Managing kangaroo grazing for the conservation of grassland and grassy woodland fauna

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Candidate's Declaration

This thesis is my own work, except where otherwise acknowledged
(See Preface and Acknowledgments).

Brett Howland

August 2016

“Grass feeds more wildlife than any other plant”

David Attenborough

Preface

This thesis is structured as a series of connected papers. With the exception of the Synthesis, these papers have been published, or submitted for publication at the time of the thesis submission. These papers are listed below and are referred to by their Roman numerals in the text.

I undertook the majority of the work for the papers that form this thesis, including developing the research questions and experimental designs, data collection and analysis, and drafting manuscripts. My supervisors, David Lindenmayer, Iain Gordon and Adrian Manning made contributions to the conceptualization and design of the research, and the editing of each paper. The addition of different co-authors to each paper, reflects contributions to the conceptualization of research ideas, data collection and the editing of manuscripts. Furthermore, Terry Neeman, Wade Blanchard, Jeff Wood and Martin Westgate provided feedback on which data analysis approaches to use in the papers of which I was the primary author. The specific contributions of each of the co-authors to each paper are outlined below. Additional assistance is acknowledged in the acknowledgments at the end of each paper.

Paper I: Brett W. A. Howland, Dejan Stojanovic, Iain J. Gordon, Adrian D. Manning, Don Fletcher, and David B. Lindenmayer (2014) Eaten Out of House and Home: Impacts of Grazing on Ground-Dwelling Reptiles in Australian Grasslands and Grassy Woodlands. *PLoS ONE* **9**, e105966. Experiment conceptualization & design: BH, DBL, IJG, ADM, DF; Data extraction: BH; Data analysis: BH; Manuscript drafting: BH; Manuscript editing & preparation: BH, DS, DBL, IJG, ADM, DF.

Paper II: Brett W. A. Howland, Dejan Stojanovic, Iain J. Gordon, Jim Radford, Adrian D. Manning, and David B. Lindenmayer (2016) Birds of a feather flock together: Using trait-groups to understand the effect of macropod grazing on birds in grassy habitats. *Biological Conservation* **194**: 89-99. Experiment conceptualization & design: BH, DBL, IJG, ADM, JR; Data extraction: BH; Data analysis: BH; Manuscript drafting: BH; Manuscript editing & preparation: BH, DS, DBL, IJG, ADM, JR.

Paper III: Brett W. A. Howland, Dejan Stojanovic, Iain J. Gordon, Don Fletcher, Melissa Snape, Ingrid A. Stirnemann[1] and David B. Lindenmayer (2016) Habitat preference of the striped legless lizard: Implications of grazing by native herbivores and livestock for conservation of grassland biota. *Austral Ecology* **41**(4): 455-464.Experiment conceptualization & design: BH, DBL, IJG, DF, MS; Data extraction: BH, MS, DF; Data analysis: BH; Manuscript drafting: BH; Manuscript editing & preparation: BH, DS, DBL, IJG, IAS, DF, MS.

Paper IV: Brett W. A. Howland, Dejan Stojanovic, Iain J. Gordon, Ingrid A. Stirnemann, Adrian D. Manning, and David B. Lindenmayer. (2016) Fear and hunger: drivers of kangaroo foraging patterns in an anthropogenically disturbed environment. *Austral Ecology*. In review. Experiment conceptualization & design: BH, DBL, IJG, ADM; Data extraction: BH; Data analysis: BH; Manuscript drafting: BH; Manuscript editing & preparation: BH, DS, DBL, IJG, ADM, IAS.

Paper V: Tiago A. Marques, Steven T. Buckland, Regina Bispo and Brett W. A. Howland (2013) Accounting for animal density gradients using independent information in distance sampling surveys. *Statistical Methods & Applications* **22**, 67-80. Experiment conceptualization & design: TAM, BH; Data extraction: BH; Data analysis: TAM, BH; Manuscript drafting: TAM; Manuscript editing & preparation: TAM, STB, RB, BH.

All papers were intended as stand-alone pieces of work. For this reason, there is some unavoidable repetition between chapters, for example in the description of study areas and experimental design within the Methods sections. In line with The Australian National

University’s College of Medicine, Biology and Environment guidelines for ‘Thesis by Compilation’, a Context Statement has been provided at the beginning of this thesis. The Context Statement is not intended to be a complete literature review, but rather a framework for understanding the relationships between all aspects of the research.

Acknowledgements

This project would not have been possible without the help of many people.

First and foremost, I would like to thank my panel of supervisors - David Lindenmayer, Iain Gordon, and Adrian Manning for their unwavering support throughout this process. They have provided critical advice, ideas and edits throughout the process. I appreciate them sticking by me through the ups and downs. David deserves special thanks for his patience, and his critical and rapid edits of countless draft papers. I have learnt so much from them all.

I also would to give thanks to Dejan Stojanovic, Jim Radford, Don Fletcher, Ingrid Stirnemann and Melissa Snape for assisting in the development of several papers. Dejan in particular, deserves extra special thanks for taking the time to talk about each paper over a beer or two, and for providing so much good advice.

This project involved a huge amount of field work, conducted over three states in Australia. For making this work possible I would especially like to thank Laura Canackle, Jordan Goulding, David Speldewinde, Roger Howland, Steven Speldewinde and Craig Williams for helping with the labour intensive laying out of tile grids. Steven Speldewinde did the lion share of this work and despite working through some 38 degree days kept me laughing and smiling throughout. I would also like to thank Steve Holliday for his expert reptile and bird identification skills, Piers Bairstow and Mauro Davanzo for helping with getting equipment and Mauro Davanzo teaching me how to drive a four wheel drive, Bruce Doran for his advice on the creation of a canopy cover map, and Clive Hilliker for his advice on how to improve the various Figures I produced.

I started this process with a very low statistical base, and the fact I have been able to complete all the analysis myself, is largely due to the advice and assistance provided to me by

Wade Blanchard, Terry Neeman, Martin Westgate and Jeff Wood. Terry especially, spent a lot of time talking me through various statistical problems and had a great way of explaining complex statistics.

Many other PhD students (mostly Dr's now) provided me with important advice - Laura Rayner, Pia Lentini, Geoff Kay, Chloe Sato, Philip Barton and John Evans. Furthermore, I would like to thank various friends, who despite thinking I spend my life counting kangaroo poo have provided crucial support - Jordan Goulding, David Speldewinde, Steven Speldewinde, Mark Greed, Dannielle Greed, and Merrin Bradford. Special thanks to Juliana Lazzari, for being there to talk through issues and for her support.

This project would not have been possible without support from landowners and funding partners. In particular, I would like to thank the ACT Government, Bush Heritage, the Australian Government, and Greg Hargreaves for allowing access to their properties and Staff at the ACT Government Environment and Sustainable Development Directorate (ESDD), Bush Heritage and Australian Government staff for their invaluable support during the project. Don Fletcher, Claire Wimpenny, Peter Saunders and Peter Mills deserve special thanks as their technical and operational support was crucial for me to complete this project. This project was largely funded by Bush Heritage Andy inc Foundation Environmental Research Postgraduate Scholarship and the Australian Government's Department of Industry, Innovation, Science, Research and Tertiary Education Australian Postgraduate Award. Further, funds were provided by Canberra Birds Conservation Fund and the Australian Government for monitoring activities undertaken at a single property.

Lastly and most importantly, I would like to thank my parents Jenny and Roger, my sister Emily and my loving partner Megan for being so supportive throughout. Thanks to my father for coming out to lay tiles over a very hot week in Victoria. I could not have done it without you all!

Abstract

Large mammalian grazers are ecosystem engineers that alter the resources available to other species through selective consumption of plant matter, redistribution of nutrients and trampling. While some level of grazing is considered critical for maintaining species diversity, alteration to natural grazing regimes can have a severe impact on native biodiversity. Restoration of grazing regimes which promote conservation of biodiversity is a priority in many protected areas. However, the ability to achieve this goal is limited by a lack of understanding of what 'appropriate' grazing regimes for conservation of biodiversity are. In south-eastern Australia, high intensity grazing by the native eastern grey kangaroo (*Macropus giganteus*) has been linked to the decline of multiple taxa. While efforts to manage the impact of kangaroo grazing on other taxa have been undertaken, the effectiveness of these interventions are limited by a lack of knowledge of what constitutes optimal grazing levels.

In this thesis, I used kangaroo population counts, tree canopy cover maps, ground vegetation structure, and reptile and birds counts to investigate the relationship between kangaroos, grass structure, and fauna. I found that: 1) there was a strong negative relationship between the abundance of kangaroos and grass structure (Paper I); 2) high intensity kangaroo grazing had a negative effect on the reptile community (Paper I); 3) birds with similar traits favoured similar grazing intensities, with different grazing intensities favoured by different trait groups (Paper II); 4) the occurrence of a threatened grassland reptile, the striped legless lizard (*Delma impar*) was positively related to fine scale grass complexity, and negatively related to kangaroo density at the broad scale (Paper III); 5) kangaroos selected forage habitat away from roads, in areas with a high cover of short grass (Paper IV); and 6) line transect sampling undertaken from vehicles driven

along tracks can provide an accurate method to survey the kangaroo population provided knowledge of kangaroo distribution relative to tracks is known and accounted for (Paper V).

My investigation into the relationships between kangaroos, grass structure and fauna indicated that grass structure has a strong effect on many reptiles and birds, and that intervention may be needed to change kangaroo habitat selection in a way that mimics natural foraging patterns in order to promote optimal vegetation structures for the conservation of native biodiversity. Therefore, to preserve a full-complement of species in these grassy habitats, I recommend that: 1) management of grazing is based on direct measures of grass structure, not herbivore abundance, 2) the extent and duration of intense grazing is limited; and 3) grazing pressure is rotated to create mosaics of different levels of grass structure in space and time. In making these recommendations, I emphasise that management of grazing by kangaroos will be necessary for ongoing conservation of biodiversity in grasslands and grassy woodland and that further research is needed on how to manage kangaroo grazing patterns for the conservation of biodiversity in grasslands and grassy woodlands in south-eastern Australia.

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Context Statement

Introduction

Grassland and savanna ecosystems cover over 20 percent of the earth land surface, and occur on every continent inhabited by humans (Bond and Parr, 2010, Woodward et al., 2004). These ecosystems occur where rainfall, temperature and soil limit the establishment of trees, or are maintained by the disturbance imposed by fire and herbivores in areas where woodlands and forest would otherwise grow (Bond and Parr, 2010, Woodward et al., 2004). The defining features of these ecosystems are the low density of woody vegetation and a grass dominated understorey. Grass is a highly productive plant and consequently, these grassy habitats support the highest animal biomass per unit area of any ecosystem (Frank et al., 1998, Sinclair, 1975), which includes some of the largest terrestrial species on the planet (e.g. the African elephant *Loxodonta africana*, the white rhino, *Ceratotherium simum*, the American bison, *Bison bison*). Through selective consumption of plant matter, trampling of vegetation and redistribution of nutrients large grazers act as ecosystem engineers, with the disturbance imposed by grazing considered critical in maintaining both flora and fauna species diversity (Bond and Parr, 2010, Mysterud, 2006, Milchunas et al., 1988, Gordon et al., 2004).

Large wild grazers were initially important sources of food and fur pelts for early human societies, and these grassy habitats have remained important with agricultural advancement, providing grass forage for domestic livestock and open land for sowing crops (Woodward et al., 2004, Sandom et al., 2014). The increased intensity of human land-use has come at substantial ecological cost, with grassy ecosystems among the most degraded and threatened ecosystems on the planet (Bond and Parr, 2010, Woodward et al., 2004, Hoekstra et al., 2005). Intensively managed grazing regimes are considered a major factor in this decline (Gordon et al., 2004, Mysterud, 2006, Milchunas et al., 1988, Foster et al., 2014). Several common themes have emerged for how anthropogenic changes affect grazing systems:

1) grazer communities have changed – the largest herbivores (i.e. the megafauna; Sandom et al., 2014) have been largely eradicated and the remaining native grazers have been suppressed and replaced by a few species of domestic grazers in most areas (Young et al., 2013, Dorrough et al., 2004b, Fleischner, 1994);

2) grazing intensity has changed – eradication of predators, provision of permanent watering points, and protection from hunting have increased the abundance of grazers (domestic and native grazers) in some areas, whereas, hunting, fencing, and disease has reduced herbivore abundance in other areas (Fuhlendorf and Engle, 2004, Gordon et al., 2004, Mysterud, 2006, Dorrough et al., 2004b); and

3) patterns of grazing in space and time have changed – barriers to movement, establishment of permanent water points, suppression of fire, and eradication of predators have concentrated grazing, often in small areas leading to a uniform grazing pressure experienced across large areas (Fuhlendorf and Engle, 2004, Gordon et al., 2004, Dorrough et al., 2004b).

Prevention of further ecological decline in the remaining grassy habitats will depend on the restoration of grazing regimes that more closely resemble those in which these ecosystems evolved (Coughenour and Singer, 2000, Gordon et al., 2004, Bengtsson et al., 2000). The establishment of large wildlife corridors to facilitate large scale migration (Rouget et al., 2006, Mduma et al., 1999) and the reintroduction of large predators (e.g. Yellowstone National Park; Ripple and Larsen, 2000) have been successfully applied to restore natural grazing regimes in some areas. However, for areas undergoing a high degree of anthropogenic change, such major restoration activities may not be socially acceptable (e.g. reintroduction of large predators; Nilsen et al., 2007) or financially viable. In these situations, direct human intervention may be required to manipulate grazing regimes to promote biodiversity (Gordon et al., 2004, Young et al., 2009, Virtanen et al., 2002).

The temperate grasslands and grassy woodlands of south-eastern Australia were among the last grassy ecosystems to be converted to intensive agriculture, but nonetheless have suffered an intense decline in both extent and species richness (Prober and Thiele, 2005). For example, in the last two hundred years it has been estimated that over 95% of grassy woodlands and 99% of temperate grasslands in south-eastern Australia have been cleared and degraded by agricultural practice (Prober and Thiele, 2005, Kirkpatrick et al., 1995). Domestic livestock are often held at artificially high densities and constrained in paddocks. This can lead to severe grazing impacts on the diverse ground-layer vegetation, as many Australian plants are poorly adapted to intense and frequent defoliation (Dorrough et al., 2004a). The hard hooves of domestic livestock, as opposed to soft feet of native marsupial grazers, has also led to soil compaction (Dorrough et al., 2004c, Bennett, 1999). Moreover, the simplification and reduction in ground vegetation has had negative effects on many ground-dwelling fauna (Dorrough et al., 2004c), and the removal of cover may have hastened the extinction of small mammals by facilitating predation by introduce predators (Fisher et al., 2003). As a consequence of these well documented and widespread impacts, livestock are commonly removed from areas as a restoration measure (Dorrough et al., 2004b, Prober and Thiele, 1995, Spooner et al., 2002). However, this action will not result in ecological recovery unless biological appropriate grazing regimes are restored.

The most common native large herbivore in south-eastern Australia, the eastern grey kangaroo (*Macropus giganteous*) is considered to have benefited from the eradication of the largest remaining predator, the dingo (*Canis lupus dingo*), reduction in hunting and the creation of permanent watering points (Grigg et al., 1989, ACT Government, 2010). The highest densities of the eastern grey kangaroos (hereafter: kangaroo) are now found in protected areas and where livestock grazing is excluded (e.g. nature reserves; ACT Government, 2010). Population appear to have increased rapidly in protected areas where information on historic densities are known (ACT Government, 2010). For example, the valley floors at the Tidbinbilla nature reserve in the Australia Capital Territory (ACT) were home kangaroo densities exceeding 500 kangaroos per square kilometre in 2002, yet in the 1960s at the opening of the park, not a single kangaroo was recorded (ACT Government, 2010, Fletcher, 2006). Not surprisingly, with these increased densities grazing by kangaroo has been linked to ecological impacts.

Evidence of impacts of grazing by kangaroos on native biodiversity first emerged in 1979, when Leigh and Holgate (1979) described changes in the cover of perennial plants in areas subject to grazing by kangaroos compared to areas protected from grazing. Since that time, a number of studies have documented negative impacts of high kangaroo densities, with overgrazing by kangaroos linked to: 1) reduced occurrence, height and seeding rates of some native grasses (Neave and Tanton, 1989); 2) reduced diversity and cover of native shrubs following fire (Meers and Adams, 2003); 3) reduced abundance and diversity of beetles (Barton et al., 2011); 4) reduced abundance of small skinks (Manning et al., 2013); 5) reduced habitat quality for some ground-nesting birds (Neave and Tanton, 1989); and 6) reduced habitat quality for endangered eastern barred bandicoots, threatening a reintroduction program (Winnard and Coulson, 2008). Concern over the impact of high grazing intensities on biodiversity resulted in several protected areas adopting strategies to manage kangaroo numbers (e.g. Hattah-Kulkyne National Park in Victoria; Cheal, 1986), with the ACT taking a multi-tenure jurisdiction wide approach to the mitigation of kangaroo grazing impacts (the ACT Kangaroo Management Plan;

ACT Government, 2010). Despite the important advances this plan has made in recognizing and implementing activities to address impacts of overgrazing by kangaroos, the effectiveness of mitigation activities is limited by a lack of understanding of what constitutes optimal grazing levels for the conservation of native biodiversity.

To address this knowledge gap and inform the management of grazing pressure, I investigated the interactions between kangaroos, grass structure and fauna (Fig. 1). Specifically, in this thesis I aimed to: 1) investigate relationships between kangaroo abundance and important aspects of fauna/habitat (i.e. grass structure); 2) investigate the relationship between grass structure and two potentially grazing-sensitive groups (birds and reptiles); 3) investigate what factors drive kangaroo foraging patterns across human-modified landscapes and; (4) investigate methods to accurately estimate the abundance of kangaroos.

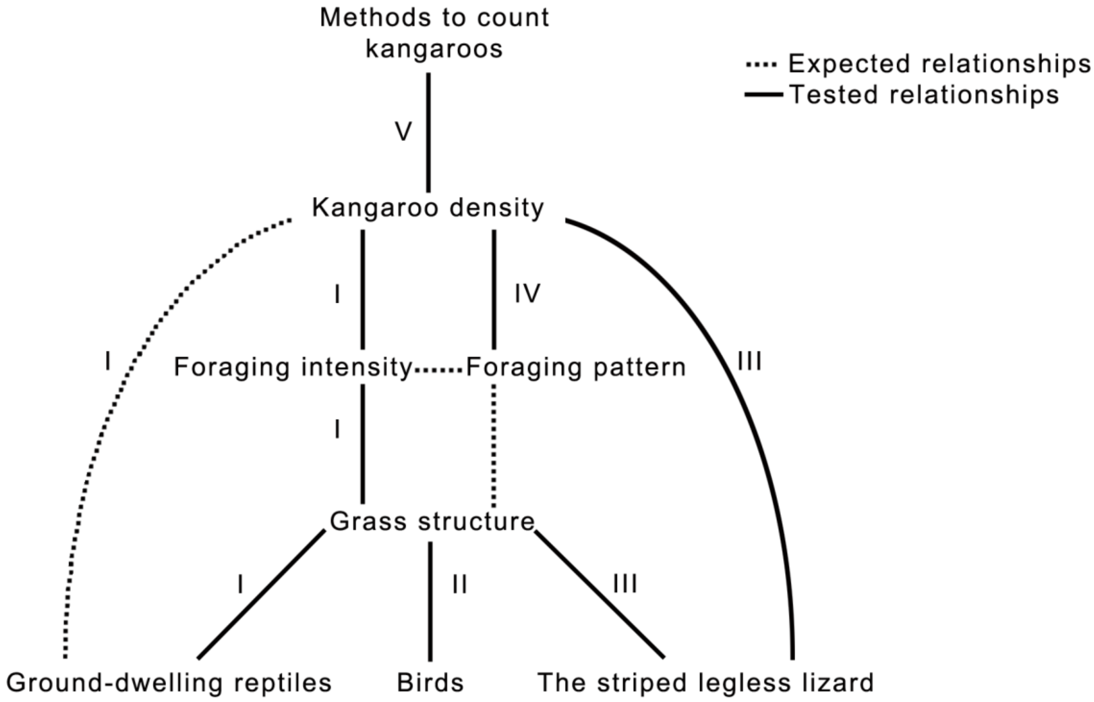

Figure 1. Flow chart outlining how each of the five papers fitted together to increase understanding of the interaction between kangaroo grazing and biodiversity in these grassy systems, with relationships explicitly tested and expected relationships shown.

Aims and methods

In Paper I, I aimed to establish guidelines for the management of kangaroo grazing intensity for the conservation of ground-dwelling reptiles in grasslands and grassy woodlands in south-eastern Australia. In particular, I was interested in whether grazing at moderate intensity provided the best outcome for reptile conservation, as was expected from studies elsewhere in the world. In 2009/2010, I collected data on kangaroo abundance, grass structure and the reptile community at 129, 1.8 ha plots located on 18 properties across the ACT, New South Wales, and Victoria. Properties were grazed predominately by kangaroos (eastern and western grey kangaroos) and were subject to a range of grazing intensities from very low to very high. I used principal component analysis (PCA) to collapse several measures of grass (i.e. grass biomass, grass height, grass percent cover) into a single measure of grass structure (PC1). I then used hierarchical generalized linear mixed models (HGLMM) to investigate the relationships between: 1) kangaroo abundance and grass structure in different tree canopy classes; and 2) grass structure and the reptile community (i.e. species diversity, species richness, abundance and occurrence of five of the more common species/genus).

In Paper II, I investigated whether a trait-based approach could be used to predict the preference of bird species for different levels of grazing intensity. I tested three predictions: 1) certain trait groups are likely to respond to differences in grazing intensity; 2) birds of the same trait group are expected to respond to differences in grazing intensity in a similar way; and 3) different traits groups should favour different grazing intensities. I sampled birds during eight 10 minute point counts conducted at the same plots used in Paper I in each season of 2010. I assigned five key life history traits (foraging stratum, predator avoidance strategy, nesting position, nest defence strategy, and body-size) to every bird species recorded, and used hierarchical clustering analysis to group birds into trait groups based on shared traits. Five trait groups contained species with traits expected to be influenced by grazing intensity (i.e. large aerial insectivore small aerial insectivore, large ground-foraging, small ground-foraging, and ground-nesting/concealment). I modelled the relationship between birds utilizing the grassy layer and measures of grazing intensity and other potentially important environment variables. The analysis was conducted in two stages using generalized linear modeling (GLM) and HGLMM.

Due to there being insufficient records for a particular threatened grassland reptile, the striped legless lizard (*Delma impar*), I ended up pooling records with a closely related species (the olive legless lizard, *Delma inornata*) to model habitat preferences of these species in Paper I. However, in Paper III, I acquired a much larger dataset on *D. impar* from the ACT Government, who had monitored reptiles in 2012 and 2013 on six properties using many of the same plots I used in Paper I. I was therefore able to model the relationships between the occurrence of *D. impar* and multiple environmental variables collected at multiple spatial scales over two years, using a HGLMM approach. I included measures of bare ground, non-grass vegetation, grass structural complexity and grass composition at the fine scale, grassland community at the moderate scale, and grassland area and kangaroo density at the broad scale.

In Paper I to III I examined the relationships between optimal grass structure and grazing levels for a range of reptile and bird species. In Paper IV, I investigated which factors influence the spatial pattern of kangaroo foraging in reserves subject to anthropogenic change. I collected foraging intensity data across 31 plots at five reserves and determined whether the spatial pattern of kangaroo foraging was predicted by: 1) food; 2) fear; or 3) a trade-off between food and fear. In all plots, I measured food quality using a lawn index and two aspects of fear (vegetation cover and distance to roads). Using an information theoretic approach (Burnham and Anderson, 2002), I identified which variables best described the observed pattern of kangaroo grazing.

I was a co-author on Paper V. This paper investigated the potential bias of undertaking wildlife surveys from tracks. I provided data on kangaroo surveys undertaken on vehicle tracks at a single study site where the true abundance of kangaroos was known. As kangaroos may avoid tracks, (and therefore bias surveys from tracks), I used GPS records collected on 23 collared kangaroos by the by the ACT Government to assess the distribution of kangaroos relative to the location of tracks. This data was provided to the primary author on this paper, Tiago Macaques, whom used the data on kangaroo counts, and track avoidance, to develop an adjustment factor for density estimates made along tracks at the study site. He then compared counts made with and without an adjustment factor to the known population of kangaroos at the study site to determine the accuracy of this method.

Summary of findings

Paper I: Eaten out of house and home: impacts of grazing on ground-dwelling reptiles in Australian grasslands and grassy woodlands. Plos One. Published.

Paper I demonstrated that grass structure declined as grazing intensity (i.e. eastern grey kangaroo *Macropus giganteus* abundance) and tree canopy cover increased, with differences in grass structure (i.e. grazing intensity) having a strong influence over the reptile community. There was little support for subjecting grassy habitats to moderate grazing, as although the legless lizard group (*Delma impar*, *D. inornata)* was more likely to be detected in areas subject to moderate grazing intensity, the abundance of reptiles, reptile species richness, reptile diversity, and the occurrence of one reptile species (eastern three-toed earless skink *Hemiergis talbingoensis*) were greatest in areas subject to low grazing intensity. To maximize reptile abundance, reptile species richness, reptile species diversity, and occurrence of several individual species of reptile, managers will need to subject different areas of the landscape to moderate and low grazing intensities and limit the occurrence of high grazing intensity.

Paper II, Birds of a feather flock together: using trait-groups to understand the effect of macropod grazing on birds in grassy habitats. Biological Conservation. In review.

Paper II showed that the value of trait-based predictions in understanding the preference of several bird species for different levels of grazing intensity. Five trait groups were considered vulnerable to grazing intensity (large aerial insectivore, small aerial insectivore, large ground-foraging, small ground-foraging, ground-nesting/concealment). The richness of small aerial insectivores and large ground-foraging species utilising the grassy layer was related to grazing intensity, with the probability of 11 individual species using the grassy layer also related to grazing intensity. However, the richness of small ground-foraging and ground-nesting/concealment trait groups and the occurrence of 11 individual species utilising the grassy layer was not related to grazing intensity. Importantly, species within the same trait group favoured similar grazing intensity, but different trait groups showed preference for different levels of grazing intensity. To maintain optimal grass structure for a variety of bird species, landscapes should contain a heterogeneous mosaic of grass structures.

Paper III: Habitat preference of the striped legless lizard: implications of grazing by native herbivores and livestock for conservation of grassland biota. Austral Ecology. In review.

In Paper III, I found that the probability of detecting the striped legless lizard (*Delma impar*) was not related to the size or quality of grassland reserves, but was positively related to grass structural complexity at a fine scale and negatively related to the density of kangaroos at a broad scale. The negative effect of the density of kangaroos on *D. impar* is likely a consequence of the negative effect of high grazing intensity on grass structural complexity. Small floristically degraded grasslands appear to provide important habitats for this species, and should be included as part of conservation efforts. Management to improve habitat quality for *D. impar* should avoid high intensity grazing (equivalent to > 1.3 kangaroos/ha), while ensuring sufficient grazing disturbance is maintained to promote the formation of complex grass structures.

Paper IV: Fear and hunger: drivers of kangaroo foraging patterns in an anthropogenically disturbed environment. Wildlife Research. In review.

In Paper IV, I found that kangaroo selection of foraging habitat in urban reserves, where native predators are absent, was the result of a compromise between food and fear. Kangaroos selected habitat where there was a high cover of short grass, away from roads. This pattern could increase variation in grass structure and create refugia from grazing, but may negatively impact on biodiversity. To maintain optimal vegetation structure for biodiversity conservation, methods such as concentrated population management, patch burning, exposure to domestic dogs and deterrents (e.g. predator scent) could be employed to better mimic foraging patterns expected under a natural system.

Paper V: Accounting for animal density gradients using independent information in distance sampling surveys. Statistical Methods and Applications. Published.

In Paper V, we found that the density of kangaroos increased with distance from tracks, resulting in an underestimation of kangaroo abundance from surveys conducted along roads. When avoidance behaviour was accounted for using independent measures of distribution (i.e. GPS collars), there was no evidence of bias in population estimates made using line transect Distance sampling. Hence, Distance sampling along tracks can provide accurate estimates of kangaroo abundance, provided the effect of tracks on kangaroo distribution is accounted for.

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PAPER I: Eaten out of house and home: impacts of grazing on ground-dwelling reptiles in Australian grasslands and grassy woodlands

Boulenger’s skink (Morethia boulengeri) found during reptile surveys (Photo: Jenny Smits)

Howland, B., Stojanovic, D., Gordon, I. J., Manning, A. D., Fletcher, D., and Lindenmayer, D. B. (2014). Eaten Out of House and Home: Impacts of Grazing on Ground-Dwelling Reptiles in Australian Grasslands and Grassy Woodlands. *PLoS ONE* **9**, e105966.

Abstract

Large mammalian grazers can alter the biotic and abiotic features of their environment through their impacts on vegetation. Grazing at moderate intensity has been recommended for biodiversity conservation. Few studies, however, have empirically tested the benefits of moderate grazing intensity in systems dominated by native grazers. Here we investigated the relationship between (1) density of native eastern grey kangaroos, *Macropus giganteus*, and grass structure, and (2) grass structure and reptiles (i.e. abundance, richness, diversity and occurrence) across 18 grassland and grassy *Eucalyptus* woodland properties in south-eastern Australia. There was a strong negative relationship between kangaroo density and grass structure after controlling for tree canopy cover. We therefore used grass structure as a surrogate for grazing intensity. Changes in grazing intensity (i.e. grass structure) significantly affected reptile abundance, reptile species richness, reptile species diversity, and the occurrence of several ground-dwelling reptiles. Reptile abundance, species richness and diversity were highest where grazing intensity was low. Importantly, no species of reptile was more likely to occur at high grazing intensities. Legless lizards (*Delma impar*, *D. inornata)* were more likely to be detected in areas subject to moderate grazing intensity, whereas one species (*Hemiergis talbingoensis*) was less likely to be detected in areas subject to intense grazing and three species (*Menetia greyii*, *Morethia boulengeri*, and *Lampropholis delicata*) did not appear to be affected by grazing intensity. Our data indicate that to maximize reptile abundance, species richness, species diversity, and occurrence of several individual species of reptile, managers will need to subject different areas of the landscape to moderate and low grazing intensities and limit the occurrence and extent of high grazing.

Introduction

Ecosystem engineers are species that alter the biotic and abiotic features of their environment and, by doing so, affect the availability of resources for other species in the habitats they occupy (Jones et al., 1994). The means by which ecosystem engineers affect their environment vary widely, and include, among others, predation (Singh et al., 2013), deforestation (Nasseri et al., 2011), nutrient cycling (Kohler et al., 2013), hydrological change (Wright et al., 2002) and herbivory (Ceballos et al., 2010). Anthropogenic factors can affect how ecosystem engineers interact with their environment, with significant impacts on ecosystems (Green et al., 2012). For example, the human extermination of the gray wolf, *Canis lupus*, within Yellowstone National Park in the early 1900's resulted in long lasting and dramatic effects, including altered stream flow and localized extinction, that are only now being reversed with the reintroduction of the gray wolf (Ripple and Larsen, 2000). The importance of ecosystem engineers in shaping the environment has made them the subject of intensive research (Wright and Jones, 2006, Jones et al., 1994, Jones et al., 1997) and management (Crain and Bertness, 2006, Young et al., 2009). Understanding the impact of anthropogenic change on ecosystem engineers is a priority for conservation because failure to do so can have dramatic, long lasting effects including loss of ecosystem function (e.g. introduced herbivores; Crooks, 2002). In this study, we examine the effects of grazing by a native ecosystem engineer on native fauna in threatened grasslands and grassy woodlands across south-eastern Australia.

Large mammalian grazers (hereafter, grazers) are arguably among the most important ecosystem engineers in grassy habitats (Mysterud, 2006). These ecosystems comprise a major proportion of the global landmass and biological diversity (Bond and Parr, 2010). By trampling/eating vegetation and redistributing nutrients, grazers influence a range of key ecosystem functions and characteristics across multiple trophic levels (Gordon et al., 2004, Mysterud, 2006). The intensity of their activity is one of the main drivers of how grazing affects the environment (Gordon et al., 2004, Mysterud, 2006). For instance, intense grazing can increase mortality and reduce recruitment of plants leading to simplification of habitat structure and reduction in species diversity (Milchunas et al., 1988, Gordon et al., 2004, Mysterud, 2006). Conversely, suppression of grazing can allow a few plant species to competitively dominate, leading to a simplification of habitat structure and reduction in species diversity (Milchunas et al., 1988, Gordon et al., 2004, Mysterud, 2006). Consequently, grazing at moderate intensities is often recommended for biodiversity conservation (e.g. Fuhlendorf and Engle, 2004, Dorrough et al., 2004b). However, there is currently limited empirical information on the benefits of moderate grazing intensities for biological conservation.

Anthropogenic impacts leading to a change in grazing intensity have occurred across terrestrial ecosystems globally (Gordon et al., 2004, Mysterud, 2006). Several common themes have emerged for how anthropogenic changes affect grazing systems: (i) release from population suppression of grazers (e.g. predator removal) leading to increased grazing intensity , (ii) suppressed grazer populations (e.g. hunting) leading to reduced grazing intensity, and (iii) changes in the pattern of grazing (e.g. domestic livestock) leading to uniform grazing across the landscape (Fuhlendorf and Engle, 2004, Gordon et al., 2004). These changes can have profound consequences for ecosystem function (Gordon et al., 2004, Mysterud, 2006, Milchunas et al., 1988). Most grazing studies have focused on intense grazing by domesticated livestock in biologically depauperate production landscapes (e.g. Matson et al., 1997, Brown et al., 2011). Relatively few studies have addressed the impact of changes in grazing intensity by native species in protected areas (Foster et al., 2014). This gap in knowledge is important because protected areas are major reservoirs of biodiversity (Brooks et al., 2006), and are often subject to anthropogenically altered grazing intensities (Gordon et al., 2004). Resumption of grazing patterns which promote conservation is a strategy adopted in restoration planning for many protected areas (e.g. Yellowstone National Park; Coughenour and Singer, 2000), but progress toward this goal is hampered by gaps in knowledge about what constitutes ‘appropriate’ grazing regimes for biodiversity conservation (Gordon et al., 2004).

Ground-dwelling species are particularly vulnerable to changes in the intensity of grazing (Hobbs and Huenneke, 1992) and are an important component of biodiversity in grassy ecosystems (Bond and Parr, 2010). Their vulnerability is due to their use of particular vegetation structures or configurations for food, shelter and reproduction (Dennis et al., 1998, Milsom et al., 2000, Barton et al., 2011, Woinarski and Ash, 2002). Additionally, the relatively limited dispersal capacity of many ground-dwelling species prevents movement to better habitat when local conditions deteriorate (Moir et al., 2005, Brown et al., 2011). Ground-dwelling reptiles are particularly sensitive to grazing because, in addition to the above vulnerabilities, they are ectothermic and thus sensitive to microhabitat change (Toft, 1985). Hence, reptiles are a good case study for investigating grazing impacts on ground-dwelling species (Brown et al., 2011). Furthermore, relative to other taxa, the direct and indirect impacts of grazers on ground-dwelling reptiles are poorly understood (Foster et al., 2014). Yet, these impacts may be profound (Michael et al., 2010, Brown et al., 2008, James, 2003, Brown et al., 2011, Castellano and Valone, 2006, Brown, 2001, Woinarski and Ash, 2002). Understanding these impacts is important because, in addition to their biodiversity value, reptiles provide an important ecological function in linking lower and upper trophic levels, as they largely feed upon invertebrates and plants, and are themselves then preyed upon by birds, mammals and other reptiles (Bennett, 1997, Tzaros, 2005)
.

In this study, we examined the impact of changes in grazing intensity by the native eastern grey kangaroo, *Macropus giganteus*, on reptiles in temperate grassland and grassy *Eucalyptus* woodland communities in south-eastern Australia. The eastern grey kangaroo (hereafter: kangaroo) is a medium-sized crepuscular and nocturnal marsupial (females; 40 kg, males; 90 kg) which occurs in open forests, woodland and grasslands, feeding predominately on grasses, with a minor component of browse (Grigg et al., 1989, Taylor, 1983, Viggers and Hearn, 2005). Kangaroos are seen as ecosystem engineers in these environments (ACT Government, 2010), as their effect on the structure, and composition of grassy vegetation (Viggers and Hearn, 2005, McIntyre et al., 2010, Meers and Adams, 2003, Neave and Tanton, 1989) influences the resources available to other species (Barton et al., 2011, Manning et al., 2013). As a consequence of anthropogenic change, populations of kangaroos have been both inflated (e.g. by predator removal, establishment of artificial water points) and suppressed (e.g. by fencing, habitat fragmentation, hunting) across our study region (ACT Government, 2010). This has resulted in a landscape-scale natural experiment characterized by a gradient of kangaroo densities and associated grazing intensities. We sampled reptiles along gradients in grazing intensity and asked: (1) Is there a relationship between the abundance of kangaroos and grass structure? (2) Does grazing at moderate intensities increase the abundance, richness, diversity and occurrence of reptiles? We aimed to provide baseline data on how changes in grazing intensity influence reptile communities, and provide recommendations for the management of grazing for conservation in these habitats.

Methods and Materials

Ethics statement

Reptile surveys were conducted with approval of the Australian National University Animal Experimentation Ethics Committee, protocol no. S.RE.10.10. There was a minor concern over impact on reptiles relating to tile searches, as turning of tiles may expose animals to predation. During surveys, care was taken to minimize adverse impact by returning tiles to initial position and not pursuing animals for identification for distances greater than 10m. Ethical clearance was given for the handling of the threatened striped legless lizard, *Delma impar.* This was necessary to accurately separate records from the similar looking olive legless lizard, *Delma inornata.*

Study region and Site selection

Our study was conducted within the range of temperate grassland and grassy *Eucalyptus* woodland communities across south-eastern Australia (Fig. 1a). These threatened communities have been extensively cleared and modified over the past 200 years (Prober and Thiele, 2005). Remnant vegetation persists mostly as fragmented, often small (< 1,000 ha) patches embedded in an agricultural matrix (Prober and Thiele, 2005).

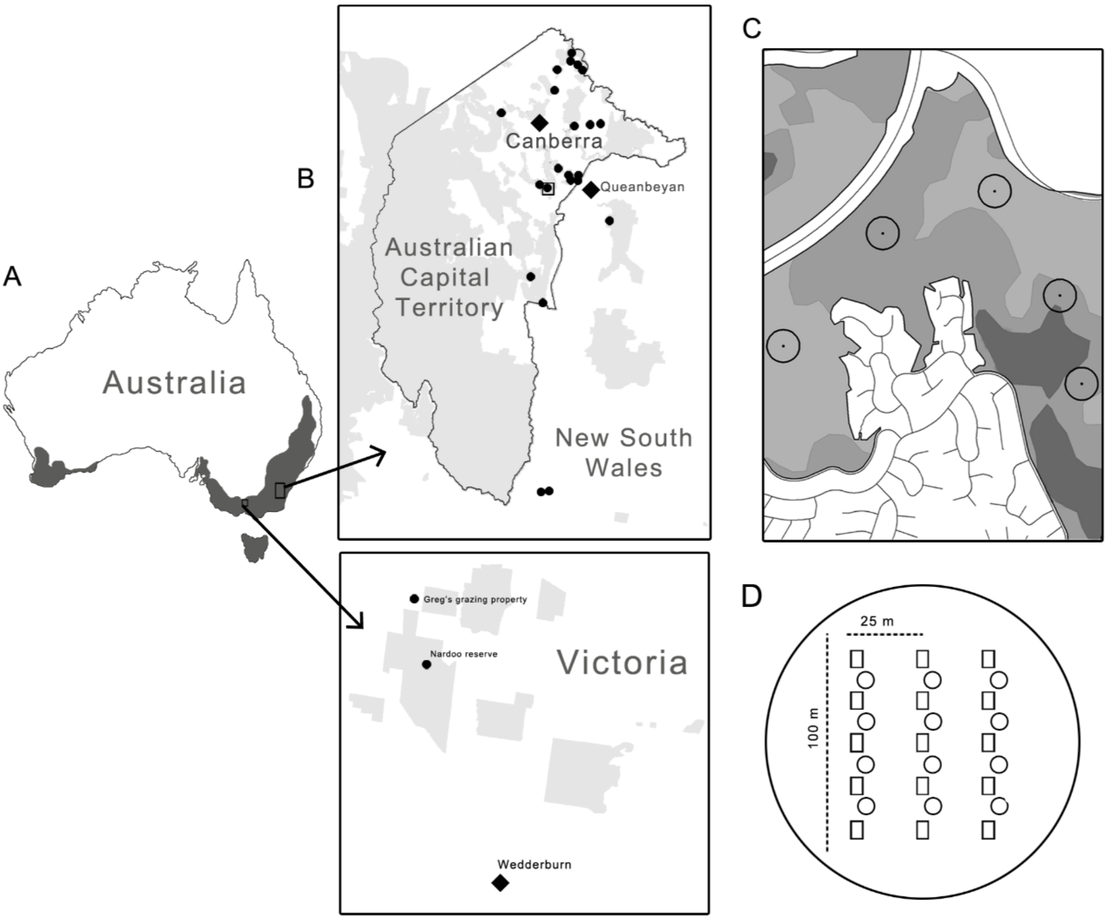

Figure 1. Study design. a) The distribution of temperate grassland and grassy woodlands (grey) across Australia. Selected study regions are shown (black outline) and expanded in b) location of study sites within south-eastern NSW and central Victoria, with protected areas shown in grey, sites shown as black dots and major towns as large black diamonds, c) an example of stratified random placement of study plots within a study site showing open woodland (light grey), woodland (grey) and open forest (dark grey) canopy types, and d) the layout of tiles (box) and circular survey disks (circle) within the study plot.

We selected 18 properties across the Australian Capital Territory (n = 14), New South Wales (n = 2) and Victoria (n = 2) where temperate grassland and grassy *Eucalyptus* woodland communities remain (Fig. 1b). The distribution of vegetation was closely aligned to topography and soil type; grasslands tend to occur in valley floors and clay soils, box-gum woodlands on lower slopes and fertile soils, with dry sclerophyll shrubby woodlands found on steeper slopes and infertile soils (Hobbs and Yates, 2000, Moore, 1970). Understorey was largely dominated by native perennial grasses (e.g. *Austrostipa spp., Bothriochloa macra, Rytidosperma spp., Themeda triandra),* although exotic perennial grasses were locally abundant at some locations (e.g. *Eragrostis curvula, Phalaris aquatica).* We assumed that by selecting sites where temperate grassland and grassy *Eucalyptus* woodland communities remained, we sampled sites with a relatively intact reptile community, as the reasons for decline of these communities (i.e. disturbance) have also negatively impacted reptiles (Hadden and Westbrooke, 1996, Brown et al., 2008). To avoid issues of small habitat islands (Smith et al., 1996), we selected large properties (>100 ha), that were, or were until recently (<15 years), connected to much larger (>500 ha) patches of remnant vegetation. Thus, we consider it unlikely that fragmentation influenced differences in fauna composition between properties (Smith et al., 1996). At the time of study, all but one property was being managed for the conservation of biodiversity, with a single property managed for livestock production. At this property, livestock had not been present for at least 12 months prior to study commencement. While selected properties covered a large geographical area, many of the same reptile species potentially occurred across all properties (Bennett, 1997, Tzaros, 2005). We did not consider geographic differences, as our intention was to explore whether the effects of changes in grass structure on reptiles was consistent across wide geographical areas. All sites fell within the 'temperate cool-season wet' climatic pattern with rainfall fairly evenly distributed throughout the year (Hobbs and McIntyre, 2005). The impacts of grazing on vegetation have likely been exacerbated by drought conditions which have prevailed over the study region for the last decade (Australian Government Bureau of Meteorology, 2014).

The kangaroo is the most common large native herbivore encountered in south-eastern Australia, and is considered to have benefited from European land-use change and eradication of the largest remaining carnivore, the dingo, *Canis lupus dingo* (see Grigg et al., 1989). Population surveys using pellet counts in the ACT and NSW, have confirmed the relative dominance of kangaroos compared to other large herbivores (ACT Government, 2010). Historically, the European rabbit, *Oryctolagus cuniculus*, has been a major contributor to grazing pressure; however national control programs (i.e. disease release; Cooke and Fenner, 2003) and ongoing management at all selected properties appear to have controlled rabbit numbers. Under current management, the contribution of rabbit grazing to total grazing pressure, appears to be substantially less than that of kangaroos (Fletcher, 2006). Both species of grey kangaroo, the eastern grey kangaroo and the western grey kangaroo, *Macropus fuliginosus*, were sympatric at Victorian properties, although the former was more common. These species are known to interbreed, and occupy similar niches, although western grey kangaroos appear more adapted to arid environments (Poole, 1975, Grigg et al., 1989). For the purposes of this study, we consider the impacts of these two species on grass to be comparable.

While all sites had a legacy of fire and grazing by domesticated livestock, with the exception of three properties, all properties had not been grazed by livestock or burnt in the last 10 years and no properties had been burnt or grazed by livestock within a year prior to study. We consider grazing by kangaroos to be the greatest contributor to grazing pressure.

We selected properties to cover a range of grazing intensities (i.e. low, medium, high) on the basis of initial visual observations of grass attributes. These categories were not used in analysis, but instead ensured we sampled from a range of grazing intensities. In most cases, the level of grazing was considered to be similar across an entire property. However, on a few properties barriers to movement (fencing, topography) had resulted in different levels of grazing being experienced. We took advantage of these differences, by stratifying sampling effort between these gradients. We recognised 24 different grazing units (hereafter: sites) across our 18 properties (see Appendix S1). A license to undertake this research on ACT reserves was obtained from the Land

Management and Planning Division of the ACT Government prior to project commencement. Additionally, permission to access Bush Heritage, Australian Government land, and a single private property were obtained from relevant authorities.

Experimental Design

Tree canopy cover influences the distribution of reptiles (Dorrough et al., 2012), grass productivity (Knowles et al., 1998) and large herbivore grazing patterns (Southwell, 1987). We therefore stratified our sites by canopy cover (Fig. 1c). A tree canopy cover map was created for each site using an unsupervised ISODATA classification technique (Franklin and Wulder, 2002) in Multispec (Biehl and Landgrebe, 2002) based on aerial photographs taken in 2008/9. The resulting map was further delineated into: grassland (0 – 2 % canopy cover), open woodland (2 – 20 %), woodland (20 – 50 %), open forest (50 – 80 %) and forest (80 – 100 %) canopy class polygons (>1 ha). These categories were similar to those in the national vegetation information system (Executive Steering Committee for Australian Vegetation Information (ESCAVI), 2003).

Within each site, we established multiple reptile survey plots (hereafter: plots) using a stratified random design, within grassland, open woodland and woodland canopy classes. We did not sample open forest or forest canopy classes as the grassy layer is suppressed in these dense habitat types. Two grassland plots were reclassified as open woodland due to the presence of several small trees within plot boundaries. Between three and nine 75 m radius (1.8 ha) plots were established at each site, with more plots established at larger sites with a greater variety of tree canopy classes (Fig. 1c). We used plots of this size because they are known to be effective in studies of reptile-habitat relationships (Brown et al., 2011). Overall, 127 plots were established, with 36 plots in grassland, 50 in open woodland, and 41 in woodland canopy classes.

Habitat characteristics

Tree canopy cover is correlated with important habitat features for reptiles (e.g. leaf litter and woody debris) and may directly affect habitat quality for reptiles by reducing light penetration (Burrow et al., 2001). We accounted for the potential confounding effect of tree canopy cover on reptiles by including tree canopy cover class as a dummy variable in analysis.

Grazing intensity

We used several grass attributes (see below) as a surrogate for kangaroo grazing intensity, rather than direct measures of grazing intensity (i.e. herbivore abundance). This approach had several advantages. First, we measured the resource for which reptiles interact directly for food and shelter (i.e. grass). Second, estimates of herbivore abundance are more error-prone than measures of vegetation condition (Morellet et al., 2007, Southwell, 1989). Third, grass structure provided an integrated, quantitative index of grazing impact among sites that vary in grazing history, soil and rainfall (Pöyry et al., 2006, Gordon et al., 2004). The value of grass structure as a surrogate for grazing pressure was tested by relating grass attributes to kangaroo abundance at a select number of sites where conditions were relatively similar.

Grass attributes

We conducted grass surveys from December 2009 to February in 2010 (coinciding with the local peak in perennial grass growth). We surveyed grass layer attributes within twelve 0.25 m^2 circular survey disks, which were systematically placed across each plot (Fig. 1d). At each grass survey point, we recorded grass height (cm), biomass (kg dry matter/ha), and percent cover of grass. We estimated grass height as the average height of above-ground leaf, with the 'comparative yield' technique (Haydock and Shaw, 1975) used to estimate grass biomass. We took vertically-oriented photographs of each grass survey point and analyzed them using the program 'SamplePoint' (Booth et al., 2006) to calculate percentage grass cover. Averaged over the plot grass height ranged from 1.7 – 18.1 cm, grass biomass from 66 – 3354 kgDM/ha and percent grass cover from 0 – 91 %.

Kangaroo density

We estimated the density of kangaroos within different tree canopy classes at a select number of sites (n = 15). We restricted analysis to sites where conditions were relatively similar to avoid factors like grazing history and rainfall confounding the relationship between herbivore abundance and grass attributes (Gordon et al., 2004). A variety of established methods were employed to survey kangaroos - pellet counts, total counts and line transect distance sampling (see Southwell, 1989). Details of kangaroo surveys can be found in Appendix S2. We believe these surveys of kangaroo abundance provided a representative assessment of grazing pressure within different tree canopy classes. For example, because kangaroo defecate more while feeding (Johnson et al., 1987a), pellet counts provide an unbiased assessment of grazing pressure. Total counts were employed only at sites where a single canopy class occurred. These sites were small and it was possible to count the entire population from vantage points. Counts were repeated on multiple days to ensure we captured an accurate representation of grazing pressure. Line transect distance sampling was undertaken early in the morning when kangaroos are actively feeding to provide an account of grazing pressure between canopy classes. We estimated kangaroo density in 2009 at 12 sites, and in 2011 at an additional three sites. Kangaroo management activities were undertaken at a single study site in the winter of 2009. Therefore, we estimated density for this site as the average between the 2008 (pre management) and 2009 (post management) kangaroo density estimates. The density of kangaroos ranged from 0.25 to 3.6 animals/ha across selected sites.

Reptile surveys

In 2010 we surveyed plots for ground-dwelling reptiles using artificial shelters (as per Michael et al., 2012). We conducted reptile sampling from February to May and from September to November, as reptiles are more likely to use artificial shelters during this time (Michael et al., 2012). We deployed artificial shelters comprising 15 concrete roof tiles at each plot 2 -3 months before reptile surveys. We did this to increase capture rates by allowing time for reptiles to grow accustomed to (and then occupy) the tiles. We spaced tiles at least 15 m apart (Fig. 1d), which is larger than the home range and movement of many small reptiles (Stevens et al., 2010). This reduced the likelihood of double counting, which was important as we considered tiles as independent sampling units for our estimation of abundance.

We conducted searches of tiles for basking and sheltering reptiles on non-rainy days, after sunrise and before sunset during periods of mild temperature (i.e. 5 – 25° C). To increase the likelihood of presence and reduce bias occurring due to variation in weather conditions, we surveyed each tile and plot on eight separate occasions. We assumed that habitat structure did not affect the likelihood of a reptile being detected under a tile. Rather, tiles provided a temporary snapshot of reptile abundance in surrounding habitat. This assumption appeared to be valid as the thermal properties of tiles (temperature extremes) prevented their permanent occupation. We could not complete reptile searches at two plots due to difficult terrain and damage to tiles, leaving a total of 125 plots for analysis.

Analysis

We performed a principal components analysis (PCA) using a correlation matrix on all grass attributes (grass height, grass biomass, grass cover) to reduce the number of covariates, and obtain a smaller number of independent variables (Manly, 1994). PCA values are the combination of multiple component variables, and cannot be quantified directly in the field, making interpretation by managers problematic. Therefore, to aid interpretation of results, we examined the relationship between each component variable and PCA values, using generalized linear modelling procedures (GLM; Nelder and Wedderburn, 1972). We modelled this relationship with a normal distribution and an identity link function.

Next we explored the relationship between PCA values, kangaroo density and tree canopy class using hierarchical generalized linear mixed modelling procedures (HGLMM; Lee and Nelder, 1996). Due to the non-trivial issues of model selection where random effects are included (Vaida and Blanchard, 2005), we opted to fit a complete model for each analysis, instead of undertaking the more common approach of choosing a 'best' model on the basis of AIC values (i.e. Burnham and Anderson, 2002). We included tree canopy cover class, as canopy cover can reduce grass growth (Knowles et al., 1998). We estimated kangaroo abundance over an entire canopy class, because the size of individual plots was at too fine a scale to estimate kangaroo abundance accurately (Southwell, 1989). To obtain values for each canopy class, we averaged PCA for all plots within the same canopy class. To account for nesting and potential similarity between canopy classes within the same property, we included property as a random effect (Lee and Nelder, 1996). The relationship was modeled with a normal distribution and an identity link function, with random effects fitted with a normal distribution and an identity link function. Prior to regression analysis, we transformed PCA values (variable + 1.5) to obtain positive values.

We calculated reptile abundance, species richness, and species diversity for each plot. We defined reptile abundance as the maximum number of individuals of a species seen at the tile in a single visit. We then summed values for all species to estimate abundance at the plot level. We defined species richness as the total number of species recorded for each plot after eight visits. We calculated diversity using the Shannon index, as this index appeared appropriate given the numerical dominance of a few species in our results (Pitkänen, 1998).

We built occupancy models for those species of reptiles which were encountered in >10 % of plots, namely: Boulenger's skink, *Morethia boulengeri* (46%), delicate skink, *Lampropholis delicata* (41%), common dwarf skink, *Menetia greyii* (23%) and the eastern three-toed earless skink, *Hemiergis talbingoensis* (16%). The striped legless lizard, *Delma impar* (9%) and the olive legless lizard, *Delma inornata*, (6%) had small sample sizes but have similar life histories (Fischer et al., 2004, Bennett, 1997), so were pooled in a 'legless lizard' group (14%) for the analysis. The delicate skink is not known to occur near our Victorian properties (Tzaros, 2005). We therefore removed all plots in Victoria (n = 9) from analysis for this species. For analysis of reptile habitat relationships, we reclassified two grassland plots as open woodland, as several small trees occurred within plot boundary. To account for zero-dominated occupancy data, we analyzed reptile data as presence/absence in a logistic regression. We considered a reptile to be present at a tile if it was recorded at least once in any of the eight visits.

Lastly, we modeled reptile abundance, species richness, species diversity and individual reptile occupancy as a function of PCA values and tree canopy cover class using HGLMM procedures. To account for nesting (i.e. plots occurred within a property) and potential similarity between plots within our study design, we included property as a random effect (Lee and Nelder, 1996). Again, we fit a complete model, with grass structure and tree canopy class included. The relationship between reptile abundance and species richness was modelled with a Poisson distribution, a logarithm link function, and random effects fitted with a gamma distribution and a logarithm link function. Reptile diversity was modelled with a normal distribution and an identity link function, with random effects fitted with a normal distribution and an identity link function. We modelled individual species with a binomial distribution, a logit link function, with random effects fitted with a beta distribution and a logit link function. Grass structure was fitted as a linear term, with a quadratic term included where exploratory analysis indicated a possible curvilinear relationship. Residual plots and distribution of residuals were examined to check model assumptions. We standardized grass structure to a mean of 0 and standard deviation of 1. All analyses was undertaken in Genstat 12 (VSN International, 2012).

Results

We recorded 781 reptiles, representing 20 species from four families, including 89 records of 'unidentified skinks' (Appendix S3).

Principal components analysis

We found the first two components of the PCA described 95.15% of the variation between grass attribute variables. The first PC explained 81.35% of variation with a latent root value of 2.441. High values corresponded to tall grass, large amounts of biomass and high grass cover with low values corresponding to short grass, low amounts of biomass and limited cover of grass. Principal component one collapses grass metrics into one unit which here we call 'grass structure'. The second PC explained only 13.8% of variation with a latent root value 0.414. We dropped the second PC as factors with latent roots less than one are considered insignificant (Joseph et al., 1984). We found a significant positive relationship between the first PCA (i.e. grass structure), and each component grass attribute (Appendix S4). To aid interpretation, we graphically represented the relationship between grass structure and each component grass attribute in Appendix S5.

Grazing intensity

Grass structure was significantly and negatively related to both tree canopy cover and kangaroo density (Table 1). Our results suggest, that to maintain the same level of grass structure, more kangaroos could be supported in grasslands, with low tree canopy cover, as compared to open woodlands and woodlands, where tree canopy cover is high (Fig. 2).

Table 1. Results of hierarchical generalized linear mixed models of PC1 (grass structure) in relation to kangaroo density and tree canopy class (dummy variable) showing trends (Slope) including standard errors (SE). Grassland has been used as a reference level for tree canopy class categories. Significance is indicated by the Wald statistic ($\chi 2$) and p-value as follows: *p<0.05, ** p<0.01, ***p<0.001.

Response	Model term	d.f.	$\chi 2$	Slope	SE	Graphical summary
Grass structure	Intercept			3.08	0.45	
	tree canopy class	2	27.81***			Fig. 2
	open woodland			-0.88	0.32	
	Woodland			-1.76	0.34	
	kangaroo abundance	1	5.94*	-0.43	0.21	Fig. 2

Habitat relationships

We developed HGLMM for reptile abundance, species richness, species diversity, and the occurrence of Boulenger’s skink, delicate skink, common dwarf skink, eastern three-toed earless skink, and legless lizards (Table 2). Tree canopy cover was an important predictor of reptile abundance, species richness and diversity, with highest values recorded in woodland habitat (Fig. 3). Reptile abundance, species richness and diversity were positively related to grass structure (Fig. 4).

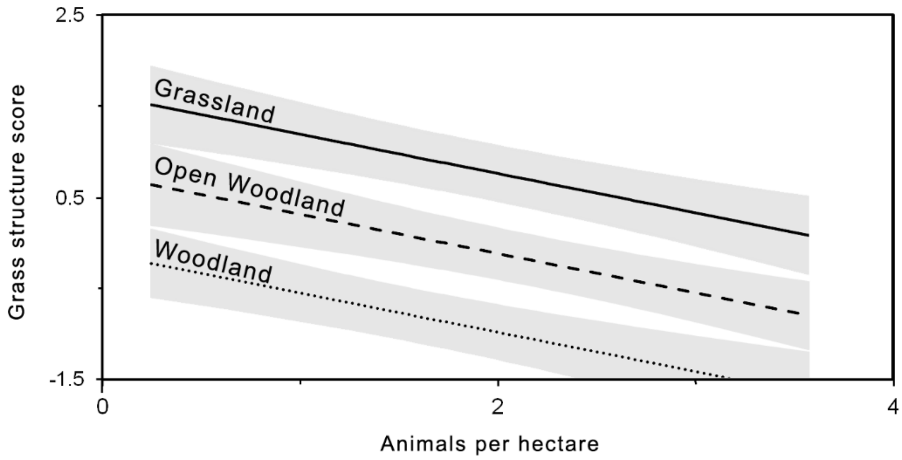

Figure 2. Graphical representation of linear regression models summarized in Table 1. The graph shows significant relationships between kangaroo density (animals/ha) and grass structure (PC1) for each tree canopy cover class (grassland, open woodland, woodland). Standard error of the model predictions are shown in grey. To aid interpretation of results, variables have been back-transformed to original scale.

Boulenger's skink and the delicate skink did not respond to grass structure but responded significantly to changes in tree canopy cover. The occurrence of the Boulenger's skink, delicate skink and the eastern three-toed earless skink increased with increasing tree canopy cover, with all three species most common under woodland habitat (Fig 5). In contrast, legless lizard presence was significantly negatively related to tree canopy cover, and was most common under grassland habitat, and did not occur under woodland habitat (Fig. 5d). The likelihood of occurrence of the eastern three-toed earless skink, and legless lizard, were significantly related to grass structure (Fig. 6). The occurrence of the eastern three-toed earless skink increased with increasing values of grass structure (Fig. 6a). The legless lizards were more likely to occur at intermediate grass structure values between 1 – 3 (Fig. 6b). Occurrence of the common dwarf skink was not related to any environmental variable.

Discussion

We have shown that the abundance, species richness, species diversity and occurrence of ground-dwelling reptiles varied over a natural gradient in grazing intensity related to the density of a native grazer, the eastern grey kangaroo. Crucially, a strong and inverse relationship between kangaroo density and grass structure existed, allowing us to use grass structure (i.e. PC1) as a surrogate for grazing intensity. Our study revealed that changes in grazing intensity affected different species in different ways. Importantly, intense grazing and associated reduction in grass structure was not favoured by any reptiles in this study. We found reptile abundance, reptile species richness, reptile diversity and the occurrence of three of six species of reptile were all lower at high grazing intensity. We found only limited evidence to support the benefits of grazing at moderate intensities in these landscapes. Therefore, across the landscape, managers will need to subject areas to different grazing intensities, to accommodate varied requirements of reptiles. We suggest that even in habitats dominated by native grazers, changes in grazing intensity can have major impacts on ground-dwelling species.

General impacts of grazing

Changes in grazing intensity by domestic livestock have been shown to have a profound effect on the reptile community. Generally, intense grazing by domestic livestock has had a negative effect on both reptile abundance and reptile species richness (Michael et al., 2010, Brown et al., 2008, James, 2003, Castellano and Valone, 2006, Brown, 2001, Woinarski and Ash, 2002, Janzen, 1976). However, studies by Brown et al. (Brown et al., 2011) and Dorrough at al. (Dorrough et al., 2012) in Australian grassy woodlands, found a weak but positive effect of the number of domestic herbivores on reptile abundance. This positive effect of grazing appeared to be driven by an increase in abundance of a few generalist species that benefit from reduction in ground cover with increased grazing (Brown et al., 2011, Dorrough et al., 2012). In this study, reptile species diversity was positively correlated with grazing intensity, with low grass structures also dominated by just a few generalist species. However, at high grazing intensities, the reptile community was less diverse, reptiles were less common and reptile species richness was lower. The only other study on native grazers and reptiles in grassy woodlands in Australia found the experimental reduction in grazer numbers resulted in increased small skink abundance (Manning et al., 2013). Prolonged intense grazing resulting in the simplification of grass structure may negatively impact reptiles through increased predation risk (Castellano and Valone, 2006), decreased prey availability (Barton et al., 2011), and loss of shelter (Michael et al., 2010, Castellano and Valone, 2006). Importantly, the impacts of grazing on reptiles is likely to cascade up the food chain as reptiles are important food sources for various other taxa, including birds, mammals and large predatory reptiles (Tzaros, 2005).

Habitat features associated with tree canopy cover, such as leaf litter and logs are known to provide important habitat features for reptiles (Fischer et al., 2004, Michael et al., 2010). In this study, reptile abundance, reptile diversity and reptile species richness was positively associated with tree canopy cover, and was higher in woodland than grassland habitats (Fig. 3). Utilization of non-grass structures may buffer the impacts of grazing by providing alternate habitat refugia (e.g. Barton et al., 2011, Manning et al., 2013). The implications for land managers of this result is that the management of grazing can be critical in grasslands which lack tree-related habitat refugia

Table 2. Results of hierarchical generalized linear mixed models for species abundance, species richness, reptile diversity, and individual species showing trends (Slope) including standard errors (SE). Grassland has been used as a reference level for tree canopy class categories. Significance is indicated by the Wald statistic ($\chi2$) and p-value as follows: *p<0.05, ** p<0.01, ***p<0.001.

Response	Model term	d.f.	$\chi2$	Slope	SE	Graphical summary
Reptile Abundance	Intercept			0.91	0.22	

	tree canopy class	2	8.006*			Fig. 3a
	open woodland			0.32	0.24	
	woodland			0.74	0.28	
	grass structure	1	7.589**	0.27	0.10	Fig. 4a
Species Richness	Intercept			0.21	0.18	
	tree canopy cover	2	6.511*			Fig. 3b
	open woodland			0.38	0.20	
	woodland			0.59	0.23	
	grass structure	1	8.627**	0.24	0.08	Fig. 4b
Reptile Diversity (Shannon index)	Intercept			0.23	0.11	
	tree canopy class	2	9.74**			Fig. 3c
	open woodland			0.26	0.12	
	woodland			0.42	0.13	
	grass structure	1	10.49**	0.17	0.05	Fig. 4c
Boulenger's skink	Intercept			-4.27	0.56	
	tree canopy class	2	10.461**			Fig. 5a
	open woodland			1.72	0.59	
	woodland			2.06	0.64	
	grass structure	1	0.017	-0.03	0.22	
Delicate skink	Intercept			-3.68	0.41	
	tree canopy class	2	20.33			Fig. 6b
	open woodland			0.39	0.43	
	woodland			1.69	0.48	
	grass structure	1	3.33	0.28	0.15	
Common dwarf skink	Intercept			-4.24	0.53	
	tree canopy class	2	1.917			

	open woodland			0.69	0.57	
	woodland			0.44	0.67	
	grass structure	1	1.504	0.37	0.31	
	grass structure^2	1	2.507	-0.37	0.23	
Eastern three-toe earless skink	Intercept			-5.61	0.54	
	tree canopy class	2	6.3*			Fig. 5c
	open woodland			-0.12	0.37	
	woodland			1.07	0.56	
	grass structure	1	35.26***	1.15	0.19	Fig. 6a
Legless lizard	Intercept			-4.34	0.61	
	tree canopy class	2	7.09*			Fig. 5d
	open woodland			-0.89	0.34	
	woodland			-10.00	16.00	
	grass structure	1	14.77***	2.44	0.63	Fig. 6b
	grass structure^2	1	14.17***	-0.89	0.24	

In addition to generating new information on broad interactions between grazing intensity and reptiles, our study provides new insights into the habitat preferences of several poorly researched reptiles. For example, legless lizards were most common in areas with moderate grazing intensity (Fig. 6b), and low tree canopy cover (Fig. 5d). While preference for low tree canopy cover is well established (Brown et al., 2011, Fischer et al., 2004), our study is the first study to identify preference for a particular grazing intensity. The eastern three-toed earless skink was more likely to occur in areas subject to under low grazing intensity (Fig. 6a), and was more common in woodland compared to open woodland and grassland habitats (Fig. 5c). The vulnerability of the eastern three-toe earless skink to intense grazing has not previously been recorded.

Unlike the other species, Boulenger's and delicate skinks did not respond to grass attributes, but instead were positively associated with tree canopy cover (Fig. 5a and 5b). The preference of these species for leaf litter and logs (Wilson and Swan, 2008), which are not directly impacted by grazing, may account for this result. Nonetheless, high intensity grazing may still impact these species over longer temporal scales via reduced tree recruitment (Fischer et al., 2004), or by impacting invertebrate prey (Barton et al., 2011).

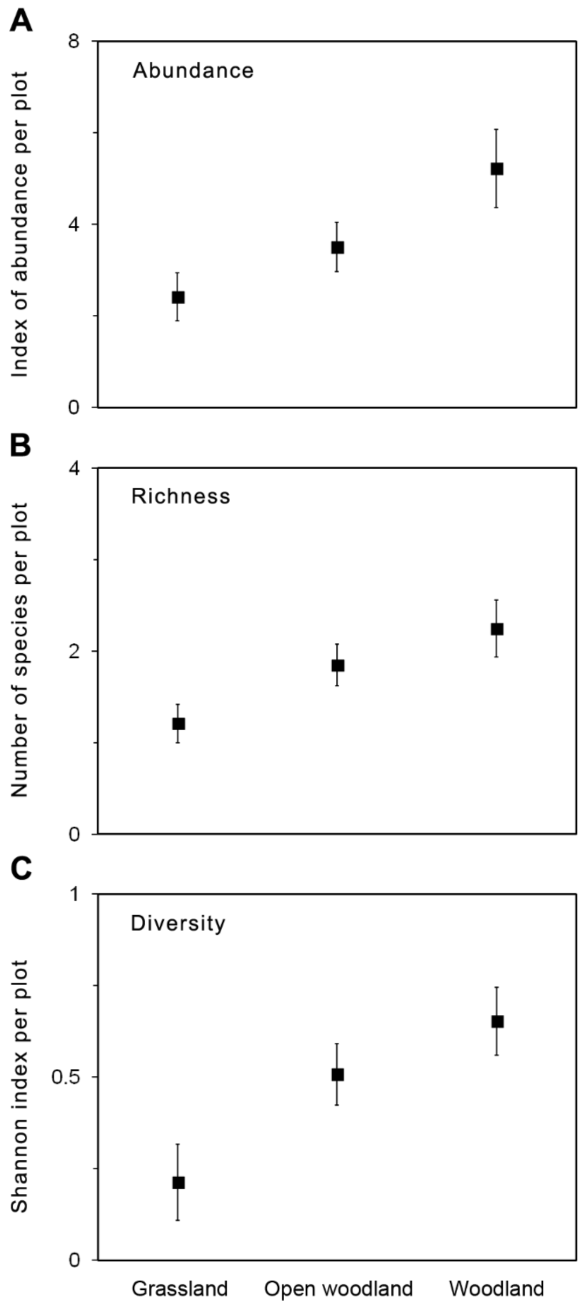

Figure 3. Graphical representation of logistic regression models summarized in Table 2. The graphs shows mean values for a) reptile abundance, b) reptile species richness and c) reptile species diversity at a given plot for each tree canopy cover class (grassland, open woodland, woodland). Standard error bars are shown. To aid interpretation of results, variables have been back-transformed to original scale.

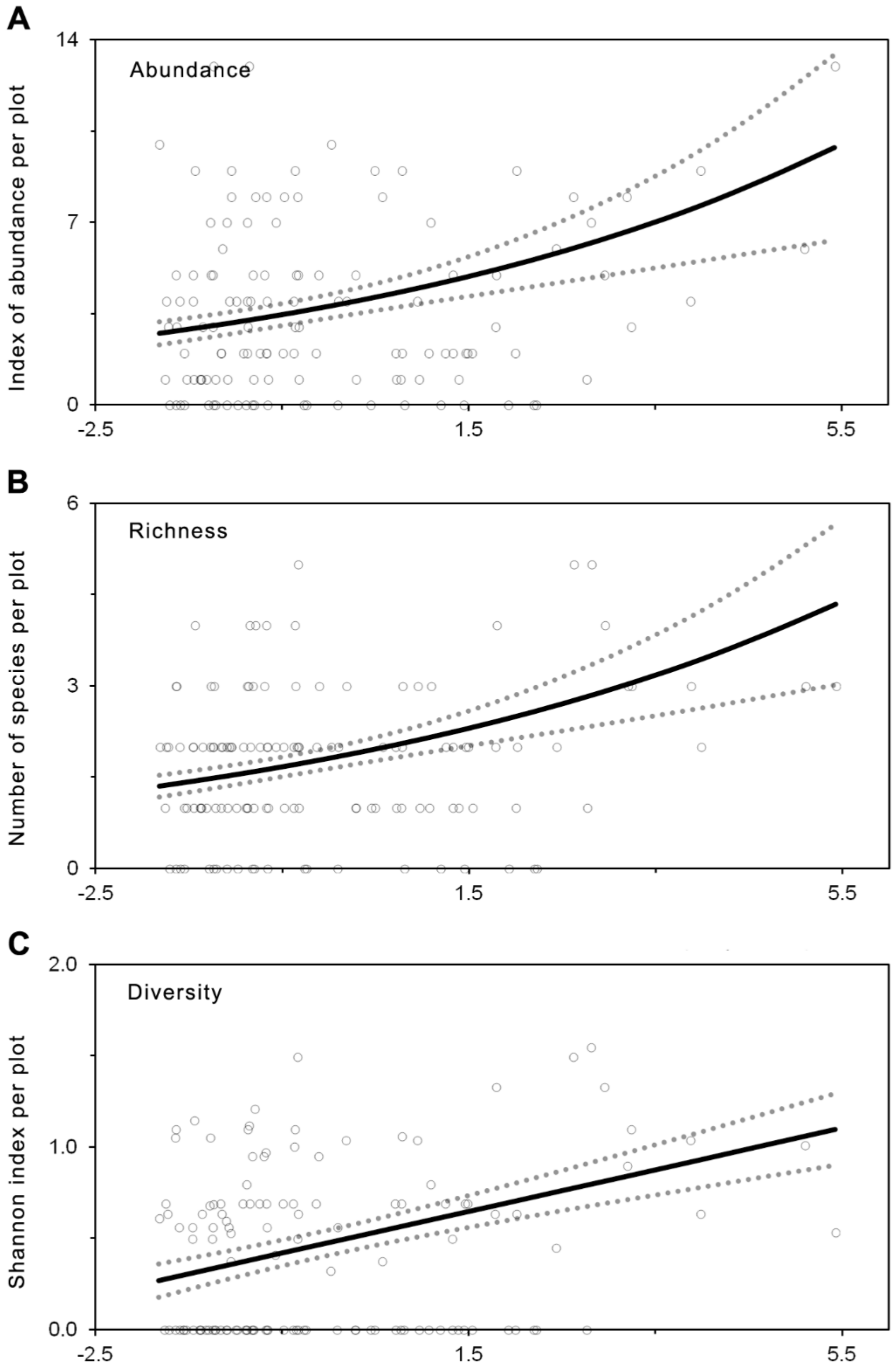

Figure 4. Graphical representation of linear regression models summarized in Table 2. The graphs show significant relationship between grass structure (PC1) for a) reptile abundance, b) reptile species richness and c) reptile species diversity in a given plot. Fitted relationships are shown as a solid line, with actual values shown as an open circle. Standard error of the model predictions are

shown as a dotted line. To aid interpretation of results, variables have been back-transformed to original scale.

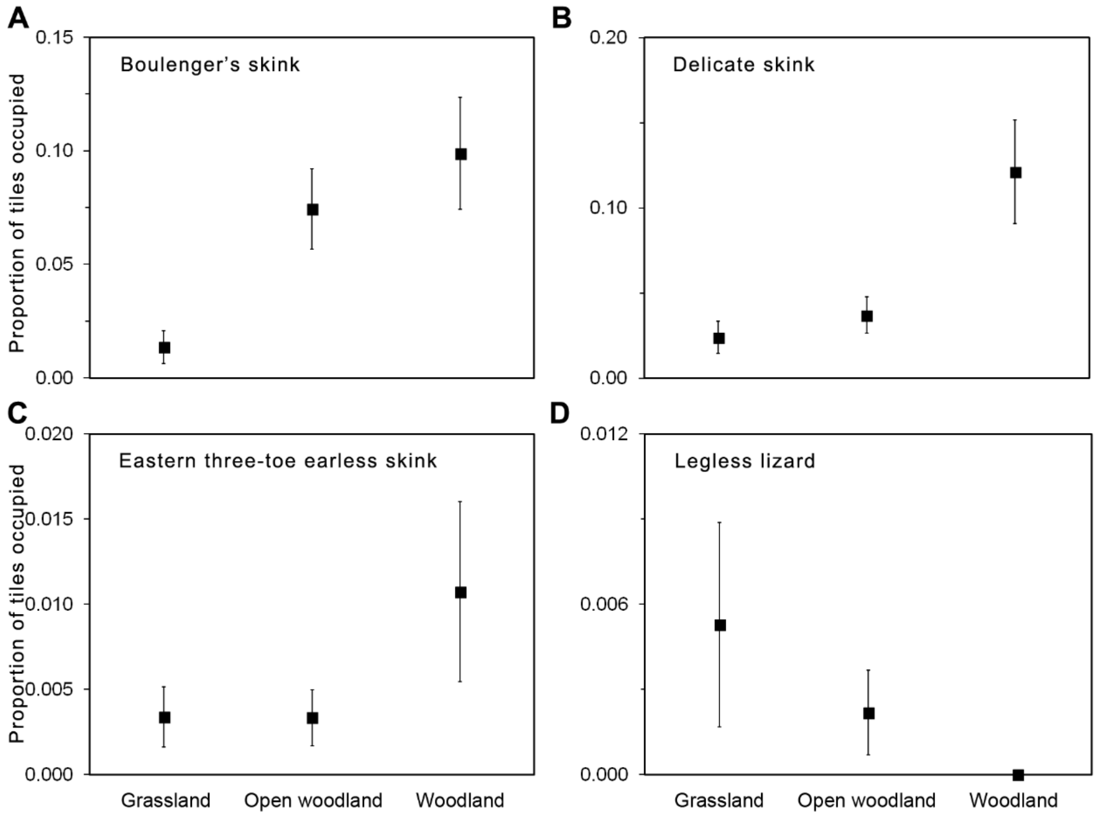

Figure 5. Graphical representation of logistic regression models summarized in Table 2. The graphs shows mean values for a) Boulenger's skink, b) delicate skink, c) eastern three-toe earless skink and d) legless lizard at a given plot for each tree canopy cover class (grassland, open woodland, woodland). Standard error bars are shown. To aid interpretation of results, variables have been back-transformed to original scale.

Management prescriptions

Managers require optimal grazing conditions to be expressed as recommended animal densities under a range of conditions (Gordon et al., 2004). The modelled relationship between kangaroo abundance and grass structure (Fig. 2) in this study could be used to develop such recommended herbivore densities based on optimal grass structure for reptiles. For instance, based on optimal grass structure for legless lizards (Fig. 6b), our model predicts a kangaroo density less than 0.5 kangaroos per hectare. However, this relationship is based on average values, at a select number of sites over a few years, thus the relationship will unlikely hold in different sites and different years. Instead of defining management prescriptions, the association between kangaroo abundance and grass structure has several important implications for managers. First, grass structure had a negative relationship to the number of kangaroos. Second, the impact of kangaroo grazing was greater where canopy cover was higher (i.e. open woodlands and woodlands). Third, regardless of kangaroo densities, grass structure was low in woodland habitat. To obtain more detailed recommendations for animal density under a range of conditions, a greater understanding of factors that affect grazing impact (e.g. grass growth and herbivore consumption) will be required.

Conservation implications

Grazing at moderate levels is often recommended for biodiversity conservation (e.g. Fuhlendorf and Engle, 2004, Dorrough et al., 2004a, Milchunas et al., 1988), as this level of grazing is considered to increase niche availability, and hence species richness (Finke and Snyder, 2008). In our study, although legless lizards (olive legless lizard, striped legless lizard) preferred moderate grazing intensity, the abundance, richness and diversity of reptiles and occurrence of the eastern three-toe skink was highest at low grazing intensity. Hence, moderate grazing intensity did not ensure conservation of all ground-dwelling reptiles in this study. In reality, few empirical studies have found support for grazing at moderate intensities for biological conservation (see Dorrough et al., 2012, McIntyre et al., 2003, Beever and Brussard, 2004) as different species require different habitat conditions. The challenge for grazing management in these environments is highlighted in this study by the preference of the threatened striped legless lizard (Dorrough and Ash, 1999) for moderate grazing intensity, rather than low grazing intensities which were associated with the most diverse reptile assemblage. Therefore, to accommodate varied requirements of reptiles, there will be a need for land managers to subject different areas of the landscape to different grazing intensities (Fuhlendorf and Engle, 2004, Vandvik et al., 2005, James, 2003).

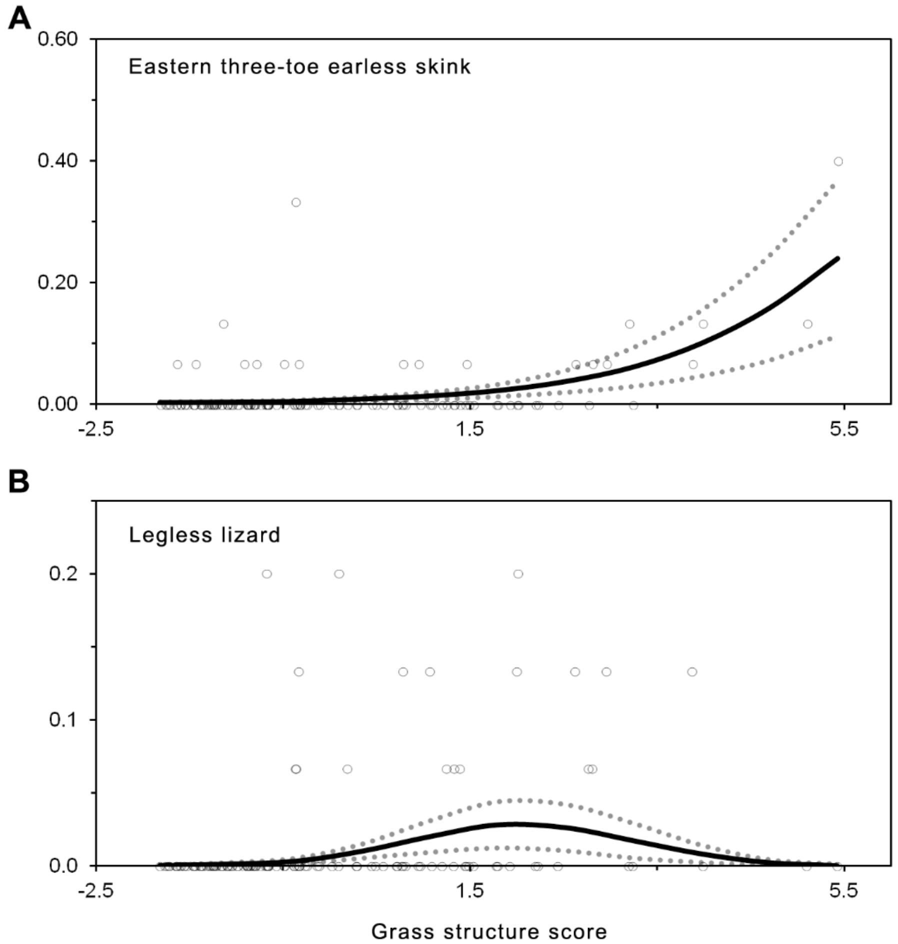

Figure 6. Graphical representation of logistic regression models summarized in Table 2. The graphs show significant relationships between PC1 values (grass structure) and the probability of encountering a species in a given plot for the a) eastern three-toe earless skink, and b) legless lizard. Fitted relationships are shown as a solid line, with actual values shown as an open circle. Standard error of the model predictions are shown as a dotted line. To aid interpretation of results, variables have been back-transformed to original scale.

Our results indicate that to maximize habitat quality simultaneously for multiple species and increase reptile abundance, diversity and richness, prolonged intense grazing resulting in areas with low grass structure should be avoided. However, a common consequence of anthropogenic management in protected areas in Australia (and elsewhere) has been an increase in herbivore density and grazing pressure (Gordon et al., 2004, Caugley, 1987). For reptile species like those in our study that prefer light to moderate grazing intensities, inflation of grazer populations can profoundly alter habitat suitability. The sensitivity of reptiles in our study is likely to be symptomatic of broader problems facing a range of species in habitats shaped by grazing. Anthropogenically altered patterns and intensity of grazing has repeatedly been shown to negatively impact biodiversity (Gordon et al., 2004, Mysterud, 2006, Foster et al., 2014), and our results conform to these broad trends for a native species of grazer. Evidence from more intensively researched study systems under livestock grazing in Australia has shown that management approaches that support both low to moderate grazing intensity across the landscape, and that limit prolonged intensive grazing, are likely to benefit biodiversity (Woinarski and Ash, 2002, Kutt and Woinarski, 2007, Martin et al., 2005, McIntyre et al., 2003). Limiting prolonged intense grazing in systems dominated by native herbivores typically relies on the re-introduction of predators (Ripple and Larsen, 2000), and/or culling (Young et al., 2009).

Conclusion

Our study provides important new insights into the impact of native herbivore grazing pressure, and indicates that intense grazing does not support an abundant or rich reptile community. In line with other studies on grazing sensitive systems around the world, the recognition of certain grazers as important ecosystem engineers, and their management in anthropogenically altered landscapes is important for the maintenance of biodiversity in grassy habitats.

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Supporting Information

Appendix S1. Characteristics of reptile study sites (listed in alphabetical order).

Property ID	Grazing unit ID	Governance	Estimated Grazing intensity	Area - Property	Area - Grazing unit	Number of canopy types	Number of reptile Plots
1	1	ACT	Low	106	106	2	4
2	2	ACT	High	143	143	2	6
3	3	ACT	High	112*	13	1	3
4	4	ACT	Low	113	113	1	3
5	7	ACT	Moderate	179	179	2	4
6	8	ACT	Moderate	239	239	2	6
7	9	NSW	High	530	530	3	9
8	6	ACT	Moderate	688	112	2	4
8	10	ACT	Moderate	688	576	2	7
9	12	ACT	Low	112	15	1	3
9	11	ACT	Moderate	112	97	1	3
10	13	ACT	Low	266	39	1	3
10	14	ACT	Moderate	266	227	3	7
11	15	ACT	Low	154	154	3	9
12	16	ACT	High	701	581	3	8
12	17	ACT	Low	701	120	1	3
13	18	ACT	Low	142	142	2	6
14	5	ACT	Moderate	429	77	2	6
14	19	ACT	High	429	352	2	6
18	24	VIC	High	825	825	2	6
17	23	VIC	High	221	221	2	3

15	21	NSW	Moderate	1151	790	2	6
15	20	NSW	Low	1151	361	2	6
16	22	ACT	High	229	229	2	6

Appendix S2. Details of the study site, canopy class, density obtained, method used and year kangaroo surveys were carried out at 14 study sites.

Grazing unit - ID	Tree canopy class	Density	Method	Year
1	OW	0.6	Pellet count	2011
1	W	2	Pellet count	2011
2	OW	2.2	Pellet count	2009
2	W	1.6	Pellet count	2009
3	G	3	Total count	2009
4	G	1.2	Total count	2009
7	OW	3.6	Pellet count	2011
7	W	1.4	Pellet count	2011
6	G	1.2	Pellet count	2009
6	OW	1.5	Pellet count	2009
8	OW	1.5	Pellet count	2011
8	W	1.8	Pellet count	2011
9	G	2.7	Pellet count	2009
9	OW	2.1	Pellet count	2009
9	W	1.7	Pellet count	2009
10	OW	2.7	Pellet count	2009
10	W	1.5	Pellet count	2009
11	G	3	Total count	2009
14	G	0.5	Pellet count	2009
14	OW	2.4	Pellet count	2009
14	W	1.9	Pellet count	2009
18	G	0.7	Pellet count	2009
18	OW	1.5	Pellet count	2009

19	OW	2	Pellet count	2009
19	W	1.6	Pellet count	2009
22	OW	2.3	Pellet count	2009
22	W	0.2	Pellet count	2009
16	G	3.4	Distance sampling	2008/2009
16	OW	2.8	Distance sampling	2008/2009
16	W	1.7	Distance sampling	2008/2009

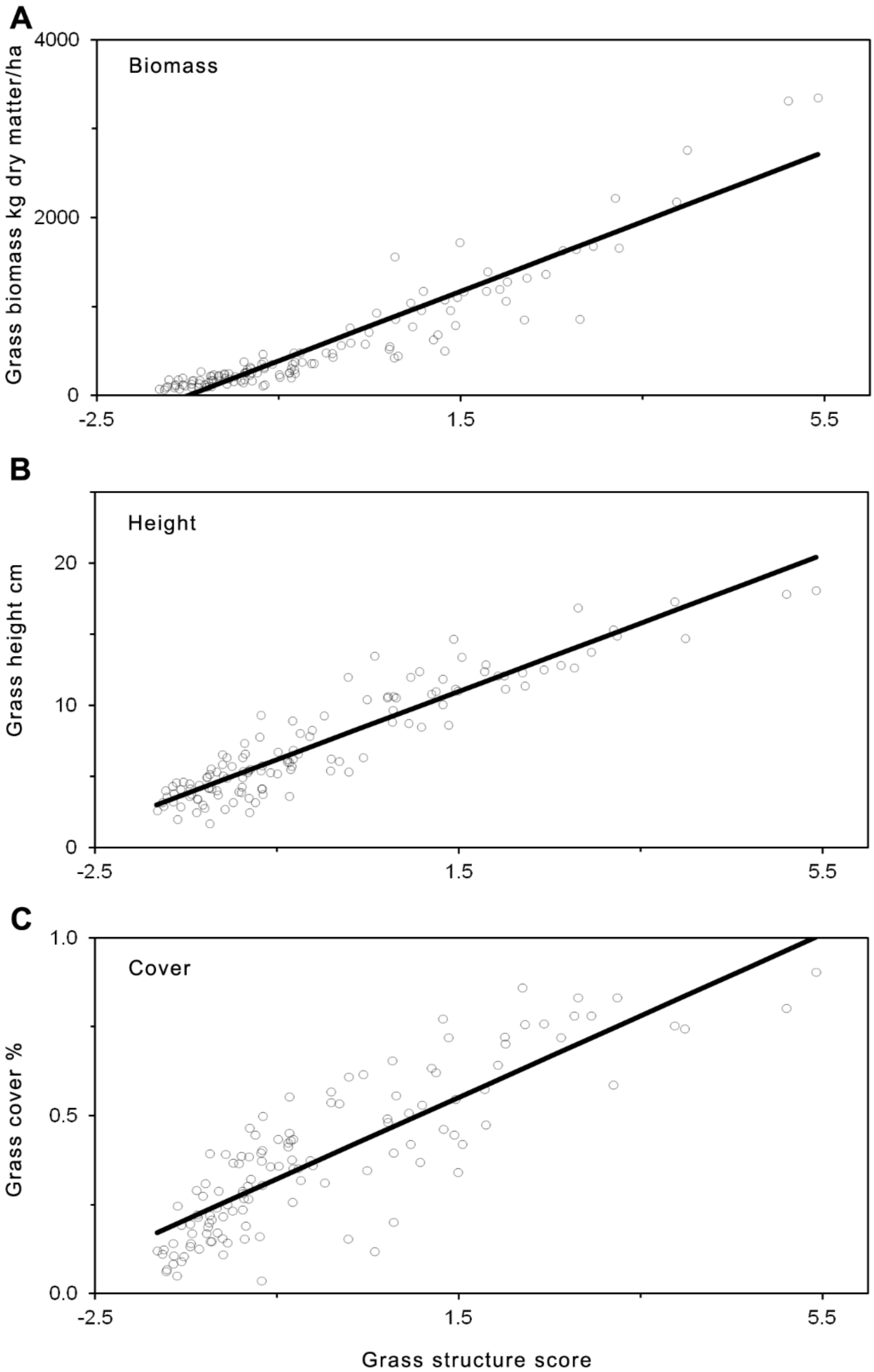
Appendix S3. Reptiles captured in this study, ordered by "Number of records".

Common name	Species name	Size (mm)	Number of records	Number of plots	Number of tiles
Boulenger's skink	Morethia boulengeri	100	261	57	141
Delicate skink	Lampropholis delicata	90	187	51	122
Eastern three-toed earless skink	Hemiergis talbingoensis.	100	66	20	37
Common dwarf skink	Menetia greyii	80	47	29	37
Striped legless lizard	Delma impar	200	26	11	21
Grass skink	Lamprophlois guitchenoti	90	19	14	17
Eastern brown Snake	Pseudonaja textilis	2000	11	8	10
Olive legless lizard	Delma inornata	400	10	7	10
Common bearded dragon	Pogona barbata	500	8	3	4
Eastern striped skink	Ctenotus robustus	300	5	3	3
Shingleback lizard	Trachydosaurus rugosus	400	4	1	2
Copper-tailed skink	Ctenotus taeniolatus	200	3	1	2
Eastern blue-tongued lizard	Tiliqua scincoides	500	2	2	2
Spotted-backed skink	ctenotus orientalis	300	2	2	2
Eastern Three-lined Skink	Bassiana duperreyi	200	1	1	1
Jacky lizard	Amphibolurus muricatus	400	1	1	1
Pink-tailed worm lizard	Aprasia parapulchella	180	1	1	1

Four-fingered skink	Carlia tetradactyla	150	1	1	1
Red-throated skink	Bassiana platynotum	180	1	1	1
Legless lizards	Delma. Sp	200-400	36	18	31
unidentified skink		-	89	45	80

Appendix S4. Results of generalized linear mixed models for grass biomass, grass height and grass cover showing trends (Slope) including standard errors (SE).

Response	Model term	d.f.	χ2	Slope	SE	Graphical summary
grass biomass	intercept			582.60	21.40	
	grass structure	1	811.3***	391.50	13.70	Appendix S5a
grass height	intercept			7.38	0.13	
	grass structure	1	825.2***	2.40	0.08	Appendix S5b
grass cover	intercept			0.38	0.01	
	grass structure	1	299.6***	0.11	0.01	Appendix S5c



Appendix S5. Graphical representation of generalized linear regression model summarized in Appendix S4.

PAPER II: Birds of a feather flock together: using trait-groups to understand the effect of macropod grazing on birds in grassy habitats.

Red-rumped parrot (Psephotus haematonotus) feeding on native grass seed (photo: Tobias Hayashi)

Howland, B., Stojanovic, D., Radford, J. Q., Gordon, I. J., Manning, A. D., and Lindenmayer, B. D. (2016). Birds of a feather flock together: Using trait-groups to understand the effect of macropod grazing on birds in grassy habitats. *Biological Conservation* **194**: 89-99.

Abstract

Restoration of appropriate disturbance regimes is a high conservation priority. However, for most species, little is known about appropriate disturbance regimes to achieve defined conservation outcomes. In this context, trait-based approaches can offer a means to generalize responses to environmental change across multiple species. Here, we investigated the potential of a trait-based approach to predict the preference of birds utilizing the grassy layers for different levels of grazing by a native grazer within grassy habitats in south-eastern Australia. We tested three hypotheses: 1) birds with particular traits (i.e. large ground-foraging, small ground-foraging, aerial insectivore, and ground-nesting/concealment) will show preferences for certain levels of grazing: 2) species within the same trait group will show preferences for a similar level of grazing intensity: and 3) different bird trait groups will favor different grazing intensities Overall, we found a significant relationship between grazing intensity and the richness of aerial insectivore and large ground-foraging trait groups utilizing the grassy layer, but not for the richness of small ground-foraging and ground-nesting/concealment trait groups. We also found that the likelihood of 3/3 aerial insectivores, 4/7 large ground-foragers, 3/10 small ground-foragers, and 1/3 ground-nesting/concealment species using the grassy layer was significantly related to grazing intensity. However, we found no significant relationship between the probability of 12 species using the grassy layer and grazing intensity, with other environmental factors potentially masking grazing response. Importantly, species within the same trait group showed a preference for similar grazing intensities, and different trait groups showed preference for different grazing intensities. For example, aerial insectivores, and a single ground-nesting/concealment species were more likely to use the grassy layer at lower grazing intensities, whereas large ground-foraging birds and small ground-foraging birds were more likely to use the grassy layer at higher grazing intensities. To

maintain optimal grass structure for birds with varying grass structure preferences, landscapes should contain a heterogeneous mosaic of grazing intensities.

Introduction

Anthropogenic changes to natural disturbance regimes are a major contributor to global biodiversity loss (Chapin III et al., 2000, Woinarski et al., 2015). Consequently, the restoration of these regimes is a high priority for conserving biodiversity (Palmer et al., 1997, Landres et al., 1999, Mori, 2011, Halme et al., 2013). For most species, exactly what constitutes their 'optimal', or even 'preferred' disturbance regime is largely unknown (Hobbs and Huenneke, 1992, Lindenmayer et al., 2006), and quantifying optimal disturbance regimes for all species is often not feasible. One approach to solving this problem is to group species based on common ecological or life-history traits and tailor land management approaches to focus on conservation of trait groups rather than individual species.

The response of an individual organisms to environmental change is dependent on multiple life history traits (e.g. dispersal method, predator avoidance strategy, diet), with species that share similar traits expected to respond to environmental change in a similar way (Langlands et al., 2011). Linking species with shared traits (i.e. trait groups) to particular environmental conditions may enable managers to apply generic approaches to conserving multiple species and reduce the need for detailed species-specific knowledge. Despite the demonstrated value of forming species trait groups based on multiple traits for understanding the effects of disturbance on plants (e.g. McIntyre, 2008), the concept has been less frequently used for studies on fauna (although see Langlands et al., 2011, Davies et al., 2010, Hanspach et al., 2012, Cumming et al., 2012). As the number of threatened species increases in response to ongoing anthropogenic degradation, there is an urgent need to manage disturbance regimes for maximum biodiversity benefit despite a lack of autecological data.

Grassy habitats are a good system in which to investigate the utility of trait-based approaches for managing species. Grassy habitats are biodiverse, in many case have been dramatically altered by human activity, and support species with a range of disturbance tolerances (Milchunas et al., 1988, Bond and Parr, 2010). Anthropogenic impacts leading to changes in the abundance and type of grazers have a profound effect on biodiversity in these systems (Gordon et al., 2004, Mysterud, 2006, Foster et al., 2014). For example, the suppression of grazer abundance (e.g. overexploitation and fencing) can allow a few fast growing plants to competitively dominate, leading to a decline in plant diversity and reduction in habitat complexity (Milchunas et al., 1988, Gordon et al., 2004, Mysterud, 2006). Conversely, with a loss of population regulation (e.g. animal husbandry, loss of large predators, barriers to migration, provision of permanent water), grazer numbers may be inflated, resulting in increased consumption of plant matter, leading to a decline in grazing-sensitive plants, and simplification of vegetation structure (Milchunas et al., 1988, Gordon et al., 2004, Mysterud, 2006). Changes in the abundance and type of grazing animals can dramatically alter the structure, function and species composition of grassy habitats (Milchunas et al., 1988, Mysterud, 2006, Foster et al., 2014), with knock-on effects on biodiversity (Foster et al., 2014, Gordon et al., 2004). Surprisingly few studies have investigated the effects on biota of a native grazer across a range of grazing intensities (reviewed by Foster et al., 2014) despite the potential for such data to provide important insight into the restoration of ‘natural’ grazing regimes (Gordon et al., 2004, Hester et al., 2000). Importantly, the impact of native grazers may differ to those of domestic livestock or feral herbivores because native grazers are more likely to mimic the natural grazing regime under which ecosystems evolved (Foster et al., 2014). Addressing the lack of data from systems dominated by native grazers is a priority for land managers because good management relies on understanding the interactions among grazing, grass structure and biodiversity.

Birds are useful for investigating the utility of a trait-based approach because they are diverse, occupy many ecological niches, are mobile, and are well researched (Davies et al., 2010, Söderström et al., 2001, Derner et al., 2009). Importantly, some birds are sensitive to changes in grazing intensity (Martin and Possingham, 2005, Foster et al., 2014), but the effects of grazing may vary depending on bird life history characteristics and environmental conditions. For example, Davies et al. (2010) found that most bird species declined as grazing intensity increased in semi-arid grassy habitats in Australia, with the largest decreases found for ground-foraging and ground-nesting species, while shrub-dwelling species declined the least. In contrast, studies in grassy habitats in Australia have found that ground-foraging species may benefit from the open grass layer created with grazing, whereas shrub-dwelling species declined at high grazing intensities (Martin and Possingham, 2005, Martin and McIntyre, 2007, Woinarski and Ash, 2002) likely due to the negative effect of grazing on shrub occurrence. While these studies have made an important contribution to understanding effects of grazing by domestic livestock on birds in Australia, they have rarely provided quantitative measures of grass structure (e.g. grass biomass) needed by conservation managers to appropriately manage grazing pressure (Gordon et al., 2004). These previous studies also have been concerned with the effects of grazing by domestic livestock rather than a native grazer, which is the focus of this study. Importantly, the impacts of native large grazers on birds also may differ due to differences in feeding behavior and plant preferences (Tiver and Andrew, 1997). In south-eastern Australia, the dominant large native grazer is the eastern grey kangaroo, *Macropus giganteus* (hereafter: kangaroo) (Taylor, 1983).

Kangaroo abundance has increased in many areas (ACT Government, 2010, Grigg et al., 1989) as a consequence of anthropogenic changes such as the provision of permanent water (e.g. dams), removal of native predators, fragmentation of habitat, and increase in pasture quality and quantity. The impacts of kangaroo grazing on birds remain largely unknown, although impacts on other groups have been reported (beetles; Barton et al., 2011, Howland et al., 2014, reptiles; Manning et al., 2013, e.g. plants; Meers and Adams, 2003, McIntyre et al., 2010). This lack of knowledge on the effects of kangaroo grazing on birds, limits effective management of grazing pressure for the conservation of birds.

We aimed to address this lack of knowledge by using a trait-based approach to investigate the impacts of a native grazer on birds occurring in the grassy ecosystems in south-eastern Australia. The main mechanism by which large grazers influence birds is through altering vegetation structure (Whittingham and Evans, 2004, Martin and Possingham, 2005) (notwithstanding more direct impacts, e.g. trampling of nests and habitat; Fondell and Ball, 2004). Changes in vegetation structure can affect bird survival through known effects on foraging efficiency, nesting success, and predation risk (see Table 1). Additionally, the impacts of grazing may vary depending on bird size, as body size affects both the size and quantity of food consumed (Brandl et al., 1994, Söderström et al., 2001). We surveyed birds along a gradient of kangaroo grazing intensity to test three hypotheses. First, birds with particular traits will show preference for certain levels of grazing intensity. We predicted that ground-foraging species, birds that forage in the air above the grassy layer and ground-nesting species would be vulnerable to changes in grazing intensity because species with these traits utilize the grass layer for food and shelter. Second, bird species within the same trait group will show preferences for a similar grazing intensity. We anticipate that species within the same trait group will show preferences for a similar grazing intensity due to shared life history and autecological characteristics. Third, different bird trait groups will favor different grazing intensities We anticipate that ground-foraging species which rely on early detection of predators would be more likely to utilize the grassy layer at higher grazing intensities (where detection of prey and predators is higher due to sparse grass cover), whereas birds that forage in the air above the grass layer, ground-nesting species and species that rely on concealment to avoid predation would show preference for lower grazing intensities where there is more prey and cover. We also expect that larger birds will favor comparatively lower grazing intensities than smaller birds as they require more food and feed on larger food items, with both food abundance and food size potentially reduced by heavy grazing (Brandl et al., 1994, Söderström et al., 2001, Woodcock et al., 2009). We used these results to provide recommendations for the management of grazing pressure for the conservation of birds in grassy habitat in south-eastern Australia.

Table 1. List of bird ecological traits likely to be influenced by changes in grazing intensity.

Ecological trait group	Trait affected	Mechanism	References
Foraging substrate	Ground-foraging	Loss of cover may increase the efficiency in which food items on the ground are discovered.	(Martin and Possingham, 2005, Söderström et al., 2001, Whittingham and Evans, 2004, Atkinson et al., 2004)
	Aerial-foraging	Loss of cover may reduce abundance of aerial invertebrates.	(Barton et al., 2011, Dennis et al., 1998, O'Connor and Pickett, 1992, Sternberg et al., 2003, Gonnet, 2001, Vickery et al., 2001b)
Predator avoidance strategy	Flight	For species that rely on flight to avoid predators, loss of cover can increase visibility of predators, reducing risk of predation.	(Whittingham and Evans, 2004, Westcott and Cockburn, 1988, Whittingham et al., 2006)
	Concealment	Loss of cover may expose species which rely on grass for concealment to greater predation risk.	(Evans, 2004)
Nesting position	Ground	Increase in herbivore numbers may increase risk of nests being trampled.	(Fondell and Ball, 2004, Whittingham and Evans, 2004)
Nest protection strategy	Concealment	Loss of cover exposes nests to a greater risk of being discovered by a predator.	(Fondell and Ball, 2004, Whittingham and Evans, 2004)
Body size		Grazing reduce size of food items, with larger birds dependent on larger prey items.	(Brandl et al., 1994, Söderström et al., 2001, Woodcock et al., 2009)

Materials and Methods

Study system

Our study was conducted within temperate grasslands and box-gum grassy *Eucalyptus* woodland communities across south-eastern Australia (Fig. 1a). These habitat types are listed as critically endangered ecological communities (Department of the Environment and Heritage, 2014b), and occur mostly as small patches (< 100 ha), that are fragmented by roads, urban development and agricultural land-use (Prober and Thiele, 2005). We selected 18 large properties (> 100 ha) across Australian Capital Territory (n = 14), New South Wales (n = 2) and Victoria (n = 2), where temperate grassland and grassy *Eucalyptus* woodland communities persist (Fig. 1b). The study area was dominated by temperate woodlands (dominant canopy spp: *Eucalyptus blackelyi, E. melliodora, E. albens*) and dry forest (*E. macrorhyncha, E. mannifera*). Lower vegetation strata were simple, and dominated by native perennial grasses (*Austrostipa* spp, *Bothriochloa macra, Rytidosperma* spp*, Themeda triandra*) and forbs, with exotic perennial grasses (*Eragrostis curvula, Phalaris aquatica*) locally abundant. While properties were selected over a wide geographic area, many of the same species of bird occur throughout this region. We did not consider these geographic differences further, as the focus of this research was on whether birds over a wide geographic area showed a consistent response to differences in grazing intensity. All properties fell within the 'temperate cool-season wet' climatic pattern, with rainfall evenly distributed throughout the year (Hobbs and McIntyre, 2005). This region experienced below average annual rainfall for the majority of the decade preceding the study period, with the drought breaking in 2009 at the beginning of this study (Australian Government Bureau of Meteorology, 2014).

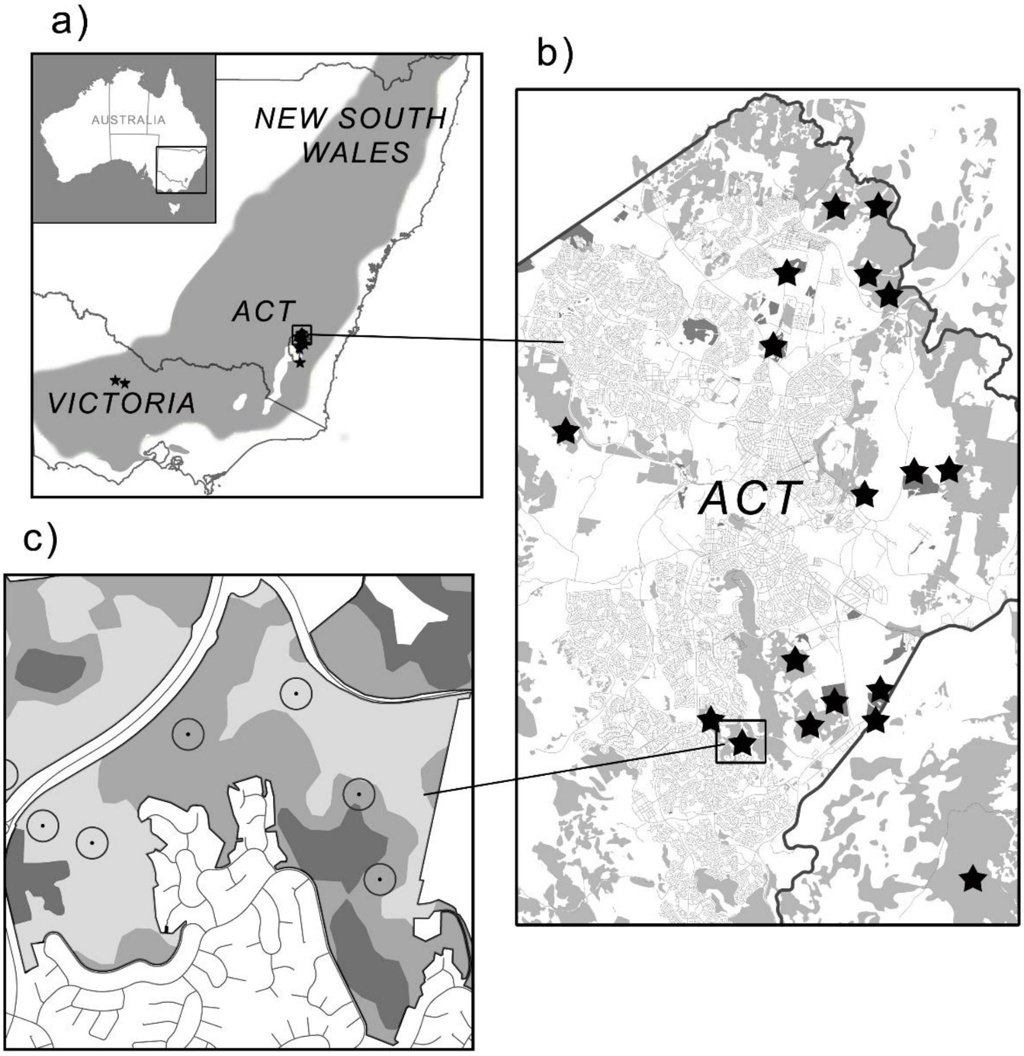


Figure. 1. a) The historic distribution of box-gum grassy woodlands and temperate grasslands (grey) in south-eastern Australia (inset). Selected study sites are shown (black star) with ACT region expanded in b) location of study sites (black star) within the Northern ACT, with box-gum grassy woodlands and temperate grasslands (grey), roads in the ACT (grey lines), and ACT border (black line) and c) an example of stratified random placement of study plots within a study site showing open woodland (light grey), woodland (grey) and open forest (dark grey) canopy types.

Outside of agricultural areas, the eastern grey kangaroo *Macropus giganteus* is the dominant large native grazer (females; 40 kg, males; 90 kg) in south-eastern Australia (Viggers and Hearn, 2005b). The eastern grey kangaroo (hereafter: kangaroo) is found in habitats from grasslands to open forest, and feeds predominately on grasses, with a minor component of browse (Grigg et al., 1989, Taylor, 1983, Viggers and Hearn, 2005b). This species was the most commonly encountered large grazer across our study properties (Howland et al., 2014), and population surveys in the ACT and NSW have confirmed the relative dominance of kangaroos compared to other large herbivores (ACT Government, 2010). Other native grazers included the brush-tailed possum *Trichosurus vulpecula*, common wallaroo *Macropus robustus*, red-necked wallaby *Macropus rufogriseus*, swamp wallaby *Wallabia bicolor*, western grey kangaroo *Macropus fuliginosus*, and wombat *Vombatus ursinus*. Non-native grazing species included fallow deer *Dama dama*, European rabbit *Oryctolagus cuniculus*, European hare *Lepus europaeus* and feral pig *Sus scrofa*, with grazing pressure by the European rabbit suppressed by control programs (Cooke and Fenner, 2003, Fletcher, 2005). On Victorian properties, both species of grey kangaroo, the eastern grey kangaroo and the western grey kangaroo, were sympatric, although the former was more common. We consider the influence of these grazers on grass to be comparable given their similar feeding ecology (Poole, 1975, Grigg et al., 1989). All properties had a history of fire and grazing by domestic livestock, but prior to this study, properties had not been burned or grazed by domestic livestock for > 12 months. For 15 properties, the last disturbance (livestock and/or fire) occurred > 10 years before the study.

Site selection and experimental design

A detailed explanation of site selection and experimental design can be found in Howland et al. (2014). Briefly, study properties were subject to a range of grazing intensities predominantly by kangaroos, whose absolute abundance was estimated at many properties using established techniques (i.e. pellet counts, distance sampling, total counts; Southwell, 1989). At six properties, barriers to grazer movement (fencing, topography) modified grazer abundance and consequently grass structure. We took advantage of these differences in grazing pressure by stratifying sampling based on these barriers. We recognised 24 different sites across 18 properties (see Table A.1).

To account for the effect of trees on birds (Hanspach et al., 2011), we stratified sites based on canopy cover (Fig. 1c) into: (1) grassland (<2% canopy cover), (2) open woodland (3-20%), and (3) woodland (21-50%). Experimental plots of 75m radius (1.8 ha) were randomly established in grassland, open woodland and woodland canopy classes at each site, with more plots placed at larger sites with a greater variety of canopy classes (Fig. 1c). We used plots of this size because they are known to be appropriate for studies of bird-habitat preferences in south-eastern Australia (Dorrough et al., 2012, Rayner et al., 2014, Martin and McIntyre, 2007). Overall, 127 plots were established, with 36 plots in grassland, 50 in open woodland, and 41 in woodland habitat. Two grassland plots were later reclassified as open woodland due to the presence of several small trees within plot boundary.

Bird Surveys

We surveyed birds from January 2010 to November 2010 using a 10 minute fixed area search method (Hutto et al., 1986, Rayner et al., 2014). Each plot was surveyed twice per season (summer, autumn, winter, spring) for a total of eight counts per plot, with all plots visited by two different observers. Surveys were conducted only during fine weather. We surveyed plots in the four hours after dawn and during autumn and winter, also in the four hours before sunset. Logistical constraints meant that we surveyed all plots at the same site on the same day. However, we varied the order plots were visited between subsequent visits.

We recorded all birds seen within 75m of the plot centre. We also recorded the stratum used by birds during surveys (i.e. on the ground, in a shrub, in a tree, flying above vegetation layer). It was possible for the same bird species record to be assigned to multiple locations during a single survey (e.g. ground and air). To account for incomplete detection and issues with estimating abundance, we recorded each species as being present or absent in a survey. To limit the effect of the observer approaching the plot on bird behavior and occurrence, birds seen leaving the plot in response to observer prior to the start of the survey were recorded along with the strata they were seen utilizing. We excluded waterbirds as their distribution is strongly correlated to water rather than grass structure (Pizzey and Knight, 2012). We also excluded birds of prey as they are naturally rare and make use of the grassy layer infrequently (during a kill) and more over much larger scales than investigated in this study.

Bird traits

We selected five life-history trait characteristics where there is a potential mechanism to explain species response to differences in grazing intensity (see Table 1). These were: 1) foraging stratum; 2) predator avoidance strategy; 3) nesting position; 4) nest defense strategy; and 5) body-size. For each bird species, we assigned traits for each of these five life-history trait characteristics based on current ecological knowledge (Ikin et al., 2013, Christidis and Boles, 2008, HANZAB, 1990-2007, Lindenmayer and Cunningham, 2011, Rayner et al., 2014)(Table A.2). We used hierarchical cluster analysis with a Jaccard dissimilarity measure (discrete data), and the complete linkage method (Jain et al., 1986, MacNally, 1994) to classify species into clusters. We defined trait groups from the resulting dendrogram as clusters that are separated from one another by similarities which are > then the mean distance between all clusters (0.5 in this case) following Holmes et al. (1979). We recognised seven trait groups: two groups contained species with traits not considered to be strongly affected by changes in grazing intensity (i.e. canopy feeders; see Table 1). The five remaining trait groups (large aerial insectivore, small aerial insectivore, large ground-foraging, small ground-foraging, ground nesting/concealment) contained 67 species in total. We classified these individual species into preferences for different habitat types (i.e. grassland, open woodland, woodland) based on current ecological knowledge of habitat associations (see Table A.2). For example, species that showed no clear habitat preferences were classified as 'generalist', species that were rarely recorded in grassland plots as 'woodland', and species largely absent from woodland plots as 'grassland'. These classifications were largely consistent with Ikin et al. (2012), although the crested pigeon, *Ocyphaps lophotes*, was assigned to generalist rather than grassland, and the stubble quail, *Coturnix pectoralis*, was assigned to grassland rather than generalist based on the habitat types they were mostly recorded using in this dataset.

Grazing intensity

We used grass attributes as a surrogate for grazing intensity. This was because: 1) grass is the resource which species interact with for food and shelter; 2) grass is easier to measure and less error-prone than estimates of grazer abundance (Southwell 1989; Morellet et al. 2007); 3) grass attributes provide an integrated, quantitative index of grazing impact among sites that vary in grazing history, soil and rainfall (Gordon et al. 2004; Pöyry et al. 2006); and 4) regression analysis between grass structure and actual kangaroo abundance at 15 sites used in this study, had previously demonstrated a significant negative relationship ($p < 0.05$), such that increases in kangaroo abundance reduced grass structure values (Howland et al. 2014). Howland et al. (2014) published detailed methodology and results for assessment of grazing intensity at our study sites. Briefly, grass attributes were measured within 12×0.25 m^2 survey quadrats at each plot in summer 2009/2010. These attributes included grass height (cm), grass biomass (kg/ha), and percent grass cover. Grass height was estimated as that average height of above-ground leaf (range 1.7–18 cm), grass biomass (range 66–3355 kg/ha) that was visually estimated using the 'comparative yield' technique (Haydock and Shaw 1975), and grass percent cover (range 0–91% grass cover) that was calculated by analyzing vertically-oriented photographs taken at each quadrat using the program 'SamplePoint' (Booth et al. 2006). These attributes were collapsed into a single variable (i.e.

‘grass structure’) represented by the first factor of a principal components analysis. The relationship between grazing intensity (i.e. grass structure) and each grass attribute in Howland et al. (2014) has been summarized in Fig. A. 2. Additionally, to aid interpretation of results we divided grazing intensity into five categories (very high, high, moderate, moderate low, very low see Table 2), and used the relationship between grass attributes and grass structure (see Fig. A.1) to provide quantitative definitions of these grazing categories (Table 2). For example, very high grazing corresponded to grass height of 3 – 6.5cm, grass biomass 0 – 438 kg/ha and grass cover 17 – 34%.

Table 2. The relationship between five grazing intensity categories and grass structure score (index of grazing intensity), grass height (cm), grass biomass (kg/ha), and grass cover (%). Values for grass height (cm), grass biomass (kg/ha), and grass cover (%) were obtained from established relationships between the grass structure score and grass attributes (see Fig A.1).

Grazing intensity category	Grass structure score (PC1)	Grass height (cm)	Grass biomass (kg/ha)	Grass cover (%)
Very high	-1.82 - -0.37	3-6.5	0-438	17-34%
High	-0.37 – 1.08	6.5-10	438-1006	34-50%
Moderate	1.08 – 2.53	10-13.5	1006-1573	50-67%
Low	2.53 – 3.98	13.5-17	1573-2140	67-84%
Very low	3.98 – 5.43	17-20.5	2140-2707	84-100

Environmental characteristics

We measured five environmental attributes that are important predictors of bird occurrence: 1) abundance of shrubs taller than 0.5 m; 2) distance to urban area; 3) distance to nearest tree > 2 m tall; 4) occurrence of noisy miners (*Manorina melanocephala*) to account for the hyper-aggressive behavior of this species on other birds (see Maron, 2007); and 5) tree canopy cover class (i.e. grassland, open woodland, woodland). We counted the number of shrubs (height > 0.5

m) within each plot, and calculated distance to nearest urban edge from plot centre using GIS techniques. Urban areas were mapped using existing government maps and satellite imagery. Distance to a tree > 2 m tall from plot centre was calculated from satellite maps.

Data preparation

As we were interested in how different bird trait-groups utilized the grassy vegetation for feeding, nesting, and cover, we restricted analysis to only those records where birds were utilizing the grassy layer. For example, all records when ground-foraging, and ground-nesting/concealment species were seen on the ground were retained, with all other records (i.e. air, shrub, tree) removed. For aerial insectivores only, records of birds actively feeding above vegetation layer were retained. We pooled bird surveys to determine: 1) trait group richness – the number of species within a given trait group per plot observed utilizing the grassy layer after eight surveys; and 2) individual species occupancy - the number of surveys in which a species was detected using the grassy layer as a proportion of all eight surveys. Hence, our measures of richness and occupancy are not true measures, but rather a measure of a species likelihood of using the grassy layer. We built probability models for all individual species that were encountered on more than 10 visits and modelled species richness for aerial insectivore, large ground-foraging, small ground-foraging, and ground nesting/concealment species. We excluded the large aerial insectivore group from analysis as only one species was recorded, and this species was not observed utilizing the grass layer during surveys. We modelled response to grazing intensity for 24 individual species. Analysis of individual bird species was restricted to their particular habitat preference. For example, analysis using all plots (n = 127) was used for trait group richness and for individual birds classified as 'generalist species', with 'woodland species' restricted to the woodland plots (n = 93), and 'grassland species' restricted to grassland plots (n = 34).

Data analysis

Prior to analysis, we checked for multicollinearity (spearman rank coefficient > 0.5), transformed skewed variables, and standardized continuous variables to enable meaningful comparison between multiple independent explanatory variables (Zuur et al., 2009b).

Next, we investigated the relationship between response variables and grazing intensity using regression techniques. Due to non-trivial issues with model selection using Akaike information criterion (AIC) and mixed models (see Vaida and Blanchard, 2005), we undertook analysis in two stages. We considered five explanatory variables (abundance of shrubs, distance to nearest tree, distance to urban area, grass structure, occurrence of noisy miners) as well as a quadratic term for grass structure because a humped response to grass structure is commonly found in studies of grazing-fauna relationships (Martin and Possingham, 2005, Foster et al., 2014). In the first stage of the analysis, we reduced the number of candidate variables using model selection techniques recommended in Burnham and Anderson (2002), but ignored the nested structure of our survey (i.e. plots within the same property). The shrub layer, noisy miner occurrence and tree canopy cover variables were not included for 'grassland' birds, as these features were largely absent from grassland plots, with the variable 'distance to tree' included only for 'grassland' birds. Records of the noisy miner were included as part of trait group richness calculation for 'small ground-foraging', as 'occurrence of the noisy miner' was included as an explanatory variable in analysis. For each response variable, we fitted all possible combinations of explanatory variables using generalized linear models (GLM; Nelder and Wedderburn, 1972). We fitted species richness with a Poisson distribution and a logarithm link function, with individual species occurrence modeled with a binomial distribution and a logit link function. We ranked each model according to AICc (adjustment for small sample size) and selected the top ranked model (lowest AICc values) for the next stage of analysis (Table A.3).

Lastly, we modelled the relationship between our response variables and candidate variables selected in the previous stages of analysis (Table A.3) using hierarchical generalized linear mixed modelling procedures (HGLMM; Lee and Nelder, 1996). We included 'property' as a random effect in the models to account for our nested study design. We fitted species richness with a Poisson distribution, a logarithm link function, and random effects fitted with a gamma distribution and a logarithm link function. Individual species occurrence was modelled with a binomial distribution, a logit link function, and random effects fitted with a beta distribution and a logit link function. If random effects were non-significant, we re-ran analyses without random effects. We checked residual plots and distribution of residuals to verify model assumptions. Regression was undertaken in Genstat 12 (VSN International, 2012b). For all analyses, the $\chi 2$ test statistics quoted are derived from Wald statistics.

Results

We classified 94 species of bird into nine trait groups based on hierarchical cluster analysis (Fig. A. 2). Five of these trait groups (large aerial insectivore, small aerial insectivore, large ground-foraging, small ground-foraging, ground nesting/concealment) contained 67 species with traits likely to be affected by grazing intensity (Table A.2). We developed HGLMMs for the richness of five trait groups: small aerial insectivore, large ground-foraging, small ground-foraging, and ground- nesting/concealment; and for the occurrence of 24 of the most common species within these trait groups (Table A.4).

Table 3. Results of hierarchical generalized linear mixed models for the richness two trait groups and the occurrence of 11 individual species predicted by grass structure showing trends (Slope) including standard errors (SE). Grassland and open woodland has been used as a reference level for tree canopy class categories for generalist and woodland species respectively. Significance is indicated by the Wald statistic (χ2) and p-value as follows: * p<0.05, ** p<0.01, *** p<0.001. For scientific names see Table A.2.

Habitat	Trait group	Response	Model term	d.f.	χ2	Slope	SE
Generalist	SAI	SAI richness	Intercept			-2.12	0.43
			tree canopy class		16.64***		
			open woodland			1.58	0.43
			woodland			2.15	0.54
			grass structure		12.14***	0.58	0.17
			No. Shrubs		1.04	-0.15	0.15
	LGF	LGF richness	Intercept			0.68	0.16

			tree canopy class		4.97		
			open woodland			0.07	0.20
			woodland			-0.25	0.23
			Distance to urban area		2.53	-0.11	0.07
			Noisy miner occurrence		9.24**	0.20	0.07
			grass structure		4.51*	-0.20	0.09
Generalist	SAI	Welcome swallow	Intercept			-6.86	0.83
			Tree canopy class	2	15.18***		
			Open woodland			1.71	0.68
			Woodland			0.64	0.86
			Noisy miner	1	21.5***	1.18	0.26
			Grass structure	1	0	0.00	0.37
			Grass structure^2	1	27.14***	0.68	0.13
			No. Shrubs	1	1.7	-0.33	0.25
	LGF	Galah	Intercept			-2.60	0.33
			Tree canopy class	2	19.01***		
			Open woodland			-0.97	0.47
			Woodland			-2.73	0.65

		Distance to urban area	1	2.09	-0.26	0.18
		Grass structure	1	12.21***	-1.16	0.33
	Sulphur-crested cockatoo	Intercept			-7.14	0.60
		Distance to urban area	1	39.87***	-1.75	0.28
		Grass structure	1	19.87***	-1.49	0.34
		No. Shrubs	1	15.66***	-2.34	0.59
SGF	Crested pigeon	Intercept			-5.90	0.92
		Tree canopy class	2	0.88		
		Open woodland			-0.73	0.96
		Woodland			-0.46	1.06
		Distance to urban area	1	19.74***	-1.79	0.40
		Grass structure	1	18.08***	-2.53	0.60
		Grass structure^2	1	5.07*	-1.66	0.74
		No. Shrubs	1	11.42***	-0.95	0.28
	Red-rumped parrot	Intercept			-4.08	0.32
		Distance to urban area	1	7.811**	0.83	0.30
		Grass structure	1	3.212	-1.27	0.71
		Grass structure^2	1	7.982**	-2.63	0.93

		Magpie-lark	Intercept			-3.67	0.37
			Tree canopy class	2	12.01**		
			Open woodland			-1.52	0.44
			Woodland			-1.13	0.49
			Distance to urban area	1	41.05***	-1.17	0.18
			Grass structure	1	11.74***	-3.47	1.01
			Grass structure^2	1	12.65***	-3.89	1.09
Grassland	GN	Australasian pipit	Intercept			-1.00	0.25
			Grass structure	1	5.726*	0.55	0.23
			Distance to tree	1	9.466**	1.15	0.37
Woodland	SAI	Dusky woodswallow	Intercept			-5.47	0.50
			Tree canopy class	1	5.946*		
			Woodland			1.35	0.56
			Distance to urban area	1	10.019**	0.89	0.28
			Noisy miner occurrence	1	6.075*	-0.75	0.30
			Grass structure	1	23.81***	0.80	0.16
			No. Shrubs	1	2.582	-0.39	0.25
		Tree martin	Intercept			-4.05	0.28

		Distance to urban area	1	8.191**	-0.58	0.20
		Grass structure	1	8.88**	1.19	0.40
		Grass structure^2	1	2.688	-0.26	0.16
		No. Shrubs	1	4.605*	-0.55	0.26
LGF	White-winged chough	Intercept			-4.92	0.43
		Tree canopy class	1	15.224***		
		Woodland			1.77	0.45
		Noisy miner occurrence	1	8.262**	0.50	0.17
		Grass structure	1	5.532*	-0.97	0.41
SGF	Superb fairy-wren	Intercept			-2.55	0.40
		Distance to urban area	1	0.968	0.41	0.42
		Grass structure	1	10.489**	1.95	0.60
		Grass structure^2	1	13.757***	-2.74	0.74

Trait-group abbreviations: "SAI" is small aerial insectivore, "GN" is ground nesting/concealment, "LGF" is large-ground foraging, "SGF" is small ground-foraging.

Hypothesis 1: Birds with particular traits will show preferences for certain levels of grazing

Grass structure (i.e. grazing intensity) was a significant predictor for the species richness of small aerial insectivore, and large ground-foraging trait groups utilizing the grassy layer (Fig. 2), but not for the richness of small ground-foraging and ground- nesting/concealment trait groups

(Table A.4). Instead, species richness of the small ground-forging trait group was positively related to tree canopy cover with species richness of the ground nesting/concealment trait group negatively related to occurrence of noisy miners and tree canopy cover.

The probability of 11 bird species (Australasian pipit *Anthus novaeseelandiae*, crested pigeon, dusky woodswallow *Artamus cyanopterus*, galah *Cacatua roseicapilla,* magpie-lark *Grallina cyanoleuca,* red-rumped parrot *Psephotus haematonotus*, sulphur-crested cockatoo *Cacatua galerita,* superb fairy-wren *Malurus cyaneus*, tree martin *Petrochelidon nigicans,* welcome swallow *Hirundo neoxena*, white-winged chough *Corcorax melanorhamphos*)(Table 3) utilizing the grassy layer was significantly related to the grazing intensity. Due to model convergence issues for the southern whiteface, *Aphelocephala leucopsis*, no HGLMM could be developed for this species. The occurrence of the common bronzewing *Phaps chalcoptera* and the willy wagtail *Rhipidura leucophrys* was not significantly related to any environmental variable. The probability of the remaining 10 bird species utilizing the grassy layer was related to environmental variables other than grazing intensity (Table A.4). Tree canopy class was the most common significant variable selected in models and was included for 11 species. Abundance of shrubs positively influenced two species and negatively influenced five species. Both grassland species (Australasian pipit, Eurasian skylark *Alauda arvensis*) favored areas further away from trees, with the probability of occurrence increasing as the distance to the nearest tree increased. Noisy miners negatively affected three species, but four species were more likely to be recorded where noisy miners also occurred. Distance to an urban area negatively affected two species, with six species more common near urban areas.

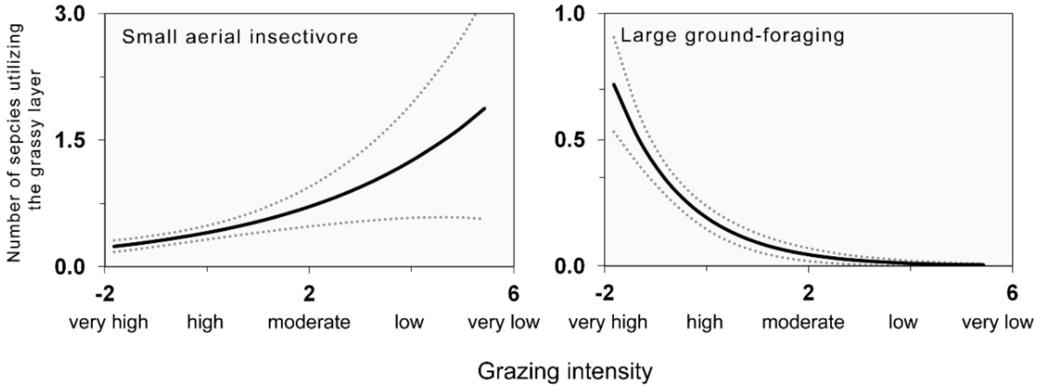


Figure. 2. Graphical representation of logistic regression models summarized in **Table** .3. The graphs show significant relationships between grass structure and the richness of aerial insectivore and large ground-foraging trait groups utilizing the grassy layer in a given plot. Fitted relationships are shown as a solid line, with standard error of the model predictions shown as a dotted line. To aid interpretation of results, variables have been back-transformed to original scale. Grazing intensity categories: "very high" is < -1, "high" is -1 – 1, "moderate" is 1 – 3, "low" is 3 – 5 and "very low" is > 5.

Hypothesis 2: Birds species within the same trait group will show preferences for a similar level of grazing intensity

For species that exhibited a significant relationship with grazing intensity (i.e. 11 species), species within the same trait groups showed a preference for a similar grazing level (Fig. 3). For example, small aerial insectivores (dusky woodswallow, tree martin, welcome swallow) were more likely to be encountered at lower grazing intensity with large ground-foraging (crested pigeon, galah, sulphur-crested cockatoo, white-winged chough), and small ground-foraging (red-rumped parrot, magpie lark, superb fairy-wren) more common at higher grazing intensities.

Hypothesis 3: Different bird trait groups will favor different grazing intensities

Different trait groups showed a preference for different levels of grazing intensity (Fig. 2, Fig. 3). Large ground-foraging and small ground-foraging species were more likely to utilize the grassy layer at plots with higher grazing intensities (i.e. grass height: <10cm; grass biomass:

<1006kg/ha; grass cover: <50%), whereas small aerial insectivores and a single ground-nesting/concealment species, the Australasian pipit, showed preference for the grassy layer at plots with lower grazing intensities (i.e. grass height: > 13.5cm; grass biomass: > 1573kg/ha; grass cover: > 67%). Three of these groups included ground-foraging species (ground-foraging, ground nesters), but the groups differed in nest position and predator avoidance strategies. Ground-foraging species that nest on the ground, and rely on cover to avoid detection appeared to favor low grazing intensity. In contrast, ground-foraging species that do not nest on the ground and rely on early detection of predators appeared to favor high grazing intensity.

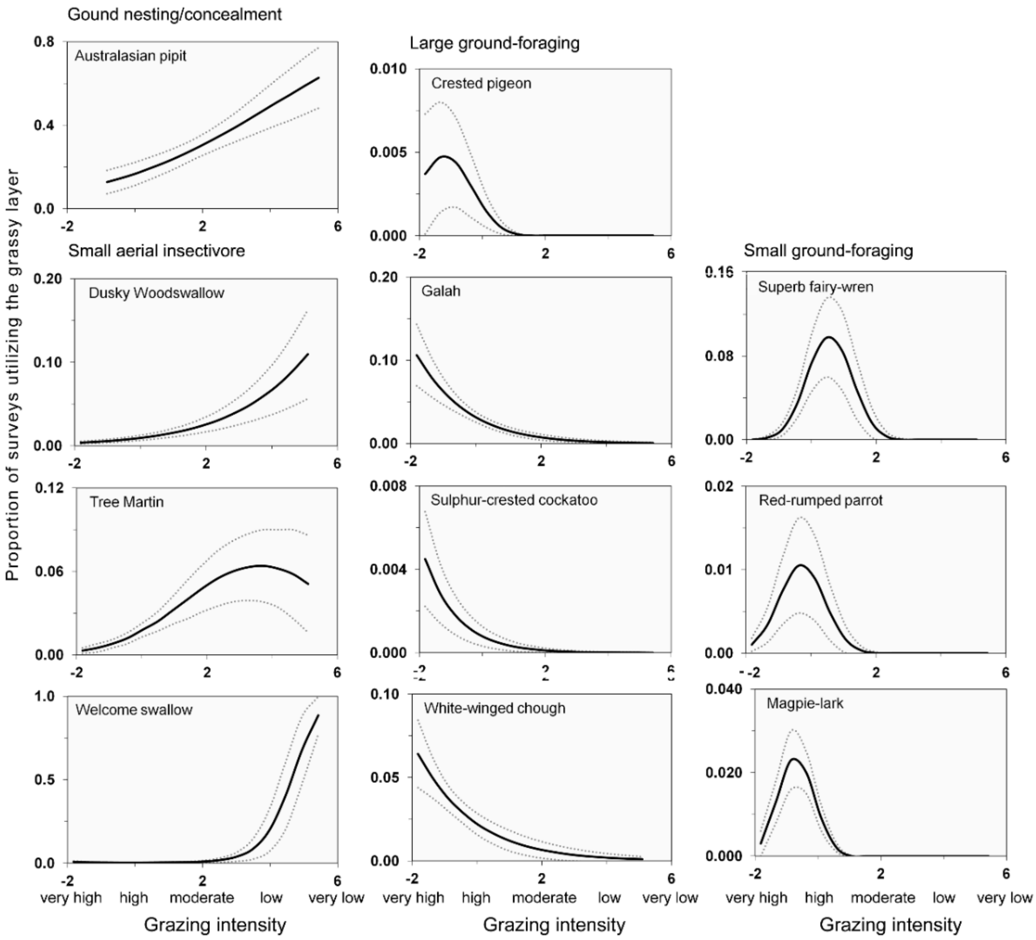


Figure. 3. Graphical representation of logistic regression models summarized in Table 3. The graphs show significant relationships between grass structure and the probability of encountering a species utilizing the grassy layer in a given plot for small aerial insectivore (dusky woodswallow, tree martin, welcome swallow), ground nesting/concealment (Australasian pipit), large ground-foraging (crested pigeon, galah, sulphur-crested, cockatoo white-winged chough) and small ground-foraging (magpie-lark, red-rumped parrot, superb fairy-wren) species. Fitted relationships are shown as a solid line, with standard error of the model predictions shown as a dotted line. To aid interpretation of results, variables have been back-transformed to original scale. Grazing intensity categories: "very high" is < -1, "high" is -1 – 1, "moderate" is 1 – 3, "low" is 3 – 5 and "very low" is > 5. See Table A.2 for scientific names.

Discussion

We have highlighted the potential for trait-based predictions to provide insights into the conservation and management of grazing intensity by a native grazer for birds that utilize the grassy layer in temperate grassland and grassy woodlands. Our study revealed that the utilization on the grassy layer by small aerial insectivores, ground-foragers, and one ground-nesting/concealment species were associated with certain levels of grazing intensity, with species within the same group showing preference for similar levels of grazing intensity. Importantly, we also found that no single level of grazing intensity was preferred by all trait groups, with different trait groups favoring different levels of grazing. Therefore, to maintain optimal grass structure for birds with varying grass structure preferences, landscapes should contain a heterogeneous mosaic of grazing intensities by native herbivores.

Hypothesis 1: Birds with particular traits will show preferences for certain levels of grazing

We expected that aerial insectivores, ground-foraging species, and ground-nesting trait groups would be sensitive to grazing intensity because changes in grass structure can affect important aspects of survival, such as foraging efficiency, predation and nesting success (see Table 1). We found that the number of small aerial insectivores and large ground-foraging species utilizing the grassy layer was significantly related to grazing intensity (Fig. 2), but this was not the case for small ground-foragers and ground-nesting/concealment species. We also found that for 11 bird species, the probability of using the grassy layer was significantly related to grazing intensity, representing at least one species in each trait group (Fig. 3). However, the probability of 12 species utilizing the grassy layer was not significantly related to grazing intensity, with the occurrence of two species (common bronzewing and willy wagtail) not related to any of the environmental variables we measured. It is possible that preference for different grazing intensities is obscured by other environmental factors, as birds select habitat for a variety of reasons (Jones, 2001). Alternatively, our dataset may have been insufficient to detect effects of grazing, because several species that did not appear to respond to grazing in this study were sensitive to it in other studies, e.g. buff-rumped thornbill, *Acanthiza reguloides*, speckled warbler, and yellow-rumped thornbill, *Acanthiza chrysorrhoa* (Martin et al., 2005, Woinarski and Ash, 2002, Martin and Possingham, 2005).

Hypothesis 2: Birds species within the same trait group will show preferences for a similar level of grazing intensity

Bird species that were more common at high and very high grazing intensity were ground foragers that fly to avoid predators and do not nest on the ground. The probability of three large ground-foraging species (galah, sulphur-crested cockatoo, white-winged chough) using the grassy layer increased with increasing grazing intensity, whereas one large ground-foraging species (crested pigeon) and three small ground-foraging species (magpie-lark, red-rumped parrot, superb fairy-wren) showed a quadratic response, being more likely to utilize the grassy layer at high grazing intensity (Fig. 3). We consider that the likely mechanism for this preference for higher grazing intensity is that a more open grass layer improves the probability of detection of prey and predators (Whittingham and Evans, 2004, Söderström et al., 2001). Studies in temperate environments have generally found that ground-foraging species benefit from a more open grass layer with (livestock) grazing (Martin and McIntyre, 2007, Maron and Lill, 2005, Whittingham and Evans, 2004, Atkinson et al., 2004). In contrast, ground-foraging birds in semi-arid grassy habitats typically respond negatively to (livestock) grazing in Australia (Davies et al., 2010, James, 2003) and elsewhere (Gonnet, 2001, Bock and Bock, 1999). The negative impacts of intense grazing pressure on ground-foraging birds in these environments may be due to the boom/bust nature of resource availability, making them less resilient to the effects of grazing (Milchunas et al., 1988).

We predicted that smaller ground-foraging birds would be more likely to utilize the grassy layer under higher grazing intensities than larger ground-foraging birds, due to negative effect of grazing on the size and quantity of food, and the requirement for a greater quantity and size of food items by larger birds (Brandl et al., 1994, Söderström et al., 2001, Woodcock et al., 2009). However, in contrast to this prediction, all four large ground-foraging species (crested pigeon, galah, sulphur-crested cockatoo, white-winged chough) favored higher grazing intensities than the three smaller species (magpie-lark, red-rumped parrot, superb fairy-wren) (Fig. 3). This result is in contrast to that found for ground-foraging birds in grasslands in Europe (Söderström et al., 2001), indicating body-size may not be a consistent predictor of response to grazing intensity. We suggest this result may be due to the ability of larger birds to consume a greater range of food items, and utilize lower quality food items (Brandl et al., 1994), thus allowing them to survive under conditions unfavorable for smaller species. For example, a small ground-foraging species, the red-rumped parrot, is almost exclusively dependent upon seeds throughout the year (Westcott and Cockburn, 1988, HANZAB, 1990-2007) and was less frequently detected using the grassy layer at very high grazing intensity in this study. In contrast, two large ground foragers, the galah and sulphur-crested cockatoo, can switch to poorer quality food items such as roots and vegetation when seeds are scarce (Westcott and Cockburn, 1988, HANZAB, 1990-2007) and were more commonly encountered using the grassy layer at very high grazing intensity in this study.

Ground-nesting birds which rely on concealment to avoid predators are especially vulnerable to higher grazing intensities. This is because reduced cover exposes both individuals and nests to higher rates of predation (Fondell and Ball, 2004, Whittingham et al., 2006), and increased likelihood of nests being trampled (Fondell and Ball, 2004). We found that the likelihood of the Australasian pipit using the grassy layer was negatively associated with grazing intensity (Fig. 3), a finding consistent with this trait group in grassy habitats in Australia (Davies et al., 2010) and elsewhere (Dobkin et al., 1998, Whittingham et al., 2006). However, we found no relationship between the likelihood of the Eurasian skylarks or the speckled warbler using the grassy layer and grazing intensity. Interestingly, the speckled warbler was significantly and positively related to shrub abundance, which may indicate that in the absence of grass tussocks, alternative habitat features like shrubs provide cover from predators and buffer the impact of grazing. The importance of non-grass structures (e.g. logs, shrubs) for buffering impacts of grazing has been reported in Australian grassy habitats for beetles (Barton et al., 2011) and reptiles (Michael et al., 2010, Manning et al., 2013). Grazing management for ground-nesting birds which rely on concealment may be of greater importance in grasslands than treed habitats as alternative refugia are lacking.

The richness of small aerial insectivores and the likelihood of all three individual small aerial insectivores (dusky woodswallow, tree martin, welcome swallow) using the grassy layer was greatest at lower grazing intensities (Fig. 2, Fig. 3), although the tree martin displayed a quadratic response, being more likely to utilize the grassy layer at low than very low grazing intensity. This result is similar to findings in other studies of aerial insectivores (Evans et al., 2007, Davies et al., 2010, James, 2003, Martin and Possingham, 2005) and is likely driven by the negative relationship between grazing intensity and abundance of aerial invertebrate prey (Evans, 2004). Reduced food availability, owing to high grazing intensity, has been implicated in the decline of barn swallow (*Hirundo rustica*) across agricultural landscapes in Europe (Evans et al., 2007) and in the decline of aerial insectivores in semi-arid landscapes in Australia (Davies et al., 2010).

Hypothesis 3: Different bird trait groups will favor different grazing intensities

As we predicted at the outset of this investigation, different bird trait groups favored different grazing intensities (Fig. 2, Fig. 3). For example, large ground-foraging and small ground-forging species were more likely to utilize the grassy layer at higher grazing intensities (i.e. grass height: < 10cm; grass biomass: < 1006kg/ha; grass cover: <50%), whereas small insectivores and a single ground-nesting species that relied on concealment were most likely to use the grassy layer at lower grazing intensities (i.e. grass height: > 13.5cm; grass biomass: > 1573kg/ha; grass cover: > 67%). Hence, to provide optimal grassy habitat for a range of species across the landscape, a mix of different grazing intensities will be needed. Across agricultural landscapes in south-eastern Australia, high and uniform grazing intensity now prevails across large areas (i.e. 1,000s km) with several ground-foraging birds (especially large species) common and thought to be increasing (Ford et al., 2001, Martin and Possingham, 2005, Lindenmayer et al., 2012).

Management implications

We recommend that because no single grazing intensity benefitted all trait groups and individual species in this study (Fig. 2, Fig. 3), mosaics of different grazing intensities should be created across the landscape at scales relevant to birds (e.g. 10 - 100 ha) to create difference grass structures in space and time. The importance of not implementing the same management regime everywhere to retain a full complement of bird species is well established in the literature (see Whittingham and Evans, 2004, Woinarski and Ash, 2002, Perkins et al., 2000) and will likely benefit a range of taxa (Vandvik et al., 2005, Howland et al., 2014, Pöyry et al., 2006, Dennis et al., 2008). Grazing mosaics may be achieved by burning, fencing or culling herbivores to rotate areas subject to grazing. Importantly, areas under higher grazing should be rotated frequently enough to enable tree and shrub recruitment and recovery of food items (< 10 years) (Fuhlendorf and Engle, 2004, Vandvik et al., 2005, James, 2003, Fischer et al., 2009, Whittingham and Evans, 2004).

Conclusion

Birds that utilized the grassy layer showed a varied response to differences in grazing intensity. Ground foragers, species with elevated nests, and birds that rely on early detection of predators were more likely to utilize the grassy layer under high grazing intensities. In contrast, small aerial insectivores, and a single ground-nesting species (that relies on concealment to avoid predators) were more likely to utilize grassy layer under lower grazing intensities. By using information on traits of bird species, we have identified the likely processes by which grazing can affect bird communities, and the trait-groups most likely to be affected by differences in grazing intensity.

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Supplementary data

Table A.1. Characteristics of study sites (listed in alphabetical order). "Governance" is the state or territory in which study site was located, ACT= Australian Capital Territory, NSW = New South Wales, VIC=Victoria. "Estimated grazing intensity", grazing category based on visual inspection of grass attributes.

Property ID	Grazing unit ID	Governance	Estimated Grazing intensity	Area - Property	Area - Grazing unit	Number of canopy types	Number of bird plots
1	1	ACT	Low	106	106	2	4
2	2	ACT	High	143	143	2	6
3	3	ACT	High	112*	13	1	3
4	4	ACT	Low	113	113	1	3
5	7	ACT	Moderate	179	179	2	4
6	8	ACT	Moderate	239	239	2	6
7	9	NSW	High	530	530	3	9
8	6	ACT	Moderate	688	112	2	4
8	10	ACT	Moderate	688	576	2	7
9	12	ACT	Low	112	15	1	3
9	11	ACT	Moderate	112	97	1	3
10	13	ACT	Low	240	15	1	3
10	14	ACT	Moderate	240	225	3	7
11	15	ACT	Low	154	154	3	9
12	16	ACT	High	701	581	3	8
12	17	ACT	Low	701	120	1	3
13	18	ACT	Low	142	142	2	6
14	5	ACT	Moderate	429	77	2	6
14	19	ACT	High	429	352	2	6

18	24	VIC	High	825	825	2	6
17	23	VIC	High	221	221	2	3
15	21	NSW	Moderate	1151	790	2	6
15	20	NSW	Low	1151	361	2	6
16	22	ACT	High	229	229	2	6

* Approximation

Table A.2. Complete list of the 94 observed bird species with assigned traits. Habitat adapted from Ikin et al. (2013). Nomenclature taken from Christidis and Boles (2008). Food, foraging, nesting, predation avoidance and ground nest protection derived from HANZAB (1990-2007), Ikin et al. (2013) and Lindenmayer and Cunningham (2011). References are provided in full below.

Habitat	Species	Scientific name	Trait						Trait-group
			Food item	Forage level	Nest position	Predator avoidance	Ground nest protection	Body size	
Generalist species	Fairy martin	Hirundo ariel	I	Air	Elvted			Sml	AI
	Rainbow bee-eater	Merops ornatus	I	Air	Borrow			Sml	AI
	Welcome Swallow	Hirundo neoxena	I	Air	Elvted			Sml	AI
	Common Myna	Sturnus tristis	Various	All	Elvted	Flgt		Sml	ALO
	Brown quail	Coturnix ypsilophora	S	Grnd	Grnd	Cvr	Cvr	Sml	GN
	Brown Songlark	Cincloramphus cruralis	I	Grnd	Grnd	Cvr	Cvr	Sml	GN
	Rufous Songlark	Cincloramphus mathewsi	I	Grnd	Grnd	Cvr	Cvr	Sml	GN
	Australian Magpie	Gymnorhina tibicen	I	Grnd	Elvted	Flgt		Lge	LGF
	Galah	Cacatua roseicapilla	S	Grnd	Elvted	Flgt		Lge	LGF
	Little Corella	Cacatua sanguinea	S	Grnd	Elvted	Flgt		Lge	LGF
	Long-billed Corella	Cacatua tenuirostris	S	Grnd	Elvted	Flgt		Lge	LGF

	Sulphur-crested Cockatoo	Cacatua galerita	S	Grnd	Elvted	Flgt		Lge	LGF
	Yellow-tailed Black-Cockatoo	Calyptorhynchus funereus	S	Grnd	Elvted	Flgt		Lge	LGF
	Australian Raven	Corvus coronoides	V	Grnd	Elvted			Lge	LGO
	Budgerigar	Melopsittacus undulatus	S	Grnd	Elvted	Flgt		Sml	SGF
	Common Starling	Sturnus vulgaris	I	Grnd	Elvted	Flgt		Sml	SGF
	Crested Pigeon	Ocyphaps lophotes	S	Grnd	Elvted	Flgt		Sml	SGF
	European Goldfinch	Carduelis carduelis	S	Grnd	Elvted	Flgt		Sml	SGF
	Magpie-lark	Grallina cyanoleuca	I	Grnd	Elvted	Flgt		Sml	SGF
	Red-rumped Parrot	Psephotus haematonotus	S	Grnd	Elvted	Flgt		Sml	SGF
	Yellow-rumped Thornbill	Acanthiza chrysorrhoa	I	Grnd	Elvted	Flgt		Sml	SGF
Grassland species	Australasian Pipit	Anthus novaeseelandiae	I	Grnd	Grnd	Cvr	Cvr	Sml	GN
	Eurasian Skylark	Alauda arvensis	I	Grnd	Grnd	Cvr	Cvr	Sml	GN

	Golden-headed Cisticola	Cisticola exilis	I	Grnd	Grnd	Flgt/Cvr	Cvr	Sml	GN
	Stubble Quail	Coturnix pectoralis	S	Grnd	Grnd	Cvr	Cvr	Sml	GN
	White-fronted Chat	Epthianura albifrons	I	Grnd	Elvted	Flgt		Sml	SGF
Woodland species	Dollarbird	Eurystomus orientalis	I	Air	Elvted			Sml	AI
	Dusky Woodswallow	Artamus cyanopterus	I/NF	Air	Elvted			Sml	AI
	Masked Woodswallow	Artamus personatus	I	Air	Elvted			Sml	AI
	Tree Martin	Petrochelidon nigicans	I	Air	Elvted			Sml	AI
	White-browed Woodswallow	Artamus superciliosus	I	Air	Elvted			Sml	AI
	Grey Shrike-thrush	Colluricincla harmonica	Various	All	Elvted	Flgt		Sml	ALO
	Noisy Friarbird	Philemon corniculatus	Various	C	Elvted			Sml	ALO
	Noisy Miner	Manorina melanocephala	Various	C	Elvted			Sml	ALO
	Black-chinned Honeyeater	Melithreptus gularis	I/NF	C	Elvted			Sml	C

Black-faced Cuckoo-shrike	Coracina novaehollandiae	I	C	Elvted		Sml	C
Brown Thornbill	Acanthiza pusilla	I	C	Elvted		Sml	C
Brown-headed Honeyeater	Melithreptus brevirostris	I/NF	C	Elvted		Sml	C
Fuscous Honeyeater	Lichenostomus fuscus	I/NF	C	Elvted		Sml	C
Golden Whistler	Pachycephala pectoralis	I/NF	C	Elvted		Sml	C
Grey Fantail	Rhipidura fuliginosa	I	C	Elvted		Sml	C
Leaden Flycatcher	Myiagra rubecula	I	C	Elvted		Sml	C
Mistletoebird	Dicaeum hirundinaceum	NF	C	Elvted		Sml	C
Olive-backed Oriole	Oriolus sagittatus	I/NF	C	Elvted		Sml	C
Red wattlebird	Anthochaera carunculata	I/NF	C	Elvted		Sml	C
Rufous Whistler	Pachycephala rufiventris	I/NF	C	Elvted		Sml	C
Silvereye	Zosterops lateralis	I	C	Elvted		Sml	C
Spotted Pardalote	Pardalotus punctatus	I	C	Elvted		Sml	C

Striated Pardalote	Pardalotus striatus	I	C	Elvted	Sml	C
Striated Thornbill	Acanthiza lineata	I/NF	C	Elvted	Sml	C
Varied Sittella	Daphoenositta chrysoptera	I	C	Elvted	Sml	C
Weebill	Smicornis brevirostris	I	C	Elvted	Sml	C
Western Gerygone	Gerygone fusca	I	C	Elvted	Sml	C
White-eared Honeyeater	Lichenostomus leucotis	I/NF	C	Elvted	Sml	C
White-naped Honeyeater	Melithreptus lunatus	I/NF	C	Elvted	Sml	C
White-plumed Honeyeater	Lichenostomus pencillatus	I/NF	C	Elvted	Sml	C
White-throated Gerygone	Gerygone olivacea	I	C	Elvted	Sml	C
White-throated Treecreeper	Cormobates leucophaeus	I	C	Elvted	Sml	C
Yellow-faced Honeyeater	Lichenostomus chrysops	I/NF	C	Elvted	Sml	C
Yellow-tufted Honeyeater	Lichenostomus melanops	I/NF	C	Elvted	Sml	C

Australian King-Parrot	Alisterus scapularis	S	C	Elvted		Lge	CG
Laughing Kookaburra	Dacelo novaeguineae	V	Grnd	Elvted		Lge	LGC
Common Bronzewing	Phaps chalcoptera	S	Grnd	Elvted	Flgt	Lge	LGF
White-winged Chough	Corcorax melanorhamphos	I	Grnd	Elvted	Flgt	Lge	LGF
Grey Currawong	Strepera versicolor	V	Grnd	Elvted		Lge	LGO
Pied Currawong	Strepera graculina	V	Grnd	Elvted		Lge	LGO
Grey Butcherbird	Cracticus torquatus	V	Grnd	Elvted		Sml	SGC
Pied Butcherbird	Cracticus nigrogularis	V	Grnd	Elvted		Sml	SGC
Sacred Kingfisher	Todiramphus sanctus	V	Grnd	Elvted		Sml	SGC
Brown Treecreeper	Climacteris picumnus	I	Grnd	Elvted	Flgt	Sml	SGF
Brush Cuckoo	Cacomantis variolosus	I	All	Elvted	Flgt	Sml	SGF
Buff-rumped Thornbill	Acanthiza reguloides	I	Grnd	Elvted	Flgt	Sml	SGF
Crimson Rosella	Platycercus elegans	S	Grnd	Elvted	Flgt	Sml	SGF
Diamond Firetail	Stagonopleura guttata	GS	Grnd	Elvted	Flgt	Sml	SGF
Double-barred Finch	Taeniopygia bichenovii	GS	Grnd	Elvted	Flgt	Sml	SGF

Eastern Rosella	Platycercus eximius	S	Grnd	Elvted	Flgt	Sml	SGF
Eastern Yellow Robin	Eopsaltria australis	I	Grnd	Elvted	Flgt	Sml	SGF
Fan-tailed Cuckoo	Cacomantis flabelliformis	I	All	Elvted	Flgt	Sml	SGF
Flame Robin	Petroica phoenicea	I	Grnd	Elvted	Flgt	Sml	SGF
Hooded Robin	Melanodryas cucullata	I	Grnd	Elvted	Flgt	Sml	SGF
Horsfield's Bronze-Cuckoo	Chrysococcyx basilis	I	All	Elvted	Flgt	Sml	SGF
Jacky Winter	Microeca fascinans	I	Grnd	Elvted	Flgt	Sml	SGF
Pallid Cuckoo	Cuculus pallidus	I	All	Elvted	Flgt	Sml	SGF
Red-browed finch	Neochmia temporalis	GS	Grnd	Elvted	Flgt	Sml	SGF
Red-capped Robin	Petroica goodenovii	I	Grnd	Elvted	Flgt	Sml	SGF
Restless Flycatcher	Myiagra inquieta	I	Grnd	Elvted	Flgt	Sml	SGF
Scarlet Robin	Petroica multicolor	I	Grnd	Elvted	Flgt	Sml	SGF
Southern Whiteface	Aphelocephala leucopsis	I	Grnd	Elvted	Flgt	Sml	SGF
Superb Fairy-wren	Malurus cyaneus	I	Grnd	Elvted	Flgt	Sml	SGF

Superb Parrot	Polytelis swainsonii	S	Grnd	Elvted	Flgt		Sml	SGF
White-browed Scrubwren	Sericornis frontalis	I	Grnd	Elvted	Flgt		Sml	SGF
White-winged Triller	Lalage sueurii	I	All	Elvted	Flgt		Sml	SGF
Willie Wagtail	Rhipidura leucophrys	I	Grnd	Elvted	Flgt		Sml	SGF
White-browed Babbler	Pomatostomus superciliosus	I	Grnd	Elvted	Flgt		Sml	SGF
Painted button-quail	Turnix varius	S	Grnd	Grnd	Cvr	Cvr	Sml	GN
Speckled Warbler	Chthonicola sagittata	I	Grnd	Grnd	Flgt/Cvr	Cvr	Sml	GN

Food item abbreviations: “Various” feeds on a range of food items, “NF” feeds on nectar and fruit, “I” feeds on invertebrates, “V” feeds on vertebrates, “S” feeds on grain and seed, “GS” feeds on grain. Foraging strata abbreviations: “Grnd” is ground-foraging, “Air” forages in the air, “All” forages across a range of strata, “C” forages above ground layer in vegetation. Nest position abbreviations: “Grnd” nests on the ground, “Elvted” nests above the ground layer. Predator avoidance abbreviations: “Cvr” relies on concealment to avoid detection by predators, “Flgt” relies on early detection and flight to avoid predators. Ground nest protection abbreviations: “Cover” relies on concealment of nest to avoid detection by predators. Body size abbreviations: “Sml” is < 250g, “Lge” is > 250g. Trait-group abbreviations: “AI” is aerial insectivore, “ALO” is all levels omnivore, “C” is canopy feeder, “CG” is canopy granivore, “GN” is ground nesting/concealment, “LGC” is Large ground carnivore, “LGF” is large ground-foraging, “LGO” is large ground omnivore, “SGC” is small ground carnivore, “SGF” is small ground-foraging.

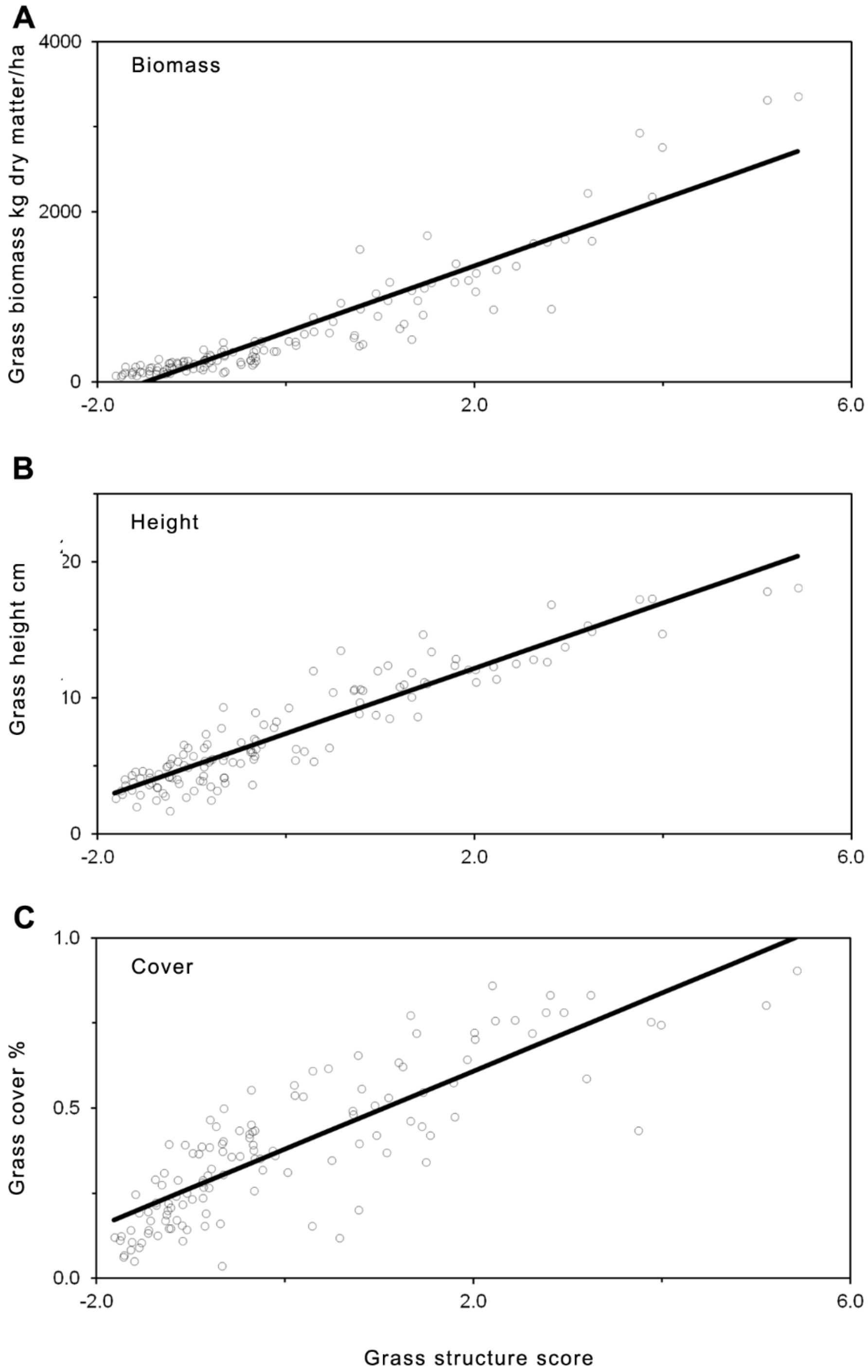
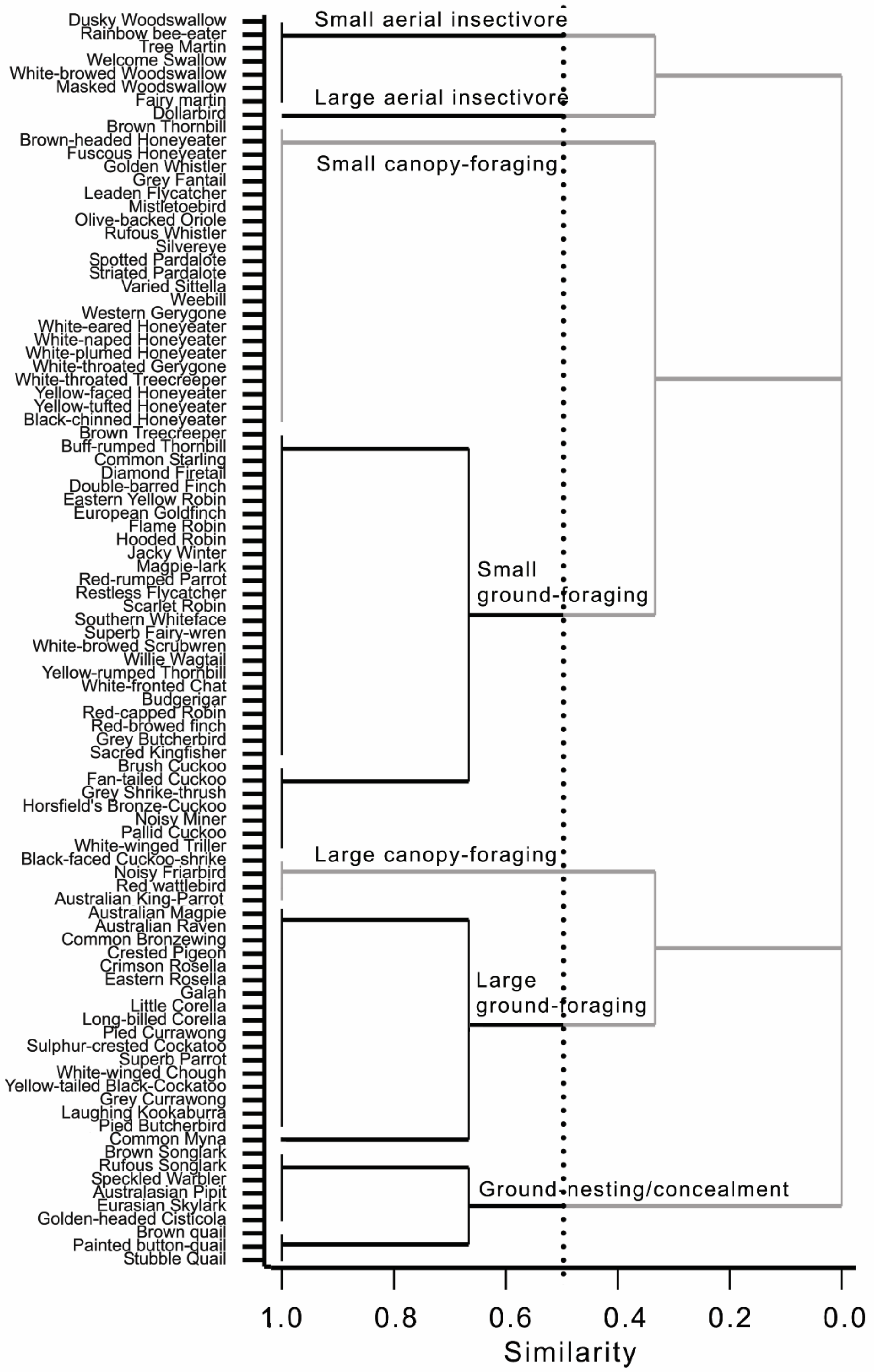


Figure. A.1. Graphical representation of the relationship between grass structure and a) grass biomass (kgDM/ha), b) grass height (cm), and c) grass cover (%). Fitted relationships are shown as a solid line, with actual values shown as open circles. Adapted from Howland et al. (2014). Reference is provided in full below.



Dusky Woodswallow
Rainbow bee-eater
Tree Martin
Welcome Swallow
White-browed Woodswallow
Masked Woodswallow
Fairy martin
Dollarbird
Brown Thornbill
Brown-headed Honeyeater
Fuscous Honeyeater
Golden Whistler
Grey Fantail
Leaden Flycatcher
Mistletoebird
Olive-backed Oriole
Rufous Whistler
Silvereye
Spotted Pardalote
Striated Pardalote
Varied Sittella
Weebill
Western Gerygone
White-eared Honeyeater
White-naped Honeyeater
White-plumed Honeyeater
White-throated Gerygone
White-throated Treecreeper
Yellow-faced Honeyeater
Yellow-tufted Honeyeater
Black-chinned Honeyeater
Brown Treecreeper
Buff-rumped Thornbill
Common Starling
Diamond Firetail
Double-barred Finch
Eastern Yellow Robin
European Goldfinch
Flame Robin
Hooded Robin
Jacky Winter
Magpie-lark
Red-rumped Parrot
Restless Flycatcher
Scarlet Robin
Southern Whiteface
Superb Fairy-wren
White-browed Scrubwren
Willie Wagtail
Yellow-rumped Thornbill
White-fronted Chat
Budgerigar
Red-capped Robin
Red-browed finch
Grey Butcherbird
Sacred Kingfisher
Brush Cuckoo
Fan-tailed Cuckoo
Grey Shrike-thrush
Horsfield's Bronze-Cuckoo
Noisy Miner
Pallid Cuckoo
White-winged Triller
Black-faced Cuckoo-shrike
Noisy Friarbird
Red wattlebird
Australian King-Parrot
Australian Magpie
Australian Raven
Common Bronzewing
Crested Pigeon
Crimson Rosella
Eastern Rosella
Galah
Little Corella
Long-billed Corella
Pied Currawong
Sulphur-crested Cockatoo
Superb Parrot
White-winged Chough
Yellow-tailed Black-Cockatoo
Grey Currawong
Laughing Kookaburra
Pied Butcherbird
Common Myna
Brown Songlark
Rufous Songlark
Speckled Warbler
Australasian Pipit
Eurasian Skylark
Golden-headed Cisticola
Brown quail
Painted button-quail
Stubble Quail
Small aerial insectivore
Large aerial insectivore
Small canopy-foraging
Small ground-foraging
Large canopy-foraging
Large ground-foraging
Ground-nesting/concealment
1.0
0.8
0.6
0.4
0.2
0.0
Similarity

Figure. A.2. Dendrogram derived from hierarchal cluster analysis. Dashed line indicates the cut off for trait groups based on mean distance between clusters (i.e. 0.5). Seven species trait groups were defined. The four trait groups considered to be affected by grazing are shown in black.

Table A.3. Top 5 models according AICc values generated using generalized linear modeling for the relationship between explanatory variables andspecies richness of four trait groups and the occurrence of 24 individual bird species. Abbreviations: “n”, number of data points (i.e. plots) used in model, “K” number of parameters included model. Variables selected in GLM are denoted with a “□ “, variables not selected with a “□” and variables not used in model with a “-”. Individual species are grouped by habitat and trait-group. For scientific names see Table A.2.

Habitat	Trait-group	Species	n	K	Aicc	Aic	Adjusted R squared	Df	Tree canopy class	Distance to Urban	Noisy Miner	Grass structure	Grass structure_2	No. Shrubs	Distance to Tree
Generalist species	AI	Welcome Swallow	127	5	135.2	134.8	33.3	7	✓	×	✓	✓	✓	✓	-
			127	5	135.3	134.8	33.3	7	✓	✓	✓	✓	✓	×	-
			127	4	135.4	135.1	32.6	6	✓	×	✓	✓	✓	×	-
			127	6	135.7	135.0	33.8	8	✓	✓	✓	✓	✓	✓	-
			127	4	137.6	137.3	30.9	5	×	×	✓	✓	✓	✓	-
	LGF	Australian Magpie	127	5	134.2	133.7	25.8	7	✓	✓	✓	✓	×	✓	-
			127	4	134.3	134.0	25.0	6	✓	✓	✓	✓	×	×	-
			127	4	134.6	134.3	24.8	6	✓	×	✓	✓	×	✓	-

	127	4	134.8	134.5	24.1	5	✓	✗	✓	✓	✗	✓	-
	127	3	134.6	134.4	24.8	6	✓	✓	✗	✓	✗	✗	-
Galah	127	3	131.3	131.1	18.4	5	✓	✓	✗	✓	✗	✗	-
	127	2	131.4	131.3	17.6	4	✓	✗	✗	✓	✗	✗	-
	127	4	131.6	131.3	19.0	6	✓	✓	✗	✓	✗	✓	-
	127	3	131.9	131.7	18.0	5	✓	✗	✗	✓	✗	✓	-
	127	3	133.3	133.1	17.1	5	✓	✗	✗	✓	✓	✗	-
Sulphur-crested Cockatoo	127	3	131.5	131.3	49.8	4	✗	✓	✗	✓	✗	✓	-
	127	4	131.6	131.3	50.6	6	✓	✓	✗	✓	✗	✓	-
	127	4	133.4	133.1	49.4	5	✗	✓	✗	✓	✓	✓	-

		127	4	133.5	133.2	49.4	5	✗	✓	✓	✓	✗	✓	-
		127	5	133.6	133.1	50.3	7	✓	✓	✓	✓	✗	✓	-
SGF	Common Starling	127	3	132.5	132.3	27.4	5	✓	✓	✗	✗	✗	✓	-
		127	4	133.0	132.7	27.8	6	✓	✓	✗	✓	✗	✓	-
		127	4	133.7	133.4	27.3	6	✓	✓	✓	✗	✗	✓	-
		127	5	134.0	133.6	27.8	7	✓	✓	✓	✓	✗	✓	-
		127	2	133.9	133.8	25.9	4	✓	✓	✗	✗	✗	✗	-
														-
	Crested Pigeon	127	5	133.9	133.4	34.3	7	✓	✓	✗	✓	✓	✓	
		127	6	135.7	135.0	34.0	8	✓	✓	✓	✓	✓	✓	-

	127	4	137.1	136.8	31.4	5	×	✓	×	✓	✓	✓	-
	127	5	137.7	137.2	32.3	7	✓	✓	✓	✓	✓	×	-
	127	4	138.7	138.3	31.1	6	✓	✓	×	✓	✓	×	-
Magpie-lark	127	4	131.7	131.4	42.5	6	✓	✓	×	✓	✓	×	-
	127	5	133.6	133.1	42.2	7	✓	✓	×	✓	✓	✓	-
	127	5	133.9	133.4	42.1	7	✓	✓	✓	✓	✓	×	-
	127	6	135.7	135.0	41.8	8	✓	✓	✓	✓	✓	✓	-
	127	3	138.9	138.7	38.1	4	×	✓	×	✓	✓	×	-
Red-rumped Parrot	127	3	131.5	131.3	15.9	4	×	✓	×	✓	✓	×	-

	127	4	131.6	131.3	16.6	5	×	✓	✓	✓	✓	×	-
	127	4	133.3	133.0	16.1	6	×	✓	✓	✓	✓	×	-
	127	5	133.5	133.0	16.8	7	✓	✓	✓	✓	✓	×	-
	127	4	133.6	133.2	15.9	6	✓	✓	×	✓	✓	×	-
Yellow-rumped Thornbill	127	2	128.9	128.8	18.3	4	✓	×	✓	×	×	×	-
	127	3	129.9	129.7	18.4	5	✓	✓	✓	×	×	×	-
	127	3	130.9	130.7	17.7	5	✓	×	✓	✓	×	×	-
	127	3	130.9	130.7	17.7	5	✓	×	✓	×	×	✓	-
	127	4	132.0	131.7	17.7	6	✓	✓	✓	×	×	✓	-

Grassland species	GN	Australasian Pipit	34	2	37.2	36.8	35.6	3	-	✗	-	✓	✗	-	✓
			34	3	37.8	37.0	37.2	4	-	✗	-	✓	✓	-	✓
			34	3	39.6	38.8	33.5	4	-	✓	-	✓	✗	-	✓
			34	4	40.4	39.0	35.1	5	-	✓	-	✓	✓	-	✓
			34	1	40.8	40.7	25.6	2	-	✗	-	✗	✗	-	✓
		Eurasian Skylark	34	1	34.5	34.3	38.0	2	-	✗	-	✗	✗	-	✓
			34	2	35.5	35.1	38.6	3	-	✓	-	✗	✗	-	✓
			34	2	36.7	36.3	36.0	3	-	✗	-	✓	✗	-	✓
			34	3	37.8	37.0	36.7	4	-	✓	-	✓	✗	-	✓
			34	3	38.9	38.1	34.3	4	-	✗	-	✓	✓	-	✓
Woodland species	AI	Dusky Woodswallow	93	5	100.9	100.2	37.4	6	✓	✓	✓	✓	✗	✓	-
			93	6	101.0	100.0	38.2	7	✓	✓	✓	✓	✓	✓	-

		93	4	101.3	100.9	36.2	5	✓	✓	✓	✓	✗	✗	-
		93	5	102.0	101.3	36.6	6	✓	✓	✓	✓	✓	✗	-
		93	4	102.8	102.3	35.2	5	✗	✓	✓	✓	✓	✗	-
	Tree Martin	93	4	97.9	97.4	31.2	5	✗	✓	✗	✓	✓	✓	-
		93	3	98.9	98.6	29.4	4	✗	✓	✗	✓	✗	✓	-
		93	4	99.0	98.6	30.2	5	✗	✓	✓	✓	✗	✓	-
		93	5	99.1	98.4	31.1	6	✗	✓	✓	✓	✓	✓	-
		93	5	99.6	98.9	30.7	6	✓	✓	✗	✓	✓	✓	-
GN	Speckled Warbler	93	3	97.1	96.8	24.6	4	✓	✓	✗	✗	✗	✓	-
		93	4	97.3	96.9	25.4	5	✓	✓	✗	✓	✗	✓	-
		93	3	97.5	97.2	24.2	4	✗	✓	✗	✓	✗	✓	-
		93	5	98.7	98.0	25.3	6	✓	✓	✗	✓	✓	✓	-

		93	4	99.2	98.8	23.8	5	✗	✓	✗	✓	✓	✓	-
LGF	Common Bronzewing	93	1	93.7	93.6	1.7	2	✗	✗	✗	✓	✗	✗	-
		93	2	94.9	94.8	1.6	3	✓	✗	✗	✓	✗	✗	-
		93	2	95.0	94.8	1.5	3	✗	✓	✗	✓	✗	✗	-
		93	2	95.1	94.9	1.4	3	✗	✗	✗	✓	✗	✓	-
		93	1	95.3	95.3	<0.00	2	✗	✓	✗	✗	✗	✗	-
	White-winged Chough	93	3	94.6	94.4	39.4	4	✓	✗	✓	✓	✗	✗	-
		93	4	96.7	96.3	38.8	5	✓	✗	✓	✓	✗	✓	-
		93	4	96.8	96.3	38.7	5	✓	✓	✓	✓	✗	✗	-
		93	4	96.8	96.3	38.7	5	✓	✗	✓	✓	✓	✗	-
		93	5	98.8	98.1	38.2	6	✓	✓	✓	✓	✗	✓	-

Buff-rumped Thornbill	93	2	94.0	93.9	11.5	3	✓	×	✓	×	×	×	-
	93	3	94.9	94.6	11.8	4	✓	✓	✓	×	×	×	-
	93	1	95.4	95.3	9.1	2	×	×	✓	×	×	×	-
	93	2	95.8	95.7	9.7	3	×	×	✓	×	×	✓	-
	93	3	95.8	95.6	10.9	4	✓	×	✓	×	×	✓	
													-
Crimson Rosella	93	4	96.8	96.4	9.7	5	×	×	✓	✓	✓	✓	-
	93	2	97.5	97.3	6.6	3	×	×	✓	×	×	✓	-
	93	5	98.8	98.1	8.9	6	✓	×	✓	✓	✓	✓	-
	93	5	98.9	98.2	8.8	6	×	✓	✓	✓	✓	✓	-
	93	3	99.1	98.9	6.0	4	×	×	✓	✓	×	✓	-
Eastern Rosella	93	2	93.1	93.0	29.6	3	✓	×	✓	×	×	×	-
	93	3	94.9	94.7	29.1	4	✓	✓	✓	×	×	×	-
	93	3	95.0	94.8	29.0	4	✓	×	✓	×	×	✓	-

	93	3	95.1	94.8	29.0	4	✓	×	✓	✓	×	×	-
	93	4	96.8	96.4	28.5	5	✓	✓	✓	×	×	✓	-
Scarlet Robin	93	3	97.6	97.3	7.8	4	✓	×	×	✓	✓	×	-
	93	4	97.9	97.5	8.7	5	✓	×	✓	✓	✓	×	-
	93	2	98.3	98.2	5.9	3	✓	×	✓	×	×	×	-
	93	1	98.4	98.4	4.7	2	✓	×	×	×	×	×	-
	93	4	98.7	98.2	7.9	5	✓	✓	×	✓	✓	×	-
Southern Whiteface	93	5	99.1	98.5	28.0	6	✓	✓	✓	✓	✓	×	-
	93	4	100.2	99.8	26.1	5	✓	×	✓	✓	✓	×	-
	93	6	101.0	100.0	27.6	7	✓	✓	✓	✓	✓	✓	-
	93	5	101.9	101.3	25.7	6	✓	×	✓	✓	✓	✓	-

	93	4	102.9	102.4	24.0	5	✓	✓	✗	✓	✓	✗	-
Superb Fairy-wren	93	3	96.0	95.7	19.8	4	✗	✓	✗	✓	✓	✗	-
	93	4	96.6	96.1	20.4	5	✗	✓	✗	✓	✓	✓	-
	93	4	97.4	97.0	19.6	5	✗	✓	✓	✓	✓	✗	-
	93	4	97.9	97.5	19.2	5	✓	✓	✗	✓	✓	✗	-
	93	2	98.5	98.4	16.5	3	✗	✗	✗	✓	✓	✗	-
Willie Wagtail	93	4	96.6	96.1	8.4	5	✗	✓	✗	✓	✓	✓	-
	93	3	97.5	97.2	6.2	4	✗	✗	✗	✓	✓	✓	-
	93	3	97.7	97.4	6.0	4	✗	✓	✗	✓	✓	✗	-
	93	2	98.1	98.0	4.3	3	✗	✗	✗	✓	✓	✗	-
	93	5	98.7	98.0	7.4	6	✓	✓	✗	✓	✓	✓	-

Trait-group abbreviations: "AI" is aerial insectivore, "ALO" is all levels omnivore, "C" is canopy feeder, "CG" is canopy granivore, "GN" is ground nesting/concealment, "LGC" is Large ground carnivore, "LGF" is large ground-foraging, "LGO" is large ground omnivore, "SGC" is small ground carnivore, "SGF" is small ground-foraging.

Table A.4. Results of hierarchical generalized linear mixed models for four trait groups and the occurrence of 23 individual species predicted by grass structure showing trends (Slope) including standard errors (SE). Grassland and open woodland has been used as a reference level for tree canopy class categories for generalist and woodland species respectively. Significance is indicated by the Wald statistic (χ2) and p-value as follows: * p<0.05, ** p<0.01, *** p<0.001. For scientific names see Table A.2.

Habitat	Trait group	Response	Model term	d.f.	χ2	Slope	SE
Generalist species	AI	Welcome swallow	Intercept			-6.86	0.83
			tree canopy class	2	15.18***		
			open woodland			1.71	0.68
			woodland			0.64	0.86
			Noisy miner	1	21.5***	1.18	0.26
			grass structure	1	0	0.00	0.37
			grass structure^2	1	27.14***	0.68	0.13
			No. Shrubs	1	1.7	-0.33	0.25
	LGF	Sulphur-crested cockatoo	Intercept			-7.14	0.60
			Distance to urban area	1	39.87***	-1.75	0.28
			grass structure	1	19.87***	-1.49	0.34
			No. Shrubs	1	15.66***	-2.34	0.59
		Australian magpie	Intercept			-0.67	0.34
			tree canopy class	2	9.874**		
			open woodland			-1.01	0.39
			woodland			-1.59	0.51

	Distance to urban area	1	1.498	-0.20	0.16
	Noisy miner occurrence	1	1.761	0.19	0.14
	grass structure	1	0.873	-0.17	0.18
	No. Shrubs	1	1.42	-0.20	0.17
Crested pigeon	Intercept			-5.90	0.92
	tree canopy class	2	0.88		
	open woodland			-0.73	0.96
	woodland			-0.46	1.06
	Distance to urban area	1	19.74***	-1.79	0.40
	grass structure	1	18.08***	-2.53	0.60
	grass structure^2	1	5.07*	-1.66	0.74
	No. Shrubs	1	11.42***	-0.95	0.28
Galah	Intercept			-2.60	0.33
	tree canopy class	2	19.01***		
	open woodland			-0.97	0.47
	woodland			-2.73	0.65
	Distance to urban area	1	2.09	-0.26	0.18

		grass structure	1	12.21***	-1.16	0.33
SGF	Red-rumped parrot	Intercept			-4.08	0.32
		Distance to urban area	1	7.811**	0.83	0.30
		grass structure	1	3.212	-1.27	0.71
		grass structure^2	1	7.982**	-2.63	0.93
	Common starling	Intercept			-6.11	0.65
		tree canopy class	2	13.174**		
		open woodland			1.90	0.54
		woodland			-6.84	11.60
		Distance to urban area	1	8.205**	-0.87	0.30
		No. Shrubs	1	3.866*	-0.80	0.41
	Magpie-lark	Intercept			-3.67	0.37
		tree canopy class	2	12.01**		
		open woodland			-1.52	0.44
		woodland			-1.13	0.49
		Distance to urban area	1	41.05***	-1.17	0.18
		grass structure	1	11.74***	-3.47	1.01

			grass structure^2	1	12.65***	-3.89	1.09
		Yellow-rumped thornbill	Intercept			-4.33	0.55
			tree canopy class	2	18.18***		
			open woodland			2.44	0.57
			woodland			2.12	0.59
			Noisy miner occurrence	1	7.92**	-0.46	0.16
Grassland species	GN	Australasian pipit	Intercept			-1.00	0.25
			grass structure	1	5.726*	0.55	0.23
			Distance to tree	1	9.466**	1.15	0.37
		Eurasian skylark	Intercept			-2.02	0.35
			Distance to tree	1	10.13**	1.75	0.55
Woodland species	AI	Dusky woodswallow	Intercept			-5.47	0.50
			tree canopy class	1	5.946*		
			woodland			1.35	0.56
			Distance to urban area	1	10.019**	0.89	0.28
			Noisy miner occurrence	1	6.075*	-0.75	0.30
			grass structure	1	23.81***	0.80	0.16
			No. Shrubs	1	2.582	-0.39	0.25

	Tree martin	Intercept			-4.05	0.28
		Distance to urban area	1	8.191**	-0.58	0.20
		grass structure	1	8.88**	1.19	0.40
		grass structure^2	1	2.688	-0.26	0.16
		No. Shrubs	1	4.605*	-0.55	0.26
GN	Speckled warbler	Intercept			-5.50	0.49
		tree canopy class	1	9.16**		
		woodland			1.25	0.41
		Distance to urban area	1	3.533	-0.53	0.28
		No. Shrubs	1	4.138*	0.48	0.24
LGF	Common bronzewing	Intercept			-4.24	0.29
		grass structure	1	1.423	-0.42	0.36
	White-winged chough	Intercept			-4.92	0.43
		tree canopy class	1	15.224***		
		woodland			1.77	0.45
		Noisy miner occurrence	1	8.262**	0.50	0.17
		grass structure	1	5.532*	-0.97	0.41
SGF	Crimson rosella	Intercept			-2.74	0.26

	Noisy miner occurrence	1	6.429*	0.52	0.21
	grass structure	1	1.224	0.36	0.33
	grass structure^2	1	2.324	-0.37	0.24
	No. Shrubs	1	5.146*	0.43	0.19
Eastern rosella	Intercept			-2.20	0.19
	tree canopy class	1	10.71**		
	woodland			-1.10	0.33
	Noisy miner occurrence	1	22.56***	0.72	0.15
Buff-rumped thornbill	Intercept			-3.47	0.31
	tree canopy class	1	3.403		
	woodland			0.62	0.34
	Noisy miner occurrence	1	8.281**	-0.66	0.23
Scarlet robin	Intercept			-4.35	0.46
	tree canopy class	1	7.251**		
	woodland			1.30	0.48
	grass structure	1	2.873	0.75	0.44
	grass structure^2	1	3.73	-0.93	0.48
Superb fairy-wren	Intercept			-2.55	0.40

	Distance to urban area	1	0.968	0.41	0.42
	grass structure	1	10.489**	1.95	0.60
	grass structure^2	1	13.757***	-2.74	0.74
Willie wagtail	Intercept			-3.60	0.42
	Distance to urban area	1	3.016	0.76	0.44
	grass structure	1	0.525	0.36	0.50
	grass structure^2	1	2.767	-1.07	0.64
	No. Shrubs	1	1.822	-0.37	0.27

Trait-group abbreviations: “AI” is aerial insectivore, “ALO” is all levels omnivore, “C” is canopy feeder, “CG” is canopy granivore, “GN” is ground nesting/concealment, “LGC” is Large ground carnivore, “LGF” is large ground forager, “LGO” is large ground omnivore, “SGC” is small ground carnivore, “SGF” is small ground forager.

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PAPER III: Habitat preference of the striped legless lizard: implications of grazing by native herbivores and livestock for conservation of grassland biota

The striped legless lizard (Delma Impar) rescued from a development site in the ACT (Photo: Brett Howland)

Howland, B., Stojanovic, D., Gordon, I. J., Stirenmann, I., Fletcher, D., Snape, M., and Lindenmayer, B. D. (2016). Habitat preference of the striped legless lizard: implications of grazing by native herbivores and livestock for conservation of grassland biota. *Austral Ecology* **41**(4): 455-464.

Abstract

Across the globe, many species of reptile are threatened with extinction, with changes in grazing pressure a significant factor in their decline. Few studies have investigated the role of native herbivores, yet studying natural grazers may provide insight into natural grazing regimes, not apparent in studies of domestic livestock. In this study, we investigate the habitat requirements of a threatened Australian grassland reptile, the striped legless lizard, *Delma impar*, in grasslands grazed by a native herbivore, the eastern grey kangaroo *Macropus giganteus*. *Delma impar* appears sensitive to habitat change resulting from altered grazing intensity, but a lack of information hinders implementation of appropriate grazing regimes. To address this gap, we investigated habitat preferences of *D. impar* at multiple spatial scales across a grazing gradient. We found that the occurrence of *D. impar* was not affected by the size of grassland remnants, but was negatively related to the density of native grazers. This result was likely a consequence of the negative effect of high grazing intensity on grass structural complexity, as the probability of encountering a *D. impar* was positively related to grass structural complexity at the fine scale (1 m^2). We recommend that conservation efforts should avoid high intensity grazing (equivalent to > 1.3 kangaroos/ha), yet ensure enough grazing disturbance is maintained to promote the formation of complex grass structures. We also recommend that small floristically degraded and fragmented grassland habitat should be included in conservation efforts. These recommendations will likely benefit a number of faunal species in grasslands grazed by domestic and native grazers. Importantly, our data highlight the need for managing grazing regimes, even in environments dominated by native herbivores.

Introduction

Animals select habitat based on various environmental factors operating across multiple spatial scales (Rodríguez et al., 2007, Luck, 2002, Mackey and Lindenmayer, 2001). Understanding what these environmental factors are is especially important for species at risk of extinction (Lindenmayer and Burgman, 2005, Caughley et al., 1996). Such information can be used to guide habitat restoration (Sato et al., 2014a), to identify priority areas for biodiversity conservation (Wintle et al., 2005), and to provide insight into likely impacts of environmental change (Lindenmayer et al., 2014). Unfortunately for many species, their ecology remains poorly understood and few data are available to assist their conservation management (IUCN Red List of Threatened Species, 2014). Addressing these data deficiencies is important for conservation managers developing management strategies to reverse population decline (Caughley and Sinclair, 1994, Morrison et al., 2006). In ecosystems where threatening processes are still acting on populations, such research should be a high priority for conservation managers.

The conservation of reptiles is seriously hampered by the global lack of basic ecological research for most species (Böhm et al., 2013, Gibbons et al., 2000). This data deficit is attributable to inherent challenges in studying reptiles because they are cryptic, occur across a diverse and often challenging terrain, and are often ignored in the allocation of research and conservation resources (Böhm et al., 2013). We address this gap for the striped legless lizard, *Delma impar*, which is a threatened semi-fossorial grassland insectivore once widely distributed in natural temperate grasslands across south-eastern Australia (Coulson, 1990, Robertson and Smith, 2010). However, over 99% of natural temperate grasslands have been lost through clearing or agricultural intensification in the last 200 years (Kirkpatrick et al., 1995, ACT Government, 2005), with natural temperate grasslands now listed as an endangered ecological community (Department of the Environment and Heritage, 2003). Consequently, *D. impar* has undergone a dramatic range contraction, and is now classified as threatened under state and federal environmental laws (Department of the Environment and Heritage, 2014a). Where *D. impar* persists, it is threatened by pasture improvement, weed invasion, urban development, and inappropriate fire and grazing regimes (Hadden, 1998, Dorrough and Ash, 1999, Robertson and Smith, 2010, O'Shea, 2005). Despite the recognition of these threats to the conservation of the species, few empirical data are available to guide the conservation management of the relict populations of *D. impar* and the maintenance of their habitat. We investigate the role of grazing regimes in influencing habitat selection by *D. impar*.

Grazing by large herbivores can have a profound influence on reptiles by changing the structural complexity of grasslands (Brown et al., 2011, Castellano and Valone, 2006, Larson, 2014, Howland et al., 2014). Intense grazing reduces grass cover and can expose small ground-dwelling reptiles to elevated rates of predation, reduced prey abundance and heat stress (Castellano and Valone, 2006, Sato et al., 2014b, Osmond, 1994). Conversely, suppression of grazing may also be detrimental, as without grazing grass can form tall and dense structures, reducing the access to sunlight needed for metabolic function in many reptiles (Scott, 1962, Hacking et al., 2014). Hence, some grazing is considered important in maintaining habitat quality for grassland reptiles (Coulson, 1990, Thompson, 2006, Candy, 2008, Robertson and Smith, 2010, Pettigrew and Bull, 2014), but information is limited on optimal grazing regimes for *D. impar*. We address this knowledge gap by determining *D. impar* habitat preferences in grasslands grazed by native kangaroos in the Australian Capital Territory.

Populations of the large native grazer, the eastern grey kangaroos, *Macropus giganteus*, have increased in many parts of Australia over the past decade, with impacts on native biodiversity recorded (Barton et al., 2011, Manning et al., 2013, McIntyre et al., 2010, Meers and Adams, 2003), including *D. impar* (Howland et al., 2014). Importantly, grazing impacts of native herbivores may provide insight into natural grazing patterns not apparent from studies of domestic livestock (Foster et al., 2014). Effective management of this impact will depend on robust quantitative investigation into links between habitat quality, species persistence and kangaroo abundance, such as being undertaken here. Furthermore, given the paucity of ecological knowledge of the impact of varying levels of grazing by native herbivores, single species studies such as ours can provide important insights that have broader relevance (Foster et al., 2014, Gordon et al., 2004, Mysterud, 2006).

We investigated the habitat preferences of *D. impar* across a grazing intensity gradient at three spatial scales (fine, [1 m^2]; intermediate, [1 ha]; and landscape, [> 10 ha]) to address four questions. First; are *D. impar* more common under low or high kangaroo densities? As high grazer densities negatively affect the amount and cover of grass (McIntyre and Tongway, 2005, Rook et al., 2004), we hypothesized that *D. impar* will be more common in areas of low kangaroo density, compared to areas of high kangaroo density. Second; does *D. impar* preferentially use areas of high grass structural complexity? We hypothesized that individuals would be more likely to be encountered where fine scale grass structural complexity is higher, due to the positive effect of complexity on important biotic conditions (prey availability, predation risk) and abiotic (microclimate) conditions, and their relationship to an individual's fitness (Sato et al., 2014b and references therein). Third; is *D. impar* associated with a particular floristic community? We hypothesized that the occurrence of *D. impar* will not vary according to floristic community as this species is found in natural grasslands as well as secondary and exotic grasslands, suggesting some flexibility in habitat choice (Dorrough and Ash, 1999, O'Shea, 2005). Fourth; does the size of grassland patches influence occupancy by *D. impar*? We hypothesized that the size of grassland patches will not have a negative effect on occurrence of *D. impar*, as small reptiles are less susceptible to the negative effects of habitat fragmentation compared to similar sized endotherms (Case, 1975, Schutz and Driscoll, 2008) and *D. impar* are known to persist in small (< 10 ha) isolated grasslands (Candy, 2008).

The results of our study provide much needed information on the habitat preferences of a grasslands specialist reptile, *D. impar*. Based on this information we provide recommendations for managing grazing pressure to improve the quality of habitat for this species. This result also has implications for the conservation of biota worldwide, where natural grazing patterns have been altered by anthropogenic change.

Methods

Study area

Our study was conducted within natural grasslands in the Australian Capital Territory (ACT, Fig. 1). Prior to European settlement, up to 20,000 ha of the ACT may have supported natural temperate grassland (ACT Government, 2005) but 95% of this habitat has been cleared or degraded. The remaining 5% occurs in small fragmented patches embedded in a urban and agricultural matrix (ACT Government, 2005). Remnant grasslands are largely dominated by native grasses (e.g. *Austrostipa spp., Bothriochloa macra, Rytidosperma spp., Themeda triandra)* and exotic perennial grasses (e.g. *Phalaris aquatica),* with a smaller component of exotic annual grass species (e.g. *Avena fatua*).

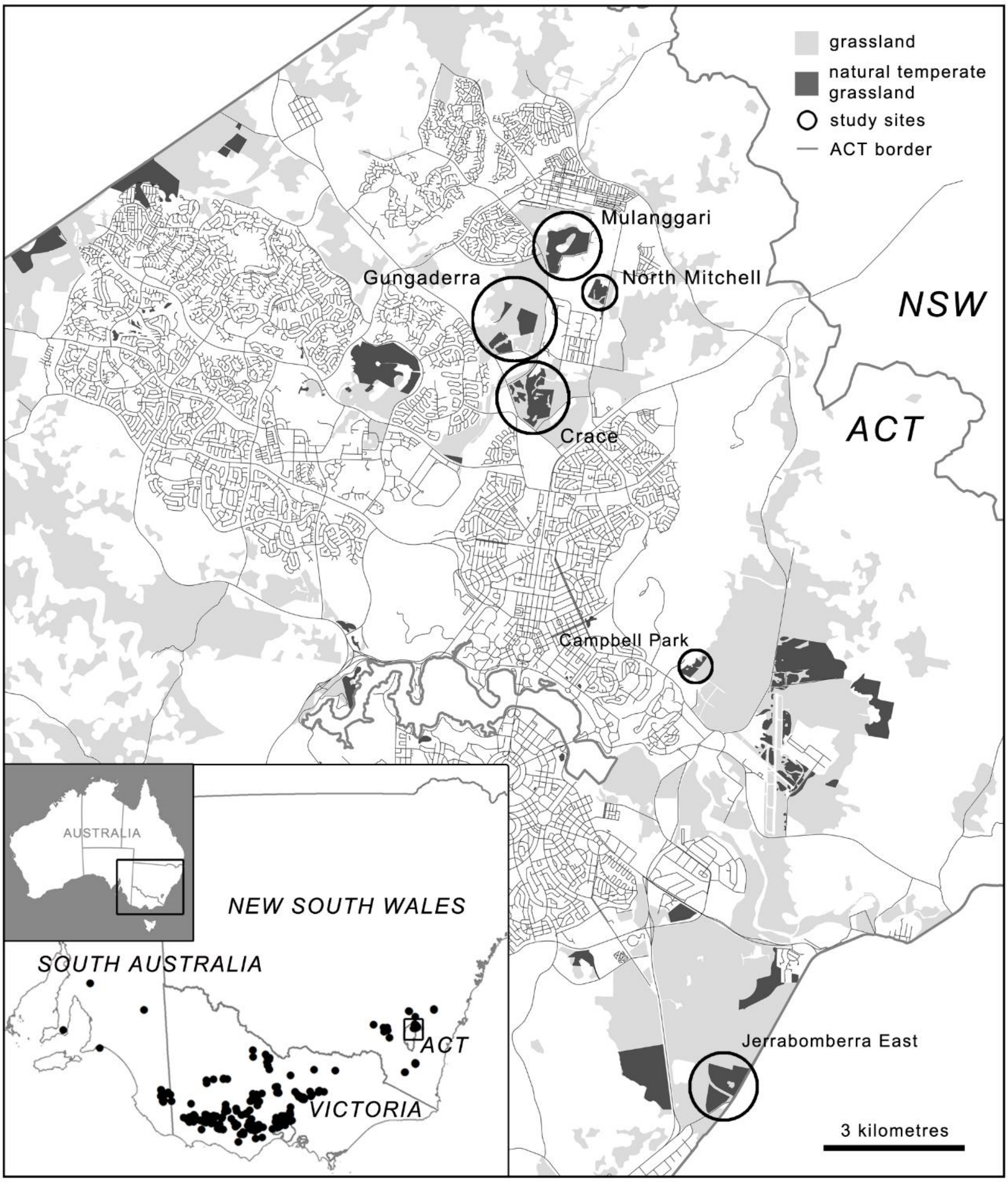

Figure 1: Current distribution of the striped legless lizard in south-eastern Australia (inset). Distribution of natural grasslands (grey), natural temperate grasslands (dark grey), and the location of our study sites (black circle) in the Australian Capital Territory. Adapted from Dorrough and Ash (1999).

Site selection

Data were collected by the ACT Government Environment and Planning Directorate for an investigation of kangaroo grazing impacts on native plants and animals, adapted from Howland et al. (2014). From this dataset, we used data from six grassland reserves (three nature reserves and three informally protected areas) where *D. impar* had been recorded (Fig. 1). Reserves varied in size and quality (Appendix S1), and were historically subject to grazing by domestic livestock (at the time of surveys, the most recent livestock grazing had occurred over five years previously). The dominant grazer in the study area is the native eastern grey kangaroo (hereafter: kangaroo). Exotic herbivores also occur in the study area, but their impact as grazers is negligible in comparison to kangaroos (Fletcher, 2006, ACT Government, 2010).

Experimental design

We investigated habitat preferences at multiple spatial scales simultaneously using a hierarchical experimental design (Meentemeyer and Box, 1987). Within the six reserves, between two and six 1 ha plots (100 x 100 m; Fig. 2a) were placed within different grassland communities (i.e. natural temperate grassland, native pasture, exotic pasture) based on mapping (see ACT Government, 2005), with a greater number of plots placed at larger properties. In 2012, 23 plots were used, with 18 of these and three new plots used in 2013. Concrete roof tiles are a cost effective, unbiased and efficient method to survey for *D. impar* (Thompson, 2006), so at each plot, 30 tiles were deployed. Tiles were arranged in either a 3 x 10, or 6 x 5 grid pattern, with tiles spaced ≥10 m apart (Fig. 2b). As *D. impar* has a very small home range (Robertson and Smith, 2010) and moves on average as little as 4 m/yr (O'Shea, 2005) , we considered tiles independent.

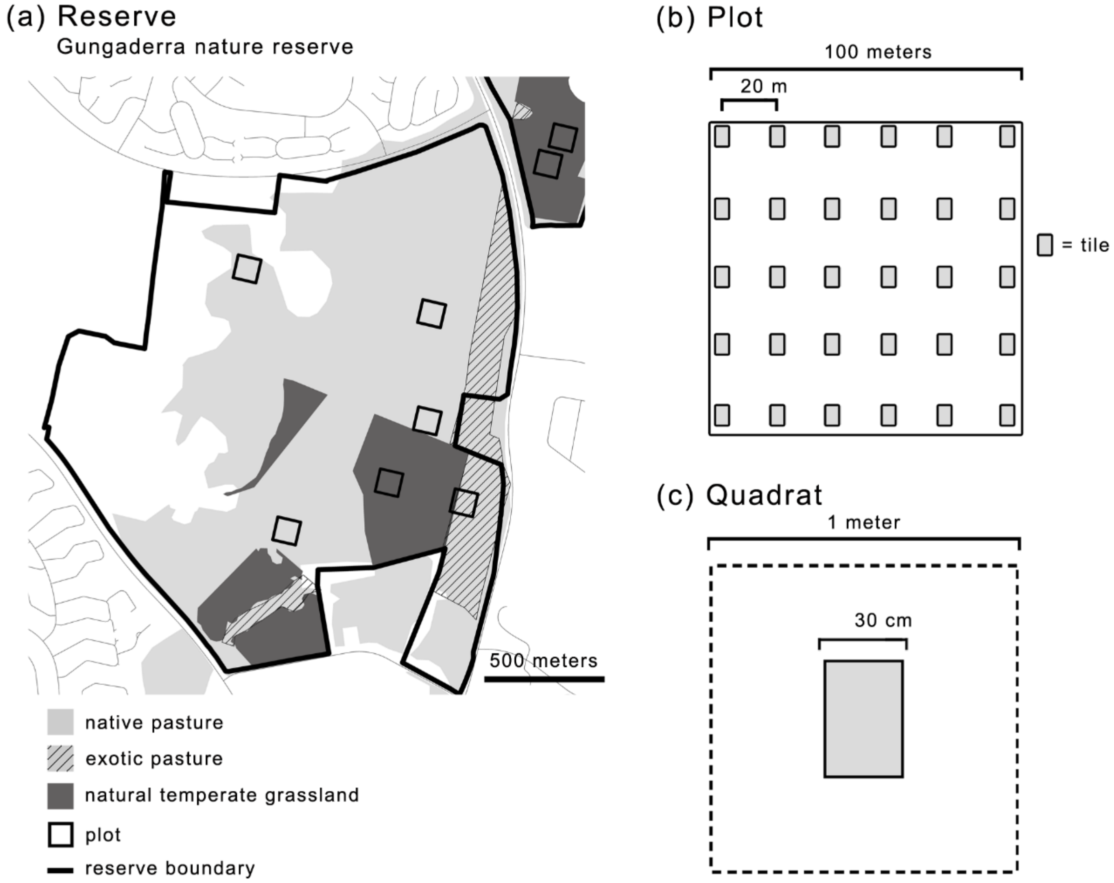

Figure 2: Experimental design. (a) an example of placement of plots within a reserve showing natural temperate grassland (dark grey), native pasture (light grey) and exotic pasture (cross hatch) grassland communities, (b) layout of tiles (box) within the plot at intermediate scale and (c) survey quadrat at the fine scale.

Reptile surveys

Surveys for *D. impar* were conducted between September and December in 2012 and 2013, with tiles deployed before spring sampling. This allowed sufficient time for reptiles to become accustomed to the tiles. At the end of the sampling period, tiles were removed to limit the impact on vegetation, so tiles were not placed in the same location in consecutive years. To improve detection, tiles were checked during daylight hours on fine days, and at temperatures between 15 to 25°C (Thompson, 2006). Overall, each tile was checked five times in 2012, and seven times in 2013. We pooled survey results from all visits to estimate presence/absence at each tile over each survey period. All field work procedures were approved by the NSW Government Department of Primary Industries ethics committee (Approved project No. 13/1641#2).

Habitat characteristics

Habitat characteristics were estimated at three spatial scales (fine, intermediate, landscape). At the fine scale, we placed a 1 m^2 survey quadrat around each tile (Fig. 2c) to measure: (1) grass structural complexity, (2) non-grass biomass (kg dry matter/ha), (3) percent bare ground, and (4) grass type. We calculated grass structural complexity following Brown et al. (2011) (ln (variance in grass height x average grass height)), where average grass leaf height was estimated using a ruler at each quadrat corner . Non-grass biomass was estimated using the 'comparative yield' technique (Haydock and Shaw, 1975) and percent bare ground was estimated visually. To assign grass type, we classified a quadrat according to whether it was dominated by native or exotic grass species.

At the intermediate scale (1 ha), we assigned plots to one of three grassland community classifications based on previous spatial mapping: natural temperate grassland (high cover of native grasses, high native forb richness), native pasture (high cover of native grasses, low native forb richness), exotic pasture (low cover of native grasses, low native forb richness) (ACT Government, 2005). Where the grassland community had clearly changed since original mapping in 2005, we reclassified plots using the same classification.

At the landscape scale, estimates of kangaroo density were made using total count of individuals and pellet count techniques (Southwell, 1989) in 2013 with a count at a single reserve done in early 2014. Density estimates for a single reserve (North Mitchell) were excluded because grazing was suppressed there for several years and hence current grazer density is not representative of grazing effects on vegetation. To assess grazing intensity, we used kangaroo density rather than a direct measure of grass structure. This was because management of grazing pressure is often undertaken based on animal densities and not grass structure at this scale (see ACT Government, 2010). We used an ACT vegetation structure map (see Howland et al., 2014) and management boundaries to estimate grassland area within a reserve in ArcGIS 10x (ESRI, 2011). Details of explanatory variables are provided in Table 1.

Table 1: Description and summary of explanatory variables which were collected at three spatial scales (fine, medium and landscape).

Scale	Variable	Description	Range (mean)	n
Fine	Grass structural complexity	Measure of complexity: Ln (mean height x variance in height)	-2.14 – 9.13 (2.77)	1320
	Non-grass biomass (kg dry matter/ha)	The weight of above ground non grass biomass.	0 – 4978 (253)	1320
	Percent bare ground (%)	Visual estimate of the exposed bare earth.	0 – 80 (20)	1320
	Grass type	Grass type within each quadrant based on origin (native or exotic).	native grass	944
			exotic grass	375
Intermediate	Grass community	Classification of pasture communities based on floristic composition.	natural temperate	24
			exotic pasture	9
			native pasture	11
Landscape	Grassland area (ha)	The area of grassland vegetation within reserve boundary.	12.1 – 237.3 (91.4)	6

Kangaroo density (animals/ha)	The density of kangaroos within reserve boundary based on pellet count and total count techniques.	1.34 – 5.23 (2.67)	5

Data analysis

Prior to analysis, we checked explanatory variables for multicollinearity (Spearman rank coefficient > 0.5), transformed skewed variables, and standardized all continuous variables to enable meaningful comparison between multiple variables (Zuur et al., 2009b). Next, we used logistic hierarchical generalized linear mixed modeling (HGLMM) (Lee and Nelder, 1996) procedures to simultaneously model the probability of occupancy (presence/absence) of *D. impar* in response to seven habitat variables (grass structural complexity, non-grass biomass, percent bare ground, grass type, grassland community, kangaroo density and grassland area) measured over three scales. We included all variables as additive effects plus an interaction between grass structural complexity and grass type. We included the interaction to test whether preference for grass structural complexity was influenced by the type of grass present. To account for our nested study design and sampling over consecutive years, we included reserve, plot and year as random effects (Lee and Nelder, 1996). Nesting structure was stipulated as reserve/plot/year. We modeled the relationship with a binomial distribution and a logit link function, with random effects fitted with a beta distribution and a logit link function. Residual plots and distribution of residuals were examined to check model fit. All analysis was undertaken in Genstat 12 (VSN International, 2012a).

Results

We recorded *D. impar* a total of 179 times across all six reserves and at 20/23 plots and under 139 individual tiles. The probability of recording an individual under a tile varied between the survey years, with *D. impar* recorded under 13% of tiles in 2012, compared to 8% of tiles in 2013. No individuals were recorded at the four plots at Jerrabomberra East in 2012, but they were recorded at one plot in 2013. The highest number of tiles occupied by *D. impar* occurred in 2013 at North Mitchell with 30% of tiles occupied during the sampling period (Appendix S2).

Regression model

The logistic regression model showed that *D. impar* occupancy of tiles was significantly related to variables at landscape and fine scales, but not on the intermediate scale (Table 2).

Table 2: Results of Hierarchical Generalized Linear Mixed Models (HGLMM) for the striped legless lizard showing trends (Slope) including standard error (S.E). Exotic pasture and exotic grass have been used as a reference level for grassland community and grass type respectively. Significance is indicated by the Wald statistic ($\chi 2$) and p-value as follows: *p<0.05, ** p<0.01, ***p<0.001.

Scale	Model term	d.f.	$\chi 2$	Slope	S.E.	Graphical summary
	Intercept			-2.02	0.35	
Landscape	Kangaroo density	1	16.93***	-1.13	0.27	Fig. 3a
	Grassland area	1	2.77	-0.34	0.20	
Intermediate	Grass community	2	1.47			
	Native pasture			-0.03	0.43	
	Natural temperate grassland			-0.33	0.36	

Fine	Grass complexity x Native grass	1	4.65*	0.35	0.16	Fig. 3b
	Grass complexity			0.06	0.13	
	Native grass			-0.56	0.20	
	Percent bare ground	1	1.29	-0.11	0.10	
	Non grass biomass	1	1.14	0.09	0.08	

Preference for low kangaroo densities

At the landscape scale, the occurrence of *D. impar* was significantly negatively related to kangaroo density ($p < 0.001$), with the encounter probability declining from 18.7% at the lowest kangaroo densities (i.e. 1.3 kangaroo/ha) to 1% at the highest kangaroo densities (i.e. 5.2 kangaroos/ha) (Fig. 3a).

Preference for high grass structural complexity and floristic community

The probability of encountering *D. impar* under a tile at fine scale was positively related to grass structural complexity with a significant interaction with grass type ($p = 0.031$). Occupancy was lower for native than exotic grass, but grass structural complexity had a greater effect on native grass than exotic grass types. For example, as grass structural complexity increased from lowest to highest values, encounter rate for exotic grass types increased from 9.1% to 12%. At tiles placed in native grass types, as grass structural complexity increased from lowest to highest values, encounter rate increased from 2.4% to 15%. Thus, exotic grasses were preferred by *D. impar* when grass structural complexity was low, and native grasses were favored when grass structural complexity was high (Fig. 3b). Other measures of fine scale structure like percent bare ground ($p = 0.26$) and non-grass biomass ($p = 0.286$), were not significantly related to the occurrence of *D. impar*. At the intermediate spatial scale, we found no significant relationship between occurrence of *D. impar* and grass community (p = 0.48).

Preference for grassland area

We found no significant relationship between probability of encountering a *D. impar* and the area of grassland (p = 0.102), despite area varying from 12 ha to> 200 ha.

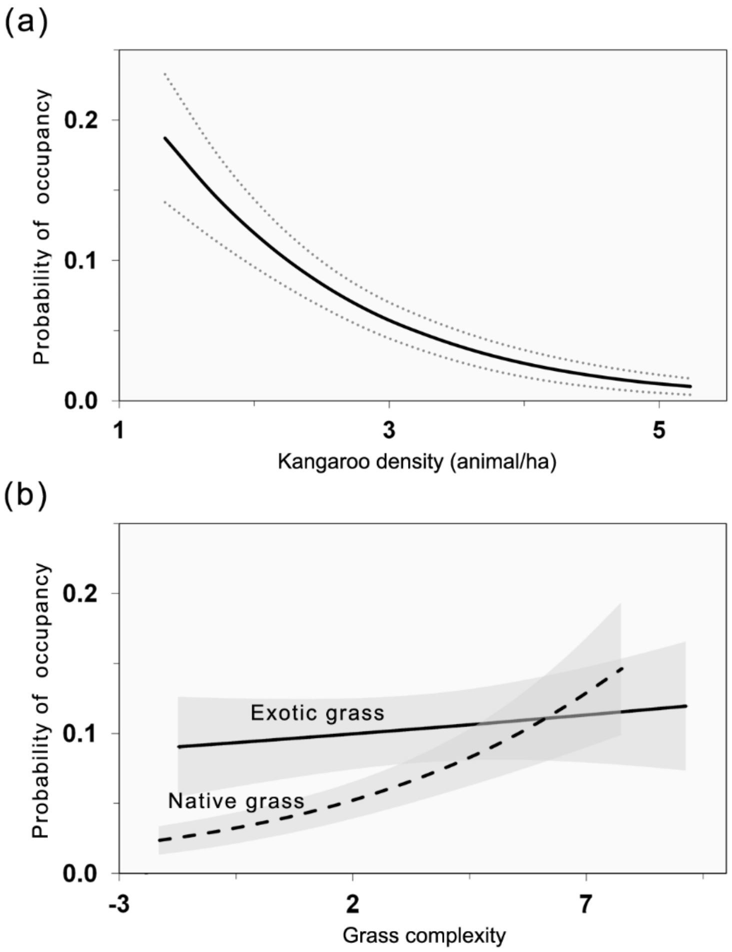

Figure 3: Graphical representation of logistic regression models summarized in Table 2. The graphs show significant relationships between the probability of encountering the striped legless lizard under a tile and (a) kangaroo density estimates at the landscape scale, and (b) grass structural complexity for two different grass types (exotic grass and native grass) at the fine scale. Standard error of the model predictions are shown. To aid interpretation of results, variables have been back-transformed to the original scale.

Discussion

Preference for low kangaroo densities

As a result of anthropogenic change, native herbivore density has either been inflated or suppressed in many areas, with cascading impacts on native biodiversity (Gordon et al., 2004, Mysterud, 2006, Foster et al., 2014). We have shown that the encounter rate of threatened *D. impar* dramatically decreased as kangaroo density increased from 1.3 animals/ha to over 5 animals/ha (Fig. 3a). While the impacts of livestock grazing on *D. impar* (Dorrough and Ash, 1999, Robertson and Smith, 2010) and other grassland biota have been documented (Dorrough et al., 2004b, Kutt and Gordon, 2012, Davies et al., 2010, Laidlaw et al., 2013, O'Connor et al., 2010), relatively few studies have considered the impact of native grazers on grassland biota. The density of large native grazers is increasing in many protected areas (Gordon et al., 2004, Mysterud, 2006, Foster et al., 2014), and our results show that irrespective of whether the grazers are native or exotic, they exert major influence on the suitability of habitat for grassland dependent species.

Preference for high grass structural complexity

The main mechanism by which large grazers affect ground-dwelling species is by altering vegetation structure. As we hypothesized at the onset of our study, the occurrence of *D. impar* was positively associated with grass structural complexity (Fig. 3b). This finding is consistent with previous research into habitat preferences of legless lizards (Brown et al., 2011, Howland et al., 2014). Small ground-dwelling reptiles such as *D. impar* may prefer complex habitats because of the diverse microhabitats they contain (McIntyre and Tongway, 2005, Pöyry et al., 2006), with flow on consequences for foraging efficiency (Pianka, 1966, Castellano and Valone, 2006, Pettigrew and Bull, 2014), thermoregulation (Scott, 1962, Hacking et al., 2014, Sato et al., 2014b, Willott, 1997), predation risk (Sato et al., 2014b, Castellano and Valone, 2006, Pettigrew and

Bull, 2012) and prey abundance (Dennis et al., 1998, Castellano and Valone, 2006). More broadly, grass structural complexity has been identified as an important driver of habitat selection for a range of taxa (Vickery et al., 2001a, Castellano and Valone, 2006, McNett and Rypstra, 2000, Whittingham et al., 2006). Unlike intense grazing, low to moderate grazing intensity can increase grass structural complexity (Rook et al., 2004, McIntyre and Tongway, 2005) and is considered necessary to maintain animal and plant species richness in many grassland ecosystems (Milchunas et al., 1988, Dorrough et al., 2004c, Kruess and Tscharntke, 2002, Fuhlendorf et al., 2006). Our results support this view because *D. impar* was most likely to occupy habitat with fine scale grass complexity.

Preference for floristic composition

D. impar has most commonly been encountered in natural temperate grasslands dominated by native grasses (Coulson, 1990). This may be an artifact of limited disturbance in these communities, rather than a particular preference for native grasses, because *D. impar* can persist in floristically degraded grasslands (Dorrough and Ash, 1999, Thompson, 2006, O'Shea, 2005). Our results confirm this tolerance for degraded native and exotic grass communities at the intermediate scale. At a fine scale, *D. impar* was more common near exotic grasses at low grass structural complexity, but more common near native grasses when grass structural complexity was high (Fig. 3b). This may be explained by the dense leafy structure formed by several common exotic grasses compared to native grasses (Lamp et al., 2001). This characteristic of exotic grasses may provide additional cover when grass structural complexity is low, but at high complexity, may impede movement and reduce solar radiation compared to native grasses. Exotic grasses are often regarded as providing poor quality habitat for reptiles (Wong et al., 2011, Michael et al., 2010, Hacking et al., 2014, Germano et al., 2001) but this was not the case in our study. This result adds to a growing body of evidence that local grassland fauna (Gilmore et al., 2008, Stevens et al., 2010) and fauna elsewhere around the world (Tews et al., 2004, Garden et al., 2007) can persist in floristically degraded habitat, provided appropriate vegetation structure is available.

Preference for grassland area

Natural grassland communities across the globe have been highly fragmented by human activities (Herkert, 1994, Kirkpatrick et al., 1995, Rösch et al., 2013), with the area of fragments known to be a major factor influencing the survival of many bird and mammal species (Andren, 1994). However, this does not appear to be the case for *D. impar* in this study (also see Candy, 2008), nor other small-bodied species (Abensperg-Traun et al., 1996, Schutz and Driscoll, 2008, Case, 1975, Wood and Pullin, 2002). Small patches of grassland are often not prioritized for conservation, but are valuable habitat for *D. impar* and other threatened grassland species (ACT Government, 2005). Protection and management of small habitat patches will increasingly become important for the conservation of grassland biota as grasslands continue to be reduced and fragmented by anthropogenic change (Wood and Pullin, 2002, Tscharntke et al., 2002, Schutz and Driscoll, 2008, Case, 1975, ACT Government, 2005, Jellinek et al., 2014).

Conservation implications

For species at risk of extinction, detailed research on habitat requirements is fundamental to developing management strategies to prevent or reverse population decline (Lindenmayer and Burgman, 2005, Morrison et al., 2006). Based on our findings, we recommend that conservation efforts for many reptile species in Australian natural temperate grassland extend beyond the large patches of high quality habitat to also encompass smaller patches of floristically degraded habitat. We also suggest that to promote the conservation of *D. impar*, management should aim to minimize high intensity grazing by kangaroos (equivalent to > 1.3 kangaroos/ha), prevent the loss of native grasses, and ensure that sufficient grass structural complexity is maintained at the fine scale. Structural complexity is often achieved by grazing at low to moderate intensity (Rook et al., 2004, McIntyre and Tongway, 2005) and this level of grazing is known to benefit biodiversity across a range of ecosystems (e.g. Fuhlendorf and Engle, 2004, Dorrough et al., 2004b, Milchunas et al., 1988).

A common consequence of anthropogenic change in grasslands is either an increase or decrease in the number of native grazers relative to historic levels (Gordon et al., 2004, Caugley, 1987). Given that management of grasslands is a global conservation challenge (Watkinson and Ormerod, 2001, Kemp and Michalk, 2007), there is an urgent need to actively manage the impact of large grazers, irrespective of whether they are native or exotic to the particular area (Foster et al., 2014, Gordon et al., 2004, Gordon, 2006). Failure to do so has already led to global loss of grassland biota, and without ongoing active management, this trend is likely to continue (e.g. Vavra et al., 2007, Ceballos et al., 2010, Dorrough et al., 2004c, Kemp and Michalk, 2007, Mysterud, 2006, Stevens et al., 2010). Because population control of native herbivores is often controversial (Herbert et al., 2006, Young et al., 2009), conservation actions need to be based on robust scientific evidence such as we have provided here, to ensure societal support and to maximize the conservation benefits (Gordon et al., 2004, ACT Government, 2010). Our results demonstrate that management intervention is necessary to minimize biodiversity loss in grasslands where native grazer densities are either elevated or suppressed by anthropogenic change.

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Supplementary material

Appendix S1: Characteristics of reserves **(**listed in alphabetical order). “Grassland communities” lists the different grassland communities found across the property.

Reserve	Protection status	Area - Property	Area - grassland	Grassland communities present
Campbell Park	Informal protected area	25.4	12.1	Natural temperate grassland
Crace Grassland Nature Reserve	Nature reserve	104.6	97.4	Natural temperate grassland, native pasture
Gungaderra Grassland Nature Reserve	Nature reserve	315	237.3	Natural temperate grassland, native pasture, exotic pasture
Jerrabomberra Grassland Nature Reserve East	Informal protected area	99.1	99.1	Natural temperate grassland, native pasture, exotic pasture
Mulanggari Grassland Nature Reserve	Nature reserve	140.4	86.2	Natural temperate grassland, native pasture
North Mitchell	Informal protected area	19.5	16.1	Natural temperate grassland, exotic pasture

Appendix S2: Details of the striped legless lizard captures at each reserve (listed in alphabetical order). Multiple records under the same tile counted as 1.

	2012			2013		
Property	Number of sites	Number of tiles	Number of tiles occupied by the striped legless lizards (%)	Number of sites	Number of tiles	Number of tiles occupied by the striped legless lizards (%)
Campbell Park	-	-		3	90	3 (3)
Crace grasslands nature reserve	6	180	29 (16)	3	90	8 (9)
Gungaderra Grasslands nature reserve	6	180	22 (12)	6	180	6 (3)
Jerrabomberra East grassland	4	120	0 (0)	4	120	2 (2)
Mulanggari Grasslands nature reserve	5	150	28 (19)	3	90	11 (12)
North Mitchell	2	60	12 (20)	2	60	18 (30)
Total	23	690	91 (13)	21	630	48 (8)

PAPER IV: Fear and hunger: drivers of kangaroo foraging patterns in an anthropogenically disturbed environment

A dingo (Canis lupus dingo) at Fraser Island -where it still persists at high numbers. (Photo: Don Fletcher)

Howland, B., Stojanovic, D., Gordon, I. J., Stirenmann, I., Manning, A. D., and Lindenmayer, B. D. (2016). Fear and hunger: drivers of kangaroo foraging patterns in an anthropogenically disturbed environment. *Austral Ecology*. In review

Abstract

Habitat selection by large herbivores has a strong influence over vegetation communities, with herbivores selecting foraging habitat often as a compromise between food quantity and quality versus fear of predation. Anthropogenic change, such as loss of native predators, may then alter natural foraging patterns potentially leading to adverse changes in vegetation cover and structure. We investigated the role of food and fear in anthropogenically disturbed habitats in driving foraging patterns of the eastern grey kangaroo in south-eastern Australia. We collected foraging intensity data (rate of pellet accumulation) across 31 plots at five reserves and determined whether the spatial pattern of kangaroo foraging was predicted by: 1) food; 2) fear; or 3) a trade-off between food and fear. In all plots, we measured food quality using a lawn index and two aspects of fear (vegetation cover and distance to roads). Using an information theoretic approach, we identified which variables best described the observed pattern of kangaroo grazing. We found that in disturbed landscapes, the eastern grey kangaroo foraged in areas of short grass away from roads. Our data suggest that herbivores can perceive novel sources of fear, like roads, to a sufficient extent to influence their habitat use. This foraging pattern may increase variation in grass structure, and create refugia from grazing in habitats near roads, but may lead to overgrazing of already grazed areas. We found no evidence for fear of predation by foxes creating foraging refugia in areas without vegetation cover. Intervention may be needed to change kangaroo habitat selection in a ways that mimics natural foraging patterns to promote optimal vegetation structures for the conservation of native biodiversity.

Introduction

Where large herbivores choose to forage can influence the structure, composition and function of vegetation communities (Gordon et al., 2004, Mysterud, 2006, Lezama et al., 2014). These choices are often a compromise between maximizing energy intake and minimizing the potential costs associated with foraging, such as predation risk (Lima and Dill, 1990). Predators can play an important role in habitat selection by their prey, through lethal means (where animals are selectively removed from certain areas), and non-lethally, where herbivores preferentially utilize areas with lower risk of predation (Peacor and Werner, 2000, Ripple and Beschta, 2004, Lima, 1998, McArthur et al., 2014). The influence of predators on altering herbivore foraging patterns is considered important in structuring vegetation communities and maintaining species richness in many habitats (Schmitz, 2003, Peacor and Werner, 2000, Ripple and Beschta, 2004).

Identifying the processes that underpin foraging behavior in herbivores is an important step in managing herbivory in degraded habitats. In habitats that have undergone major anthropogenic change, processes which affect foraging patterns can be altered, with flow-on effects for many species (Berger et al., 2001, Duffy, 2003, Massé and Côté, 2009, Pople et al., 2000). For instance, following the eradication of the gray wolf (*Canis lupus)* in Yellowstone National Park, the intensity of elk (*Cervus elaphus*) foraging increased in areas previously avoided because of a high predation risk leading to a decrease in aspen trees and a trophic cascade (Ripple and Beschta, 2012, Eisenberg et al., 2014). Likewise, there are important implications for human wildlife conflict when foraging patterns of large herbivores become altered, as habitat selection is important in predicting and managing problems like wildlife on roads, competition with domestic herbivores and depredation of crops (Sitati and Walpole, 2006, Lehnert and Bissonette, 1997, Viggers and Hearn, 2005a, Bonnot et al., 2013).

We aimed to assess whether food, fear or a trade-off between both food and fear could explain foraging habitat selection by herbivores in a modified landscape. We used an index of foraging intensity (i.e. pellet counts) of the eastern grey kangaroo (*Macropus giganteus*) in urban reserves to investigate effects of anthropogenic change on foraging patterns. The eastern grey kangaroo (hereafter: kangaroo) is a medium-sized (40–80 kg), crepuscular, marsupial grazer found throughout south-eastern Australia (Grigg et al., 1989, Taylor, 1983). The only remaining native predator of the kangaroo is the dingo (*Canis lupus dingo*), however persecution by pastoralists has extirpated the dingo from most of south-eastern Australia (Pople et al., 2000). In contrast, the red fox (*Vulpes vulpes*), an introduced mesopredator (5–6 kg), is common throughout the region and preys on juvenile kangaroos (Banks, 2001). South-eastern Australia also has undergone significant anthropogenic change; many habitats are cleared and/or fragmented, with roads being an important source of kangaroo mortality (Fletcher, 2006, Ramp and Roger, 2008).

The loss of the dingo, provision of permanent watering points, and barriers to movement are factors considered to have led to increased kangaroo numbers and altered foraging activity (Grigg et al., 1989, ACT Government, 2010), with increased kangaroo numbers linked to negative impacts on biodiversity (Barton et al., 2011, Howland et al., 2014, McIntyre et al., 2015, Howland et al., 2016a, Howland et al., 2016b). However, there is still only a limited understanding about the role altered foraging patterns may have on native biodiversity, and how to address altered foraging patterns through management interventions.

Previous studies have found that the intensity of kangaroo foraging is related to the quality of grass resources (Maguire et al., 2006, Ramp and Coulson, 2002, Ramp and Coulson, 2004). However, these studies did not specifically consider predation risk, although they acknowledge this also may influenced foraging patterns (e.g. Maguire et al., 2006). Conversely, other workers (Banks, 2001, Caughley, 1964, Frith, 1973) have emphasized the role of predation risk (both of dingoes and foxes) on forage selection by kangaroos. This was because kangaroo distribution in those studies was found to be related to cover, with risk of predation considered to be less in areas with high cover. The only study to consider both food and fear in determining kangaroo foraging patterns (Hill, 1981), found that kangaroos selected foraging habitat based on both availability of food and vegetation cover (surrogate for reduced predation risk). To our collective knowledge, no study to date has considered the role of novel sources of mortality, such as roads, in shaping patterns of kangaroo foraging. Yet, motor vehicles travelling on roads inflict a high rate of mortality on urban kangaroos (Fletcher, 2006), with roads associated with avoidance behaviors by large herbivores elsewhere (Fahrig and Rytwinski, 2009).

Kangaroos are typical of many large herbivores living in modified landscapes in that their populations are simultaneously exposed to the combined effects of fluctuations in food (driven by rainfall and season), predation risk and anthropogenic change (Smuts, 1978, Bjørneraas et al., 2011, Fletcher, 2006, Dussault et al., 2012). Interpreting foraging behavior relative to any one of these factors in isolation of the others may be misleading (Smuts, 1978, Bjørneraas et al., 2011, Fletcher, 2006, Dussault et al., 2012). We considered the role of food and fear in explaining observed kangaroo foraging patterns across multiple study sites. We tested seven possible hypotheses to explain the distribution of kangaroo foraging intensity: 1) food quality; 2) vegetation cover; 3) distance to roads; 4) vegetation cover and distance to roads; 5) trade-off between food quality and vegetation cover; 6) trade-off between food quality and distance to roads; and 7) trade-off between food quality, vegetation cover and distance to roads. We represented each of these hypotheses with candidate models (Table 1). The relative strength of each model in explaining the observed foraging patterns was used to provide inferences on the mechanisms driving kangaroo foraging patterns in this study system.

The results of this investigation will provide important insights into the drivers of kangaroo foraging patterns in anthropogenically disturbance habitats, but also in other habitats where new and novel sources of mortality may be driving foraging patterns in unexpected ways.

Table 1. Predictions of expected outcomes in response to three drivers of kangaroo foraging patterns: 1) food driven, 2) fear driven, and 3) food and fear driven. We represented each of these drivers by one or more hypothesis.

Possible driver	Hypothesis	Candidate model	Predicted response
Food	Kangaroo foraging is affected by food quality	Food quality (F)	Kangaroo foraging intensity positively

			correlated with quality of food
Fear	Kangaroo foraging is affected by vegetation cover	Cover (C)	Kangaroo foraging intensity positively correlated with vegetation cover
	Kangaroo foraging is affected by intermediate vegetation cover	Cover (C^2)	Kangaroo foraging intensity positively correlated with intermediate vegetation cover
	Kangaroo foraging is affected by distance to roads.	Roads (D)	Kangaroo foraging intensity is negatively correlated with distance to road
	Kangaroo foraging is affected by both vegetation cover and distance to roads.	Cover (C) + Roads (D)	Kangaroo foraging intensity is positively correlated with vegetation cover and negatively correlated with distance to road.
	Kangaroo foraging is affected by both intermediate vegetation cover and distance to roads.	Cover (C^2) + Roads (D)	Kangaroo foraging intensity is positively correlated with intermediate vegetation cover and negatively correlated with distance to road.
Food and Fear	Kangaroo foraging is a trade-off between food quality and vegetation cover.	Food (F) + Cover (C)	Kangaroo foraging intensity is positively correlated with food and vegetation cover.
	Kangaroo foraging is a trade-off between food quality and intermediate vegetation cover.	Food (F) + Cover (C^2)	Kangaroo foraging intensity is positively correlated with food and intermediate vegetation cover.
	Kangaroo foraging is a trade-off between food quality and distance to roads.	Food (F) + Roads (D)	Kangaroo foraging intensity is positively correlated with food and negatively correlated with distance to road.
	Kangaroo foraging is a trade-off between food	Food (F) + Cover (C) + Roads (D)	Kangaroo foraging intensity is positively correlated with food and vegetation cover

	quality, vegetation cover and distance to roads.		and negatively correlated with distance to road.
	Kangaroo foraging is a trade-off between food quality, intermediate vegetation cover and distance to roads.	Food (F) + Cover (C^2) + Roads (D)	Kangaroo foraging intensity is positively correlated with intermediate food and vegetation cover and negatively correlated with distance to road.

Material and methods

Study location

Our study was undertaken within the Australian Capital Territory (ACT), Australia (Fig. 1a). Our survey area is covered by temperate grassland and grassy *Eucalyptus* woodland communities. These habitat types are critically endangered *(e.g. Environmental Protection and Biodiversity Conservation Act 1994; Department of the Environment and Heritage, 2014b)*. Modification of the grazing regimes in which these ecosystems evolved is considered a major factor in historic and ongoing decline of these two ecological communities (Prober et al., 2005). We selected five study areas within the ACT to conduct our research. These five sites satisfied five criteria: 1) the eastern grey kangaroo were the dominant grazers; 2) there was a mix of habitat types; 3) kangaroo density was moderate (1.05 to 2.36 kangaroos per hectare; Appendix S1) to allow some level of selectivity in the forage matter consumed to occur; 4) tree and shrub cover was not uniformly distributed across the study area; 5) at least one major road (speed limit: 60-80 km/hr) adjoined the study area and; 6) all reserves were within 2 km of moderate to high-density housing. These criteria enabled us to model kangaroo foraging habitat selection among urban reserves that varied in food quality, vegetation cover and distance to roads.

Our study region has a temperate cool-season wet climatic pattern, rainfall evenly distributed throughout the year (Hobbs and McIntyre, 2005). The ACT experienced below average annual rainfall for the majority of the decade preceding this study (Australian Government Bureau of Meteorology, 2014). However, during collection of foraging data in spring 2009, average to above average rainfall was recorded for the region (Australian Government Bureau of Meteorology, 2014). Consequently, water was not considered to be limited, with access to permanent water (e.g. dams) not found to be an important factor in the distribution of kangaroo foraging patterns in non-drought conditions in two previous studies on this subject (Montague-Drake and Croft 2004, Newsome, 1965). For this investigation, we assumed all our study areas supported foxes because they are widely distributed and abundant throughout south-eastern Australia (Menkhorst and Knight, 2010), and were commonly seen in reserves during this study. Fire, an important disturbance regime in the evolution of grassy ecosystems (Lunt and Morgan, 2002), is now largely suppressed across this region (ACT Government, 2004), with no burns occurring during, and for several years prior to this study. Kangaroo populations were not culled during, or for at least three years before, the study.

Sampling Design

To ensure we sampled from a range of cover types, we stratified our five study areas on the basis of tree canopy cover: 1) grassland (<2% canopy cover); 2) open woodland (3-20%); 3) woodland (21-50%); 4) open forest (51-80%); and 5) forest (81-100%), using a canopy cover map developed for the ACT region (Howland et al., 2014). Within each study area, we established between five and seven 1.8 ha randomly selected sampling plots across the tree canopy classes, with more plots in larger sites (Fig. 1b). Overall, 31 plots were established, with seven plots in grassland, 14 in open woodland, and 10 in woodland.

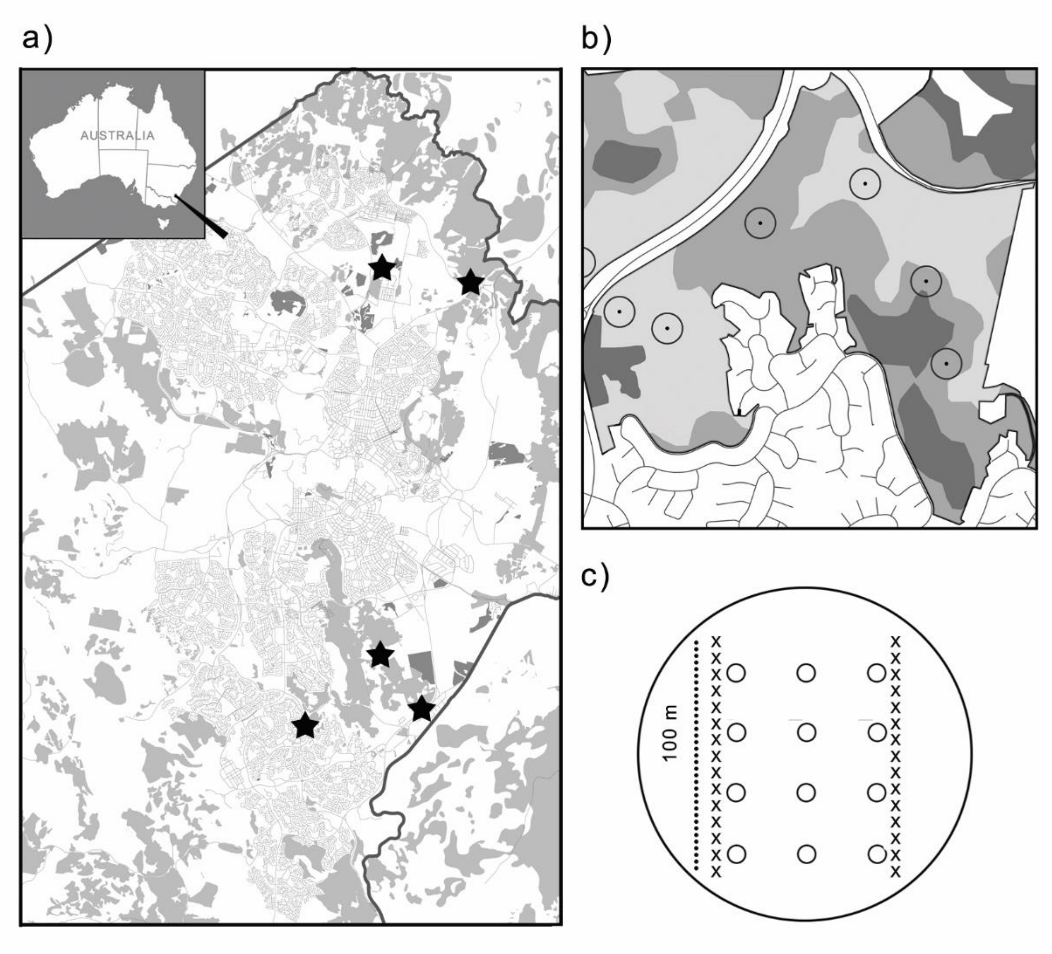

Figure. 1: a) The location of the five study sites (black star) across the Australian Capital Territory, with box-gum grassy woodlands and temperate grasslands (grey shading), roads in the ACT (grey lines), and ACT border (black lines). b) an example of stratified random placement of study plots within a study site showing open woodland (light grey), woodland (grey) and open forest (dark grey) canopy types, and c) the layout of 30 pellet count quadrats (x) and 12 vegetation quadrats (circles) within each study plot.

Foraging intensity

We used pellet accumulation as an index of kangaroo foraging intensity (Maguire et al., 2006, Banks, 2001, Ramp and Coulson, 2004, Ramp and Coulson, 2002), because kangaroos defecate more while feeding (Johnson et al., 1987). In each plot, we estimated the rate of pellet accumulation by clearing pellets from 30 3.125 m^2 quadrats that were placed evenly along two parallel 100 m transects, with transects spaced 80m apart (Fig. 1c). Sampling was undertaken at the beginning of spring (September/October), when grass is actively growing (Hutchinson et al., 2005), and when the energy requirements of kangaroos is greatest (Fletcher, 2007, Tyndale-Biscoe, 2005). We revisited quadrats three to four weeks after initial pellet removal to count the number of new pellets. We divided the number of new pellets encountered by the time since quadrats were cleared to calculate the rate of pellet accumulation for each plot (pellets ha^{-1} day^{-1}). A previous investigation suggested that the loss of pellets through decay was minimal over this short time span (Howland, 2008). We converted pellet accumulation rates at each plot to a proportional measure (i.e. pellet accumulation rate per plot / total pellet accumulation for site) to enable meaningful comparisons between sites with differing kangaroo density. This conversion was important as pellet accumulation rates varied largely between plots (see Table 2) and would have skewed results toward reserves of higher kangaroo density.

Forage quality

Large herbivores select habitats based on the quantity and quality of food (Alm et al., 2002, Van Beest et al., 2010), with grass lawns more attractive to herbivores than scattered tall tussocks, because short grasses are of higher nutritional value (Ramp and Coulson, 2004, Stephens and Krebs, 1986, Cingolani et al., 2005, McIntyre, 2005). To account for this structure-quality relationship, we calculated a lawn index: percent grass cover/grass height, with grass measurements made in 12, 0.25 m^2 quadrats spaced evenly along three 100 m transects within each plot (Fig. 1c). We estimated grass height as the average height of grass leaf in each quadrat, with grass percent cover calculated by analysing vertical photographs taken of each quadrat in the software package SamplePoint (Booth et al., 2006). We measured vegetation variables in summer 2009/2010.

Fear

We used vegetation cover as a surrogate for predation risk because kangaroos forage closer to cover when they fear predators (Banks, 2001, Caughley, 1964, Frith, 1973). We calculated an index of vegetation cover by summing the DBH (diameter breast height) estimate of all shrub and trees greater than 1 m in height recorded within the plot boundary.

The distance from the centre of each plot to the nearest major road, was calculated using the NEAR function in ArcGIS (ESRI, 2011) from digitized maps of ACT roads.

Statistical Analysis

The response variable in our analysis was the kangaroo foraging intensity for each plot (i.e. pellet accumulation rate per plot / total pellet accumulation for site). We considered four explanatory variables: lawn index, vegetation cover, distance to roads and reserve (Table 2).

Table 2. Details of study sites and the range (mean) of values of each of the three explanatory variables used in the analysis.

Study site	No of plots	Area (ha)	Forage intensity (pellets ha^{-1} day^{-1}).)	Lawn index	Vegetation cover	Distance to roads (m)
Callum Brae	6	142.6	70.73-1145.03 (715.08)	0.03-0.06 (0.05)	232-777 (489)	306-1014 (636)
Goorooyarroo	7	551.4	493.38-1764.67 (895.25)	0.02-0.11 (0.06)	102-618 (417)	150-2431 (1356)
Jerrabomberra West	7	220.2	4.82-1702.705 (621.56)	0.03-0.06 (0.05)	0-637 (198)	185-1327 (673)
Mulanggari	6	117.1	249.11-981.45 (474.48)	0.04-0.07 (0.06)	0-134 (52)	88-498 (270)
Wanniassa	5	212.2	0-1818.22 (830.89)	0.02-0.13 (0.08)	121-974 (405)	134-446 (253)

To prepare our data for analysis, we divided each explanatory variable values by the mean value of that explanatory variable for that site. We did this to account for relative differences in plots nested within sites, i.e. plots in some sites have less grass, less vegetation cover and are closer to roads on average than plots in other sites. We then pooled our data across all sites (n = 31) and standardized variables to allow meaningful comparison between the three potential explanatory variables (Zuur et al., 2009b). We assessed our explanatory variables for strong collinearity ($r > 0.5$), the presence of extreme outliers, and leverage effects in the explanatory variables using pairwise scatterplots, correlation coefficients and boxplots (Zuur et al., 2009b). We found the potential explanatory variables were not strongly collinear, contained no extreme outliers, and had no strong multi-collinearity. Therefore, all three variables could initially be included in the analysis.

We modelled the response of kangaroo foraging intensity as a function of the four potential explanatory variables, using generalised linear models (GLM) within the software package Genstat 12 (VSN International, 2012a). We used a normal error distribution with an identify link function (Zuur et al., 2009a). We used an information-theoretic approach, as recommended by Burnham and Anderson (2002), to test our hypotheses about kangaroo foraging. We tested the seven candidate models from Table 1, and we also tested a 'null model' with the single term 'reserve', to determine if the candidate models predicted any more than our study design. We evaluated the strength of each model by ranking models according to their AIC value, adjusted for small sample size (AICc, Burnham et al., 2011). We calculated the difference in the Akaike Weight for each model, and estimated the coefficient and standard error for the models within 2 delta AIC of the top model. We also calculated an adjusted R-squared value as a measure of goodness of fit of each model to observed data on kangaroo foraging intensity. The top ranked models were tested for over-dispersion by inspecting both the Pearson and deviance residuals. These tests confirmed that our models contained no dependent structure. Therefore, we did not further consider over-dispersion in the estimation of parameters.

Results

Our findings provided strong support for food and fear as the driver underpinning kangaroo foraging habitat selection. Two models predicting the probability of kangaroo foraging had strong support (i.e. within 2 delta AIC of the top ranked model; Table 3), with the food and fear model having greater support (adjusted R squared = 15.06, model weight = 0.37) then the fear model (adjusted R squared = 8.75, model weight = 0.26)(Burnham et al., 2011). The food and fear model predicted that the probability of kangaroo foraging was highest in areas with a high lawn index and in areas away from roads (Table 4). The fear ranked model predicted a similar directional response for distance to roads but did not include lawn index (Table 4).

Table 3. Outcomes of generalised linear modelling (GLM) of kangaroo foraging intensity in response to seven candidate models. The GLMs were ranked using Akaike's Information Criterion, adjusted for small sample size (AICc). Showing the model rank (Rank), associated hypothesis (Candidate model), terms included in each models (Model), degrees of freedom (d.f.), Akaike's Information Criterion (AICc), delta Akaike's Information Criterion (dAIC), the model weight (w) and the R2 value for each model. Terms in the models included lawn index [F], vegetation cover [C], vegetation cover with quadratic [C^2], distance to roads [D], and reserve [R].

Rank	Candidate model	Model	d.f.	AICc	dAIC	w	R2
1	Food and fear	F + D	3	33.31	0.00	0.43	19.03
2	Fear	D	2	35.30	1.98	0.16	9.4
3	Food and fear	F + C + D	4	35.76	2.45	0.13	16.07
4	Food	F	2	36.71	3.40	0.08	5.29
5	Fear	C + D	3	37.49	4.18	0.05	6.45
6	Food and fear	F + C^2 + D	5	37.54	4.22	0.05	15.67
7	Food and fear	F + C	3	38.25	4.93	0.04	4.18
8	Fear	D+C^2	4	38.93	5.62	0.03	6.17

9	Fear	C	2	39.53	6.22	0.02	<0.00
10	Food and fear	F+C^2	4	40.08	6.77	0.01	2.58
11	Fear	C^2	3	41.06	7.75	0.01	<0.00
12	Null	R	2	46.06	12.75	0.00	<0.01

Table 4. Slope and standard error (S.E.) table for the two top ranked models (see Table 3)

Model	Term	Slope	S.E.
1	Constant	-1.70	0.01
	F	0.29	0.01
	D	0.36	0.01
2	Constant	-1.67	0.01
	D	0.31	0.01

Discussion

By understanding the mechanisms underlying habitat selection for large herbivores, we can help address conflicts between humans and wildlife and mitigate the negative effects of altered foraging patterns in sensitive ecosystems. We found that in disturbed landscapes, the eastern grey kangaroo selected foraging habitats through a trade-off between food quality and distance to roads, by foraging in areas of short grass away from roads. Our data suggest that herbivores can perceive novel sources of fear, like roads, to a sufficient extent to influence their habitat use. Foraging patterns by large herbivores are under a high degree of anthropogenic influence in many areas, and our results show that, even in absence of native predators, fear can exert strong influence over forage habitat selection, and, therefore, potentially the structure of vegetation communities.

Fear

We anticipated that kangaroo foraging intensity would be positively correlated with vegetation cover, because kangaroos have been found to utilize areas with high cover when under risk of predation (Banks, 2001, Caughley, 1964, Hill, 1981). However, we found limited support for kangaroos using areas with greater vegetation cover (Table 3). There are several possible reasons for this finding. First, kangaroos in our study region have never encountered dingo predation, and may have consequently lost their fear of many such predators (similar to what has been documented for macropods on predator-free islands; Blumstein and Daniel, 2002). However, we consider the complete loss of fear to be unlikely, as both foxes and domestic dogs represent a threat to kangaroos, and would be encountered by kangaroos at all sites. Second, our investigation was at a finer scale and sites contained more scattered vegetation cover compared to the investigation by Banks (2001) study, where there was a sharper demarcation from large areas of cleared grasslands to forested areas over the landscape. At larger scales, and in areas with more open foraging habitat, fox predation may have a stronger effect on selection for cover than was apparent in our study. Third, the red fox may elicit a weaker behavioural response on our sites than the dingo, because fox predation is limited to young animals (Banks, 2001, Fletcher, 2006). Our results indicate that cover may have a more limited effect on foraging patterns of kangaroos in landscapes with a mix of vegetation cover (e.g. variegated; Hobbs and McIntyre, 2005) over fine spatial scales (several hectares), lack of clear delineation between forested areas and large grassy areas, and where there has been a long absence of larger quadruped predators such as the dingo.

As expected, kangaroo foraging intensity was negatively related to distance from the nearest road (Table 3), confirming the tendency for large herbivores to avoid areas near roads (Fahrig and Rytwinski, 2009). The mechanism underlying the avoidance of roads shown by kangaroos in this study, (and other large herbivores elsewhere; Fahrig and Rytwinski, 2009) remains unclear. Avoidance of roads may be attributed to direct effects, such as perceived collision risk, fear of traffic light and noise, fear of the road itself (Fahrig and Rytwinski, 2009, Forman and Alexander, 1998, Jaeger et al., 2005), or indirect effects, such as through natural selection, where there are heritable differences in behavioral traits for road crossings and animals that avoid roads have higher survival (Shepard et al., 2008) and increase in predator densities along road edges (Fahrig and Rytwinski, 2009, Forman and Alexander, 1998), although predator densities may also decline near roads (see Berger, 2007). In this study, roads may have created refugia for plants from foraging intensity, which may benefit native species that favor tall grass structures (Howland et al., 2014, Howland et al., 2016a). However, avoidance of roads will intensify foraging in areas distant from roads, which may create conflicts, where grazing sensitive species perceive roads as poor habitat. For example, a declining woodland bird, the dusky woodswallow (*Artamus cyanopterus*), has been shown to avoid areas close to human infrastructure, and is also dependent on a high cover of dense tall grass (Howland et al., 2016a). Furthermore, the high predator densities often found along road sides (e.g. to consume carrion) may create population sinks for some species, for example songbirds (Schmidt, 2003) and desert tortoises (Kristan and Boarman, 2003) in North America. Hence, the benefits of roads in creating refugia for grazing sensitive species will depend on how roads influence other aspects of habitat quality.

Food

The lawn index (our index of food quality) was an important driver of kangaroo habitat selection in this study (Table 4). Our finding that kangaroos prefer grass lawns for foraging, supports those of other studies on kangaroos (Southwell and Jarman, 1987, Roberts et al., 2011, Ramp and Coulson, 2004) and other wild herbivores (Roberts et al., 2011, Archibald, 2008, Kanga et al., 2013, Gordon, 1989, Fuhlendorf and Engle, 2001). Once these lawns are created, they can be maintained in this nutritious state by grazing, creating a positive feedback loop with herbivores (Verweij et al., 2006, Kanga et al., 2013, Roberts et al., 2011). Interestingly, the selectivity shown for grass lawns, will limit foraging intensity in tall grass, thus promoting variation in grass structure. Variation in grass structure is considered important for conservation of biota in grassy habitats in Australia (Howland et al., 2014, Woinarski and Ash, 2002, Howland et al., 2016a, Howland et al., 2016b), and worldwide (Whittingham and Evans, 2004, Fuhlendorf et al., 2006).

Conservation implications

The collision of large macropods with motor vehicles is a major economic cost in the study region (ACT Government, 2010, Ramp and Roger, 2008). Our results suggest that the current management practice of mowing roadside grass in the ACT for line of sight, access and fire fuel reduction, may increase forage quality and encourage kangaroos to utilize areas they otherwise avoid. We anticipate that kangaroos would make use of these higher quality roadside verges, when forage habitat elsewhere has declined (e.g. during winter and drought). Studies into deer-vehicle collisions in North America have identified how modifying the width (> 40 m) and timing (early growing season) of mowing of roadside vegetation and the installation of fencing and appropriate wildlife crossings can reduce deer-vehicle collisions (McCollister and Van Manen, 2010, Barnum and Alt, 2013, Rea, 2003). Hence, abandoning or altering the timing and width of mowing of roadside vegetation and/or the installation of fencing and wildlife crossings may reduce kangaroo use of roadside verges and potentially reduce incidences of car collision with kangaroos.

Grazing by kangaroos exerts a profound influence over vegetation and associated biodiversity in Australian temperate grassland and grassy woodland ecosystems (Barton et al., 2011, Manning et al., 2013, Howland et al., 2014, Meers and Adams, 2003). Our finding that kangaroos concentrate grazing on lawns and avoid areas with tall grass tussocks has two important implications for conservation and management. First, this selectivity in foraging will be greatest at moderate grazing intensities when animals are able to select between patches that vary in quality, with a more uniform grass structure expected under low or high grazing intensities (Rook et al., 2004, McIntyre and Tongway, 2005). Second, if kangaroo foraging remains concentrated on already heavy grazed lawns throughout the year (as opposed to just spring), this could result in the replacement of perennial, tall more palatable species with annual, short, and unpalatable species (Kemp and Dowling, 2000, McIntyre, 2005, Monaco et al., 2003). This loss of perennial species represents a loss of stability and resilience, and is linked to land degradation world-wide (Cingolani et al., 2014, Monaco et al., 2003), particularly in grazing enterprises in Australia (Kemp and Dowling, 2000). Methods that move kangaroo foraging across reserves and prevent prolonged heavy grazing of the same grass patches are needed, and could include concentrated population management, patch burning, exposure to domestic dogs and deterrents such as predator scent used in other parts of the world (Archibald, 2008, Cromsigt et al., 2013, Parsons and Blumstein, 2010, Silva-Rodríguez and Sieving, 2012, Fuhlendorf and Engle, 2001).

Conclusions

We found that in a five disturbed reserves in the absence native predators, kangaroos selected foraging habitat as a trade-off between food and fear, foraging in areas with a high cover of short grass away from roads. This foraging pattern may increase variation in grass structure, and create refugia from grazing in habitats near roads, but may lead to overgrazing of already grazed areas. We found no evidence for selection of cover expected under fear of predation creating foraging refugia in areas without vegetation cover. Importantly, intervention may be needed to change kangaroo habitat selection, in a way that mimics natural foraging patterns, in order to promote optimal vegetation structures for native biodiversity conservation.

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Supplementary Material

Appendix S.1. Details of the density of kangaroos estimated through pellet counts undertaken in spring 2009 at all five study site.

Study site	Density (animals/ha)
Callum Brae	2.08
Goorooyarroo	2.36
Jerrabomberra West	1.21
Mulanggari	1.05
Wanniassa	1.29

Synthesis

Large grazers have a profound effect on vegetation communities and associated biodiversity (Gordon et al., 2004, Mysterud, 2006). While some level of grazing is considered critical in maintaining species diversity, alteration to grazing regimes to which species are adapted can lead to biodiversity loss (Gordon et al., 2004, Mysterud, 2006). In south-eastern Australia, the abundance of the eastern grey kangaroo (*Macropus giganteus*) has increased in many areas, owing to a loss of predators, the provision of permanent watering points and protection from hunting (Grigg et al., 1989, ACT Government, 2010). Several studies have demonstrated that high grazing pressure by the eastern grey kangaroo (hereafter: kangaroo) can negatively affect native biodiversity (Cheal, 1986, Meers and Adams, 2003, McIntyre et al., 2010, ACT Government, 2010, Barton et al., 2011, Manning et al., 2013). These studies have provided valuable insights into the potential impacts of high kangaroo numbers on biodiversity, but do not provide information on what constitutes optimal grazing levels may be. However, information on optimal grazing levels for species is necessary to effectively conserve biodiversity (Gordon et al., 2004, Hester et al., 2000). Below I draw together key results from my investigation into the effects of kangaroo grazing on grass and fauna in grassy habitats in south-eastern Australian. I also discuss the implications of my results for conservation of biodiversity in these habitats.

This thesis has added to our knowledge on the management of kangaroo grazing pressure for the conservation of biodiversity by investigating the relationship between kangaroos, grass structure and fauna. I found that: 1) there was a significant and negative relationship between kangaroo density and grass structure (Paper I). 2) High intensity grazing had a negative effect on reptile abundance, reptile species richness, reptile species diversity, and the occurrence of several ground-dwelling reptiles (Paper I). 3) Birds with similar traits favoured similar grazing intensities, with different bird traits groups showing a preference for a range of grazing intensities (Paper II).

4) A threatened grassland reptile, the striped legless lizard (*Delma impar*), was more likely to occupy habitat with a complex grass structure, and a low kangaroo density (Paper III). 5) Kangaroo abundance can be accurately estimated using line transect sampling from vehicles driven along tracks provided the distribution of kangaroos in regards to the track are known (Paper V).

Overall, I found only limited support for the management recommendation suggesting that moderate grazing intensities was best for conserving fauna biodiversity. Instead, my results highlighted the importance of varying grazing management so as to retain grass heterogeneity, and a full complement of species (Woinarski and Ash, 2002, Fuhlendorf et al., 2006, Lindenmayer et al., 2008). Another important finding was the discovery that kangaroos, within reserves that are undergoing a high degree of anthropogenic change, selected foraging habitat as a compromise between resource quality and fear (i.e. kangaroos select areas with a high cover of short grass away from roads; Paper IV). These foraging patterns may conflict with conservation objectives where species that favour low grazing intensities also avoid roads, and where grazing remains concentred on already grazed areas.

Recommendations

Based on my findings, I recommend that mosaics of grass structures should be maintained across the landscape at spatial scales relevant to reptiles and birds (10s of ha), with few (if any) areas subject to prolonged high intensity kangaroo grazing. To achieve this, I suggest:

1. Management of kangaroo grazing pressure (and indeed all grazing pressure) be based on grass structural attributes (e.g. such as grass height, grass biomass, grass percent cover) optimal for reptiles and birds (see Paper I, II, and III).

2. Limit the extent and duration of high intensity grazing events. Areas of very low grass structure subject to intense grazing was sub-optimal for all fauna expect large-ground

foraging birds (Paper I, II, and III), and even these species may be negatively affected in the long-term, due to detrimental effects on tree and shrubs recruitment and reductions in food abundance (Paper II). Management to prevent prolonged intense grazing events could involve predator reintroduction, culling, the use of deterrents and fertility control.

3. Rotate grazing across the landscape to prevent pasture degradation under continuous grazing and to create mosaics of areas characterised by different grass structure at spatial scales relevant to reptiles and birds. Patch-scale burning also could be used to redistribute grazing pressure, and increase heterogeneity between burnt and unburnt patches. Burning has been recognised as an important tool in management of biomass, either directly through incineration, or indirectly through redistribution of herbivore foraging intensity (McIntyre et al., 2015, Fuhlendorf and Engle, 2001b)

Future research and limitation of study

In suggesting these management actions, I recognize that further research is needed into how some of the general principles outlined in this study can be used to effectively manage kangaroo grazing pressure in grassy habitats in south-eastern Australia. Most importantly, further investigations are needed into how to create mosaics of grass structure at scales relevant to reptiles and birds. This could involve implementing a rotational patch burning (> 10 ha) program across a reserve (e.g. Fuhlendorf and Engle, 2001a), and subsequently monitoring to determine how this burning regime influences kangaroo foraging patterns, grass structure and grazing sensitive fauna.

My thesis focussed on the optimal grazing levels for two vertebrate groups – reptiles and birds. However, another abundant and diverse group in grasslands – invertebrates (Watkinson and Ormerod, 2001) was not investigated. Invertebrates are known to be sensitive to changes in grass structure and may show varying preferences for grass structures depending on the species' size, dispersal abilities, foraging behaviour, and feeding guild (Dennis et al., 1998, Barton et al., 2011, Read, 1999, Watkinson and Ormerod, 2001, Woodcock et al., 2009). Sampling the invertebrate community across a gradient of grazing intensity (as done for reptiles and birds in my thesis), could provide important insights into how grass structure influences invertebrates. Given the important role invertebrates play in ecosystem function (Lavelle et al., 2006, Swift and Anderson, 1994, Jouquet et al., 2006), and as food for higher order taxa (Evans et al., 2007, Vickery et al., 2001, Castellano and Valone, 2006), a greater understanding of the effects of grazing is warranted.

Another important aspect of research not addressed in this thesis was the mechanisms underlying the selection for different grass structures by reptiles and birds, with variation in grass structure potentially influencing important factors of survival – predation risk, thermoregulation, food and breeding (Evans, 2004, Sato et al., 2014b, Castellano and Valone, 2006, Vickery et al., 2001). Investigation into the mechanisms driving faunal species responses could involve manipulating grass structure to different amounts/heights and recording how these different structures affected microclimate, predation risk, and food availability for different fauna, in a similar way to mowing experiments that were undertaken in Australian ski resorts (see Sato et al., 2014b, Whittingham and Devereux, 2008). Such an investigation could increase our understanding of how grass structure affects the quality of habitat the fauna, and may offer other additional management options to mitigate impacts of grazing on the fauna community.

In summary, this thesis has added to our knowledge on the management of kangaroo grazing pressure for conservation by undertaking an investigation into: 1) how grazing intensity and grass structure influence habitat selection by reptiles and birds; 2) how food and fear influences kangaroo forage habitat selection in landscapes subject to anthropogenic change and; 3) developing a method to accurately estimate kangaroo abundance along vehicle tracks. This research offers important quantitative measures of optimal grass structure for the conservation of a variety of many species and species groups, and has outlined several strategies on how to manage grazing intensity for conservation. Ultimately, this thesis highlights that the management of grazing by large native herbivores in anthropogenically-altered grassy habitats is vital for the maintenance and retention of biodiversity in threatened Australian ecosystems, such as temperate grassland and box-gum grassy *Eucalyptus* woodland communities.

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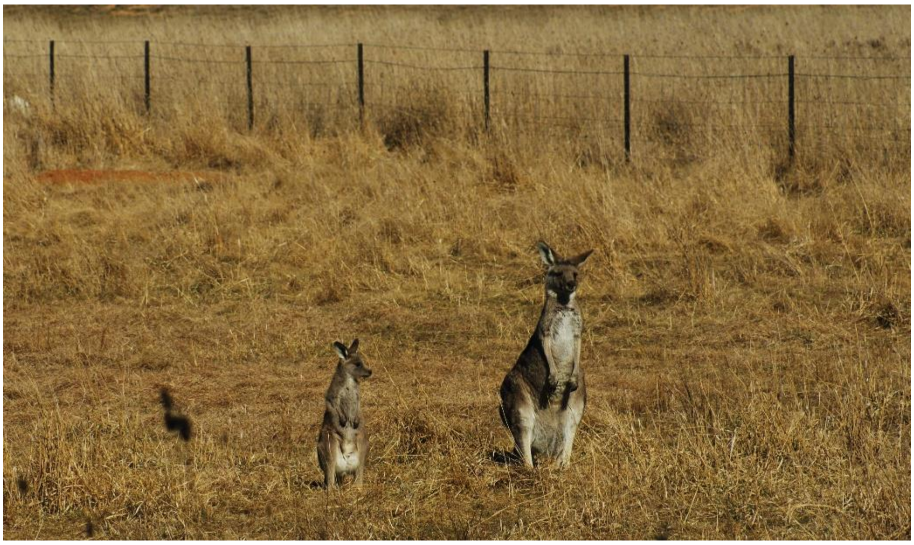
Appendix 1. Paper V: Accounting for animal density gradients using independent information in distance sampling surveys



View of kangaroos from vehicle driven along tracks. (Photo: Brett Howland).

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Accounting for animal density gradients using independent information in distance sampling surveys

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Abstract Distance sampling is extensively used for estimating animal density or abundance. Conventional methods assume that location of line or point transects is random with respect to the animal population, yet transects are often placed along linear features such as roads, rivers or shorelines that do not randomly sample the study region, resulting in biased estimates of abundance. If it is possible to collect additional data that allow an animal density gradient with respect to the transects to be modelled, we show how to extend the conventional distance sampling likelihood to give asymptotically unbiased estimates of density for the covered area. We illustrate the proposed methods using data for a kangaroo population surveyed by line transects laid along tracks, for which the true density is known from an independent source, and the density gradient with respect to the tracks is estimated from a sample of GPS

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collared animals. For this example, density of animals increases with distance from the tracks, so that detection probability is overestimated and density underestimated if the non-random location of transects is ignored. When we account for the density gradient, there is no evidence of bias in the abundance estimate. We end with a list of practical recommendations to investigators conducting distance sampling surveys where density gradients could be an issue.

Keywords Density gradients · Distance sampling · Kangaroo · Road surveys · Line and point transects · Wildlife abundance

1 Introduction

In a world of limited resources and increasing human population, there is a growing need to accurately and efficiently assess animal populations, to allow their effective management and conservation. Therefore, methods for estimating animal abundance or density are increasingly required. There are a number of methods available, with mark-recapture and distance sampling being those most frequently considered (Williams et al. 2002). Unfortunately, the choice of a given method is often driven by logistics and cost considerations rather than statistical rigour or adequacy. In particular, all methods have assumptions, and their failure leads to bias. Nonetheless, these are too frequently ignored for the sake of pragmatism. While sometimes this decision results from a carefully considered compromise between clearly defined objectives and available resources, quite often this is motivated by the lack of understanding of the assumptions and the exact consequences of their violation.

Distance sampling is arguably the most widely used method for estimating absolute animal density or abundance. While the standard distance sampling reference (Buckland et al. 2001) specifies the requirement that a sufficiently large number of samplers, line or point transects, need to be laid at random with respect to the animal distribution, all too often surveys are reported where landscape features are used to lay the samplers. Such landscape features might include natural structures like rivers (Fletcher and Hutto 2006), vantage points (Vargas et al. 2002), and shore lines (George et al. 2004), but also man-made structures like roads (Giunchi et al. 2007; McShea et al. 2011), fences and power lines (del Rey and Rodriguez-Lorenzo 2011). Although the random location requirement might seem just a "statistician's caprice", it is paramount for the derivation of the estimators involved, as we show in Sect. 2. Ignoring it can therefore potentially introduce severe bias in density estimates (e.g., Marques et al. 2010). In fact, this bias might be as large as, or even larger than, that introduced by violations of the three other key distance sampling assumptions: (1) no animals go undetected at the line or point, (2) no animal movement, (3) no measurement error. Therefore, the consequences of the failure to use transects located at random must be understood. For features to which the animals respond, and hence present a non-uniform density gradient with respect to samplers laid along them, resulting density estimates will be biased in the absence of additional information about the density gradient. However, as we show here, if one can obtain independent information about the density gradient, it can be incorporated in the estimation process by extending the conventional distance sampling likelihood.

Here we address the use of independent information about the animal density gradient with respect to samplers to derive asymptotically unbiased estimates of density. In Sect. 2, we describe why the random location of samplers is so important: it allows us to assume a known distribution of animals with respect to the lines or points. This in turn is a corner-stone for further inference. Building on this, we show how one might, given independent knowledge about the animal distribution with respect to the samplers, extend the methods to deal with a spatial distribution of animals that is not independent of the samplers. We illustrate the application of the proposed methods with an Australian population of kangaroos in Sect. 3, sampled from road-based transects. The kangaroo distribution with respect to roads along which the transects are located is obtained from animals fitted with GPS collars. We discuss the results in Sect. 4, and present some recommendations that practitioners should consider when dealing with surveys for which density gradients with respect to samplers are likely to occur.

2 Methods

In this section we present an overview of the key aspects of distance sampling, giving the methodological basis required to develop our proposed methods. The reader is referred to Buckland et al. (2001) for further details. We consider that N animals exist in a study area of size A, leading to animal density $D = \frac{N}{A}$. Distance sampling assumes that a sufficiently large number of samplers (lines or points) is placed at random in the area for which inferences are required. Usually, the entire area cannot be sampled, and hence there are two steps involved in estimating abundance for the wider survey area: (1) using the data collected, abundance is estimated for the covered area using model-based methods; (2) based on the estimate for the covered area, density is estimated for the wider region of interest usually by a design-based approach, which led Fewster and Buckland (2004) to refer to distance sampling as a "composite" inferential approach. Recently, the second (traditionally design-based) step has been implemented in a model-based framework (e.g., Hedley and Buckland (2004), Katsanevakis (2007)). We emphasize differences in model- and design-based inference here because, under the presence of a density gradient, obtaining density estimates for the wider survey area based on those from the covered area is unlikely to be feasible under a design-based approach, as we discuss below.

For the first step, typically a systematic random sample of transects is recommended. This complicates estimation of the variance associated with encounter rate, but that variance is typically lower than that from simple random designs (Fewster et al. 2009). The distances $y_i (i = 1, 2, \ldots, n)$ from the line or point to each of the n detected animals are recorded. These distances are used to model a detection function $g(y|\theta)$, which represents the probability of detecting an animal, given that the animal is at distance y from the line or point and θ represents the detection function parameters to be estimated. Note that, unless otherwise required, we often drop θ in the notation for readability. Typically, semi-parametric models are assumed for $g(y)$, along the lines of Buckland (1992). These models are fitted to the sample of detected distances, and conventional model selection tools are used to choose a parsimonious model, from which inference is drawn. Practitioners rarely implement model fitting themselves, relying on dedicated software to do so. The software most commonly used to analyse distance sampling data is Distance (Thomas et al. 2010). In practice, the modelling proceeds by fitting the probability density function (pdf) of detected distances, $f(y)$, which relates directly to the detection function as:

$$f(y) = \frac{g(y|\theta)\pi(y|\lambda)}{\int_0^w g(u|\theta)\pi(u|\lambda)du} = \frac{g(y|\theta)\pi(y|\lambda)}{P} \tag{1}$$

where w is a truncation distance (a distance beyond which distances are ignored), and $\pi(y|\lambda)$ represents the pdf of the distances available to be detected. Note that P is by definition the expected value of the detection function with respect to the distribution of the distances available for detection; in other words, the average probability of detecting an animal in the covered area. Note also, in contrast with the traditional representation (e.g. Borchers and Burnham (2004), equation 3.32), the explicit use of a parameter vector λ associated with the pdf of distances available to be detected. This is fundamental for the current formulation, as we will later use non-conventional models for this distribution, indexed by λ. For conventional methods, the random location of samplers is fundamental. Assuming that the location of lines or points is random, the animal distribution within the covered areas is uniform on average, and hence $\pi(y) = \frac{1}{w}$, for lines (Fig. 1a), and for points, $\pi(y) = \frac{2y}{w^2}$ for points (Fig. 1b). Thus for conventional methods, the only unknown parameters are those from the detection function (i.e. θ), and hence we maximize the likelihood for θ given a sample $\underline{y_1} = (y_{1,1}, y_{1,2}, \ldots, y_{1,n_1})$,

$$\mathcal{L}(\theta|\underline{y_1}) = \prod_{i=1}^{n_1} \frac{g(y_{1,i}|\theta)\pi(y_{1,i}|\lambda)}{\int_0^w g(u|\theta)\pi(u|\lambda)du} \tag{2}$$

allowing the estimation of θ. Following Buckland et al. (2001), the expression for conventional distance sampling density estimators is

$$\hat{D} = \frac{n\hat{f}(0)}{2L} = \frac{n}{2Lw\hat{P}} \tag{3}$$

in the case of line transects, where $\hat{f}(0)$ represents the estimated pdf of detected distances, evaluated at distance 0, and L represents the total line length and

$$\hat{D} = \frac{n\hat{h}(0)}{2\pi k} = \frac{n}{k\pi w^2\hat{P}} \tag{4}$$

for the case of point transects, where $\hat{h}(0)$ represents the slope of the estimated pdf of detected distances, evaluated at distance 0, and k represents the number of points surveyed. Note in both Eqs. 3 and 4 $\hat{P}$ represents an estimator of the detection probability,

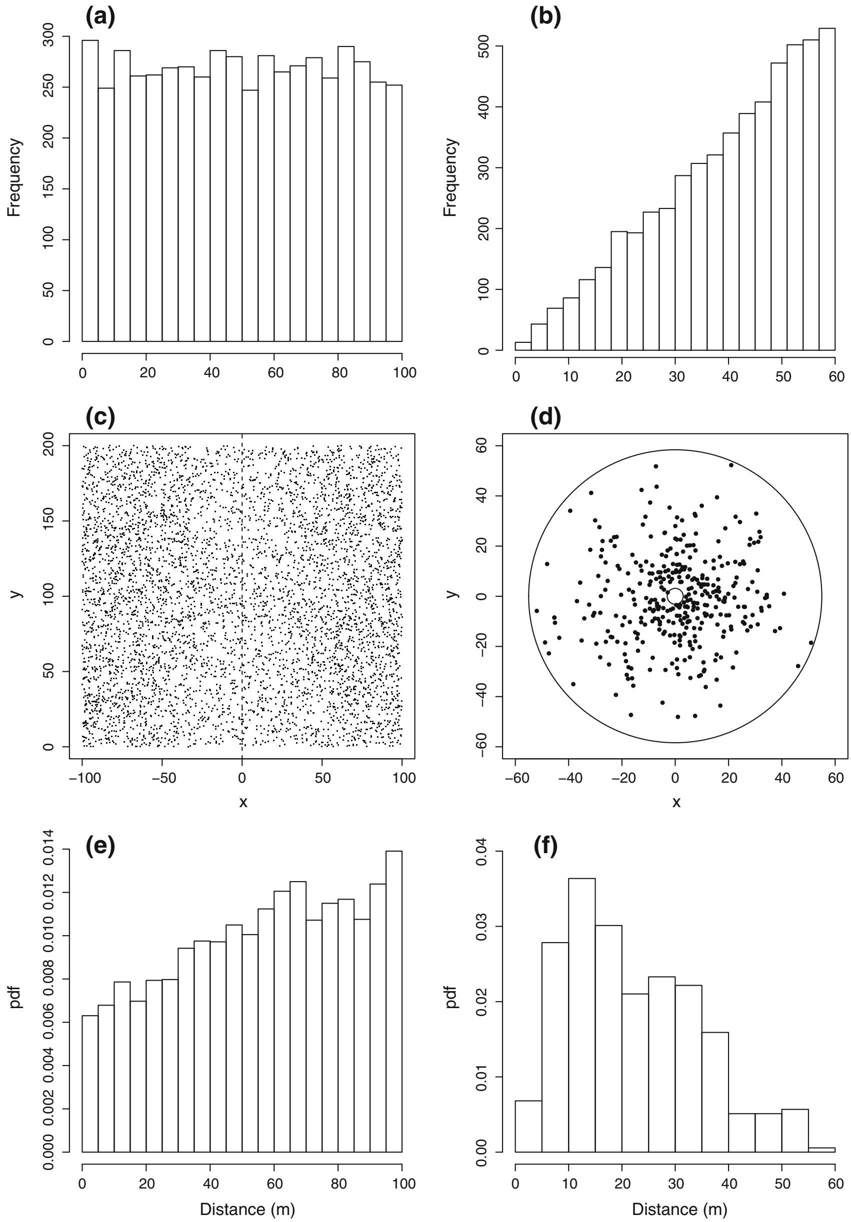

Fig. 1 Distributions of distance with respect to line (*left column*) and point (*right column*) transects (note these distribution results from pooling the data from a large number of samplers). **a** histogram of available distances under random line transect placement; **b** the same as **a**, for point transects; **c** real example of two dimensional locations of kangaroos with respect to *line* transects laid along roads, obtained from GPS collared kangaroos (distance along the transect is not real, and was simulated from a uniform distribution for visual display); **d** the same as **c**, for birds with respect to point transects located at wind farm turbines, obtained from extensive bird searches; **e** histogram of available perpendicular distances with respect to the samplers resulting from the data depicted in **c**; **f** histogram of available radial distances with respect to the samplers resulting from the data depicted in **d**

obtained by evaluating the expression for P (cf. Eq. 1) substituting the parameters by their maximum likelihood estimates.

For line transect sampling, if transects are laid in such a way that the distribution $\pi(y|\lambda)$ cannot be assumed uniform, then $g(y)$ cannot be separately estimated in the absence of independent data, as $\pi(y)$ and $g(y)$ always appears as a product. The information about detectability and availability for detection is completely confounded in the sighting distances, and hence $g(y)$, and therefore P, are estimated with bias. Therefore, we need independent information about one of these two processes to proceed. By contrast, for point transect surveys in which points are not located randomly, Marques et al. (2010) and Cox et al. (2011) present methods in which independent data are not required to incorporate the density gradient in the process; these are based on assumptions for the sighting process (radial symmetry) and collection of both radial distances and angles. However, even here, if the density gradient extends further than the truncation distance w from the points, and design-based methods are used to extrapolate beyond the covered area, then bias will occur.

Suppose that an independent sampling process, such as secondary transects perpendicular to the density gradient, or GPS location data in two-dimensional space (Fig. 1c–f), provide a sample $\underline{y_2} = (y_{2,1}, y_{2,2}, \ldots, y_{2,n_2})$, drawn directly from $\pi(y|\lambda)$. Then one can easily obtain maximum likelihood estimates for λ from the following likelihood

$$\mathcal{L}(\lambda|\underline{y_2}) = \prod_{j=1}^{n_2} \pi(y_{2,j}|\lambda). \tag{5}$$

Assuming that $\underline{y_1}$ and $\underline{y_2}$ are independent (which can be enforced by proper design and survey methods), a likelihood combining the two data sources follows naturally, allowing the joint estimation of the parameters of both processes:

$$\mathcal{L}(\theta, \lambda|\underline{y_1}, \underline{y_2}) = \mathcal{L}(\theta|\lambda, \underline{y_1})\mathcal{L}(\lambda|\underline{y_2}) = \prod_{i=1}^{n_1} \frac{g(y_{1,i}|\theta)\pi(y_{1,i}|\lambda)}{\int_0^w g(u|\theta)\pi(u|\lambda)du} \prod_{j=1}^{n_2} \pi(y_{2,j}|\lambda). \tag{6}$$

Given the parameter estimates, the usual estimate for P follows as

$$\hat{P} = \int_0^w \hat{g}(u|\theta)\hat{\pi}(u|\lambda)du \tag{7}$$

and we can therefore obtain the corresponding estimator for density (see Eqs. 3 and 4).

The above approach provides an estimate of density for the covered area. Given this estimate, and the estimated density gradient, one should implement a model-based abundance estimation for the wider survey region of interest, as described in (Marques et al. (2010), section 2.5). A purely design-based extrapolation would not be valid, as given that the density gradient exists, by definition that density is not the same near the samplers as away from the samplers. Hence we need to model density as a function of distance to the samplers, rather than inferring it by design-based considerations.

As for the conventional analysis methods, a straightforward way to obtain the variance of these density estimators might be to consider a nonparametric bootstrap. For the distance sampling survey, the recommended units for resampling are either the lines or the points. For the independent source of information about the density gradient, the appropriate sampling unit will usually be easy to identify. In the example we provide below, in which the density gradient is estimated based on a sample of animals with GPS collars, the animals themselves would represent a reasonable sampling unit for resampling. Note that, alternatively, one could obtain variances for the probability of detection based on the numerically differentiated Hessian matrix (which e.g. R's `optim` function returns), and incorporating these with the traditional cluster size and encounter rate variances via the delta method to obtain a density estimate.

3 Estimating grey kangaroo abundance

The motivating data set comes from an eastern grey kangaroo *Macropus giganteus* survey conducted at Farrar Ridge nature reserve (FRNR). The FRNR is located in the Australia Capital Territory (ACT) in south-eastern Australia (35°23°S, 149°06°E), and covers 178.60 ha (Fig. 2). The reserve is characterized by temperate grassy woodland vegetation with an overstorey of *Eucalyptus* sp. and an understorey of grasses and forbs (Dorrough et al. 2004). Steeper slopes also have a dense shrub mid-storey. On the basis of canopy cover, the vegetation can be divided into three canopy classes:

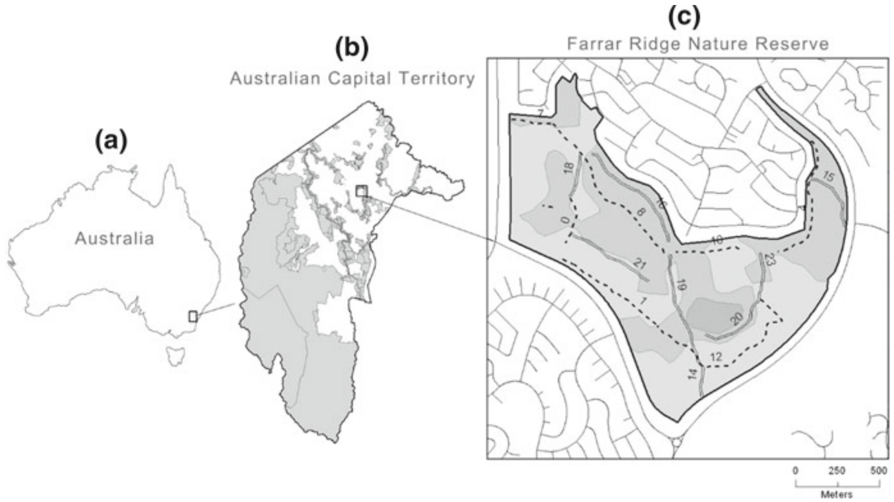

Fig. 2 Study area **a** location of study site within Australia, **b** the Australian Capital Territory, with protected areas shown in *grey*, and **c** location of Farrar Ridge Nature Reserve, showing transects as *dotted* and *parallel lines*. Different canopy types are indicated by *light grey* (*open woodland*), *grey* (*woodland*) and *dark grey* (*open forest*). Roads surrounding reserve are shown in black

open woodland, woodland and open forest. For simplicity here we ignore the effect of habitat on both detectability and availability for detection.

Distance sampling surveys of kangaroos were conducted in the 7th, 13th and 18th July and 5th August 2011, coinciding with a period of population stability (Fletcher 2007). All transects were surveyed twice, with approximately 3.5 + 3.5 h (3.5 h in each of 2 days) of driving required to cover the full transect length. Surveys were undertaken 3 h after dawn, to increase the dispersion of animals, hence improving the efficiency of data collection. Transects were laid along existing trails. The trail network was split into 15 transects based on changes in canopy type, or abrupt change in track direction (>45 degrees). Due to the closeness to the reserve boundaries, some transects were treated as one-sided transects.

Vehicle surveys were conducted along transects, with one person driving and recording, while the other spotted kangaroos from an elevated position at the rear of the vehicle. Between spotting events, the vehicle was driven at speeds between 10 and 15 km/h. Sighting distance and angle to kangaroos were recorded using a rangefinder (Leupold Wind River RB800). We consider the object of interest to be groups, not individual animals: where kangaroos occurred in close proximity (within 2 m), animals were recorded as a single group, with distance and angle recorded to centre of the group, and group size was recorded. Each encounter was recorded using a GPS (E-trex), with the actual location of kangaroos spatially mapped in ArcGIS 9.3 (ESRI 2011) based on sighting coordinates and the distance and angle measurements. Perpendicular distance was calculated from the location to the nearest point on the track using the NEAR command in ArcGIS. To minimize errors associated with reactive movement, the observer scanned ahead to record animals prior to movement. Where recorded animals moved ahead of the vehicle, the behaviour (vigilance) of newly encountered animals was gauged to determine if animals were previously sighted, and if so, they were not included again.

A total count of the kangaroo population was conducted in 15th May 2011 using 'drive counts' (Lancia et al. 2005; Southwell 1989). Due to population stability, it was assumed that abundance would change negligibly between this count and the distance sampling surveys. Drive counts involve observers walking across the length of reserve within sight of each other, and counting kangaroos as they pass back through the line of observers. Drive counts can provide a very accurate estimate of population size when animal movement is restricted to within a relative small area, as at FRNR (Southwell 1989). Roads and housing on all sides limited kangaroo movement outside of the reserve, so that all animals which occur on FRNR should have been counted. Population size was estimated at 516 on the first drive and 517 on the second. Given the close agreement between repeat counts no further counts were undertaken.

To illustrate the methods, a single author (TAM) carried out all the analyses, without knowing the true kangaroo density. Only after the analysis was concluded was he informed of the above estimates; taking true abundance to be 516.5 animals, density is 2.89 animals per hectare. For illustrative purposes, to estimate mean density in the reserve, we make the simplifying assumption that average density within the truncation distance $w = 150$ m is representative. We note that most of the reserve is within 150 m of a track.

Conventional line transect analysis, ignoring the density gradient, was implemented in Distance 6 (Thomas et al. 2010). Numerical maximization of the required likelihoods for the proposed methods was implemented in R (R Development Core Team 2012) using the general purpose optimization function `optim`.

3.1 Conventional distance sampling analysis

In total, 372 groups of kangaroos were detected. Preliminary data inspection suggested moderate track avoidance, and suggested that 150 m would be a reasonable truncation distance for analysis (resulting in 351 distances). To account for possible size bias, we considered a size-bias regression, regressing the log of the observed cluster size on the log of the estimated detection function. We considered three combinations to model the detection function: (1) half-normal + cosine; (2) uniform + cosine; (3) hazard-rate + simple polynomial. It is interesting that none of the conventional goodness-of-fit tests including the χ^2, the Cramér-von Mises and the Kolmogorov-Smirnov tests, showed evidence of a bad fit for any of these three models, with a truncation distance of either 100 or 150 m. Based on minimum AIC, the hazard-rate model with no adjustment terms was selected for further inference. There was moderate evidence of size bias, with the mean cluster size being 2.13 animals per group and the size-bias regression estimate being 1.94 animals per group. The estimated parameters of the hazard-rate were $\hat{\sigma} = 94.9$ and $\hat{b} = 3.1$ for the scale and shape parameter, respectively. The average probability of detection of an animal in the covered strip was estimated to be 0.73 (95 % CI 0.67,0.81). The estimated density was 2.3 animals per hectare (95 % CI 1.60,3.31).

3.2 Modelling the distribution of animals with respect to the road

As part of a separate movement study being conducted by the Conservation Planning and Research unit of the ACT Government, location information on a sample of 23 kangaroos spread across 15 properties in the Australian Capital Territory (ACT) and one property in neighbouring New South Wales (NSW) was available from GPS collar data. Of these, two animals were actually collared at FRNR. We assume that the distribution of animals with respect to the road was constant across reserves. The implications of this assumption are further addressed in the discussion. GPS fixes were restricted to 3 h following sunrise in order to match the timing of line transect surveys. To reduce the influence of temporal correlation in animal positions, GPS fixes were separated by 50 min, resulting in the maximum number of three fixes per animal per day.

In ArcGIS 9.3 (ESRI 2011) we calculated the distance of each GPS fix to the surrounding tracks. These distances were assumed to represent a sample from the density gradient with respect to the tracks. A myriad of models could be used here, but selecting the best model for the existing density gradient is outside the scope of this paper. We simply considered the model proposed by (Marques et al. 2010, equation 12) as a plausible candidate:

$$\pi(y|\beta,\tau) = \frac{1-\beta f(y|\tau)}{\int_0^w [1-\beta f(u|\tau)]\,du},\ y \geq 0, \tau > 0, \beta \leq \tau\sqrt{2\pi} \tag{8}$$

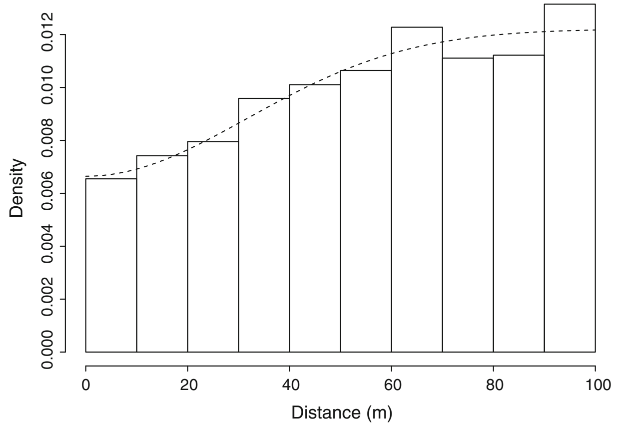

Fig. 3 Observed distribution of animals with respect to the transects, overlaid with a fitted density gradient model

where $f(y|\tau)$ is the Gaussian density with mean 0 and standard deviation τ. This is a versatile model with an intuitive parameter interpretation. The shape parameter τ reflects the extent to which the road (or any other feature considered) has an impact on the animal distribution. The model accommodates both attraction to ($\beta < 0$), and avoidance of ($\beta > 0$), the linear feature, while $\beta = 0$ gives a uniform. Numerical maximization of the likelihood resulted in parameter estimates ($\hat{\tau} = 31.7$, $\hat{\beta} = 36.2$) that provided an excellent fit to the data (Fig. 3). As can be seen, this model is far from uniform, and hence we can expect the estimates reported in the previous section to be biased.

3.3 Estimating kangaroo density accounting for the density gradient

We now implement the likelihood from Eq. 6 which incorporates both sets of data, the survey data analysed in Sect. 3.1, and the GPS data providing direct estimates of the density gradient parameters introduced in Sect. 3.2. In an analogous context, Borchers et al. (2010, online appendix) showed that this is more efficient than treating the parameter estimates from the previous section as known and estimating the detection function parameters based on these. For the detection function, AIC now favours a half-normal model, with parameter estimate $\hat{\sigma} = 73.2$ ($\Delta AIC = 0$) rather than the hazard-rate, with parameter estimates $\hat{\sigma} = 73.14$ and $\hat{b} = 5.88$ ($\Delta AIC = 2$). This probably reflects that, when the density gradient is ignored, the data suggest that the detection function has a broader shoulder, better represented by the hazard-rate model, than does the true detection function. The comparison between the estimated detection functions ignoring and accounting for the density gradient is shown in Fig. 4. The estimated probability of detection in the covered strip is now 0.54 (with either the half-normal or hazard-rate detection function). As was anticipated, the observed long tail was partially due to the increased availability of animals away from the line; hence, when accounting for the availability of animals, the detectability decreases and our density estimate increases.

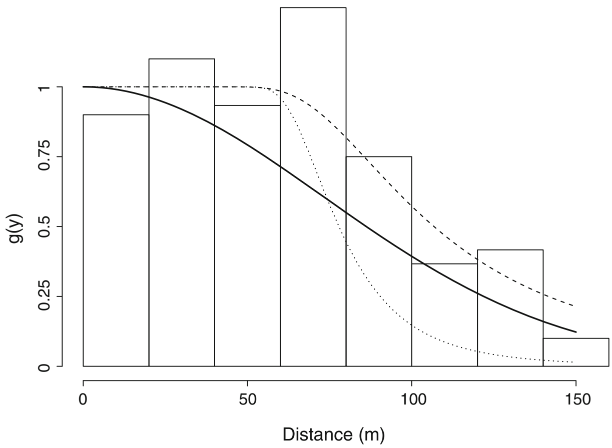

Fig. 4 Detected distances with overlaid estimated detection function ignoring the density gradient (*dashed line*) and incorporating the GPS data to account for the density gradient, for both the hazard-rate (*dotted line*) and the half-normal (*solid line*, model with lower AIC)

Using the estimated mean cluster size of 1.94 derived in Sect. 3.1, we estimate that the density to be 3.13 (95 % CI 2.36,4.16, bootstrap percentile method) animals per hectare. If instead we estimate mean cluster size using size-bias regression with the (now preferred) half-normal detection function, the mean cluster size is estimated to be 1.75 animals per group, and this density is estimated at 2.82 (95 % CI 2.14,3.60).

Being based on a single sample, it is hard to generalize the above result. However, assuming the estimated detection function and density gradient, we simulated a sampling procedure of the same population, repeated 1,000 times. For simplicity, we considered individual animals rather than clusters, with the simulated density being equal to the group density in the real data set. We also assumed that 500 distances were available to estimate the density gradient. This resulted in a mean bias of −1.92 %, showing that the proposed procedure is close to unbiased, provided the models assumed are good representations of truth. If the density gradient was assumed not to exist, mean bias was −28.1 %.

4 Discussion

Placing transects along features with respect to which animals might not distribute themselves at random leads to biased distance sampling estimates if conventional approaches are used. Depending on the actual distribution of animals one might expect overestimation or underestimation of density. In general, animals avoiding the features will lead to an overestimation of detection probability, and a corresponding underestimation of density. For animals which are actually attracted to these features, the opposite is expected. In our example, for which true density was 2.89 animals per hectare, a conventional distance sampling estimate assuming that animals are uniformly distributed led to −20 % bias. When we account for the density gradient using the information available from the GPS fixes, which reveals that animals avoid the vicinity of the roads along which transects were laid, the bias was reduced to 8.3 %. Note that the bias introduced in the detection function estimation also propagates into the cluster size bias correction via the size-bias regression, because the log of the estimated detection function is used as the independent variable. The effect of the size bias was stronger if one conducted the analysis using the detection function estimated accounting for the density gradient, with the estimated mean cluster size being 1.75 animals per group, leading to a density estimate of 2.82 animals per hectare. This translates to a further improvement in terms of percentage bias, now as low as −2.4 %. A similar value of around −2 % bias was obtained for a small simulation based on the same parameters as observed during the survey.

When looking at the survey data (Fig. 4), one could have anticipated problems because there was a slight increase in number of detections with distance from the tracks. In general, ignoring the density gradient, this could have been attributed to responsive movement away from the observer. As we have shown here, it is actually more likely that this was simply the combined effect of detection and availability. An important point to make is that for lines, and especially if animals avoid the features with respect to which transects were laid, visual inspection of the data might hint at potential problems. However, if the animals are attracted to the linear features along which line transects are laid (as in e.g. Butler et al., 2005), or in the case of point transects, the recorded detection distances might not contain any features indicative of the failure of the uniformity assumption. Therefore, extra care should be taken in this case. In particular for points, as suggested by Marques et al. (2010), recording the sighting angle might allow assessment of the plausibility of the uniformity assumption, and even better, allow incorporation of non-uniform distributions. However, due to the added complexity and inherent additional sources of variability, we only recommend accounting for the density gradient when it cannot be avoided by proper survey design.

Two particular features arising from the case study are worth discussion. First, the model required for the detection function becomes simpler (one parameter rather than two) when one accounts for the density gradient. This is intuitive: if part of the variation in the data is explained by the density model, less remains to be explained by the detection function model. Second, the bias introduced by the density gradient has an impact on the estimated detection function, and hence on the probability of detection, but it can also have an impact on the estimation of the mean group size. Again, this is obvious (at least after the fact!), because mean group size is estimated building on the estimated detection function.

For the analyses of the kangaroo data, several simplifying choices were purely pragmatic, and justified on the basis of the proof-of-concept nature of this work. However, these could be improved upon if approximately unbiased density estimation was the key objective. The first point to raise is that strictly the corrected density estimate is valid in the vicinity of 150 m from the roads. Due to the spatial scale involved, we assume that this was a reasonable approximation to the density in the reserve. One could argue that the spatial density model should be used to calculate density in the entire reserve, as described by Marques et al. (2010). We assumed that the density gradient, estimated from the available sample of 23 kangaroos with GPS collars from 16 reserves, was representative of the density gradient with respect to roads in the sampled reserve. Additional analysis of similar GPS data as a function of spatial location might be required to confirm, or disprove, this assumption. Further we assumed that there were no differences in detectability or availability for detection as a function of habitat. One should try to account for habitat differences in both of these processes to meet biological or ecological objectives. Also, a more elegant way of dealing with size bias would be to include group size as a covariate, along the lines of Marques and Buckland (2003) and Marques et al. (2007). Finally, model selection and goodness-of-fit evaluation could be improved.

Testing the uniformity assumption for the species and place of interest when conducting distance sampling surveys should not be overlooked, especially if the transect placement is not random. For logistical and safety reasons, roads are often preferred to random line placement. Their effect on wildlife can be diverse. Venturato etal. (2010) showed an example in which pheasant distribution was unaffected by roads. Butler et al. (2005) showed that a wild turkey density gradient with respect to roads was absent in some seasons, but present in others. This suggests that care should be taken when quoting work from other times and places to support claims on uniformity. Quoting directly from Erxleben et al. (2011), "We recommend researchers and managers investigate animal distributions around roads before implementing road-based monitoring programs". Similarly, whenever lines are placed along linear features that are not randomly located with respect to the study population, the same cautious approach should be adopted.

Our advice for dealing with distance sampling surveys in the potential presence of density gradients is simple: (1) design the survey to avoid having a density gradient if at all possible; (2) collect data to assess to what extent a density gradient might exist. If a density gradient is expected to exist or your data point towards its existence (3), interpret results from conventional methods with extreme caution, discussing possible direction and extent of bias and (4) consider using methods that account for the density gradients, either by collecting independent information on the density gradient, as presented here, or as presented exclusively for point transect based surveys in Marques et al. (2010) or Cox et al. (2011).

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