Pasture height and crop direction influence reptile movement in an agricultural matrix.

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ABSTRACT

Tackling the global threat of habitat fragmentation on biodiversity requires knowledge of how species move within agricultural landscapes. However, the specific mechanisms influencing dispersal within such landscapes remain poorly understood. The objective of our study was to assess how matrix type (improved pasture, native pasture or crop) and structure (grass height) influence fine-scale reptile movement, as well as influences of crop sowing direction and setting-sun position. In an agricultural region of south-eastern Australia, we first released 20 individuals of an arboreal gecko (*Christinus marmoratus*) at set distances from trees to determine the distance at which they could perceive their tree habitat (perceptual range). We then translocated 36 individuals into six matrix environments within their perceptual range of isolated trees to examine how gecko movement was modified by the type and structure of the matrix. We also recorded crop sowing direction and setting-sun position and examined all recorded tracks using angular statistics. We found that geckos exhibited a perceptual range of 40-80m. Short matrix environments promoted direct movements towards trees, irrespective of matrix type. Furthermore, movements were significantly affected by crop sowing direction with individuals following the planted lines. Our study has three significant implications: (i) restoring mature tree spacing to 80m apart will assist gecko movements, (ii) targeted management for low pasture height, such as by maintaining directional narrow strips of low vegetation among taller pastures, might assist movement and facilitate increased connectivity, (iii) directional sowing of crops between habitat patches presents a simple but potentially effective tool for reconnecting fragmented landscapes.

KEYWORDS
1. INTRODUCTION

Globally, expanding agricultural practices are creating increasingly fragmented landscapes, with patches of habitat that can support high biodiversity becoming interspersed with a matrix of crops and pastures (Alexandratos and Bruinsma, 2012). The persistence of biodiversity in these fragments depends crucially on an individual’s capacity to move through the agricultural matrix (Ricketts, 2001; Zollner and Lima, 2005). The degree to which the matrix genuinely represents a barrier to movement has therefore been the focus of intense research effort in recent years (e.g. Anderson et al., 2015; Cooney et al., 2015; Driscoll et al., 2014; Malekian et al., 2015; Rodríguez-San Pedro and Simonetti, 2015; Smith et al., 2013; Sozio et al., 2013). Landscape-scale occupancy studies, as well as expert opinion, have dominated assessments of species movements (Driscoll et al., 2014). More recently, mark-recapture and molecular studies have also shown that certain matrix environments represent a barrier to movement for many species (e.g. Anderson et al., 2015; Prevedello and Vieira, 2010a). Despite increasing evidence for the impact of the matrix on some elements of biodiversity, previous studies have tended to remain correlative, focused on broad (>1km) movements and have rarely identified the specific mechanisms that influence fine-scale movement (Lechner et al., 2015). Understanding specific mechanisms explaining why movement might be poorer in some matrix environments at fine-scales would allow us to implement effective management strategies to improve biodiversity conservation (Hawkes, 2009).

The type and structure of the matrix represents a key factor influencing the fine-scale movements of terrestrial animals through agricultural landscapes (Driscoll et al., 2013). The
composition and height of vegetation can greatly influence the distance at which individuals may perceive neighboring habitat – its perceptual range (Pe’er and Kramer-Schadt, 2008; Prevedello et al., 2010). For example, lower vegetation obstruction associated with certain land-use types (i.e. grazed pastures) support greater perceptual range in some Brazilian marsupials (Prevedello et al., 2011). Despite the important role of the matrix on perceptual range, empirical data quantifying this impact is lacking for most taxa. Additionally, the type and structure of the matrix can directly influence a species’ ability to orientate and move, even when within the perceived range of habitat. For example, the fine-scale movements of some small mammals are strongly guided by the linear structure of cereal crops despite proximity to habitat (Prevedello and Vieira, 2010b; Sozio et al., 2013) but this important effect has not been examined for any other terrestrial fauna in cropping landscapes. Comprehensive examinations of the effects of matrix type and structure on the fine-scale movements of small, ground-dwelling organisms would be useful but are rare (but see Haynes and Cronin, 2006; Sozio et al., 2013). Additionally, how the fine-scale movements of non-mammalian organisms are affected by a broad suite of different agricultural environments has yet to be explored. Understanding fine-scale movements within different matrix environments could be particularly useful for enhancing connectivity for reptiles (Southwood and Avens, 2010) and amphibians (Pittman et al., 2014b), both of which are undergoing major declines in agricultural landscapes globally (Böhm et al., 2013; Gibbon et al., 2000). These groups are consistently under-studied in connectivity science (Driscoll et al., 2013), yet are likely to show strong movement patterns between different matrix environments due to their direct associations with management-specific groundcover habitats (Moore et al., 2008; Schutz and Driscoll, 2008). For example, cultivated pasture and crop matrices generally support
fewer micro-habitat features critical for many reptiles (Kay et al., 2016) and may illicit more “directed” movements than required in native pastures where these micro-habitat features are more common. Our understanding of reptile navigation has mostly focused on long-range movements of marine turtles (Rivas et al., 2015; Southwood and Avens, 2010) and a crocodilians (Read et al., 2007), while our knowledge of the specific cues terrestrial reptiles use for guiding fine-scale movements is comparatively limited. For example, extensive review of the literature reveals evidence only for the role of sun position in orienting movements in some terrestrial turtles (DeRosa and Taylor, 1978) and lizards (Beltrami et al., 2010; Freake, 2001), as well as homing (“map and compass”) senses in some pythons (Pittman et al., 2014a) and geckos (Marek et al., 2010). A further examination of the influence of matrix and non-matrix cues on the perceptual range and movement of small terrestrial reptiles within agricultural landscapes is needed.

Here, we provide a novel examination of the influence of a range of matrix environments on the fine-scale movements of small terrestrial reptiles to better understand mechanisms guiding habitat perception and orientation within the matrix. First, we examined the impact of a range of matrix types (native pasture, improved pasture, and cropped landscapes) and structures (tall or short) on habitat detection and orientation. Visual cues are thought to be most important for guiding fine-scale movements for small terrestrial reptiles (e.g. Freake, 2001; Gruber and Henle, 2004), and so we expect the structure (specifically short pastures) would have strongest influence on habitat perception and movement. Second, we examined the influence of crop sowing direction on fine-scale movements. Based on strong effects observed for small mammals (Prevedello and Vieira, 2010b; Sozio et al., 2013), we hypothesized crop sowing direction would also strongly influence reptile orientation.
We selected a nocturnal arboreal gecko (*Christinus marmoratus*) as a model species to test the influence of the matrix because it is arboreal with limited dispersal capability. Translocation experiments are an ideal approach to test orientation ability (Betts et al., 2015; Wiltschko and Wiltschko, 1999), and so we used field experiments to address the following two questions:

i) How does the type (improved pasture, native pasture or crop) and structure (pasture height) of different agricultural matrix environments influence the fine-scale habitat detection and movement of reptiles?

ii) How does crop sowing direction influence fine-scale movement of reptiles?

2. METHODS

2.1 Study area and design

Our study was conducted in the highly fragmented mixed cropping/grazing agricultural landscape near Boorowa (-34.437°S, 148.717°E), south-eastern Australia (Fig. 1a). The predominant form of agriculture in this area is pasture dominated by native groundcovers with no or infrequent fertilization (native pasture), pasture dominated by exotic groundcovers and a regular history of fertilization (exotic pastures), and cereal cropping of either wheat (*Triticum vulgare*) or canola (*Brassica napus*) (see Appendix A for details).

We undertook movement experiments during October-November 2014 within fields comprising six different matrix environments: short native pasture, short exotic pasture, long native pasture, and long exotic pastures plus two cereal crops: wheat and canola (Fig. 1b).
A.1) We replicated these treatments three times in separate fields (spaced >2 km to ensure spatial independence) giving a total of 18 sites. We measured pasture height at each site using a rising-plate pasture meter (Correll et al., 2003) and defined short pastures where the site mean height was <10 cm and long pastures where the mean height was >20 cm (Appendix A). Both crops (canola and wheat) were cultivated along rows spaced approximately 20 cm apart, with plants closer within lines creating semi-permeable guides without acting as a barrier for movement. We examined two crops with contrasting growth-form to provide a wider test of the general influence of crops on species movement that was not possible in previous studies that examine only a single crop type (Prevedello and Vieira, 2010b; Sozio et al., 2013). At ground-level, both crops formed visible lines of planted stems although wheat crops were more closely planted (1-2 cm apart) than canola crops (5-10 cm apart) and allowed greater ground-level visibility than within the leafy multi-stem branching canola crops. For both native and exotic pastures, the distribution of plants did not follow any regular pattern.

2.2 Movement experimental protocol

Our experiment involved releasing individuals of a nocturnal arboreal gecko (*Christinus marmoratus*) into fields comprising an isolated tree surrounded by different matrix environments and recording the direction of movement (or orientation). Trees are key habitat structures for this species (Michael et al., 2015; Taylor et al., 2015; Wilson and Swan, 2013) and we therefore expected animals would move quickly towards them if released within their perceptual range. We therefore considered all groundcovers as “matrix” given the non-core use of this environment by the target species (following the definition of Driscoll et al., 2013).
A critical first step was to identify the perceptual range of *C. marmoratus* to determine the distance for release in subsequent experiments. Perceptual range of a species cannot be considered absolute, and will vary depending on the matrix context (Pe’er and Kramer-Schadt, 2008). We interpreted perceptual range relative to short pastures to find the maximum possible distance our target species may realistically detect habitat within our study environment (i.e. pastures where no visual obstruction is present given the environmental conditions). To quantify this, we released animals into short (<10 cm high) pastures (representing a mix of both native and exotic pastures) with no visual obstruction at set distances (40 m, 80 m and 120 m) from isolated “target” trees (Fig. 1b). Each target tree was isolated from the nearest tree by a distance of >250 m, and occurred on flat landscapes presenting similar horizons for all released animals. Five animals were released at each distance interval simultaneously, separated by 10 m to minimize conspecific interference. We repeated this at two trees. The release position for all distance categories was kept constant (due west of the target tree) to minimize the influence of confounding cues (e.g. the visual silhouette of the target tree) and animals were carried to the release point in a dark bag that was gently spun to ensure disorientation prior to release. Animals were released by hand, with the observer moving quickly away in a consistent direction (south) for all releases, in order to reduce their influence on subsequent movements of lizards.

To examine the impact of matrix type (native pasture, improved pasture, and cropped landscapes) and structures (tall or short grass) on habitat detection and orientation (Question 1), we selected three target trees for each of the six treatments, resulting in a total of 18 sites. At each site, we released two animals at a distance of 40 m (the perceptual
range in short pastures), one due east and one due west of the target tree (Fig. 1c), once again keeping release positions consistent and disorientating individuals to minimize confounding influences. To explore the influence of crop plantings on orientation (Question 2), at each point we recorded the bearing of sowing direction. Because sun position can influence orientation in some reptiles (Beltrami et al., 2010; DeRosa and Taylor, 1978), we also measured the direction of sun-down so that we could control for this effect (Fig. 1c).

Animals were hand caught in remnant fragments within the same landscape but more than 5 km distant from the release landscape to remove any influence of learnt behavior on movements. Individuals were fed and housed for a maximum of 72 hours before being released to ensure optimal physiological condition and minimal stress (sensu Betts et al., 2015). Each animal was released only once. Prior to release, animals were marked with fluorescent powders of different colors. Animals were released at dusk, on evenings with no wind, clear skies and at the new moon-phase to maximize perceptual ability of animals and reduce confounding non-target factors able to influence navigation (Dacke et al., 2003; Rivas et al., 2015). We tracked animals six hours after release, recording the movements of each individual using a hand-held GPS from the release point until no additional powder was detected or until reaching the target tree. We defined this as an individuals’ “track” (i.e. the path between an individuals’ release point and the tree or final point of powder detection).

2.3 Data analysis

We use circular statistics (Batschelet, 1981) to quantify the orientation of individuals by subdividing entire tracks (i.e. entire path from release to final detection) into vectors recording the distance and direction of each composite movement (Appendix B). We corrected each track and subsequent vectors to have the same position relative to the tree.
(e.g. tracks in the west were reflected to the east). We then calculated weighted mean vectors of each track (at least 1 m long), with segment lengths as weights (following Sozio et al., 2013) to provide a series of directional and weighted vectors per track. We calculated the perceptual range as the maximum distance at which released animals demonstrated they had perceived the target tree by heading directly towards it (V-test for the significance of mean angles around a specified direction; Batschelet, 1981).

To test for the influence of type and structure of matrix on fine-scale movement (Question 1), we tested whether the target weighted mean vectors orientated towards the target tree in each of the six treatments. To test for the influence of crop plantation lines on movement (Question 2), we recorrected tracks relative to target directions of the crop sowing direction (V-test with mean angles as axial data; Sozio et al., 2013). We used the same approach to test for the influence of sun-setting direction. All analyses were performed using Oriana 4 software (Kovach, 1994).

3. RESULTS

We captured and released 56 individuals: 20 to determine the perceptual range and 36 for the main movement experiment (six per treatment; Table 1). The mean track length was 32.7 m with minimum and maximum track lengths of 16.7 and 86.3 m.

3.1 Matrix type and structure

The perceptual range trials revealed that all individuals released at 40 m moved towards the target tree (u=3.135, p<0.001; Table 1). There was no overall significant movement towards the tree at distances of either 80 m (u=-0.543, p=0.703) or 120 m (u=1.00, p=0.165). This
suggests the perceptual range of *C. marmoratus* within short pastures is at least 40 m but less than 80 m.

For the main movement experiments, orientation within different matrix environments revealed that *C. marmoratus* oriented directly towards the target tree in matrix environments with short native pasture (*u*=3.43, *p*<0.001) and short exotic pasture (*u*=3.30, *p*<0.001), but not for long native pasture (*u*=-0.916, *p*=0.814), long exotic pasture (*u*=-1.883, *p*<0.971), or either wheat (*u*=0.815, *p*=0.212) or canola (*u*=-0.714, *p*=0.756) crops (Table 1, Fig. 2, Fig. 3).

### 3.2 Influence of crop sowing direction

Movement of *C. marmoratus* within crops was significantly oriented along the direction of the planted crop lines (Table 1, Fig. 2). This effect was present in both crop types but was stronger for wheat (*u*=3.128, *p*<0.001) compared to canola (*u*=2.278, *p*=0.01). The position of the setting sun did not influence *C. marmoratus* movement in any matrix environment (Table 1, Fig. 2).

### 4. DISCUSSION

Our study aims to help fill a research gap examining the movement of reptiles within a range of different matrix environments, providing new insights into the role of matrix environments for fine-scale species movement and habitat connectivity. We found that *C. marmoratus* have a perceptual range of at least 40 m and less than 80 m within short pastures. Examining different matrix environments, we found that, when released within
their perceptual range in short pastures (i.e. <40 m), the height of pasture rather than the
type of matrix (native pasture, exotic pasture or crop) was the most important factor driving
habitat detection. We also found that individuals strongly followed planted crop lines during
their movement, irrespective of the direction of habitat, supporting previous studies of
small-mammals to provide compelling evidence for the impact of crops on the movement of
ground-dwelling fauna.

4.1 Ecological response to the matrix

Our result for a 40-80m perceptual range for C. marmoratus is consistent with the previous
few examinations of perceptual range for arboreal geckos (Gruber and Henle, 2004).
Although perceptual range may depend upon matrix context (Pe’er and Kramer-Schadt,
2008), our results indicate that effective movement within the matrix for this arboreal gecko
may be achieved when mature trees are spaced at an equivalent (or reduced) distance.
However, less than 3% of the original remnant vegetation persists across the landscapes
examined here (Lindenmayer et al., 2012b; Sato et al., 2016) and our results suggest fine-
scale orientation and dispersal capability could be eroded by historic and ongoing tree
clearing. The loss of large old scattered trees is a pervasive issue across agricultural
landscapes globally (Lindenmayer et al., 2012a and references therein). Our result highlights
significant challenges to sustaining important connectivity processes relevant beyond the
landscapes and taxa examined here. Restoring agricultural landscapes in ways that enhance
perceptual range could address this issue in line with the recent call for incorporating fine-
scale dispersal behavior into conservation planning (Lechner et al., 2015). Such restoration
approaches could include establishment of “stepping stone” visual structures that could
assist orientation (sensu Saura et al., 2014) and may enhance connectivity over relatively
immediate (~1-10 years) timeframes compared to timeframes required to restore the target habitat (~100-300 years; Sato et al., 2016). For example, natural (i.e. young planted trees) or even artificial (i.e. erected) structures (Goldingay et al., 2011) could be used but require testing.

Our study revealed clear patterns of reptile orientation in shorter rather than longer pastures, irrespective of whether this was native or exotic pasture. This supports vision as a primary tool for orientating between habitats for this species as found for another arboreal gecko species in this system (Gehyra variagata; Gruber and Henle, 2004). An ability to orientate and move decisively in short pastures has clear benefits when considering the multiple threats to ectothermic reptiles in exposed landscapes. For example, low vegetation could cause a loss of thermal buffering and a reduction in operative function in ectotherms, or subject individuals to a higher predation risk (e.g. Sato et al., 2014) causing a need to exit the matrix quickly. Moreover, short pastures provide limited apparent ecological benefit to arboreal geckos, but have been found to have negative impact on reptile occupancy (Howland et al., 2014) and landscape/ecosystem function generally (Gaitàn et al., 2014). Nevertheless, this ‘substandard’ matrix environment evidently assists orientation and so reconciling its utility for enhancing connectivity, as well as developing a better understanding of species’ motivations for movement, is critical. Importantly, while short pastures appear useful for individuals orientating within the matrix, we have not considered the edge permeability (or willingness of individuals/species to enter) of such environments (Youngquist and Boone, 2014). Doing so, for a range of taxa, will help determine the value of short pastures for enhancing connectivity, and for understanding the degree to which it also represents a dispersal barrier.
Although individuals were unable to move towards habitat in cropped environments, we found that movements were strongly aligned with crop plantation rows. This was true for two structurally different types of crop (wheat vs canola), suggesting the effects may be more general than previously known based on studies focusing on single crop types.

Previous studies show orientation is driven by the visual effects of stem-lines (Prevedello and Vieira, 2010b). Our results support these findings (Table 1, Fig. 2g-h), revealing stronger influence within wheat crops which are visually clearer at ground-level compared to the “bushy” less clear rows within canola. Importantly, our finding for a small reptile concords with previous studies of some small mammals (Prevedello and Vieira, 2010b; Sozio et al., 2013) and has implications for theoretical movement ecology in matrix environments. That is, the influence of crops for guiding small mammal movements proposed by Prevedello and Vieira (2010b) and Sozio et al. (2013) appear applicable to a broader range of taxa, including small reptiles. Our results therefore contribute to a wider understanding of the impact of cropping on the movement of ground-dwelling fauna, which represent key groups associated with high conservation risk (e.g. small mammals, amphibians) in agricultural landscapes. A thorough investigation of this issue for additional species is required to further test the generality of this for ground-dwelling fauna in other agricultural landscapes globally.

Despite the clear findings of our study, a number of key questions remain. First, how does the perceived range of habitat change with (i) different matrix contexts, (ii) the characteristics of target habitat (i.e. age, size, type of tree in this study), (iii) the background (horizon) context, and (iv) the taxa examined? Second, how are our observations influenced by temporal dynamics of the matrix, such as the seasonality of pasture and crop growth (Bertrand et al., 2015), and how do these interact with temporal patterns (if present) in
dispersal events? Third, we selected an arboreal species that uses trees which are generally visible landmarks at ground-level. However, it is less clear how species associated with “less-visual” habitats orientate. For example, outcrops and hilltops are critical habitat for many saxicolous (rock-dwelling) reptiles (Michael et al., 2008), yet the cues (if any) that individuals use to orientate towards such habitats remain unknown but are of key conservation significance.

4.2 Conservation implications

Understanding how species move through the agricultural matrix at fine-scales can help identify mechanisms influencing dispersal efficacy and inform decisions about the conservation of biodiversity in fragmented landscapes (Barton et al., 2015; Lechner et al., 2015). Our study highlights how different matrix environments influence the fine-scale movements of small terrestrial reptiles, a group of global conservation concern, to enhance connectivity and survival within fragmented agricultural landscapes. Considering the extent of agricultural modification of habitats globally (Alexandratos and Bruinsma, 2012) as well as the challenges facing conservation managers in these landscapes, our findings have three clear management implications relevant for the conservation of poor-dispersing fauna that extend beyond our system.

First, our results for perceptual range suggest that tree spacing should be close (i.e. <80 m) to facilitate direct movement. Our study provides novel evidence for the role of large mature trees in orienting reptiles, and although we acknowledge that our study focusses on a single species, our findings join a host of others advocating the ecological value of scattered trees (Allnutt et al., 2008; Gibbons, 2010; Lindenmayer et al., 2012a; Manning et al., 2006; Moga et al., 2016). Ongoing tree loss is a major issue in this landscape (Evans,
and our study highlights risks associated with maintaining low tree densities within agricultural landscapes for maintaining important ecological function.

Second, targeted management of pasture height can influence species movements with potential to help facilitate increased connectivity yet is rarely considered in management plans tasked with reconnecting fragmented landscapes (Prevedello and Vieira, 2010a). Maintaining tall pastures is a targeted priority in many conservation programs because it benefits occupancy for poor-dispersing fauna at-risk of agricultural fragmentation (e.g. Howland et al., 2014), reduces threatening processes like predation (Sato et al., 2014; e.g. Schneider et al., 2012), and prevents loss of ecosystem function (Gaitàn et al., 2014). Our results suggest that species move directly towards habitat in low pastures, even in highly modified (non-native) landscapes. One opportunity for enhancing movement could be to maintain narrow strips of low vegetation among taller pastures to facilitate directional movement but that minimize predation and increase perceptual range. This could be achieved by strip grazing or mowing pastures directionally between habitat patches, but first needs to be experimentally tested.

Third, our study provides evidence for the influence of cropping on the fine-scale movements of small reptiles, suggesting that targeted management of cropping could enhance connectivity for at least some reptiles in fragmented landscapes. Specifically, directional sowing between habitats represents an important opportunity to link isolated habitat remnants to facilitate greater directional movements for species who otherwise remain exposed to hostile effects of the matrix. Our work corroborates recent studies that demonstrate similar effects for small mammals (Prevedello and Vieira, 2010b; Sozio et al., 2013), suggesting that directional cropping management can enhance connectivity for
multiple taxa within two vertebrate groups of key conservation concern (Böhm et al., 2013; Ceballos et al., 2005). Furthermore, by revealing consistent response across two globally wide-spread crop types (wheat and canola), we provide important evidence for the generality of this response that is of increasing need as human demand for food continues to increase (Alexandratos and Bruinsma, 2012). Strategies that encourage directional cropping to link habitats therefore provide a promising approach for conserving some significant ground-dwelling fauna in cropping landscapes globally.

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**SUPPLEMENTARY MATERIAL**

Appendix A: Details of the study area and agricultural matrix environments.
Appendix B: Visual example of track quantification.