (Rufli et al., 2008; Scaramuzza et al., 2006a,b) and an example panoramic image sampled from the ant habitat is shown in figure 6.3 (a).

Initial model testing was conducted using the real world panoramic images as

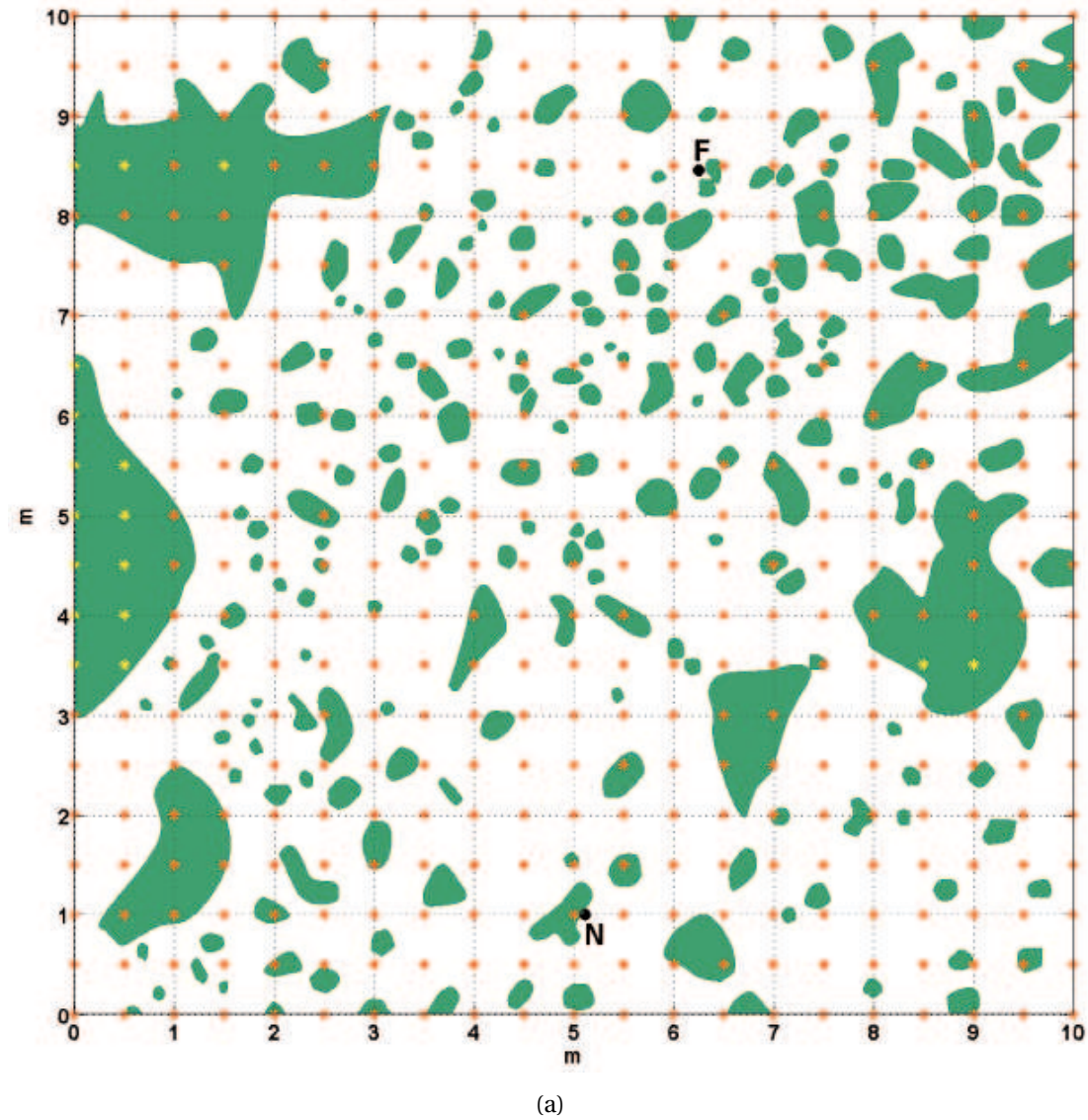


Figure 6.2: **Image sampling within ant habitat.** Locations where images are sampled are indicated by red stars and locations where images were not able to be sampled due to dense vegetation are indicated by yellow stars.

visual input. However no model produced reliable home vectors for any combination of parameters. A variety of factors may have influenced the failure including sun glare, dynamic light changes, cloud contamination, camera tilt and orientation offsets. Considerable effort was invested to correct for these possible sources of error. Sun glare was removed by manually identifying patches of glare in images and filling with RGB values sampled from surrounding pixels. Tilt was identified in images by fitting a sinusoid to the visible horizon and images realligned accordingly. Furthermore, offset in camera orientations was compensated for by allowing models to optimise across a series of rotational displacements. Regardless of these amendments homing performance remained poor for all models.

Further image preprocessing may have improved results, however the search space of possible solutions rendered such an approach infeasible for this work. Additionally it remains possible that the 50cm spacing between images was larger than the catchment area of models even when supplied with reliable guidance cues. Instead a simulated ant habitat was created allowing models to be supplied ideal visual input sampled at high spatial resolution.

6.2.2 Simulated Ant Habitat

A simulated ant habitat is created using information derived from both the panoramic image database and the overhead map of the ant environment. Every grass tussock visible in all panoramic images is mapped to a corresponding tussock outlined in the top-down map of the ant area. The angle of elevation to the peak of each tussock was recorded in every panoramic image that it appears. The top-down map then provides an estimate of distance from the image capture point to each tussock allowing computation of every tussock height by simple trigonometry. Combining the height data of tussocks with the top-down map provides sufficient information to construct a 3-dimensional model of the entire 10m*10m ant world.

Panoramic images are then generated through a simple ray-tracing procedure. From the defined agent location, rays are projected through 0° to 45° degrees vertically and 0° to 360° horizontally at 1° resolution maintaining consistency with the unwrapping resolution of real world images. Note that the height at which images were created was held constant at 1cm above the surface. Rays are traced in space until either a tussock or the world boundary is encountered and the pixel value set to green or blue respectively.



(a) Real world image.



(b) Artificial world image



(c) Real world image passed to the models after image processing.



(d) Artificial world image passed to the models after image processing.

Figure 6.3: **Panoramic images sampled at the same location in both real and simulated ant habitats.** (a) and (b) shows the unprocessed images generated in the real and simulated ant habitats. (c) and (d) present the same images after being passed through the ant eye model. Note that the grass tussocks in the artificial world generally appear larger as their heights were defined by the peak height visible in the real images.

The images generated in the simulated habitat provide the simplest possible input for models free from all noise and error sources thought to affect the real-world images. Furthermore, images can be sampled at virtually infinite spatial resolution in the simulated world. These factors allows normative testing of visual homing models with highly controlled visual input. Testing of this form also provides an upper limit of model performance possibly providing insight into the reasons for model failure using real images.

Figure 6.3 shows examples of the images produced at the same location in both the real and simulated ant habitats.

6.2.3 Models of Visual Homing

All biologically plausible visual homing models outlined and tested in chapter 4 are included in this study:

1. Average Landmark Vector (ALV).
2. Centre-of-mass Average Landmark Vector (COMALV).
3. First Order Optic Flow (FO).
4. Second Order Optic Flow (SO).
5. Image Difference Function (IDF).

6.2.4 Parameter Tuning

As in chapter 4 visual homing models are allowed to optimise across a number of parameters such that there is no bias towards any particular model.

Image area used: Due to the panoramic images being generated with the image horizon close to the ground the image regions optimised for are altered to:

1. Horizon pixels only (0°).
2. 5° above the horizon.
3. 10° above the horizon.
4. 20° above the horizon.
5. 30° above the horizon.

6. Full image (0° to 45°).

Down-sampling rate: Visual input is supplied from the image data-base as a panoramic image at 1° resolution rising from the horizon at 0° to an elevation of 45°. Note that interommatidial angle of *Cataglyphis bicolor* is smallest at the horizon at around 4° (Land, 1997), thus the native image resolution far exceeds the resolution of the ant eye. However, to maintain consistency with earlier work models are again optimised for 1°, 2° and 4° image resolution.

Image Smoothing: Images are again blurred using a first order Butterworth filter with a cut-off frequency of 3° as observed in *Cataglyphis bicolor* (Labhart, 1986). Models are again allowed to optimise the amount of further image smoothing through 0, 1, 3 or 5 applications of the Gaussian filter.

Image Type: Models also optimise for either greyscale images or black and white using the thresholding technique described previously.

6.2.5 Model Metrics

6.2.5.1 Catchment Area

In this study model performance is assessed using the catchment area (CA) size as metric. The CA is defined as the continuous area surrounding the target location from which an agent could successfully home. More specifically the CA is calculated by first computing home vectors at all image locations in the defined vicinity - a 10cm grid extending +/- 1.5m from the target in both x and y is used. Note this range was chosen as it extends further than the maximum catchment area observed by Basten and Mallot (2010). Homing trials are then initiated at all locations and path traced until either the home location is reached or a time limit is reached. The CA is then computed using a region growing algorithm.

CAs are measured at sixty pre-selected target locations as shown in figure 6.4. The sixty locations are intentionally distant from grass tussocks as proximal landmarks are known to influence the performance of some models. Furthermore, all target locations are more than 2m from the world boundary to mitigate boundary effects present in the simulated habitat.

6.2.5.2 Number of Visual Memories Required For Routes

A second metric is also defined to quantify the number of visual memories required for models to replicate the routes observed in ants. That is, for each model the number of reference images necessary to traverse the median routes of all ants (both outward and inward) is assessed. Thus, models that generate small CAs, or fail completely in specific habitat conditions will require a larger memory set than models that are robust across the environment.

All routes are traced from nest to feeder, and the goal of the model is to require as few memories as possible to traverse the path. To trace the path an initial route memory is defined. Ideally this would have been situated at the nest entrance, however many ants entered the nest via the adjacent grass tussock. Travelling inside designated landmarks causes problems for the simulation and therefore the first memory on each route is pre-defined as 25cm from the nest. The model being investigated then computes the CA surrounding the first route memory, and draws its boundary. The algorithm then traces the ant path until the CA boundary is breached: the location at which the current visual memories no longer provides reliable guidance cues. The algorithm then stores the panoramic scene at this location as a new visual memory, the surrounding CA is computed, and the ant path traced until the new CA is breached. This procedure is repeated until the feeder is reached. The result is a list of memory locations necessary for each model to traverse the paths of every ant.

It should be noted that in some regions of the simulation certain models fail to generate any accurate guidance cues, and thus the CA falls to zero. In such circumstances (when no CA can be generated meaning that the route cannot be traversed by the means outlined above), the algorithm jumps 5cm along the ant path and a new memory is stored. This procedure penalises models that fail completely by increasing the memory requirements, but also prevents the algorithm becoming locked in loops.

6.3 Results

The general effectiveness of the various homing models within the simulated ant habitat was assessed by optimising CA sizes from sixty target locations and assessing the number of memories required to navigate a route. Figure 6.5 (a) and (b) show

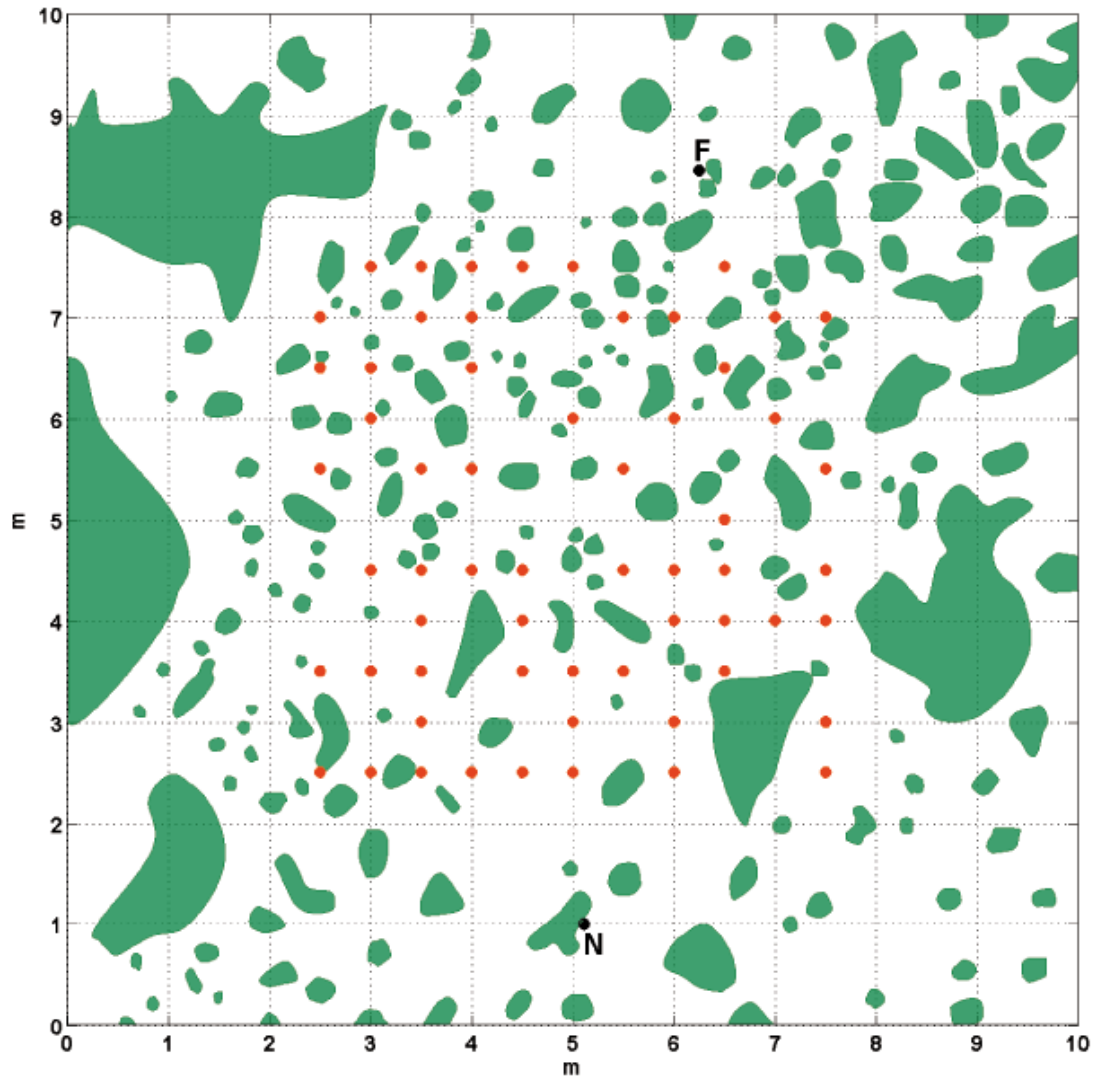


Figure 6.4: **60 homing target locations.** Each model is tested on its ability to home to the 60 locations shown from test areas spreading $\pm 1.5\text{m}$ in both x and y . Target locations were chosen randomly from the 424 image locations on the 50cm grid from which real images were sampled.

boxplots of the optimal CA sizes calculated across the sixty test locations and the number of route memories required to reconstruct the paths recorded in real ants.

6.3.1 ALV Model

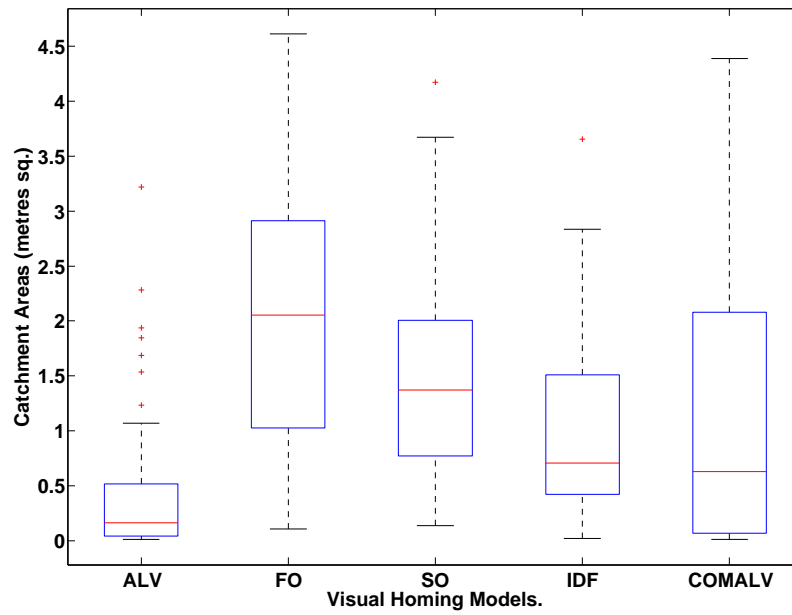
The optimal parameter settings found for the ALV model were: image resolution of 1°; 1 application of the Gaussian filter; image region 20° above the horizon; using greyscale images.

It is clear that ALV Model generates small CAs across target locations, and correspondingly requires a relatively large number of visual memories to reconstruct the ant routes. The median CA size for the ALV Model across test locations was 0.17m² which was the smallest of all models with statistical significance ($p < 0.01$ for all comparisons). The second model metric revealed that the median number of memories required to trace the ant routes was 59.

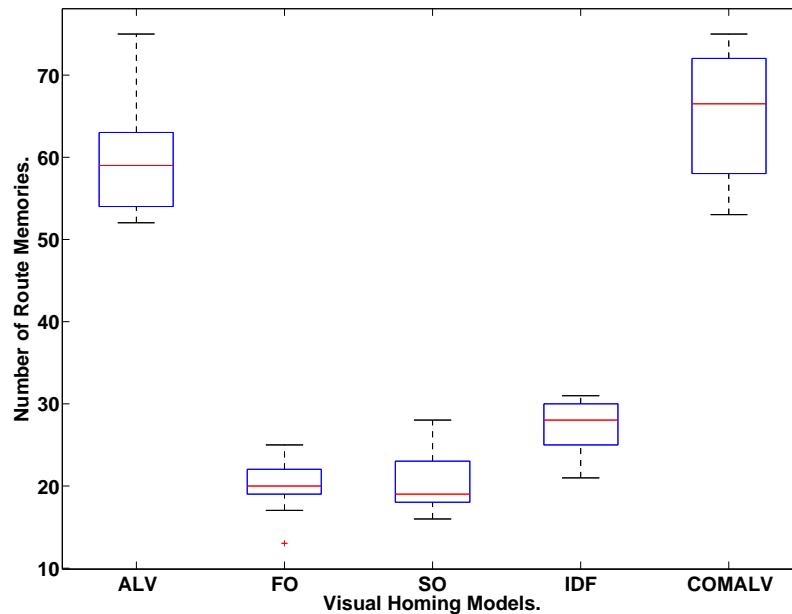
The poor performance of the ALV model in the simulated, as in the hot-plate paradigm, is due to the difficulty in reliably extracting edges. The simulated visual input may have in some cases made edge extraction tougher. For example, as all grass tussocks are coloured solid green in the simulated world then visually segmenting overlapping landmarks may be harder than in the real-world images where different landmarks may appear visually distinct. However it should also be noted that the vertical edges, which the ALV model seeks to extract, are exaggerated in the simulation.

The small CAs generated by the ALV model leads to the large number of visual memories needed to reconstruct the observed routes of ants. Figure 6.6 (a) shows the visual memories needed to reproduce one ant route. It is clear that there are large portions of the ant habitat in which the model completely fails. This is indicated by the red dots that indicate where insufficient guidance cues were available such that the route could be traced.

Given that the simulated ant habitat offers the simplest possible representation of the world in which to navigate it seems unlikely that the ALV performance would be significantly improved using real images. The ALV model is therefore unlikely to be a strategy employed by foraging ants.

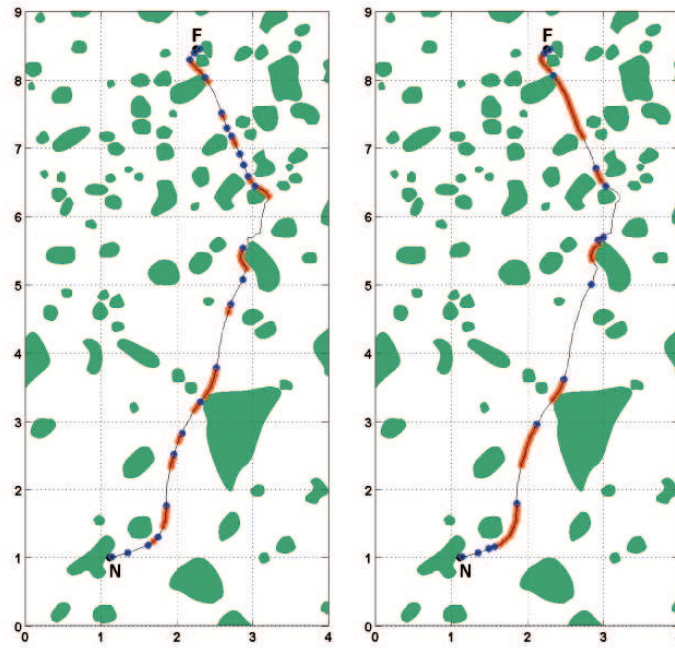


(a) Optimal catchment area sizes.



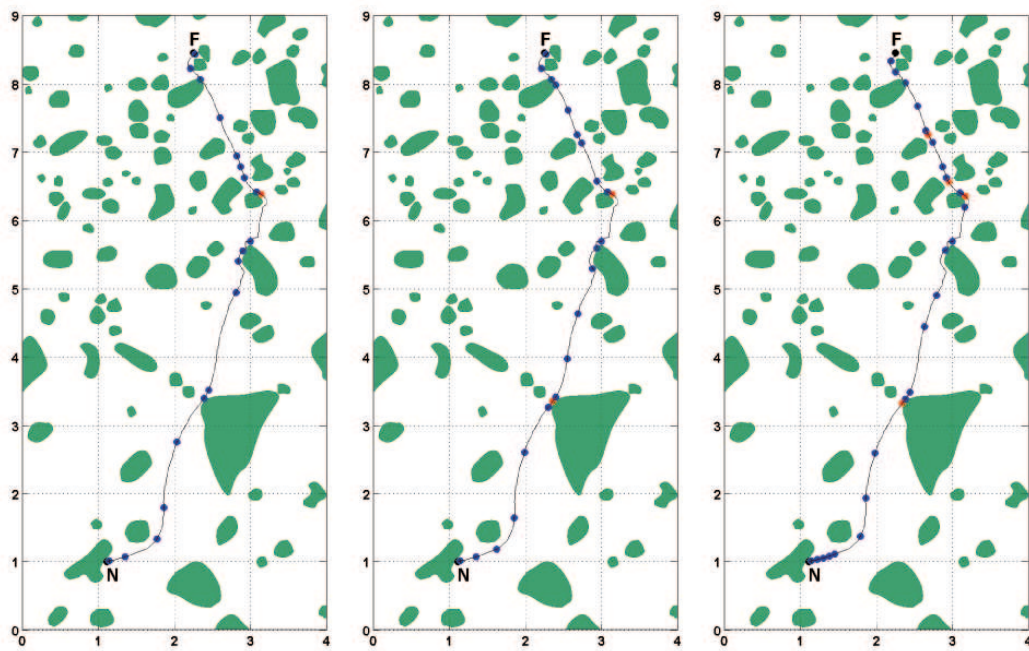
(b) Number of memories to retrace ant paths.

Figure 6.5: **Optimal performance of visual homing model in ant habitat.** (a) Box-plots showing the Catchment Area sizes generated across the 60 test locations using the optimal parameter settings for each model. Medians: ALV=0.17m², FO=2.05m², SO=1.37m², IDF=0.71m², COMALV=0.63m². (b) Box-plots showing the number of visual memories required to reproduce the routes recorded with foraging *C. velox* (n=14). Medians: ALV=59, FO=20, SO=19, IDF=28, COMALV=66. Boxes show lines at the lower quartile, median, and upper quartile values. Whiskers indicate the most extreme values within 1.5 times the interquartile range from the ends of the box. Outliers are shown as + signs.



(a) ALV - 61 memories

(b) COMALV - 67 memories.



(c) FO - 20 memories

(d) SO - 23 memories.

(e) IDF - 28 memories.

Figure 6.6: **Number of visual memories required by the various models to traverse the example route.** The black line shows the median route of an ant observed in the field study. The blue dots show where visual memories are stored and the red dots show locations where the model fails to generate any useful homing cues.

6.3.2 COMALV Model

The optimal parameter settings found for the COMALV model were: image resolution of 2°; 1 application of the Gaussian filter; image region 30° above the horizon; and using greyscale images. Performance of the model appears robust to changes in image type, resolution and smoothing. CA sizes decrease however when the image region used is small (horizon only and 10° above the horizon), where the input would likely be saturated with landmarks in all directions.

Given the good performance of the COMALV model in chapter 4 it is surprising that it produces the second smallest CAs across test conditions, indeed failing completely at various sites (median CA 0.63m²). The reason for the failure is that in some regions of the ant habitat the COMALV generated at the target location is negligible. This occurs at locations in the simulated habitat where landmarks on all sides appear similar. For example, in the case where only two landmarks are visible which are identical in size but located at opposite sides of the agent. When the COMALV at this location is computed the influence of each landmark will be cancelled by the other and therefore the overall vector will have a negligible magnitude. The effect is that in the vector subtraction step required to generate home vectors ($h = ALV_C - ALV_H$), the influence of the (ALV_H) is negligible. This is the same problem reported for the COMALV model within the Blank Walls surround in chapter 4.

It should be noted however, that in some locations the COMALV performs very well leading to the large variance in CA size (see figure 6.5). The COMALV is statistically outperformed by both optic flow models ($p < 0.01$) however the performance of the COMALV model and the IDF model cannot be statically distinguished using the CA size criteria ($p = 0.12$).

The model performance drops significantly when tested using the second performance metric. The median number of visual memories required to reconstruct the ant routes is 66 - marginally larger than that required by the ALV Model ($p = 0.09$). This result is due to the complete failure of the model in large regions of the simulated ant habitat for the reason outlined above.

6.3.3 Image Difference Model

The optimal parameter settings found for the IDF model were: image resolution of 4°; 5 application of the Gaussian filter; image region 45° above the horizon; and

using greyscale images. Performance of the IDF Model is however robust to changes of all parameters barring the image region. Performance drops when image regions 10° above the horizon and horizon pixels alone are used. This is likely due to the visual input being saturated by uniform landmarks in these regions which prevents error gradient formation.

The IDF is statistically outperformed by the optic flow based models ($p < 0.01$) when comparing CA sizes. It does however produce CA sizes that are marginally larger than the COMALV (median CA = 0.71m^2). Attention is drawn to the robustness of the model: there are few test locations in which performance fails altogether. Correspondingly the IDF model requires far fewer visual memories than the COMALV model to recreate the ant routes (median memories 28). In this test the model outperforms the COMALV model with statistical significance ($p < 0.01$).

6.3.4 Optic Flow Based Models

Both optic flow based models generate large CAs (median CA: First Order 2.05m^2 ; Second Order 1.37m^2) and correspondingly required the fewest visual memories to reconstruct the ant routes (median CA: First Order 20; Second Order 19). The First Order Model produced significantly larger CAs ($p < 0.01$), however performance could not be separated in the route generating test ($p = 0.83$).

The optimal parameter settings computed for the First Order Model are: image resolution of 1° ; 5 application of the Gaussian filter; image region 20° above the horizon; and using greyscale images. And for the Second Order Model: image resolution of 2° ; 5 application of the Gaussian filter; image region 20° above the horizon; and using greyscale images. Both models are robust to changes in image resolution, and to most image regions conditions although performance drops using only 10° above the horizon images. This is likely due to the reasons outlined above for the other models.

The optic flow based models are highly sensitive to image smoothing with significant improvement in performance with every application of the Gaussian filter. The smoothing effect of the Gaussian filters on the simple binary images (blue and green) introduces and extends intensity gradients across the visual input. This in turn increases the robustness of translation vector accuracy in the foci of expansion and contraction which are crucial to accurate home vector generation. It should be noted that similarly smooth and continuous image gradients are unlikely to be

present in the natural images.

6.4 Conclusions

This chapter assessed the efficacy of five biologically plausible models of visual homing. Models were initially supplied with unwrapped real-world images directly as visual input however, a combination of image corruption and large inter-image spacing rendered all models ineffectual. Instead a 3-D simulation of the ant habitat based on the captured images was created allowing models to be supplied with noise-free visual input images at high spatial resolution. The five biologically plausible models of visual homing implemented in chapter 3 were then tested for efficacy using this *ideal* input.

All models were assessed on their ability to generate catchment areas surrounding sixty hand picked target locations. That is, the area surrounding the target location from which an agent could return to the reference position. Models were free to optimise over various parameters including smoothing, image type and regions, and resolution. The magnitude, and variance of CA sizes over the sixty test locations offers a good measure of the efficacy of models.

The results presented allow the specific research questions posed in the Introduction to be answered directly.

- *Can any of the biologically plausible models of visual homing provide robust guidance in the ant habitat?*

It is clear that both optic flow and IDF Models of visual homing could provide insects with robust guidance in the ant habitat. While the COMALV Model generates accurate guidance in some regions of the habitat, it also fails completely in others. Due to the high environmental pressures facing foraging desert ants it seems unlikely that insects would utilise a homing strategy with such variance. However, it should be noted that in a similar work Basten and Mallot (2010) did not report the same level of variance and therefore further investigation, possibly through performance testing in both simulated habitats, is required before firm conclusions can be drawn. The ALV Model fails to generate robust guidance cues across the ant habitat and therefore is very unlikely to be the strategy employed by ants.

In this work the optic flow based models generated accurate homing signals over the largest range. Although it should be noted that this performance range is likely

to decrease as real world visual input is provided, as the smooth image gradients on which these models are so reliant are unlikely to be maintained. At this juncture the range of insect homing is unknown and therefore it is not possible to state which model is more likely to be used by insects. Indeed, empirical experimentation to quantify the CA range and also shape could be a powerful paradigm against which to assess models.

- *If so, can a single visual memory provide guidance over the entirety of the observed routes - or are multiple memories required?*

The Catchment Areas generated in the first test condition demonstrate that none of the models can provide guidance over a sufficient range such that a single visual memory could guide an ant over its entire route. Thus models were subjected to a second test condition that sought to quantify the number of visual memories that would be required for the various models to home from the feeder to the nest.

Despite producing large CAs in some regions of the ant habitat, in others the COMALV failed completely. This resulted in the COMALV model requiring the most visual memories to retrace the ant routes (median memories required: 66). Similarly, the ALV model also performed poorly with a median of 59 visual memories required to re-trace the ant paths.

In contrast the three remaining models required a consistently small number of visual memories across routes (median memory requirements: 20 for FO, 19 for SO and 28 for IDF). The variance in required route memories was also tightly bounded for each of these models showing a robustness in performance across the ant habitat.

6.5 Discussion

This study describes the performance of the most biologically plausible visual homing models in a simulated ant habitat. It should be noted that the simulated world was based not only on a mapping of the environment but on an image database collected within the natural habitat. Thus, the height and width of the grass tussocks that populate the desert ant habitat are true to that which the animals observed. Moreover when the simplistic blue and green images are converted to greyscale, the simulated visual input corresponds well to the real images. It should also be noted that the various models not only differ in how they compute a homing signal but

also in what information they extract and process from their visual surroundings. Therefore the data presented can be considered at one level an analysis of the presence and robustness of differing visual cues visible to the insect.

Most interesting amongst the results is the CAs derived for the COMALV and IDF models which are similar in magnitude to that described by Basten and Mallot (2010). However, this study reports large levels of variance in the performance of the COMALV model in specific regions of the habitat which is not found in the other study. At this time it is unclear whether this is due to slight model differences (*Basten et al* did not explicitly implement the COMALV model), or a feature of either simulation.

(Basten and Mallot, 2010) also assessed the range of both a IDF model and an equivalent COMALV model when provided with a one dimensional vector representing the panoramic skyline. Performance of the IDF did not improve whereas the COMALV model range increased to approximately 2m^2 to match that of the optic flow models in this work. The desert ant compound eye is known to be well suited extracting the location where terrestrial cues give way to sky (Möller, 2002). A number of studies have shown that the skyline is the dominant cue driving visual homing in ants (Fukushi, 2001; Graham and Cheng, 2009a) but the exact encoding of the information remains unclear. Further experimentation, with tight controls on the visual information available to the homing insect is needed to tease out the exact information encoding at play. Validation of behavioural results using simulated habitats such as those in Basten and Mallot (2010) and in this work, where visual input can be artificially amended, may prove invaluable to this effort.

Chapter 7

Conclusions and Discussion

The motivation for this thesis was to investigate the visual navigation strategies employed by insects. In chapter 2 a review of the current literature was presented from which two timely research questions were developed:

- *Are visual homing capabilities conserved across diurnal insects indicating a general navigational ability across species?*
- *If so, is there a single method of visual homing that can account for such behaviours?*

The remainder of this chapter presents an analysis of the success of this study in answering these questions. Specifically, the key contributions of this thesis are summarised before a discussion of how the results presented fit within the context of current research. Moreover, future research avenues that can build upon this thesis shall be outlined.

7.1 Key Contributions

- In chapter 3 the homing ability of the field cricket *Gryllus bimaculatus* was assessed in an experimental paradigm analogous to the Morris water-maze (Morris et al., 1982). It was shown that crickets successfully learned the location of a hidden cool-spot using surrounding visual cues. Performance was best when a natural scene stimulus was supplied, followed by blank walls, and finally distinct landmarks. No learning was observed in the dark control. To the best of the authors knowledge this is the first conclusive proof that crickets are capable of visual homing.

- Chapter 4 presented a biorobotic study aiming to verify if any biologically plausible model of visual homing could account for the cricket data when tested in the same experimental conditions. To the best of the authors knowledge this is the first study in which the foremost models of visual homing have been ranked with respect to their ability to replicate real insect data.

Of the five models implemented only the COMALV and IDF Models replicated the performance trend observed in crickets. Feature-based and optic flow based models failed to match the cricket performance when provided with either the natural image, or blank arena walls stimulus respectively.

- Chapter 5 presents a field study investigation into the natural foraging behaviour of the European desert ant species *Cataglyphis velox*. This is the first recording of the navigational strategies employed by this species. Foragers were shown to learn idiosyncratic routes by which they travel to and from a regular feeding site. These paths are distinct from the routes of other ants despite their journeys having identical start and end points. Moreover, visual cues are shown sufficient for route recall and guidance. Thus, it is shown that visual navigational strategies are closely matched to those reported in geographically distant desert ant species that exploit a similar ecological niche (for example *Melophorus bagoti* in Australia).
- Chapter 5 also shows the development of multiple distinct routes by individual *Cataglyphis velox* foragers. These route memories are stored concurrently allowing ants to switch between routes when appropriate. The data presented also suggests that these novel routes are learned after only one instance. While desert ants have been shown capable of learning multiple routes through experimental manipulation (Sommer et al., 2008), this is the first report of their natural occurrence.
- Chapter 6 presents an analysis of the efficacy of the same biologically plausible models of visual homing implemented in chapter 3, in the natural ant habitat. None of the models generated sufficiently large catchment areas that an ant could navigate their route using a single visual memory. Models were instead ranked on the number of visual memories required to reproduce the routes observed in the field study. The COMALV Model failed to generate accurate homing cues in extended regions of the ant habitat, and thus scored

second last of all models. In contrast the IDF Model showed robust performance across locations and required a low number of visual memories to reconstruct the routes observed in ants. Thus the IDF model is the only model to offer robust cues in the ant habitat as well as replicating the cricket data.

7.2 Discussion and Future Work

7.2.1 Hot-plate Paradigm

The hot-plate paradigm has proven a powerful tool for the study of visual homing capabilities in a series of insect species including cockroaches (Mizunami et al., 1998b), crickets, and more recently fruit flies (Foucaud et al., 2010; Ofstad et al., 2010). Recent enhancements of the experimental apparatus have included the use of heating tiles to heat the arena floor, and in the case of Ofstad et al. (2010) provision of visual stimuli via a matrix of LEDs. These augmentations open up novel experimental possibilities, for example by coupling insect movement to dynamic changes in the visual stimulus.

In chapter 3 two models of visual homing were shown to reproduce the performance trend of crickets given various static stimulus: COMALV and IDF models. The COMALV model relies upon robust intensity vectors to generate accurate homing signals, whereas the IDF model compares raw pixel values directly. It is therefore feasible that a carefully selected visual stimulus could be created more suited to each model type. Differing results in one or other condition would add significant support to the case for its use in homing insects.

A similar model-driven adaptation of the paradigm could occur through the introduction of physical landmarks as stimulus. In the case where azimuthal intensity values balance, a robust COMALV cannot be generated and thus the COMALV model fails (see chapter 6). An intensity balanced visual environment could be easily produced using identical landmarks spaced 180° apart with a blank background. Indeed, it may be possible to replicate landmark manipulation studies performed in ants (Wehner et al., 1996; Graham et al., 2003; Narendra et al., 2007) and bees (Cartwright and Collett, 1983) offering further insights into the generality of visual homing strategies across insects. Moreover, physical landmarks provide insects with a more realistic environment containing motion parallax cues absent in the current paradigm.

A final research avenue could explore the neural firing patterns in freely moving insects within the hot-plate paradigm. Neural recording in cockroaches was demonstrated by Mizunami et al. (1998a). Studies of this kind would allow for the investigation of the information pathways and specific neuropils crucial to visual homing. Such efforts would be complementary to any genetic studies that are possible in smaller insects such as fruit flies in which direct neural recording in freely moving animals would be impractical.

7.2.2 Multiple Visual Memories

All visual homing models implemented in this work rest on the assumption that the current visual scene is aligned with the visual memory stored at the target location. This premise holds in many cases as various insect species infer their orientation from allothetic cues such as polarised light from the Sun. Knowledge of the angular offset between the animal's current orientation and the orientation at which the reference image was sampled provides sufficient information for correction: either through internal image manipulation or adjustment of the animal's current heading.

When homing in the hot-plate paradigm crickets did not have access to any external compass cues; magnetic or celestial. (Zeil et al., 2003) demonstrated that an IDF also exists in the rotational dimension with pixelwise errors decreasing as the angular match between current and reference image decreases. Such a process would require the animal to rotate to align images yet such behaviour was not evident across crickets. Thus, without extension the current models cannot completely account for the homing performance of the animals.

One could hypothesise that crickets store multiple visual memories at various orientations when at the target location. When homing the insect would then select the visual memory most closely matching its current visual input to act as the reference image. Autoassociative networks (e.g. Hopfield Net (Hopfield, 1982)) provide one possible framework by which multiple memories could be stored, and later retrieved. Such networks can retrieve complete memories from partial information, and thus may be able to recall the appropriate reference memory even when the displaced from the goal location.

It is worth noting that the results from chapter 6 indicate that ants require multiple visual memories to navigate along their routes. It may be possible that the

a similar network to that outlined above could store the chain of visual memories making up a route.

7.2.3 Integrating Multiple Navigational Cues

In chapter 5 *Catahlyphis velox* were shown to navigate predominantly through visual and path integration strategies in common with other species of desert ant. This study and others (Kohler and Wehner, 2005) have also shown that when the global home vector and visual cues placed are out of context, desert ant species tested in cluttered environments adopt the route as indicated by the visual surroundings. In contrast, desert ants tested in featureless terrain will ignore landmarks indicating the nest position until their home vector nears completion (Wehner et al., 1996).

Furthermore, visual cues are known to influence the extent to which the home vector is followed. Narendra (2007a) showed that ants trained and tested within a channel, thus without influence of external visual cues, will complete their full home vector path before engaging a search in a test channel. Yet, when the test is conducted in open terrain, where the visual surround does not match that as in training, ants consistently expire only 50% of their home vector before initiating search. The mechanism by which these redundant navigational cues are integrated remains undefined.

Cheng et al. (2007) have recently discussed multi-sensory cue integration in animal navigation within a Bayesian context. The question is therefore raised as to whether ants combine their visual and path integration cues using an optimal strategy. That is, do ants predict the nest position by weighting the different sensory cues relative to their variance. Encouragingly, studies in both honeybees (Chittka and Geiger, 1995) and desert ants (Merkle and Wehner, 2010) provide data that fits within such a framework.

In a controlled experiment it should be possible to measure the accuracy of homing when ants have access to only one of their navigational cues, and contrast this with the accuracy when both cues are present. A similar procedure has been followed to assess optimal cue integration in humans (Nardini et al., 2008). The variance of the homing cues can then be increased systematically, for example by overhead light diffusers to scramble polarised light, and the resultant change in homing accuracy recorded. The behaviour of the insects should be markedly dif-

ferent if they are utilising a mixture model or a Bayesian strategy, which could be confirmed through a modelling study.

It should be noted that Bayesian methods have achieved great success when applied to robot navigation problems (Thrun et al., 2005, 2007). If ants are shown to combine sensory cues in Bayesian fashion then the overlap between insect navigation and robot applications will only increase. To give a specific example, ants relocated from the nest to feeder (section 5.3.2.2) resolve their location without the aid of self-generated motion cues as during normal foraging. This situation is conceptually identical to the classic "kidnapped robot" problem in robotics which has been addressed by Bayesian methods (Durrant-Whyte et al., 2003).

7.2.4 Navigating The Ant Habitat

Chapter 6 reported on the performance of the various visual homing models within a simulated ant habitat. This is somewhat contrary to the stated aim of this work: to assess models using real-world visual stimuli as experienced by insects. However, as all models failed to generate robust guidance cues when supplied with real image data simulated visual input offered a highly controlled stimulus with which to test models.

The model catchment areas range from approximately 0.17m^2 to 2.05m^2 , indicating that even if supplied with noise-free input many models could not have generated accurate homing signals in the image database. Yet, the impact that other error sources such as camera tilt, cloud contamination, and dynamic lighting would have on models remains unknown.

Animals are known to actively compensate for error sources. For example many species of bird actively compensate for motion blur by co-ordinating head and body movements (Necker, 2007). Insects also engage strategies that reduce homing error likelihood. For example the learning walks of foraging are characterised by the individual stopping, and rotating to face the nest directly (Müller and Wehner, 2010), or most conspicuous nest-based landmark (Nicholson et al., 1999). Thus when the ant is later returning to the nest, possibly guided by path integration, they shall encounter a familiar and correctly aligned visual scene which can offer precise guidance in the final stages of their journey.

Such behaviours offer insights into the homing strategies employed by insects as some mechanisms will be more robust to some error sources than others. The

simulated ant habitat provides an tool with which to address these issues in an controlled manner. By adding real-world inspired noise to the visual and motor systems in a systematic manner and then analysing the impact on performance it may be possible to infer the likelihood that individual models are sufficiently robust to offer guidance in real world conditions. Furthermore, it should be possible to define novel strategies that mitigate, or at least reduce, the influence of these errors. Comparing the strategies required by various models could in turn inspire empirical studies in insects seeking to identify if insects engage similar behaviours or not. Indeed, it may then also be possible to design future experimental design by manipulating the habitat in which the models are tested.

7.3 Closing Remarks

This work was motivated by the confounding ability of the humble insect to navigate complex habitats over large distances and with great accuracy. This amazement is only compounded when considering the meager neural resources at the disposal of these animals. Yet it is this meeting of complex behaviour with simple nervous system that offers so much promise to the investigation of control and cognition, and inspired this author to complete this work.

The behavioural studies undertaken have reported on the visual homing abilities of two insect species for which little was previously known. In both cases, the experimental design was explicitly driven by current modelling theory, and correspondingly models were assessed on their ability to replicate the animal data. Implementation and testing of models in this comparative methodology has been crucial to the results reported and conclusions drawn from this work. Indeed, with increasing computer power, continued miniaturisation of electronics, and improved batteries, biorobotics will likely play an increasingly prominent role in the neuroethological investigation in the future.

It is hoped that the conclusions of this study act to validate this biorobotic methodology and lay the foundations upon which future work can be built.

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