The impacts of feral ungulates on ephemeral savanna waterholes in the Northern Territory, Australia and their flow-on effects for native wildlife

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A dissertation submitted in fulfilment of the requirements for the degree of

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“We’re replacing the wild with the tame. Half of the fertile land on earth is now farmland ... We account for over one-third of the weight of mammals on earth. A further 60% are the animals we raise to eat. The rest, from mice to whales, make up just 4%.”

- Sir David Attenborough

From: “A life on our planet: My witness statement and vision for the future” (2020)
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Certificate of Authorship

I hereby declare that this submission is my own work and to the best of my knowledge and believed, understand that it contains no material previously published or written by another person, nor material which to a substantial extent has been accepted for the award of any other degree or diploma at Charles Sturt University or any other educational institution, except where due acknowledgement is made in the thesis. Any contribution made to the research by colleagues with whom I have worked at Charles Sturt University or elsewhere during my candidature is fully acknowledged. I agree that this thesis be accessible for the purpose of study and research in accordance with normal conditions established by the Executive Director, Library Services, Charles Sturt University or nominee, for the care, loan and reproduction of theses, subject to confidentiality provisions as approved by the University.

Helenna Mihailou

May 2022
Preface

This thesis is comprised of an abstract, a general introduction (chapter 1), a literature review (chapter 2), three data chapters (chapters 3-5), and an overall discussion of the findings of the study (chapter 6). Each chapter covers a different aspect of the overall study and have been prepared for publication in peer reviewed scientific journals. As a result, some principal concepts are repeated in chapter introductions. To date, chapters 2 and 4 have been published in peer reviewed scientific journals, chapter 3 is currently under peer review with a publisher, and chapter 5 has been prepared for submission to a journal. Publication information is available at the beginning of each of the published chapters, which are included in their published format.

All data used in this thesis was collected from 2018-2020 in Limmen National Park in the Northern Territory, Australia. All data pertaining to wildlife was collected by the author, while vegetation data was collected by James Vincent for use in this study. The entirety of this thesis has been written by myself with supervision and advice provided by Assoc. Prof. Melanie Massaro and Assoc. Prof. Dale Nimmo.
Acknowledgements

This thesis is the result of years of unwavering support from colleagues, friends, and family; both old and new. Without your collective support, the completion of this body of work would not have been possible.

To my principal supervisor, Associate Professor Melanie Massaro: I cannot thank you enough for your untiring encouragement and enthusiasm for adventure over the last decade that we have known each other. I’m not sure I would ever have pursued a PhD without your belief in me and willingness to take me on as a distance student. Your mentorship and friendship along the way has been invaluable and I have learned so much. May our adventures continue for many years to come!

To my secondary supervisor, Associate Professor Dale Nimmo: Thank you for your guidance in the incredibly complex and ever-changing world of ecological statistics. From the outset, this was the part of my PhD which was always going to be the most challenging, so thank you for sharing your knowledge and most importantly, your patience.

To Deanna Duffy of the Spatial Data Analysis Network of Charles Sturt University: Thank you for your immense help with the spatial analyses for this project. Your continued enthusiasm in the face of many unexpected hurdles has been amazing. Thanks also to Gary McKenzie and Simon McDonald for their assistance.

To my partner James Vincent: You’ve been my biggest supporter throughout this entire journey and have sacrificed so much time, effort, and energy to help me achieve this. Your curiosity for and dedication to the wilderness continues to inspire me and I cannot wait to see where life leads us next.

To Mum and Dad: I’m ridiculously lucky to have parents who aren’t just family but are great mates too. Thanks for instilling in me an interest in nature from a young age and for always being there despite my pursuit of field research in far-flung places.

To Aunty Chris: Thanks for your support and for putting me up whenever I rolled through Melbourne on my way to Albury, not to mention while in Vietnam. Where are we going next?

To the rest of my family and friends: Thank you all for helping keep me sane over the duration of this process. Doing this from one of the most remote places in Australia has had its challenges, and I have leant on you all immensely for mental and social support. A special shout out to the fabulous Rhiannon Pigdon, Alisha van Vliet, and Cheryl McIlroy – thanks for keeping me grounded along the way and (most importantly) for the belly laughs.
To the volunteers: A big thank you to Allison Roberts, Tom Freire, Matilda Terry, and Sara Petrovic for taking a leap of faith and coming all the way up to the Top End to lend a hand. It was so good to get to know you all, especially while out and about in the bush. A big thanks to Reece Verdoorn as well for helping maintain fences.

To fencing contractor, Wally Snelling and workmates: Thanks for your help putting up the fences crucial to this project despite the ridiculous September heat.

To the Parks and Wildlife Commission of the Northern Territory and its staff: This project would not have been possible without your support. Thank you.

To the anonymous reviewers, editors, and associate editors who have reviewed publications submitted to peer reviewed journals: Thank you for your invaluable professional feedback which has helped improve our papers along the way.

And last but certainly not least, to the organisations which have funded this research; The Hermon Slade Foundation, the Ecological Society of Australia, Birdlife Australia, the Institute for Land, Water and Society, and the Australian Government Research Training Program: Without your generous financial support this project would never have been possible. Thank you.
Statement of Contribution

Two published papers, one submitted manuscript, and one manuscript in preparation for submission are reproduced in full as chapters in this thesis. The contributions that myself and others made to these chapters are as follows:


   Conceptualisation, writing, and review of the manuscript were performed by myself with supervisor contributions as follows: Melanie Massaro provided guidance and feedback on draft versions of the manuscript, and contributed to the review and editing of the final manuscript following reviewer comments.

**Chapter 3:** Submitted manuscript - Mihailou, H., Nimmo, D.G., & Massaro, M. Water scarcity exacerbates feral ungulate use of ephemeral savanna waterholes in northern Australia. Currently under peer review with Biological Invasions.

   Conceptualisation, methodology, data collection, data analysis, and written work were performed by myself with supervisor contributions as follows: Melanie Massaro and Dale Nimmo provided guidance during the conceptualisation and methodological development of the study. Dale Nimmo provided guidance and assistance with the statistical analysis of data. Melanie Massaro provided feedback on draft versions of the manuscript. Both Melanie Massaro and Dale Nimmo contributed to the review and editing of the final manuscript prior to submission.


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Permits

Approval to conduct this study was granted by the Animal Care and Ethics Committee of Charles Sturt University (Approved protocol numbers A17035 and A20056). Research was conducted in Limmen National Park with permission from the Parks and Wildlife Commission of the Northern Territory under scientific permit number 61071.
Abstract

Globally, savannas have been severely degraded through their conversion to pastureland for domesticated ungulate species. Grazing pressure from ungulates has negative impacts on native savanna flora and fauna species, particularly in areas where large herbivores have been absent for long periods, such as in northern Australia. Over the last ~200 years, several ungulate species have been introduced to northern Australia and have established large feral populations, including cattle (Bos taurus, B. indicus), Asian water buffalo (Bubalus bubalis), and pigs (Sus scrofa). These species have high water requirements and thus, congregate around water points. Water is a limited resource in savannas, particularly during periods of seasonal and interannual water scarcity. Hence, many native species also rely on savanna waterholes, which provide habitat, food, and water resources. However, it is largely unknown how periods of water scarcity affect feral ungulate behaviour around waterpoints and what flow-on effects this has on native flora and fauna communities in Australian savannas. In this study, I investigate these knowledge gaps using an ungulate exclusion experiment at ephemeral savanna waterholes in Limmen National Park, Australia.

To investigate how water scarcity affects feral ungulate use of waterpoints, I studied changes in the seasonal and interannual visitation behaviours of feral cattle, water buffalo, and pigs at savanna waterholes. All three species visited waterholes more often, for longer periods, and in larger numbers during a drought year, compared to an average rainfall year. Cattle considerably increased their use of waterholes as the dry season progressed, while buffalo did not change their waterhole use. Pig visitation to waterholes only increased when water scarcity was most extreme at the end of the dry season during the drought.

In African savannas, large herbivores can competitively exclude smaller species from accessing water. Yet, no studies have investigated whether the presence of large feral ungulates at waterholes affects the behaviour of smaller native herbivores in Australia. I found that macropods avoided waterholes when cattle presence was high but did not preferentially use waterholes where ungulates were excluded. The potential for competition between feral and native herbivores is exacerbated by water scarcity.

Australian savannas support a rich diversity of birds, which rely on waterholes for drinking and bathing, particularly when water is scarce. Ungulates aggregate around waterholes, but few Australian studies have investigated how this impacts native plant and bird communities in water limited savannas. I found that ungulate presence affected vegetation recovery during a drought and bird diversity was significantly lower as the dry season progressed.
Overall, this study demonstrates that even highly mobile fauna, such as macropods and birds, suffer negative impacts from ungulate activity around waterpoints, particularly during water scarcity events. Vegetation communities closest to water are the most vulnerable and are damaged even at very low ungulate densities. The use of fencing to exclude ungulates from small, but resource rich areas in Australian savannas provides important refugia sites for native fauna. Collectively, we must find practical, scientifically informed solutions to control feral ungulate species before vulnerable native species are lost.
Chapter 1: General Introduction

1.1: Savannas and introduced ungulates

Distributed across the tropical and sub-tropical latitudes, savannas cover approximately 20% of the global land surface (Whitley et al. 2017; Pennington et al. 2018). Savannas are ecosystems where enough light penetrates the tree canopy to support the growth of dense perennial and annual grass communities, as well as shrubs and mid-level tree species (Haynes et al. 1991). Due to the availability of grasses, savannas typically support many herbivorous grazing and browsing mammal species, as well as a diverse array of small granivorous mammals and birds which feed predominately on grass-seed. Generally, the dry diets of these savanna species make them highly dependent on reliable sources of surface water for drinking (Fisher et al. 1972; Western 1975; Harrington 2002; Chamaillé-Jammes et al. 2007). However, rainfall in savanna environments is highly seasonal, whereby the majority of rain each year is concentrated over several months (wet season) and is then followed by ~5-7 consecutive months of little to no rain (dry season) each year (Solbrig et al. 1996). Moreover, rainfall in savannas can vary greatly between years, but because rain is concentrated over the wet season months, below average rainfall during this period can quickly lead to severe drought (Valeix et al. 2008). As a result, savanna waterholes act as natural hubs for animal activity where the density and diversity of species is more concentrated than in the surrounding landscape (Thrash et al. 1995; Redfern et al. 2003; Valeix 2011).

Globally, savannas have been extensively degraded by human activity (de Lima et al. 2018), and almost 50% of their total area had been converted to pasture and crop land by the year 2000 (Ramankutty et al. 2008). Savannas have likely been further impacted over the last ~20 years, as pastoralism has continued to intensify, particularly in South America (Williams and Anderson 2020). Pastoralism results in the replacement of the native herbivore fauna with domestic livestock species, particularly ungulates such as cattle (Bos spp.) and goats (Capra hircus). Domestic ungulate populations can be maintained at much greater densities than in their natural habitats because human intervention provides protection against disease, predation, and resource bottlenecks (Freeland 1990; Skarpe 1991; Oesterheld et al. 1992). One of the most expansive savanna ecosystems on Earth is found in northern Australia (Woinarski et al. 2007). Unlike those on other continents (e.g., Africa, South America), plant species in Australian savannas evolved in the absence of hooved mammals (Skarpe 1991; Scogings and Sankaran 2019), such as deer (Family Cervidae) and wildebeest (Connochaetes spp.). Following the extinction of the megafauna
~45,000 years ago (Skarpe 1991; Scogings and Sankaran 2019), the biggest extant grazers native to Australian savannas are marsupials of the family Macropodidae (including kangaroos and wallabies), of which the largest northern species typically weigh <55kg (Reid et al. 2020b). Thus, many native plant species in Australian savannas do not possess physiological adaptations to cope with grazing pressure from introduced ungulate species (Ash and McIvor 1998). In addition, due to high rainfall variation in savannas, vegetation communities can be slow to recover from periods of water stress (Schwalm et al. 2017). Together, these factors have made Australian savanna ecosystems particularly vulnerable to disturbance caused by increased grazing pressure following the introduction of large exotic herbivore species (Freeland 1990; Ash and McIvor 1998; Sankaran 2019). Since the establishment of pastoralism in northern Australia in the 1860s, several species of ungulate have been introduced to the region (Woinarski and Ash 2002) including cattle (*B. taurus* and *B. indicus*), Asian water buffalo (*Bubalus bubalis*), and pigs (*Sus scrofa*). Following their escape or intentional release from settlements and pastoral lands, these species have successfully established large feral populations across northern Australia (Ridpath 1991; Wilson et al. 1992; Woinarski et al. 2007). However, feral ungulate populations in northern Australia have not been comprehensively surveyed since the 1980s, despite their presence in conservation reserves, indigenous protected areas, and national parks (Bayliss and Yeomans 1989; Kakadu National Park Board of Management 2016; Clancy and Vincent 2021). Furthermore, there is evidence that feral ungulate populations have recently expanded in size and distribution, including dispersal into new areas (Caley 1997; Cowled et al. 2009; Saalfeld 2014). What impacts this ongoing population growth and dispersal has had on native ecosystems is largely unknown.

### 1.2: Ungulates and their water requirements

Ungulates need to drink regularly and require high volumes of water, with some species drinking up to 10 percent of their body weight daily (Hunt et al. 2013; Bray et al. 2015). In hot climates, Australian beef cattle can drink up to 75 litres of water per day (Watts et al. 2016). The amount of water ungulates require daily can also change depending on the dryness of available fodder, salt intake, lactation, and external temperatures (Schlink et al. 2010). Some ungulate species also require water for other reasons. For example, water buffalo and pigs need access to mud in hot climates to thermoregulate efficiently because they have fewer sweat glands than other ungulates (Tulloch and Litchfield 1981; Ridpath 1991; Bracke 2011). Mud is used because it has a greater evaporative potential than water
(i.e., keeps the animal cool for longer) and has the added benefit of limiting skin exposure to biting insects (Tulloch and Litchfield 1981; Bracke 2011).

The dependency of ungulates on water usually results in their congregation in areas where water is easily accessible (Tomkins and O'Reagain 2007; Graz et al. 2012). However, rainfall in Australian savannas can fluctuate greatly between years and drought is a major cause of ungulate mortality due to thirst, starvation, bogging in mud, and ingestion of toxic weeds (Ridpath 1991; Dobbie et al. 1993). In northern Australia, the availability of surface water declines each year as the dry season progresses (i.e., time since last rainfall increases) and is also limited during years of low annual rainfall (Haynes et al. 1991; Woinarski et al. 2007). During such periods of seasonal and interannual water scarcity, ungulate activity in natural savanna ecosystems becomes concentrated around a shrinking number of water resources (Valeix 2011; Pettit et al. 2012). This also concentrates grazing pressure around waterpoints, as ungulates rarely distribute themselves more than 5km from a water source (Tomkins and O'Reagain 2007; Graz et al. 2012). This can lead to the formation of a spherical gradient of disturbance surrounding waterpoints known as a piosphere, where areas closest to water are the most impacted by ungulate trampling and grazing damage (Thrash and Derry 1999; Illius and O'Connor 2000). As water is a limited resource in savanna ecosystems, the dependency of ungulates on water has the potential to impact native wildlife, particularly species with high water requirements.

1.3: The study area
To date, most research concerning ungulate impacts on the savannas of northern Australia has focussed on the more mesic areas of the Northern Territory, Western Australia, and Queensland. In particular, water buffalo impacts in the areas surrounding Kakadu National Park and the Alligator Rivers regions have been well studied (see Chapter 2). Comparatively little research has been done in the more xeric regions of northern Australia, hence there is a significant knowledge gap concerning the effects of ungulates in the drier savannas of northern Australia. An area which has been particularly poorly studied is the Gulf of Carpentaria region of the Northern Territory. In this region lies Limmen National Park (Fig. 1), which protects over a million hectares of open savanna plains and rocky ridgeline country.

Limmen National Park was declared in 2012 and is currently the third largest national park in Australia. It is comprised of several land parcels which were previously operated as cattle stations. Today, Limmen National Park is surrounded by a number of private and commercial pastoral properties (Department of Environment, Parks, and Water Security
2022). The perimeter of the national park measures over 700km (Fig. 1) and fences separating the park from bordering pastoral properties are either non-existent or are rarely maintained (pers. obs.). As a result, cattle from the surrounding properties are able to access the park freely. Many of these cattle are typically mustered off the national park by neighbouring pastoralists on an annual or biennial basis (unpublished: Clancy and Vincent 2021). However, between musters, these cattle continue to reproduce and may have substantial detrimental impacts on the soils, vegetation communities, wetlands, and wildlife of the national park (see Mihailou and Massaro 2021). This has led to the establishment of a feral cattle population in Limmen National Park, which consists primarily of European long- and short-horn breeds (pers. obs.). These unbranded cattle are sometimes mustered off park land via a public tenure system, but are otherwise largely left alone, as property law in the Northern Territory complicates culling by land managers (unpublished: Clancy and Vincent 2021).

Fig. 1: Location and size of Limmen National Park (NP) in the Gulf of Carpentaria region of the Northern Territory, Australia.

A recent aerial survey of the feral ungulate population within Limmen National Park by Clancy and Vincent in 2021 (unpublished) found that cattle were the most abundant species (0.75 individuals/km²), followed by water buffalo (0.24 individuals/km²; Fig. 2). Horses (*Equus caballus*), donkeys (*E. asinus*), and pigs were also present at very low
densities (<0.1 individual/km²), but the precision for sighting pigs from a light plane was impaired by their smaller size and preference for denser habitats compared to other ungulates. As pigs and their sign (scat, tracks) were often observed around study waterholes in the lead up to data collection, pigs were included in the study, while horses and donkeys (of which there was little sign) were not. Overall, ungulate densities within the park were found to be low (<1 individual/km²). However, it is important to note that because this survey was conducted in May 2021 following an above average wet season, ungulates were still widely dispersed throughout the park and harder to detect, compared to the late dry season when water is scarcer. In addition, the park experienced a severe drought over the two years prior to the survey, hence the reported ungulate densities are likely to be lower than during the period data were collected for this research project (i.e., due to drought related mortality).

Fig. 2: Feral cattle (a) and water buffalo (b) at ephemeral savanna waterholes in Limmen National Park.
1.4: Thesis overview

Ungulate visitation to natural wetlands has negative impacts on native Australian flora and fauna communities (e.g., Skeat et al. 1996; Ludwig et al. 1999; Fordham et al. 2006; van Doorn et al. 2015). Yet, few studies have investigated whether the waterhole visitation behaviour of feral ungulates affects native fauna communities in the water limited savanna habitats of northern Australia. Furthermore, how periods of seasonal and interannual water scarcity affect feral ungulate behaviour has not been comprehensively investigated in Australia and the flow-on effects for water dependant native species are largely unknown. Hence, the overarching aim of this study was to investigate whether feral ungulate visitation to waterholes in the water limited savanna habitats of northern Australia affects native flora and fauna communities, particularly during periods of interannual and seasonal water scarcity. To address these questions, I surveyed feral ungulates, native plants, and wildlife communities surrounding 20 ephemeral savanna waterholes in Limmen National Park in the Gulf of Carpentaria region of the Northern Territory, Australia. I also conducted a fencing experiment to determine if native flora and fauna communities were significantly affected by the exclusion of feral ungulates from savanna waterholes.

To provide context for this thesis, I first presented a brief history of ungulate introductions to northern Australia and conducted a comprehensive review of the literature about how domestic and feral populations have impacted the savannas, wetlands, and biota of the region (chapter 2). This review focuses on three key ungulate species; cattle, water buffalo, and pigs. Other ungulate species with feral populations in northern Australia were excluded either because their distributions were limited, or there has been little research done on their impacts in the region. First, I discussed the impacts of cattle, water buffalo, and pigs on soil, water quality, wetland hydrology, vegetation, fire regimes, and the spread of exotic plants in Australia’s tropical savannas and associated wetland habitats. I then examined what flow-on effects these impacts have had on native terrestrial wildlife communities and identify current knowledge gaps which are further addressed in the remaining chapters of this thesis.

As highlighted in my literature review, the impacts of ungulates are concentrated around waterpoints (Ludwig et al. 1999; Illius and O’Connor 2000; Landsberg et al. 2003). However, the extent to which feral ungulates use waterholes in the water limited savannas of northern Australia is largely unknown. In chapter 3, I investigated the behavioural similarities and differences in how cattle, water buffalo, and pigs used ephemeral savanna waterholes in Limmen National Park. I also examined whether these species changed the way they used waterholes during periods of seasonal and interannual water scarcity.
Despite the large size and high water needs of feral ungulates, no Australian studies have investigated how their visitation to waterholes can affect the behaviour of native species, despite evidence of detrimental impacts overseas (e.g., Ostermann-Kelm et al. 2008; Gooch et al. 2017; Hall et al. 2018). In chapter 4, I investigated the potential for competitive overlap in waterhole use between feral ungulates and native macropods based on their temporal activity patterns. I also tested whether the exclusion of feral ungulates from savanna waterholes and changes in predation risk during different moon phases affected macropod visitation to waterholes.

Much of the research on exotic ungulate impacts globally has focussed on their effects on other mammals, particularly native ungulate species (e.g., Ostermann-Kelm et al. 2008; Hall et al. 2018), small marsupials, and rodents (e.g., Legge et al. 2011; Woinarski et al. 2011; Neilly and Schwarzkopf 2018). While some recent studies have been conducted (e.g., van Doorn et al. 2015; Hall et al. 2016, Neilly and Schwarzkopf 2019), comparatively little research has focussed on ungulate impacts on native bird assemblages, presumably because they are typically highly mobile. However, Australia’s savannas support a rich diversity of bird species, many of which have high water requirements (Fisher et al. 1972; Harrington 2002). Furthermore, some species have suffered severe declines in their abundance and distribution due to the combined negative effects of grazing and fire on vegetation structure (Garnett and Crowley 1997; Franklin 1999; Legge et al. 2015). Hence, there is potential for ungulate impacts on the vegetation communities surrounding savanna waterholes to have impacts on bird assemblages, particularly in water limited environments. Hence, in chapter 5, I investigated how the exclusion of feral ungulates during periods of seasonal and interannual water scarcity affected the plant communities in the receding water zone and wider savanna surrounding waterholes. I then tested whether the species richness and abundance of birds from several different feeding guilds was influenced by ungulate presence and seasonal and interannual water scarcity. Finally, I tested whether the amount of cover of different plant lifeforms affected the distribution of bird assemblages around savanna waterholes.

This thesis concludes with a final synthesis of the main outcomes of my research and identifies important directions for future research (chapter 6). I also discussed potential implications for the conservation management of native savanna flora and fauna communities affected by feral ungulate presence. Finally, I highlight how conflicting opinions regarding the management of domestic and feral ungulate populations in northern Australia is perpetuating the problem at the cost of native species.
Throughout this thesis, the term ‘refugia’ is used as defined by Seddall et al. (1990): “Habitats or environmental factors that convey spatial and temporal resistance and/or resilience to biotic communities that have been impacted by biophysical disturbances.”
Chapter 2: An overview of the impacts of feral cattle, water buffalo and pigs on the savannas, wetlands and biota of northern Australia

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An overview of the impacts of feral cattle, water buffalo and pigs on the savannas, wetlands and biota of northern Australia

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Abstract Since the extinction of the megafauna some 45 000 to 50 000 years ago, grazing pressure on Australian savannas has been relatively low compared to that on savannas in other continents. However, the introduction of several species of ungulate, primarily during the 1800s, and the establishment of large feral populations in northern Australia has resulted in an increase in grazing pressure compared to pre-colonial times when soft-footed macropods were the largest extant grazers. Here, we provide an overview of the introduction of three key ungulates to northern Australia: cattle (Bos taurus, B. indicus), Asian water buffalo (Bubalus bubalis) and pigs (Sus scrofa), and the impact of these populations on both abiotic and biotic elements of savanna habitats in northern Australia. Feral ungulate populations have considerable impacts on soil, water quality, waterhole hydrology, vegetation, fire regimes and the spread of exotic plants, and resulting changes to habitat have flow-on effects for native wildlife. Ungulate impacts on vegetation communities and associated changes in fire regimes are particularly concerning given that sustained grazing can lead to the permanent removal of key grass species and changes in fire intensity and frequency can result in the conversion of grassland to woodland. Native wildlife can be affected by ungulate disturbance in a multitude of ways, but overwhelmingly, habitat loss or degradation is the main driver for declines in biodiversity. Based on current knowledge gaps, we discuss potential directions for future research about how feral ungulate activity affects Australian native species and their impact on savanna habitats.

Key words: Australia, disturbance, feral ungulate, grazing impacts, savanna.

INTRODUCTION

Since the extinction of the Australian megafauna species 45 000 to 50 000 years ago, soft-footed macropods represent the largest extant native herbivores in Australian savannas (Freeland 1990; Skarpe 1991; Scogings & Sankaran 2019). Australian macropod species exhibit a variety of feeding strategies ranging from grazing to browsing, however, given their lower metabolic biomass compared to herbivores in other savannas, Australian savannas have received considerably less historical grazing pressure (Calaby 1980; Skarpe 1991). As a result, plant species in Australian savannas do not exhibit the same capacity to compensate for grazing pressure compared with those on other continents (e.g. Africa) (Ash & McIvor 1998) and are thought to be particularly susceptible to change from grazing by large introduced ungulates (Freeland 1990; Ash & McIvor 1998; Sharp & Whittaker 2003). In addition, some Australian savannas occur in areas with nutrient-poor soils that support vegetation which is low in minerals and unable to sustain a large biomass of grazing animals (Skarpe 1991). These differences in the evolutionary history of Australian savannas, paired with recent evidence of expansive declines in native fauna (e.g. Woinarski et al. 2001; Franklin et al. 2005; Garnett et al. 2010; Woinarski et al. 2011), warrant a review of how the introduction of several large ungulate species has affected the savannas, wetlands and biota of northern Australia.

In this review, we focus on the impacts of three key ungulates: cattle (including Bos taurus and B. indicus), Asian water buffalo (Bubalus bubalis) and pigs (Sus scrofa) on the savannas, wetlands and biota of northern Australia. First, we provide an overview of the introduction of cattle, water buffalo and pigs to northern Australia. Second, we discuss how current feral populations in northern Australia are impacting the soil, water quality and wetland hydrology, vegetation, fire regimes and the spread of exotic plants in tropical savannas and associated wetland habitats. Throughout, we acknowledge that present-day ungulate impacts may not necessarily reflect historical change. Finally, we discuss the flow-on impacts of these feral species on native terrestrial wildlife and make recommendations for future research about how feral ungulate activity affects Australian native species and their impact on savanna habitats.

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research in Australia based on current knowledge gaps. While several other ungulate species have been introduced to northern Australia, either their populations within northern savannas are small or restricted in distribution (banteng: B. javanicus, sambar deer: Rusa unicolor, rusa deer: Rusa timorensis, chital deer: Axis axis, red deer: Cervus elaphus, goats: Capra hircus, camels: Camelus dromedarius) (Freeland 1990; Wilson et al. 1992; West 2018), or there has been little study on their impacts in Australian savannas (horses: Equus caballus, donkeys: E. asinus). For these reasons, we have excluded these species from this review.

BACKGROUND

Due to its wet-dry monsoonal rainfall patterns and fire regimes, northern Australia is dominated by savannas, which cover approximately 1.5 million square kilometres (Fig. 1a) and support a diverse range of flora and fauna (Woinarski et al. 2007). A rainfall gradient exists in the northern savannas, with the greatest rainfall occurring in the mesic northern coastal regions and the lowest in the southern xeric regions towards the arid interior of Australia (Fig. 1b). Given that the vast majority of the northern savannas occur in latitudes above the Tropic of Capricorn (Fig. 1a), we refer to them throughout this review as ‘tropical savannas’.

Pastoralism in Australia’s northern savannas began with the establishment of cattle ranches in northern Queensland in the 1860s (Woinarski & Ash 2002). From there, pastoralism spread westward across the Northern Territory and into Western Australia (Woinarski & Ash 2002). In addition to cattle, several other exotic species of ungulate were introduced to provide food and animal labour for establishing European settlements. As most livestock were not kept in fenced enclosures, some eventually escaped into the wild or were released when settlements failed and these livestock went on to establish feral populations (Ridpath 1991). Introduced ungulates, including cattle, water buffalo and pigs, occur at greater densities in northern Australia than in their respective natural habitats, most likely due to the general lack of large predators and comparatively fewer pathogens than in their native ranges (Freeland 1990). Ungulates need to drink frequently due to their dry diet; hence, they are typically distributed close to water sources (Tomkins & O’Reagain 2007; Graz et al. 2012). Pastoralists have traditionally favoured wetlands and their surrounds for stock grazing because high concentrations of nutrients in these areas produce good quality feed (Finlayson et al. 1999). Drought and late wet season onset are a major cause of mortality for some ungulates in northern Australia due to thirst, the ingestion of toxic plants which would normally be avoided (horses: Dobbie et al. 1993), starvation, and bogging of animals in thick mud surrounding drying water points (water buffalo: Ridpath 1991).

Two species were initially introduced in northern Australia: European breeds of Bos taurus (e.g. European long-horn, European short-horn) and the heat and drought tolerant brahman (B. indicus) which originated in the drier regions of south-western Asia (Epstein 1971; Ridpath 1991). Brahman have lower metabolic rates, are resistant to ticks common in northern Australia and can utilise less nutritious vegetation than European breeds (Frisch 1981; Frisch & Vercoe 1982; Ridpath 1991), making them well suited to the region. However, the establishment of feral brahman populations was limited by slow growth rates and reduced fertility when compared with European breeds (Ridpath 1991). Despite this, by 2007 the total population of cattle in northern Australia was estimated to include 5 million animals distributed over 75% of the landscape (Woinarski et al. 2007). While this figure includes both domesticated and feral cattle, it is important to note that pastoral properties in northern Australia are typically very large, undeveloped parcels of land in which water sources are widely separated (Hunt et al. 2013). As fencing is expensive to install and maintain, it is rarely expansive, and cattle are usually left free to roam the landscape and forage on unimproved native pasture until mustering (Hunt et al. 2014). This ‘free-ranging’ approach to most cattle management in the region means that the damage domestic herds cause to the landscape is likely comparable to feral populations. However, the degree of cattle damage to the landscape will vary based on animal densities and is most concentrated within 5km of waterpoints (Hunt et al. 2013).

Asian water buffalo (Bubalus bubalis) were introduced from South-east Asia to northern Australia several times between 1825 and 1866 (see Ridpath 1991). When settlements were abandoned, buffalo were released into the wild and rapidly established feral populations (Ridpath 1991; Skeat et al. 1996; Woinarski et al. 2007). In the mid-1880s, buffalo herds containing several hundred animals were a common occurrence in the Alligator Rivers region (Carrington 1885). However, populations were suppressed by the advent of the buffalo hide industry, which harvested thousands of animals annually for the manufacture of machinery belts (Skeat et al. 1996; Petty 2008; Werner 2014). The hide industry collapsed in 1956 (Skeat et al. 1996; Petty 2008), and by 1985 the feral buffalo population in the Northern Territory had grown to over 340 000 individuals (Bayliss & Yeomans 1989). In the late 1980s, high densities and fear of buffalo acting as reservoirs

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for disease which could impact northern Australia’s beef industry, initiated a large-scale government-sponsored eradication program known as the ‘Brucellosis and Tuberculosis Eradication Campaign’ (Skeat et al. 1996; Robinson et al. 2005; Petty et al. 2007). This program reduced buffalo densities in Kakadu National Park from 5.6 animals/km² to below 0.1 animals/km² by 1992 (Skeat et al. 1996). However, little population control has been conducted in the region since (Petty et al. 2007). Substantial populations still exist in Kakadu and in nearby Arnhem Land (Finlayson et al. 1999; Petty et al. 2007), where the buffalo population was recently estimated at around 97 000 (Saalfeld 2014). The eradication campaign in Kakadu had large-scale impacts on vegetation communities, with both native and introduced plants rapidly recolonising grazed out areas and obstructing waterways (Minchin & Dunlop 1989; Ridpath 1991; Finlayson et al. 1999; Werner 2014). Buffalo is still widely distributed across northern Australia, particularly the Northern Territory, however, their management is complicated by their ability to range long distances and by local opposition to their removal due to their value to the tourism industry and as food and revenue for Aboriginal landholders (Skeat et al. 1996; Robinson et al. 2005; Ens et al. 2016).

Pigs (Sus scrofa) first established feral populations on the Cobourg Peninsula between 1829 and 1849, but were also introduced from Timor at Escape Cliffs near Darwin in 1866 (Letts 1964; Ridpath 1991). Feral pigs are now widely distributed across northern Australia and are still dispersing into some parts of east Arnhem Land and the Kimberley region at an estimated rate of 2km per year (Choquenot et al. 1996; Caley 1997; Cowled et al. 2009). Pigs cause significant damage to wetland verges and surrounding woodlands (Ridpath 1991; Finlayson et al. 1999), which they favour as habitat due to the availability of water, shade and food, as the alluvial soils surrounding wetlands allow for easy foraging (Caley 1997). Pigs are omnivorous, feeding on subterranean vegetation (e.g. tubers and rhizomes), as well as terrestrial vegetation, small wildlife (e.g. turtles) and carrion (Bowman & McDonough 1991; Ridpath 1991; Fordham et al. 2006; Waltham & Schaffer 2017). Feral pigs can breed at any time of the year and are able to produce a litter of 4–8 piglets twice a year under
good conditions (Ridpath 1991). Pig populations are known to increase following the removal of buffalo from suitable habitats (Corbett 1995; Finlayson et al. 1999; Werner 2014). This is because buffalo outcompete pigs for food resources, damage favoured pig habitats and compact soil around wetland verges, making foraging more difficult for pigs (Corbett 1995; Finlayson et al. 1999).

IMPACTS OF FERAL UNGULATES ON SAVANNA HABITATS

Impacts on soil

Grazing by feral ungulates has been correlated with changes in the characteristics of savanna grass communities, where deep-rooted vegetation is replaced by shallow-rooted species, which can lead to increased erosion due to decreased soil stability (Skeat et al. 1996; Finlayson et al. 1999). Where grazing has been severe enough, scald areas can develop where erosion completely removes the topsoil to expose the denser subsoil beneath which can greatly impede the regeneration of vegetation (Fogarty 1982; Tothill & Mott 1985; Winter 1990; Sharp & Whittaker 2003). In addition, areas which experience high ungulate traffic, such as 'camp' sites and along tracks leading to water sources, can become completely denuded of vegetation, exhibit high soil compaction and reduced soil aggregate size (Tothill & Mott 1985; Skeat et al. 1996). Such compaction impedes the permeation of water through soils, which affects plant recruitment, can increase plant mortality and can lead to the formation of erosion gullies following heavy rain (Braithwaite et al. 1984; Macdonald & Frame 1988; Skeat et al. 1996). However, these impacts can be reversed under some conditions. For example, fencing floodplain sites to exclude buffalo in Kakadu National Park resulted in a marked improvement of soil quality, with soils developing a more friable consistency (i.e. crumbly and better able to support plant root development) (Tothill & Mott 1985). Ungulates also cause soil disturbance around the margins of wetlands by creating pugs and wallows, which can have impacts on waterhole hydrology and water quality (Skeat et al. 1996). Wallows are created by rolling in mud around wetland margins and are used by buffalo and pigs to reduce insect attack and thermoregulate, as mud dries much more slowly than water (Tulloch & Litchfield 1981; Bracke 2011). In northern Australia, the impacts of feral ungulates on soil are most prevalent in floodplains and around perennial waterholes (Skeat et al. 1996). Those floodplains with silty or sandy soils are particularly susceptible to erosion and regenerate slowly following disturbance, while black-clay floodplains are more susceptible to physical disturbance from pugging and wallowing, but recover quickly (see Skeat et al. 1996; Petty et al. 2007; Petty 2008).

Impacts on water quality and wetland hydrology

Feral ungulates increase water nutrient levels through direct contamination of wetlands with excrement and indirectly when waste from surrounding areas is washed into wetlands by wet season rains (Finlayson et al. 1999). For example, cattle access to waterholes increases nitrogen and phosphorous levels in water and in littoral zones (Pettit et al. 2012). Such increases in nutrient loads may cause eutrophication of waterholes, triggering algal blooms and decreasing overall water quality (Ridpath 1991; Pettit et al. 2012). In addition, the foraging actions of pigs result in the overturning of benthic soils (Ridpath 1991), which can lead to increased water turbidity due to particle resuspension in nearby waterbodies and can contribute to eutrophication (Waltham & Schaffer 2017). Resuspension of organic material in the water column can also decrease dissolved oxygen levels and may affect habitat suitability for aquatic plants and animals (Waltham & Schaffer 2017). The action of wallowing increases water turbidity both directly and through erosion by runoff (Finlayson et al. 1997). Buffalo and pigs wallow more frequently than other ungulates, such as cattle, because they have fewer sweat glands (Tulloch & Litchfield 1981; Bracke 2011). Buffalo use wallows preferentially over shade and spend more time grazing when a wallow is available than when there is shade alone (Tulloch & Litchfield 1981). Pugging and wallowing of wetland margins by buffalo can also increase the surface area exposed to evaporation and cause decreased water retention over dry periods (Skeat et al. 1996). In addition, a study at Kapalga in Kakadu National Park, found that feral buffalo can drink up to 21 litres of water daily in the mid dry season, which may have considerable impacts on water availability at high population densities (Williams & Ridpath 1982).

The potential for perennial waterholes to recover from cattle disturbance relies on wet season flooding either directly by rains or by water flow from seasonally connected watercourses (Pettit et al. 2012). In addition, the depth of perennial waterholes may affect their resilience to cattle damage, with deeper waterholes less susceptible to increases in water turbidity than shallow ones (Pettit et al. 2012). This is thought to be due to the greater accessibility of shallow waterholes to cattle during the late dry season and the compounding effects wind has on the resuspension of particulate matter into the water column.
(Pettit et al. 2012). Hence, the flushing of waterholes by wet season rains may be more important for maintaining the health of shallow waterholes than for deeper ones (Pettit et al. 2012).

Wetland hydrology can also be affected at a landscape scale, as grazing of soil-stabilising, salt-tolerant grasses, trampling of levees and creation of swim channels by buffalo prior to the eradication campaign in the South Alligator River region resulted in the intrusion of saltwater into freshwater wetland systems (Fogarty 1982; Tothill & Mott 1985; Finlayson et al. 1997; Petty 2008). This had widespread impacts on wetlands in the region, including increased salinity and siltation due to tidal infiltration, die-off of salt-intolerant vegetation, increased erosion and accelerated drying times (Stocker 1970; Fogarty 1982; Finlayson et al. 1997; Petty 2008).

Impacts on vegetation and fire regimes

In general, grazing by cattle and buffalo in Australian savanna environments results in a shift from dominant perennial grass species to annual grasses (Tothill & Mott 1985; Minchin & Dunlop 1989; Skeat et al. 1996; Ash & McIvor 1998; Kutt & Woinarski 2007; Petty 2008). The exclusion of either of these ungulate species and/or declines in stocking rates results in the regeneration of some perennial grasses (Fogarty 1982; Foran & Bastin 1984; Minchin & Dunlop 1989; Skeat et al. 1996). Long-lived perennial grass species are more susceptible to cattle grazing impacts than shorter-lived perennial species, particularly under drought conditions (Orr & O’Reagan 2011). Nonetheless, areas which have been subjected to heavy erosion are less responsive to changes in grazing pressure and either remain bare or support mostly weeds and annual native forbs and herbs (Fogarty 1982). Grazing by feral ungulates can also greatly affect vegetation biomass. For example, a fence line comparison study showed that areas grazed by buffalo had a ground level biomass of 2–3 tonnes/hectare compared with 5-8 tonnes/hectare in areas where buffalo had been excluded (Werner 2005).

The timing of grazing is also an important factor which can have lasting impacts on plant growth and recovery. A study in the Northern Territory found that native perennial grasses which had been exposed to moderate or heavy cattle grazing across an eight week period at the start of the wet season had a lower standing biomass that year and suffered reduced abundances for the following two years (Ash & McIvor 1998). As in other studies, declines in native perennial grass species abundance were linked to increases in the abundance of annual grasses and forbs (Ash & McIvor 1998). A similar study of native perennial grass, Allotropis semialata, found that grazing during the early wet season resulted in lower seed yields for at least two years, even when plant size was not affected (Crowley & Garnett 2001). By comparison, grazing during the dry season had no impact on grass composition and productivity, because the studied grasses had already produced seed and were not actively growing during this period (Ash & McIvor 1998). Another important factor which influences the impacts of grazing is rainfall, with heavy cattle grazing during drought years exacerbating the detrimental impacts on mitchell grasslands in the Northern Territory (Foran & Bastin 1984).

Proximity to water also affects impacts on plant communities, as trampling and grazing by cattle and buffalo causes a decrease in the species diversity and structural complexity of vegetation, including the removal of the grassy understory, reduction in the shrub layer and damage to woody vegetation in riparian areas and around the periphery of waterholes (Ludwig et al. 1999; Landsberg et al. 2003; Petty et al. 2007; Skroblin & Legge 2012; van Doorn et al. 2015). These impacts can extend in a gradient (known as a piosphere) for several kilometres around water points (Lange 1969; Ludwig et al. 1999; Hunt et al. 2013) and are further exacerbated during the dry season, as the drying of water points concentrates grazing around those waterholes still containing water (Harrington et al. 1984; Pettit et al. 2012). Feral ungulate activity also has impacts on aquatic vegetation, such as the floating grass mats found in Northern Territory floodplains (Fogarty 1982; Hill & Webb 1982; Skeat et al. 1996). Grazing and trampling by buffalo in the Alligator Rivers region resulted in the rapid decline of billabong grass mat coverage, which dropped from 30% to only 5% coverage over a 15 year period (Hill & Webb 1982).

While buffalo grazing during the dry season may have fewer direct impacts on vegetation productivity than at other times of the year, it has been shown to reduce understory vegetation biomass (Skeat et al. 1996; Werner 2005), which can impact fire regimes due to changes in fuel loads (Woinarski et al. 2007). Selective grazing can also cause a shift in dominance from perennial grass species which remain green well into the dry season, to more palatable, earlier drying annual species which can increase the intensity and frequency of burns, as well as reducing the patchiness of late dry season fires (Skeat et al. 1996). Heavy sustained grazing by cattle in savanna can remove the herbaceous layer of vegetation and result in fires that are smaller and of lower intensity than would naturally occur (Sharp & Whittaker 2003). Such changes in fire regimes caused by cattle grazing can lead to rapid increases in woody vegetation due to decreased fire mortality and can result in permanent changes to savanna habitats (Sharp & Whittaker 2003).
Buffalo can cause direct mortality to small monsoonal rainforest trees (Braithwaite et al. 1984) and palms (Riley 2005) by trampling, scratching and knocking them over by graze on leaves. Buffalo is also known to suppress woody vegetation on floodplains by grazing on seedlings and saplings (Lucas & Russell-Smith 1993; Riley 2005; Petty 2008). However, contrary to these findings, a fencing experiment at Kapalga, Kakadu National Park, found that buffalo removal resulted in reduced recruitment rates and 20% lower coverage of woody vegetation after 8 years compared to sites where buffalo had been free to graze (Werner 2005). The removal of buffalo grazing pressure resulted in an increase in herbaceous biomass, which is thought to have increased competition for resources and negatively affected woody recruitment (Werner 2005).

However, the impacts of buffalo on floodplain and savanna habitats have been disputed, as Bowman et al. (2008) speculated that changing CO₂ levels, rainfall and fire regimes may have had a greater influence on savanna ecosystems than buffalo. This was countered by Petty and Werner (2010), who highlighted that aerial photographs of a buffalo-proof fence line (photographs published in Petty et al. 2007) showed more shrubs and young trees on the side buffalo had been excluded for 4 years, despite experiencing common changes in other environmental factors flagged by Bowman et al. (2008). In any case, interactions among factors affecting vegetation communities are complex and disturbance from feral ungulates may have substantial impacts (Sharp & Whittaker 2003).

It is also important to note that present-day ungulate disturbance to vegetation may not necessarily reflect historical disturbance. For example, wetland plant species sensitive to grazing and trampling by pigs may have already been removed from ecosystems by persistent disturbance since pig introduction (Doupé et al. 2010) and hence, measures of plant species richness in areas where ungulates have been excluded in recent times may be significantly lower than prior to their introduction. Studies in northern Australia have found that heavy cattle stocking rates result in irreversible changes to savanna vegetation communities (Walker et al. 1997; Sharp & Whittaker 2003). Grazing by cattle can strip the ground layer of vegetation to bare soil, with the only vegetation left being unpalatable species or those of low nutritional value (Sharp & Whittaker 2003). This is of concern in savanna systems, as removal of 90% coverage for three consecutive years is enough to prevent the re-establishment of Themeda triandra, a dominant native perennial grass species (Walker et al. 1997). This grass species is highly palatable to cattle and is selectively grazed, hence, even when grazing intensity is low, there is a high probability of local extinction when stocking is continuous (Ash & Corfield 1998).

Another important consideration of ungulate impacts on Australian plant communities is the hysteresis effect, where the process of recovery may lag after ungulate removal or may not mirror that of the original degradation (Searle et al. 2009). Hence, the removal of grazing pressure may not result in a direct return of the ecosystem to the same state prior to disturbance, as demonstrated following removal of buffalo from Kakadu National Park (Werner 2005; Werner et al. 2006; Petty et al. 2007). In addition, it has been theorised that the interaction between rainfall and the history of grazing in a given ecosystem may affect the tolerance of native plant species to grazing (Milchunas et al. 1988). Plant communities that evolved without much grazing pressure may be more vulnerable to change caused by increased grazing pressure from large, introduced grazers.

Spread of invasive plants

Grazing not only affects native plant communities, but also creates disturbances which allow the establishment of invasive plant species. Introduced plant species are common in northern Australia and considered to be one of the biggest threats to biodiversity in the region (Humphries et al. 1991). For example, the impacts of several exotic pasture grass species, including gamba grass (Andropogon gayanus) and mission grass (Pennisetum polystachion), are formally recognised as a key threatening process under the Australian Environmental Protection and Biodiversity Conservation Act (Department of Sustainability, Environment, Water, Population & Communities 2012). Exotic grasses have been shown to affect fire intensity and seasonality (Rossiter et al. 2003; Ferdinands et al. 2006; Setterfield et al. 2010), deplete soil nutrient loads (Rossiter-Rachor et al. 2008), encroach on wetland habitats and replace breeding grounds for aquatic wildlife (Humphries et al. 1991). Pasture grass encroachment facilitated by cattle grazing has also been shown to impact fauna assemblages, with declines in some ground nesting birds and terrestrial reptiles (Kutt & Fisher 2011). Grazing by feral ungulates may also lead to the loss of disturbance-susceptible plant species and assist the spread of invasive terrestrial and aquatic plants (Skeat et al. 1996; Pettit et al. 2012).
communities in areas associated with high ungulate traffic, such as the margins of floodplains and woodlands, have been found to be some of the most severely affected by exotic plants (Cowie & Werner 1993). For example, *Hypstis suaveolens* is readily spread by cattle and buffalo via epizoochory (i.e. seed attachment to animal exterior for dispersal) and flourishes in riparian zones, particularly those where native perennial species have already been removed by grazing (Ridpath 1991; Skeat et al. 1996). Fence line comparisons in Kakadu National Park have also found that buffalo presence is correlated with increased densities of several other invasive plant species, including *Sida cordifolia, Triumfetta rhomboidea* and *Stylosanthes humilis* (Skeat et al. 1996). The removal of grazing pressure can also benefit some exotic plants, such as *Stylosanthes scabra*, which significantly increased in cover over 10 years following the conversion of a QLD pastoral cattle property to a conservation reserve (Kemp & Kutt 2020).

**IMPLICATIONS FOR TERRESTRIAL WILDLIFE**

The advent of pastoralism and establishment of feral ungulate populations in northern Australia coincided with the breakdown of traditional Aboriginal fire regimes, which together are considered the primary factors contributing to a regional decline in the biodiversity of native fauna (Woinarski et al. 2001; Franklin et al. 2005; Woinarski et al. 2011; Stobo-Wilson et al. 2020). Vegetation communities affect habitat suitability for a wide range of animal species, as they provide physical structure to an environment (Tews et al. 2004). Structural complexity influences the resources available to animals, including food (either provided by the vegetation itself or the invertebrates it attracts), shelter and breeding grounds (Woinarski 2000). Changes in structural complexity due to the direct (e.g. reduced vegetation cover) and indirect impacts (e.g. changed fire regimes, exotic plant invasion) of ungulate grazing have also been associated with increased predation due to reduced cover (McGregor et al. 2014) and altered fauna community compositions (Hill & Webb 1982; Friend 1984; Friend & Cellier 1990; Bromham et al. 1999; Woinarski & Ash 2002; Woinarski et al. 2002; James 2003; Tassicker et al. 2006; Kutt & Woinarski 2007; McKenzie et al. 2007; Woinarski et al. 2007; Thomaz et al. 2008; Kutt & Fisher 2011; Legge et al. 2011; Kutt & Gordon 2012; Fisher et al. 2014; van Doorn et al. 2015).

**Invertebrates**

The species richness of some invertebrate species, including grasshoppers and crickets, has been found to decrease with increasing proximity to cattle watering points (Ludwig et al. 1999). Buffalo impacts on vegetation structure in northern Australia have also been shown to affect grasshopper abundances (Friend 1984). While some species benefitted from loss of vegetation structure, other species were disadvantaged (Friend 1984). This could also be attributed to the food preferences of the grasshopper species involved, as a study in the United States found that obligate grass-feeding species were more common in grazed areas due to the higher abundance of short grass species rather than the tall grass species which dominated ungrazed areas (Quinn & Walgenbach 1990). Ant and spider species are also affected by grazing, with lower species richness for both groups in grazed areas compared to ungrazed areas (Woinarski et al. 2002) and declines in the abundance of some spider families with increasing proximity to cattle watering points (Churchill & Ludwig 2004). The densities and species richness of soil macroinvertebrate communities have also been shown to be affected by ungulate grazing and trampling due to the simplification of vegetation structure, loss of ground cover and compaction of soil (pigs: Vtorov 1993, cattle: Bromham et al. 1999). Ungulate grazing of aquatic plants can also affect invertebrates, as water-dwelling species richness and abundances decline with reduced macrophyte cover due to changes in habitat complexity and food availability (Hill & Webb 1982; Thomaz et al. 2008). In contrast, ants (Formicidae) have been found to increase in abundance at sites under heavy grazing pressure, possibly due to reduced habitat complexity and declines in ant predator communities at heavily grazed sites (Neilly et al. 2020). However, this is not always the case, and different ant species may show different responses to grazing based on their habitat and food preferences (Hoffmann 2000; Arcoverde et al. 2017). For example, some thermophilic ant species which prefer open habitats benefit from the removal of grassy vegetation by cattle grazing, while seed-harvesting ant species suffer declines for the same reason (Arcoverde et al. 2017).

**Reptiles and amphibians**

A study of pig-nosed turtles (*Carettochelys insculpta*) found that the sandy banks of billabongs which provide nesting habitat for the species, were severely degraded by buffalo disturbance in the Kakadu region, while trampling by livestock in the Daly River region is a known source of turtle nest mortality (Georges & Kennett 1989). The authors concluded that under heavy stocking conditions, turtle recruitment would decline severely and supported the removal of buffalo from the Kakadu region. Feral
pigs are a major predator of northern snake-necked turtles (Chelodina rugosa) and when abundant, can account for 96% of turtle mortalities during dry conditions (Fordham et al. 2006). Modelling of C. rugosa populations has predicted that pig predation levels of ≥ 40% may lead to local extinction within 50 years (Fordham et al. 2008). The habitat niche occupied by different reptile species may affect their response to cattle grazing, as several studies in Queensland have demonstrated that some terrestrial species have significantly lower abundances in grazed areas due to changes in habitat and microclimate (Kutt & Woinarski 2007), while some arboreal species are not affected or may increase under the same conditions (Woinarski & Ash 2002; Neilly et al. 2018). In contrast, amphibian populations appear less susceptible to disturbance from cattle grazing, with no difference in the abundance or species richness of amphibians at grazed and ungrazed sites (Woinarski & Ash 2002). Other studies on water buffalo disturbance have found amphibian responses may vary based on their habitat preferences, with ground-dwelling species benefitting from the creation of small bodies of still water caused by pugging and wallowing, while arboreal species were disadvantaged by changes in plant communities (e.g. grazing of pandanus palms) (Friend 1984; Friend & Cellier 1990).

**Mammals**

Native mammal populations are declining in northern Australia, particularly those species with ground-dwelling habits and which favour open habitats (Fisher et al. 2014). Environmental changes due to the combined impacts of grazing and fire are thought to be contributing to this decline (Woinarski et al. 2001; Woinarski & Ash 2002; McKenzie et al. 2007; Legge et al. 2011; Fisher et al. 2014; Reid et al. 2020), as the simplification of habitats increases the vulnerability of small mammals to predation by feral cats (Felis catus) (Fisher et al. 2014; McGregor et al. 2014; Stobo-Wilson et al. 2020), which have existed in northern Australia since at least 1845 (Abbott et al. 2014). Additionally, grazing by livestock and feral ungulates degrades habitat and resources available to small marsupials, which may further contribute to their decline (Woinarski 2015). A study in Western Australia found that the large scale (> 40 000 ha) removal of cattle from a fenced wildlife reserve resulted in the rapid recovery of local small mammal populations (Legge et al. 2011). Similarly, a pastoral grazing trail in the Northern Territory found that small mammal abundance increased significantly within 5 years following cattle exclusion (Hunt et al. 2013). However, a comparable study by Kutt et al. (2012) in north-eastern Queensland found that small mammal populations continued to decline following cattle removal and this contrast may be attributable to the longer history of pastoralism and greater stocking densities in the region compared to western Australia. A CSIRO study of native dusky rats (Rattus colletti) in Kapalga, Kakadu National Park, found that a reduction in buffalo numbers on flood plains (and their margins) resulted in a significant increase in rat populations, as well as other small vertebrates (Skeat et al. 1996). Some Queensland species have been shown to have greater abundances in areas ungrazed by cattle, including the eastern grey kangaroo (Macropus giganteus) and eastern chestnut mouse (Pseudomys gracilicaudatus), while others show no difference in abundance at grazed or ungrazed sites, including common planigale (Planigale maculata) and squirrel gliders (Petaurus norfolcensis) (Woinarski & Ash 2002). Arboreal brush-tailed possums (Trichosurus vulpecula) have also been shown to prefer areas heavily grazed by cattle, as reduced ground cover makes ground movement easier in areas where the canopy is not connected (Neilly & Schwarzkopf 2017). By contrast, rufous bettongs (Aepyprymnus rufescens) avoid areas with high cattle densities, possibly due to the combined impacts of grazing on vegetation communities, soil compaction restricting access to subterranean food sources and trampling of nest burrows (Neilly & Schwarzkopf 2018). Analysis of dung samples from the northern Kimberley region has also indicated that feral cattle compete with native macropods for high-quality forage that becomes available after fire (Reid et al. 2020).

**Birds**

Cattle have had significant impacts on bird assemblages in north-eastern Queensland, as shown in a long-term study at a pastoral property, which found that 45% of species recorded in 1873 had declined or were no longer recorded on the property by 1999 (Woinarski & Catterall 2004). Over the same time period, 13% of bird species on the property had increased in abundance or colonised the area, however, most of these were common and widely distributed species which favour open habitats, such as grey butcherbirds (Cracticus torquatus), magpie-larks (Grallina cyanoleuca) and grey fantails (Rhipidura fuliginosa) (Woinarski & Catterall 2004). These changes in species composition were attributed to a combination of factors, including altered fire regimes, pastoralism and land clearance (Woinarski & Catterall 2004). While grazing pressure across most of the property was high by 1999, the bird species most affected were those favouring densely vegetated wetland verges, such as black bitterns (Ixobrychus flavicollis) and buff-banded rails (Gallirallus philippensis),

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which were replaced by more open wetland species, including masked lapwings (Vanellus miles), cattle egrets (Ardea ibis) and dusky moorhens (Gallinula tenebrosa) (Woinarski & Catterall 2004).

Granivorous bird species can also be affected, as grazing of flowering grasses can reduce seed availability and result in food shortages (Crowley & Garnett 2001). Such disruptions in seed availability, combined with an inability to switch diet easily and limited ability to move to more favourable foraging grounds during the breeding season, are thought to be responsible for the recent and severe decline of Gouldian finches (Erythrura gouldiae) across their range (Dostine & Franklin 2002; Legge et al. 2015). Following the introduction of cattle to a previously protected area, grazing of riparian grasses was found to drastically decrease the survival and presence of purple-crowned fairy-wrens (Malurus coronatus) from one breeding season to the next (i.e. the percentage of individuals persisting at a site from one year to the next), which declined from 89% prior to grazing, to 24% in just one year (van Doorn et al. 2015). Similarly, the abundance of red-backed fairy-wrens (M. melanocephalus) and golden-headed cisticolas (Cisticola exilis) has been shown to decrease with increasing grazing pressure from domesticated cattle (Hunt et al. 2013; Neilly & Schwarzkopf 2018).

A study in Kakadu National Park found that buffalo activity degraded the habitat of magpie geese (Anseranas semipalmata), affecting their nesting and foraging behaviour. A 10-fold decline in goose populations between 1950 and 1972 corresponded with a rapid increase in buffalo densities within the park, but goose numbers rose quickly after buffalo were widely culled in the region (Ridpath 1991). These fluctuations in goose numbers were thought to be caused by buffalo trampling and grazing on vegetation favoured by the geese for nest building (Eleocharis sphacelata) and as a wet season food source (Hymenachne acutigluma), which increased in abundance following buffalo removal (Skeat et al. 1996). Declining buffalo densities in Kakadu also corresponded with a shift in the location of magpie goose nests, which were most abundant in the centre of floodplains when buffalo were abundant, but moved to wetland margins following buffalo removal (Corbett et al. 1996). Buffalo also compact soils in wetland verges, making it more difficult for magpie geese to forage for subterranean reed tubers, which form an important part of their diet during the dry season (Skeat et al. 1996).

DIRECTIONS FOR FUTURE RESEARCH

This review highlights some of the known impacts of feral cattle, buffalo and pigs on the savannas, wetlands, and biota of northern Australia; however, there are still many gaps in our knowledge. Few ungulate exclusion or removal experiments have been conducted in Australian savannas, but those which have been performed demonstrate that affected ecosystems may be able to recover (e.g. references in Fogarty 1982; Tothill & Mott 1985; Skeat et al. 1996; Legge et al. 2011; Ens et al. 2016). There are little long-term data available about how native flora and fauna recover over time and what adaptive management can be taken to accelerate the process of recovery. The resistance, resilience and recovery of savanna systems after the removal of ungulates can be complex (e.g. Kemp & Kutt 2020) and is dependent on a number of factors, including the role of interannual and seasonal rainfall patterns (across rainfall gradients: Petty et al. 2007) and particular fire regimes (e.g. Legge et al. 2015). Given that feral ungulates cause changes to fuel loads in savanna habitats, more studies which assess how the combination of ungulate control, fire history and fire management affects the recovery of biodiversity are needed across northern Australia (such as Legge et al. 2019).

In addition, more studies are needed which experimentally test how grassland plant communities with different evolutionary histories of grazing respond to contemporary grazing pressure from domestic and feral ungulates.

The location of studies assessing savanna recovery is also an important consideration, as most research to date has concentrated on ungulate impacts in riparian and floodplain areas of tropical savannas (e.g. Kakadu and Alligator Rivers regions) rather than the drier savanna woodlands in the southern extent of the tropics. Given that waterpoints in drier tropical savanna regions are often small waterways, ephemeral waterholes and springs, they may be more sensitive to ungulate disturbance. The reduced availability of surface water for use by native wildlife in the late dry season may also exacerbate ungulate impacts in drier savannas. Another consideration is that lower seasonal rainfall and the frequency of drought may also affect the recovery of vegetation communities in drier regions compared to those in higher rainfall areas. Hence, exclusion experiments should consider recording rainfall events as they may also influence recovery time.

Scale is another important consideration for future exclusion experiments. Studies in northern Australia which have demonstrated that the removal of feral ungulates can facilitate the rapid recovery of native fauna populations (e.g. those conducted in Kakadu), have involved the use of large-scale fencing (> 10 000 ha) and aerial shooting programs to control ungulate numbers. However, such programs are extremely expensive and, hence, are not feasible control approaches for many landholders. Recent small-
scale (<10ha) fencing experiments in northern Australian have found vegetation and water quality can improve within two years of ungulate exclusion (Douqué et al. 2010; Ens et al. 2016) and may be a viable alternative to large-scale fencing. Little data are available about the effects of small-scale fencing projects on terrestrial wildlife, however, those conducted have shown that many small terrestrial fauna avoid areas grazed heavily by cattle (Neilly & Schwarzkopf 2018; Neilly et al. 2018). Another consideration is that the protection of a given area has been shown to provide benefits to adjacent unprotected areas in a phenomenon known as the ‘halo effect’ (Ricketts et al. 2001; Tubelis et al. 2004; Otter et al. 2007; Anand et al. 2010). Hence, the use of small-scale fencing to exclude ungulates may provide benefits for surrounding habitat available for native wildlife and warrants further study. While both small-scale and large-scale fencing experiments yield valuable information, the former is particularly useful to determine changes to flora and smaller animals, whereas the latter is useful for the study of larger animals that require more than one type of habitat to persist. Hence, it is important to consider that the response of different fauna species following a relaxation in grazing pressure may vary based on enclosure size (Hunt et al. 2013).

To date, most research assessing how habitat change in Australian savannas affects wildlife has focused on native mammal populations. However, more work is needed to understand the impacts of habitat change on savanna invertebrates, reptiles, amphibians and birds. In addition, future studies assessing species richness and abundance in altered habitats, such as those affected by grazing, should be supplemented by assessments of population health and fitness to gain a more comprehensive view of how disturbance affects wildlife communities. Several threatened bird species, such as the Gouldian finch and golden-shouldered parrot (Psophotellus chrysopterygius), rely on northern savannas and have suffered recent and expansive contractions in their distributions which have been attributed (at least in part) to habitat changes caused by feral ungulates (Garnett & Crowley 1997; Crowley et al. 2004; Lewis 2007). In addition, many nomadic and migratory bird species also rely on northern savannas, including near threatened waders such as red-necked stint (Calidris ruficollis) and curlew sandpiper (C. ferruginea), which use the floodplains of the Alligator Rivers region as a staging area on their annual migration from Siberia to southern Australia (Morton & Brennan 1991). Given that pastoralism remains a dominant land use in northern Australia and feral ungulate populations continue to rise (Saalfeld 2014; Kakadu National Park Board of Management 2016), such species may suffer further declines across their range unless action is taken. The ongoing spread and growth of feral ungulate populations in the northern savannas of Australia cannot be disregarded without severe consequences for our native biota.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTION

Helenna Mihailou: Conceptualisation (equal); Funding acquisition (supporting); Project administration (equal); Writing-original draft (lead); and Writing-review & editing (lead). Melanie Massaro: Conceptualisation (equal); Funding acquisition (lead); Project administration (equal); Supervision (lead); and Writing-review & editing (supporting).

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Chapter 3: Water scarcity exacerbates feral ungulate use of ephemeral savanna waterholes in northern Australia

This chapter has been prepared as a paper which is currently under peer review for publication in the journal Biological Invasions. It contains all references as part of the chapter.
Water scarcity exacerbates feral ungulate use of ephemeral savanna waterholes in northern Australia

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Abstract
Australian savannas evolved in the absence of hooved mammals and hence, are particularly prone to disturbance from exotic ungulates. Several ungulate species have established feral populations in Australia’s northern savannas. As most ungulate species have high water requirements, seasonal and annual changes in water availability are likely to affect their behaviour and the extent of their impacts on native ecosystems. However, few studies have investigated how water scarcity affects feral ungulate use of waterpoints in Australia. We studied changes in the seasonal and annual visitation behaviours of feral pigs, cattle, and water buffalo at ephemeral savanna waterholes within Limmen National Park, Australia. All three species visited waterholes more often, for longer periods, and in larger numbers during a drought year, compared to an average rainfall year. Cattle and buffalo spent more time drinking from waterholes during the drought, while pigs and cattle also spent longer periods foraging. Buffalo also wallowed more during the drought. Responses to dry season progression varied between species. Cattle considerably increased their use of waterholes as the dry season progressed, while buffalo did not change their waterhole use. Pigs only increased their visitation to waterholes when water scarcity was most extreme at the end of the dry season during the drought. Our results demonstrate that water scarcity exacerbates feral ungulate use of savanna waterholes. As climate change is predicted to reduce surface water availability in northern Australia, feral ungulate use of savanna waterholes may intensify in the future, risking further biodiversity losses and irreversible ecosystem damage.

Key words: feral ungulate, savanna, water scarcity, cattle, water buffalo, pig
Introduction

Northern Australia supports one of the largest and least developed savanna ecosystems in the world, which covers approximately 1,500,000 km$^2$ (Woinarski et al. 2007). Australian savannas are thought to be particularly susceptible to disturbance from introduced ungulate species (Freeland 1990; Ash and McIvor 1998), because they did not evolve with native ungulates and have been devoid of large herbivores (>100kg) since the extinction of the megafauna ~45,000 years ago (Skarpe 1991; Scogings and Sankaran 2019). However, several ungulate species have been introduced to the region since the 1800’s (Ridpath 1991) and pastoralism is now a major land use (Woinarski and Ash 2002; Holmes 2010). Pigs (Sus scrofa), cattle (Bos taurus, B. indicus), and Asian water buffalo (Bubalus bubalis) have established widespread feral populations in tropical savanna habitats (Mihailou and Massaro 2021), including in conservation reserves, indigenous protected areas, and national parks (Bayliss and Yeomans 1989; Kakadu National Parks Board of Management 2016). In addition, domestic cattle in northern Australia are rarely confined to enclosed paddocks, but instead, roam freely over vast areas of ‘unimproved’ native savanna until mustering (Chilcott et al. 2020). Boundaries between pastoral properties and protected land are often delineated by lines on a map rather than fences, which are costly to build and maintain (Hunt et al. 2014). Hence, domestic cattle often make their way onto national parks (at least until the next tenured muster), where they likely cause the same damage to the landscape as feral populations, making the distinction between the two more academic than ecological.

The pervasiveness of pastoralism and the continuous ungulate intrusions of protected areas in northern Australia raises concern that refugia (as defined by Seddall et al. 1990) for native wildlife may not be as extensive as it appears. Over the last few decades, many native mammal and bird species have suffered sudden and severe declines in their distribution and abundance in northern Australia, including in protected areas, such as Kakadu National Park (Woinarski 2000; Woinarski et al. 2001; Franklin et al. 2005; Woinarski et al. 2011). These declines are often attributed to predation by feral cats (Felis catus) and the impacts of altered fire-regimes on native habitat (Pardon et al. 2003; Firth et al. 2010; Fisher et al. 2014; Lawes et al. 2015). However, researchers are increasingly considering the impacts of introduced ungulate species on vegetation communities as a factor which exacerbates the combined effect of both cats and fire on native wildlife (Legge et al. 2011; McGregor et al. 2014; Woinarski 2015; Legge et al. 2019).

Most ungulates, particularly grazing species, need to drink regularly due to their dry diets and hence, are often distributed near waterpoints (Tomkins and O’Reagain 2007; Graz et al. 2012). Ungulate visitation to waterholes can reduce water quality through faecal contamination and by increasing turbidity through the overturning of benthic soils (Skeat et al. 1996; Finlayson et al.
1999; Pettit et al. 2012; Waltham and Schaffer 2017), reducing suitability for native wildlife. Additionally, ungulates can drink up to 10% of their body weight daily (Hunt et al. 2013; Bray et al. 2015) and can increase the evaporative potential of waterholes through pugging and wallowing (Skeat et al. 1996), directly reducing the amount of water available for native wildlife. In northern Australia, rainfall can vary greatly between years and surface water availability declines as the dry season progresses each year, resulting in interannual and seasonal periods of water scarcity (see Cook and Heerdegen 2001; Kanniah et al. 2013). Such periods concentrate animal activity around those areas where surface water is still available (Pettit et al. 2012). Both permanent and ephemeral waterholes provide important drought and dry season refugia for many savanna species (Thrash et al. 1995; Redfern et al. 2003; Valeix 2011). Hence, ungulate visitation to and use of savanna waterholes may have greater impacts on native biota when water scarcity is high compared to times when water is more readily available across the landscape. Despite this, little research has been conducted in Australia on the behaviour of ungulates in the wild and whether water scarcity affects how they use waterholes in savanna environments. Understanding how feral ungulates respond to water scarcity may inform land managers and conservationists about potential threats to native biota due to changes in ungulate disturbance and allow targeted control and management of ungulates in protected areas.

In this study, we used remote triggered wildlife cameras to investigate changes in the annual and seasonal visitation behaviours of three feral ungulate species (pigs, cattle, and buffalo) at ephemeral savanna waterholes in Limmen National Park in northern Australia. Rainfall varied considerably over the two years the study was conducted. The first year received a relatively normal amount of rainfall, while the second year was a drought year with well below average rainfall. Hence, surface water availability within the landscape varied considerably between years, as well as over the progression of the two dry seasons (i.e., with increasing time since last rainfall each year). We hypothesised that ungulates would respond to increasing water scarcity (both during the drought and as the dry season progressed) in the following ways: 1) visiting waterholes more frequently, 2) visiting waterholes for longer time periods, 3) visiting waterholes in larger numbers, and 4) spending more time drinking, foraging, and wallowing at waterholes.

**Methods**

**Study area**

This study was conducted in Limmen National Park, a large savanna reserve (>1,000,000 ha) in the Northern Territory, Australia. Vegetation communities in the region were comprised of a mosaic of grasses, shrubs, and trees in a range of densities, from treeless grasslands to wooded forests, provided that enough sunlight can penetrate the canopy to support grass growth (Woinarski...
et al. 2007). Rainfall follows a monsoonal wet-dry cycle, whereby rain predominately falls between November-April (wet season), while the months of May-October (dry season) receive little or no rain. Rainfall can be highly variable between years (Taylor and Tulloch 1985; Haynes et al. 1991), and hence, surface water availability can be restricted on both a seasonal (i.e., as the dry season progresses each year) and interannual basis (i.e., during years of below average rainfall). On average, the park receives 859mm of rain annually (as measured at Nathan River Ranger Station, Bureau of Meteorology 2021). The park received totals of 970mm and 371mm of rain over the 2017/2018 (hereafter 2018) and 2018/2019 (hereafter 2019) wet seasons respectively (Bureau of Meteorology 2021).

Data collection

Ephemeral waterholes within the park are typically small clay basins, which dry completely by the end of the dry season and are refilled by rain each wet season. To collect pig, cattle, and buffalo visitation data, we selected 10 main waterholes of comparable size, depth, soil type, and surrounding vegetation. As pilot sampling indicated pig numbers within the study area were lower than the other ungulates studied, we selected a further 10 sites for pig sampling only (following the same selection criteria). All waterholes were situated in open, mixed savanna woodland. Those near ridgelines, rivers, or billabongs were excluded.

Field work was conducted from April-October in 2018, and March-August in 2019. The length of the field season varied between years due to the accelerated drying of waterholes during the drought (2019). As data was collected from multiple sites per day, the total number of sampling days also varied between years and for different species (Table 1). All species were sampled for a total of 173 calendar days in 2018. While in 2019, cattle and buffalo were sampled for 138 calendar days, and pigs for 150. The duration of pig sampling in 2019 and the number of sampling days per year was higher for pigs than for cattle and buffalo because pigs were sampled over 20 sites instead of 10 sites. Four study sites were sampled each week on a 5-week rotation over the course of each dry season. Accessibility to sites at the start of the dry season determined their sampling order, which was maintained thereafter. To sample ungulate visitation to and use of study waterholes, three Reconyx Hyperfire HC600 motion triggered wildlife cameras (‘camera traps’) were mounted to trees around waterholes at ~1.2m above ground level and positioned to capture as much of the waterline as possible (see Fig. 1 for photo capture examples showing each ungulate species utilising study waterholes at various times of season and year). When triggered by movement or body heat, cameras captured 3 photos at 1 second intervals (key settings used; trigger: sensitive, night mode: max range, quiet period: no delay). Once set, cameras were left to sample waterhole visitation for ~5 continuous day/night cycles.
Collation and processing of data

Photos captured by cameras were processed using the database program, CPW Photo Warehouse version 4.3.0.5 (Newkirk 2016). A visit was defined as any event where target species were caught on camera. A visit began when a camera was triggered by an ungulate and ended when the last individual of that species left the camera field of view. Multiple visits within a 30-minute time frame were not considered to be independent events, unless the animals involved could be identified as different individuals/groups which appeared to be moving independently from each other within the 30-minute time frame. For example, if a mixed group of female buffalo and calves entered the trigger zone from the right and begin grazing for several minutes before eventually moving off to the left, then 25 minutes later a male buffalo entered from the right, before exiting to the right – this series of triggers would be considered two distinct visits. The total number of individuals in a visit was determined by looking at all cameras stationed around a waterhole and counting the lowest possible number of individuals present, based on their identifiable markings (e.g., coat colour, horn/tusk shape, gender, size).

The behaviour of ungulates during visits was then classified into several categories, including drinking, foraging (either grazing or grubbing with head down posture moving slowly over fodder), and wallowing (for buffalo only). Other behaviours, such moving through sites, resting (other than wallowing), and fighting were not included in the analysis. To account for slight variations in camera times and to prevent double counting of behaviours, a time buffer of 3 minutes was applied when multiple cameras stationed around a waterhole captured activity within a single visit. This buffer was determined by turning on all 20 cameras used for sampling at once and observing the maximum and minimum times displayed, then calculating the offset required so that no time overlap was possible. Where multiple cameras simultaneously captured activity in a visit and the 3-minute buffer had to be applied, the configuration of cameras which captured the most activity was used.

Data were analysed at a daily scale per site (i.e., per sampling day). Visitation response variables included the number of visits, the total duration of visits, and the total number of individuals visiting per sampling day. Behavioural response variables included time spent foraging (i.e., grazing in cattle and buffalo, grubbing in pigs), drinking (cattle and buffalo), and wallowing (buffalo). Although pigs were also observed drinking and wallowing, there were not enough records to allow analyses of these behaviours. The estimated time (in minutes) spent conducting a given behaviour in each sampling day was calculated as a function of camera triggers by dividing the number of camera triggers in which a given behaviour was observed by the total number of camera
triggers, and then multiplying this by the total duration (in minutes) of all visits in that sampling day.

Data analyses

We used generalised linear mixed models (GLMMs) to analyse all data because they are well suited for modelling count data correlated by repeated sampling of study sites (Bolker et al. 2009; Bolker 2015). GLMMs modelled each response variable against two fixed factors (predictor variables): year, and days since the dry season started (i.e., year+days since the dry season started), as well as the interaction between the two (i.e., year*days since the dry season started). Days since the dry season started was included as a continuous variable. Study site was included as a random effect to account for repeated sampling. Given that much of the data was over-dispersed and zero-inflated (because there were many days where species did not visit waterholes), we tested the suitability of the two model variations for each response variable which included different model families (e.g., poisson, quasi-poisson, negative binominal, hurdle) and several zero-inflation factors (including year, days since the dry season started, year+days since the dry season started, and year*days since the dry season started). The most parsimonious model was then determined using Akaike’s information criterion (AIC; Akaike 1973). Full model component details and AIC values for the most parsimonious model for each response variable are presented in Table S1 in the Supplementary Information. Results for co-efficients are presented for the conditional models using a quasi-poisson or negative binominal family with a log-link, while zero-inflation models used a logit-link. All data was analysed using the statistical program, “R” (R Core Team 2020), with library “glmmTMB” (Brooks et al. 2017). Model dispersion was assessed using the “testDispersion” and “simulateResiduals” functions from the “DHARMa” package (Hartig 2020). Figures were generated by using models to calculate predicted values for each response variable using the “ggpredict” function from library “ggeffects” (Lüdecke 2018) and plotted with “ggplot2” (Wickham 2016).
Table 1 Sampling day averages and standard deviations of the number of visits, visit duration, number of visiting individuals, time spent drinking, foraging, and wallowing by pigs, cattle, and buffalo. Values in brackets represent raw totals (over all sampling days). Hyphens denote variables not included in analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Factor</th>
<th>Number of sampling days</th>
<th>Number of Visits</th>
<th>Duration of visits (mins)</th>
<th>Number of individuals</th>
<th>Time spent drinking (mins)</th>
<th>Time spent foraging (mins)</th>
<th>Time spent wallowing (mins)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pig</td>
<td>Year</td>
<td>2018 446</td>
<td>0.03587 ± 0.2571</td>
<td>0.1166 ± 1.342</td>
<td>0.1480 ± 1.339</td>
<td>-</td>
<td>-</td>
<td>0.06054 ± 0.6278</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2019 294</td>
<td>0.1327 ± 0.4667</td>
<td>1.415 ± 8.889</td>
<td>0.6429 ± 3.105</td>
<td>-</td>
<td>0.5034 ± 3.133</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Dry season progression</td>
<td>Overall 740</td>
<td>0.07432 ± 0.3584</td>
<td>0.6324 ± 5.729</td>
<td>0.3446 ± 2.228</td>
<td>-</td>
<td>0.2365 ± 2.043</td>
<td>-</td>
</tr>
<tr>
<td>Cow</td>
<td>Year</td>
<td>2018 226</td>
<td>0.1593 ± 0.4436</td>
<td>1.580 ± 8.692</td>
<td>0.4823 ± 1.797</td>
<td>0.1814 ± 0.7819</td>
<td>0.6372 ± 5.311</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2019 168</td>
<td>0.5119 ± 0.9969</td>
<td>6.655 ± 26.46</td>
<td>3.083 ± 7.988</td>
<td>1.077 ± 3.682</td>
<td>1.976 ± 8.967</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Dry season progression</td>
<td>Overall 394</td>
<td>0.3097 ± 0.7520</td>
<td>3.744 ± 18.63</td>
<td>1.591 ± 5.533</td>
<td>0.5635 ± 2.512</td>
<td>1.208 ± 7.124</td>
<td>-</td>
</tr>
<tr>
<td>Buffalo</td>
<td>Year</td>
<td>2018 226</td>
<td>0.2965 ± 0.6638</td>
<td>2.301 ± 8.460</td>
<td>0.8363 ± 2.524</td>
<td>0.2080 ± 1.329</td>
<td>1.407 ± 6.509</td>
<td>0.1327 ± 0.9522</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2019 168</td>
<td>0.4762 ± 0.8683</td>
<td>3.833 ± 14.42</td>
<td>1.345 ± 3.521</td>
<td>0.5833 ± 2.260</td>
<td>1.423 ± 5.166</td>
<td>0.5060 ± 2.445</td>
</tr>
<tr>
<td></td>
<td>Dry season progression</td>
<td>Overall 394</td>
<td>0.3731 ± 0.7619</td>
<td>2.954 ± 11.40</td>
<td>1.053 ± 2.996</td>
<td>0.3680 ± 1.793</td>
<td>1.414 ± 5.966</td>
<td>0.2919 ± 1.759</td>
</tr>
</tbody>
</table>
Fig. 1 Photos of feral ungulates using study waterholes captured by Reconyx automated wildlife cameras. Top: pigs grubbing for food around a waterhole verge (mid dry season, 2018). Middle: cattle drinking from an almost dry waterhole (late dry season, 2019). Bottom: buffalo wallowing (early dry season, 2019)
**Results**

**Number of visits**
Both cattle and buffalo visited waterholes more frequently during the drought (2019) compared to the non-drought year (Table 2, Fig. 2a). Cattle also significantly increased their number of visits to waterholes as the dry season progressed, while buffalo did not. For pigs, the interaction between year and dry season progression was significant and positive, hence they visited waterholes more frequently towards the end of the dry season during the drought year (for full results, see Table S2 in Supplementary Information).

**Visit duration**
The duration of cattle and buffalo visits to waterholes increased during the drought (2019) compared to the non-drought year (Table 2, Fig. 2b). In addition, cattle significantly increased the duration of their visits as the dry season progressed, while buffalo did not. For pigs, the interaction between year and dry season progression was significant and positive, hence the durations of their visits increased towards the end of the dry season during the drought year. Dry season progression was included as a zero-inflation factor in the pig model but was not significant (for full results, see Table S3 in Supplementary Information).

**Number of individuals visiting**
The number of cattle and buffalo visiting waterholes increased significantly during the drought year (Table 2, Fig. 2c). Cattle numbers also increased significantly as the dry season progressed, but buffalo numbers were not significantly affected. For pigs, the interaction between year and dry season progression was significant and positive, hence their numbers increased towards the end of the dry season during the drought year. Dry season progression was included as a zero-inflation factor in the pig model but was not significant (for full results, see Table S4 in Supplementary Information).

**Time spent drinking**
The time cattle and buffalo spent drinking at waterholes increased significantly during the drought year (Table 2, Fig. 3a). Cattle also spent significantly more time drinking as the dry season progressed, but buffalo did not. Model selection supported the inclusion of an interaction term between year and dry season progression for the cattle model, but this result was not significant (i.e., the time cattle spent drinking at the end of the dry season was not significantly different between years; for full results, see Table S5 in Supplementary Information).
**Time spent foraging**

Cattle spent significantly more time foraging around waterhole verges during the drought and as the dry season progressed, however buffalo did not alter their behaviour in response to either factor (Table 2, Fig. 3b). For pigs, the interaction between year and dry season progression was significant and positive, hence they spent more time foraging towards the end of the dry season during the drought year. Dry season progression was included as a zero-inflation factor in the pig model but was not significant (for full results, see Table S6 in Supplementary Information).

**Time spent wallowing**

Buffalo spent significantly more time wallowing during the drought compared to the non-drought year (Table 2, Fig. 3c). However, dry season progression had no significant effect on their wallowing behaviour (for full results, see Table S7 in Supplementary Information).
Table 2 Results of most parsimonious GLMMs determined from model selection. All results represent values per sampling day sampled for different species (e.g., time spent drinking (minutes)/sampling day). Both conditional and zero-inflation components of models are presented where applicable. Significant values are presented in bold and significance levels presented in brackets are as follows: *** (p < 0.001), ** (p < 0.01), * (p < 0.05). Hyphens denote factors not included in models. “Interaction” denotes the interaction between year and dry season progression.

<table>
<thead>
<tr>
<th>Species</th>
<th>Model component</th>
<th>Factor</th>
<th>Number of visits</th>
<th>Duration of visits (mins)</th>
<th>Number of individuals</th>
<th>Time spent drinking (mins)</th>
<th>Time spent foraging (mins)</th>
<th>Time spent wallowing (mins)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pig</td>
<td>Conditional</td>
<td>Year</td>
<td>-0.6828</td>
<td>-1.696</td>
<td>-3.145 (*)</td>
<td>-</td>
<td>-0.9811</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dry season progression</td>
<td>-0.1002</td>
<td>-0.0001981</td>
<td>-0.005210</td>
<td>-</td>
<td>0.01529</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Interaction</td>
<td>0.02781 (***)</td>
<td>0.06865 (***)</td>
<td>0.07196 (***)</td>
<td>-</td>
<td>0.05981 (*)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Zero-inflation</td>
<td>Dry season progression</td>
<td>-</td>
<td>0.2612</td>
<td>0.2447</td>
<td>-</td>
<td>0.3342</td>
<td>-</td>
</tr>
<tr>
<td>Cow</td>
<td>Conditional</td>
<td>Year</td>
<td>1.068 (***)</td>
<td>1.319 (***)</td>
<td>1.565 (***)</td>
<td>3.578 (***)</td>
<td>1.316 (***)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dry season progression</td>
<td>0.006311 (*)</td>
<td>0.01818 (***)</td>
<td>0.01784 (***)</td>
<td>0.04112 (***)</td>
<td>0.01222 (*)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Interaction</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-0.01934</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Zero-inflation</td>
<td>Dry season progression</td>
<td>-</td>
<td>0.02234</td>
<td>0.01356</td>
<td>0.1149</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Buffalo</td>
<td>Conditional</td>
<td>Year</td>
<td>0.4262 (*)</td>
<td>0.4006 (*)</td>
<td>0.4315 (*)</td>
<td>0.8088 (*)</td>
<td>0.3881</td>
<td>1.044 (***)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dry season progression</td>
<td>-0.001080</td>
<td>-0.001357</td>
<td>-0.001331</td>
<td>0.003916</td>
<td>-0.004762</td>
<td>-0.001254</td>
</tr>
</tbody>
</table>
Fig. 2 Effect of year and dry season progression on the waterhole visitation behaviours of feral ungulate species. (a) Number of visits by feral ungulate species per sampling day, (b) duration of feral ungulate visits per sampling day (mins), (c) number of visiting individuals per sampling day. Solid lines represent predicted mean values, shaded areas represent upper and lower confidence intervals. Colours of lines and shaded areas correspond to different years: blue (2018 – normal rainfall year) and red (2019 – drought year)
Fig. 3 Effect of year and dry season progression on the waterhole use behaviours of feral ungulates. (a) Time feral ungulate species spent foraging around waterholes per sampling day (mins), (b) time cattle and buffalo spent drinking at waterholes per sampling day (mins), (c) time buffalo spent wallowing per sampling day (mins). Solid lines represent predicted mean values, shaded areas represent upper and lower confidence intervals. Colours of lines and shaded areas correspond to different years: blue (2018 – normal rainfall year) and red (2019 – drought year)

Discussion

Responses to drought

In this study, we found that water scarcity exacerbates feral ungulate use of ephemeral waterholes in Australian savannas. All ungulates increased their number of visits to waterholes, visited for longer durations, and visited in greater numbers during the drought year. We also found that the behaviours which ungulates exhibited during visits were significantly affected by drought: cattle and buffalo
spent more time drinking, pigs and cattle spent more time foraging, and buffalo spent more time wallowing during the drought year. Our findings support the hypothesis of Illius and O'Connor (2000) that seasonal and climactic variability leads to the spatial concentration of ungulates around key resource areas, such as waterholes.

High waterhole use by ungulates can lead to severe defoliation of vegetation communities in a spherical gradient surrounding waterpoints, known as a piosphere (Thrash and Derry 1999; Illius and O'Connor 2000). Thus, our findings suggest that drought may exacerbate ungulate impacts on vegetation communities surrounding savanna waterholes. Piospheres have been shown to have long lasting (>100 years) and possibility irreversible effects on vegetation and soil characteristics in Australian arid areas, even after grazing pressure is removed (Croft et al. 2007). Hence, further research which defines how feral ungulates affect vegetation communities surrounding Australian savanna waterholes during drought, and how this may impact native fauna communities is needed. Additionally, studies over longer time periods of fluctuating water availability (>2 years) are needed to verify our findings.

Responses to dry season progression

Dry season progression affected waterhole visitation and behaviour of cattle, pigs, and buffalo differently. Cattle were the most responsive to water scarcity: they significantly increased their number of visits, they visited for longer durations, and more individuals visited per sampling day as the dry season progressed. They also spent significantly more time drinking and foraging when visiting waterholes as the dry season progressed. Cattle were the most numerous feral ungulates observed during the study (Table 1) and were detected 4.6 and 1.5 times more per sampling day than pigs and buffalo, respectively. The number of cattle we detected across just 10 small waterholes is concerning, because each adult can drink ~40-80 litres of water daily depending on sex and body condition (Hunt et al. 2013; Bray et al. 2015). Hence, increased cattle visitation to savanna waterholes during dry and hot conditions (i.e., drought, end of dry season) may deplete already scarce water resources available to native fauna. In addition, cattle presence could affect patterns of waterhole visitation by native fauna, as has been observed with other feral ungulate species in water limited habitats (e.g., Perry et al. 2015; Hall et al. 2016; Gooch et al. 2017; Brim Box et al. 2019). For example, feral camel presence reduces the frequency that native dingoes (Canis lupus dingo) and birds visit waterholes in central Australia, as well as impacting their temporal activity patterns (Brim Box et al. 2019).

Pigs only changed their waterhole visitation and use behaviours at the end of the dry season during the drought, when water scarcity was most extreme. They visited waterholes more, for longer
periods, in greater numbers, and spent more time foraging at the end of the dry season during the drought than at any other times. This suggests that pigs are more reliant on larger waterbodies (e.g., lagoons, swamps, and billabongs) than cattle and buffalo, which provide better foraging opportunities for pigs than the small, ephemeral waterholes studied here (Ridpath 1991). Lower surface water availability during the drought may have led pigs to move into less preferred habitat as the year progressed. This also explains why pigs spent more time foraging around study waterholes as the drought progressed, as larger waterbodies may have dried earlier than in the previous year (i.e., did not fill to capacity), forcing pigs to find alternative foraging sites.

Buffalo only changed their waterhole visitation and use in response to drought, and not dry season progression. This may be because buffalo evolved in hot, humid wetland habitats (Ridpath 1991) where evaporative cooling from sweating is impaired. Buffalo have highly vascularised skin and rely on frequent wallowing to keep cool (Tulloch and Litchfield 1981; Ridpath 1991), and their water requirements appear to be high year-round. This may explain why their visitation to and use of waterholes was relatively consistent across the dry season. By contrast, drought may have had greater impacts on buffalo behaviour because reduced surface water availability would have increased their dependence on those waterholes still containing water (e.g., our study waterholes). Unlike cattle, buffalo did not spend more time grazing riparian vegetation on waterhole verges with increasing water scarcity. This may be explained by the wider dietary niche of buffalo, whose diet consists of <30% grasses (Bowman et al. 2010), compared to ~50% for cattle (Reid et al. 2020). Hence, riparian food resources may be a more important for buffalo than cattle, which they may use more consistently throughout the year.

Broader implications of feral ungulate aggregations at ephemeral waterholes

Feral ungulates have extensive impacts on Australian savanna habitats, which have substantial detrimental flow-on effects for native wildlife, particularly the destruction or degradation of primary habitat (Mihailou and Massaro 2021). As our study indicates that water scarcity concentrates ungulate activity around savanna waterholes, these areas are particularly vulnerable to ungulate disturbance and negative flow-on effects for wildlife are potentially worsened at critical times. Studies elsewhere have shown that feral ungulate presence at waterholes may deter visitation by native fauna (Ostermann-Kelm et al. 2008; Hall et al. 2018; Brim Box et al. 2019). In northern Australia, aggregations of feral ungulates at savanna waterholes during periods of water scarcity may affect waterhole use by important native species, such as dingoes (Australia’s largest terrestrial predator) and macropods (Family Macropodidae, including kangaroos and wallabies - the largest extant grazers in Australia). Vulnerable fauna communities already suffering declines in Australia’s
northern savannas, such as small mammals (Woinarski et al. 2011; Woinarski 2015) and granivorous bird species (Franklin 1999; Franklin et al. 2005) may also be negatively affected by ungulate disturbance around waterholes during water scarcity events. Ungulate damage to understory vegetation surrounding waterpoints may be particularly detrimental for small species with frequent drinking requirements (e.g., granivores), as habitat simplification provides better visibility for predators, such as feral cats (Fisher et al. 2014; McGregor et al. 2014; Stobo-Wilson et al. 2020).

Our findings also highlight that management and control programs for feral ungulates in northern savannas may benefit from targeting different species under different water scarcity conditions. Cattle control operations should be targeted around waterholes in the late dry season, irrespective of annual rainfall. Contrastingly, pigs are best targeted (at least around ephemeral water sources) during extreme water scarcity events (i.e., late dry season during drought years). As buffalo utilise waterholes consistently across the dry season, land managers should instead focus control programs during years of low rainfall for optimal results.

As climate change is predicted to reduce surface water availability in northern Australia (Dai et al. 2018; NESP Earth Systems and Climate Change Hub 2020), increasing feral ungulate use of waterholes may exacerbate stress on native flora and fauna communities in an increasingly turbulent environment. This could lead to the loss of resilience in the ecosystem to recover from high water scarcity events and potentially lead to irreversible damage to sensitive habitats. Hence, more research is warranted to assess feral ungulate impacts on native flora and fauna. Furthermore, due to the social and economic value of ungulates, conflicting values between stakeholders and land managers complicate conservation efforts in the region (Robinson et al. 2005; Spear and Chown 2009; Sloane et al. 2021). Many local stakeholders view feral ungulates as a source of income (e.g., tourism operators and safari hunters – buffalo), or as a self-sustaining food source (e.g., recreational hunters – pigs and buffalo; some traditional Aboriginal landowners – cattle and buffalo), rather than a threat to native ecosystems (Skeat et al. 1996; Robinson et al. 2005; Ens et al. 2016). Hence, we must urgently work to align the attitudes of stakeholders and conservationists regarding feral ungulate control in northern Australia before it is too late.

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Statements and Declarations

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Conflicts of interest
The authors declare no competing interests.

Availability of data
All data analysed during this study are available in the supplementary material.

Code availability
The modelling used for the statistical analysis is described in detail in the text and supplementary material, including the “R” packages used.

Authors’ Contributions
All authors conceived and designed the study; Melanie Massaro and Helenna Mihailou secured funding for the project; Helenna Mihailou conducted the field data collection and collation; Helenna Mihailou and Dale Nimmo conducted the statistical analysis; Helenna Mihailou and Melanie Massaro drafted the manuscript; all authors contributed to the review and editing of the final manuscript.

Ethics Approval
Approval to conduct this study was granted by the Animal Care and Ethics Committee of Charles Sturt University (Approved protocol number A17035).

Consent to participate
Not applicable.

Consent for publication
The authors consent to the publication of this manuscript in Biological Invasions.
Chapter 4: Feral ungulate and macropod responses to resource scarcity and predation risk at savanna waterholes

This chapter has been published as a paper in the journal Behavioral Ecology and Sociobiology in January 2022. The paper is presented as per the complete publication within Behavioral Ecology and Sociobiology and contains all references as part of the chapter.

Feral ungulate and macropod responses to resource scarcity and predation risk at savanna waterholes

Helenna Mihailou1 · Dale G. Nimmo1 · Melanie Massaro1

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Abstract
When exotic species are introduced to new environments, they often have a competitive advantage over native species. In northern Australia, pigs, cattle, and water buffalo have established widespread, feral populations. As ungulates have high water requirements, they typically congregate near waterpoints. We used a fencing experiment to test whether native macropods preferentially visited savanna waterholes where large ungulates were excluded. We also investigated whether water scarcity affected the visitation behaviour and temporal activity patterns of herbivores at waterholes and whether increasing prey aggregation at waterholes increased dingo presence. We found that macropods did not use fenced waterholes preferentially over unfenced ones. Cattle presence at waterholes increased as water became scarce, while macropod and pig presence peaked in the middle of the dry season. Macropod activity declined rapidly at the end of the dry season when cattle activity was greatest, suggesting that macropods may avoid waterholes in areas utilised by cattle when competition for resources is high. Macropods and all ungulates visited waterholes more during a drought year compared to an average rainfall year. Despite increasing prey activity, dingo presence at waterholes did not increase when water became scarce. However, dingo presence increased significantly on moonless nights. Our results suggest that competition between macropods and ungulates may intensify during periods of water scarcity. Climate change and pastoral intensification are likely to increase competition for resources between ungulates and macropods in Australian savannas, potentially threatening macropod populations across the landscape in the future.

Significance statement
In northern Australia, feral populations of pigs, cattle, and water buffalo compete with native wildlife for access to water sources. As interspecific competition favours species with a size advantage, we tested whether kangaroos and wallabies (macropods) preferentially use waterholes where large ungulates (cattle and buffalo) were excluded. We found that macropods avoided waterholes when cattle presence was high but did not preferentially use waterholes where livestock were excluded. When water scarcity peaked during a drought, macropods and all three feral ungulate species visited waterholes more. However, increased prey presence at waterholes during the drought did not correspond with increased predator (dingo) presence. Our study advances the understanding of behavioural interactions between invasive and native species at important shared resources, and how this may affect wildlife conservation in an increasingly unpredictable environment.

Keywords  Feral ungulate · Macropod · Savanna · Interspecific competition · Resource scarcity · Predation risk

Introduction
Niche separation minimises competitive interactions amongst sympatric species (Hasui et al. 2009; Staniewicz et al. 2018). Interspecific competition operates in two key ways: interference competition occurs when competitively dominant species directly limit the access of other species to a shared resource (e.g., aggressive interactions, food theft), while exploitative competition occurs when competitively
dominant species indirectly limit resource access by depleting a shared resource (e.g., faster food processing) (Latham 1999; Linnell and Strand 2000). Interference competition is more likely to lead to temporal segregation of the competing species’ activity because it allows inferior competitors to avoid the dominant competitor (Carothers and Jakiści 1984; Valeix et al. 2007). Interference competition can be exacerbated when competitors are forced into close contact, such as when resources are scarce and concentrated (Petren and Case 1996; Vahl et al. 2005; Valeix et al. 2007). For example, in African savannas, smaller herbivore species shift their temporal activity patterns (Valeix et al. 2007) or increase their vigilance around waterholes to minimise interactions with elephants (Loxodonta africana) (Valeix et al. 2009), which are keystone competitors in this ecosystem (Ferry 2018).

When species have a shared evolutionary history, mechanisms to reduce competition, such as differences in food selection and habitat, evolve over time (Frere et al. 2008; Beaulieu and Sockman 2012; Staniewicz et al. 2018). However, when exotic species are introduced to new environments, such mechanisms may be absent due to a lack of shared evolutionary history with native species (Goodyear 1992; Wauters et al. 2002; Baskaran et al. 2016). Predation risk and vulnerability to pathogens is often lower for exotic species in new environments (Bloxsie and Notzold 1995), which can provide fitness benefits and give them a competitive advantage over native species (Holway 1999; Amarasekare 2002; Brim Box et al. 2019). This may result in fitness costs for native competitors, including exclusion from preferred habitat (Ayala et al. 2007; Cheeseman et al. 2018). For example, the introduction of eastern grey squirrels (Sciurus carolinensis) to Europe caused population declines in native Eurasian red squirrels (S. vulgaris) (Bertolino et al. 2014) because red squirrels were unable to change their spatial and dietary niches to avoid competition with grey squirrels (Wauters et al. 2002).

In northern Australia, several ungulate species have established feral populations since their introduction in the early 1800s (Ridpath 1991). Of those, three key species are common in Australia’s tropical savanna habitats: pigs (Sus scrofa), cattle (Bos taurus, B. indicus), and Asian water buffalo (Bubalus bubalis) (Mihailou and Massaro 2021). Ungulates have high daily water requirements and congregate close to water sources, such as rivers and waterholes (Skeat et al. 1996; Tomkins and O’Reagain 2007; Graz et al. 2012). Rainfall is highly variable throughout the region (Taylor and Tulloch 1985), and the monsoonal wet-dry cycle of rain affects vegetation and surface water, with water becoming scarce as the dry season progresses (see Cook and Heerden 2001; Kanniah et al. 2013). As water is a limiting resource in savanna habitats (Valeix et al. 2008) and interference competition favours organisms which have a size advantage (Persson 1985; Peters and Peters 1986; Nakayama and Fuiman 2010), water points may concentrate interference competition between feral ungulates and smaller native herbivores, such as macropods (family Macropodidae, including kangaroos and wallabies). As there is considerable overlap in the diets of feral ungulates and macropods in Australian savannas (Reid et al. 2020), they may also compete for food resources. Yet little is known about the competitive interactions between the two groups for access to shared resources in savanna habitats.

Along with food and water availability, predation threat is an important factor influencing macropod densities in northern Australia (Ritchie et al. 2008). As water scarcity may concentrate herbivore activity around water sources (Thrash et al. 1995), these areas can become targeted hunting grounds for predators (Valeix et al. 2010). In African savannas, increased prey aggregation at the end of the dry season causes lions (Panthera leo) to focus their hunting within 2 km of waterholes (Valeix et al. 2009; Valeix et al. 2010; Davidson et al. 2013). Similarly, dingoes (Canis lupus dingo)—Australia’s largest terrestrial predator (excluding humans)—use waterpoints as focal hunting grounds for native macropods and feral ungulates (Shepherd 1981; Thomson 1992; Forsyth et al. 2019). Hence, herbivores become increasingly more exposed to dingo predation as the dry season progresses, because they congregate in areas near available water and must drink more frequently due to the drying of fodder (Letnic et al. 2012). Additionally, the nocturnal activity and hunting efficacy of some predatory animals increase during the full moon, when night-time illumination is greatest (e.g., Cozzi et al. 2012; Pratas-Santiago et al. 2016). By contrast, prey animals may reduce their activity when night-time illumination is high (e.g., full moon, reduced cloud cover) to decrease predation risk (e.g., Harmsen et al. 2011; Linley et al. 2020). Healthy adult cattle and buffalo are considered too large for dingoes to kill, but calves and weak adults are vulnerable to predation (Thomson 1992; Corbett 1995b; Fleming et al. 2001). Dingoes also prey on feral pigs of all ages in tropical Australia (Corbett 1995a; Fleming et al. 2001; Brook and Kutt 2011).

Exclusion fencing provides a method to identify interspecific competition and its impacts on the spatial and temporal behaviour of species (Ziv et al. 1993; Hall et al. 2016, 2018). In this study, we conducted a fencing experiment to investigate whether the exclusion of large feral ungulates (cattle and buffalo) from ephemeral savanna waterholes affected the behaviour of native macropods in northern Australia. We also assessed whether the visitation behaviour and temporal activity patterns of these species varied with increasing water scarcity and the activity of dingoes, a predator of both macropods and ungulates. We hypothesised that competition from feral ungulates leads macropods to preferentially use sites where cattle and buffalo were excluded,
particularly when water becomes scarce (i.e., as the dry season progressed). At sites accessible to cattle and buffalo, we expected macropods to shift their temporal activity to avoid overlap with large ungulates. We also hypothesised that water scarcity increases prey visitation to waterholes, leading to increased dingo visitation. We also expected that dingo activity around waterholes increases during the full moon, while prey species decrease their activity. The reverse was expected when night-time illumination was low.

**Methods**

**Study area**

This study was conducted in Limmen National Park, a reserve which protects over a million hectares of mixed savanna woodland in the Gulf of Carpentaria region of the Northern Territory, Australia. The park has an average annual rainfall of 859 mm (as measured at Nathan River Ranger Station, Bureau of Meteorology 2021), which falls throughout the “wet season” (~November to March), while little to no rain is received throughout the “dry season” (~April to October) (full rainfall statistics for the site (014,719) from 1979 to present are available via the Bureau of Meteorology at http://www.bom.gov.au/climate/data). Ephemeral waterholes are common within the park and are typically small clay basins, which dry completely by the end of the dry season and are refilled at the start of each wet season. Rainfall varied considerably in the region over the sampling period, with 970 mm and 371 mm falling over the 2017/2018 and 2018/2019 wet seasons respectively (Bureau of Meteorology 2021). For simplicity, hereafter we refer to the 2017/2018 wet season as “2018” and the 2018/2019 wet season as “2019.”

**Site selection and experimental design**

All waterholes used in this study were ephemeral clay basins located in predominately clay soils with open mixed savanna woodland in the surrounding area. Rocky and sandy basin waterholes and those located at the base of ridgelines and within 1 km of larger watercourses (e.g., rivers, large permanent billabongs) were excluded. We selected 20 waterholes that were similar in size, depth, surrounding vegetation, and soil type (see Fig. 1 for an example). We then used a paired experimental design where we assigned the most similar waterholes into pairs based on their physical properties (as outlined above) and estimated ungulate disturbance (e.g., determined from foot pugging, dung pats, tracks, wallows). From each pair of waterholes, we then randomly selected one site as a control (unfenced) and the other as a treatment site (fenced). Distribution of study waterholes is shown in Fig. 2. All study waterholes were located within 1–2 km of an alternative water source to minimise the likelihood that fencing would affect animal visitation to unfenced study waterholes.

Fences were erected in September 2017 to prevent waterhole access by cattle and buffalo, as well as horses (*Equus caballus*) and donkeys (*E. asinus*), which occur in much lower densities in the study area and were not included in this study. Macropods, dingoes, and other native wildlife were able to move beneath fences and had continued access to fenced waterholes. We were not able to exclude pigs from fenced sites because the use of meshed, pig-proof fencing would have also hindered the access of native wildlife, including macropods and dingoes. Hence, our paired

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**Fig. 1** A typical savanna waterhole in Limmen National Park (left) and an example of the reinforced, four-strand wire fencing design used to exclude cattle and buffalo (right)
experimental design allowed us to assess if there were differences in the temporal and visitation behaviours of species which could access both fenced and unfenced sites (i.e., macropods, pigs, and dingoes).

Fences were 150 × 150 m long and were positioned around treatment sites, such that the waterhole was in the centre of the fenced area. Fencing design was a standard four-strand, star picket fence, with barbed wire at approximately 120 cm and 60 cm above the ground (top and third line of fence) and galvanised plain wire in between (see Fig. 1). Fences were reinforced against ungulate damage by spacing pickets at 7-m intervals (rather than the 10 to 12-m spacing typically used) and including a steel dropper between pickets to help maintain tension under stress. Regular fence checks and maintenance were carried out at roughly 4-week intervals and fences re-stretched as necessary. Fences were breached occasionally (< 1 per month across all sites) but were always repaired prior to cameras being
deployed. Hence, large ungulate access was restricted during all sampling.

Sites were protected from fire as much as possible over the duration of the study by using controlled, early season burns to create fire breaks around each site (> 1 km away). Despite these precautions, lightning strikes in December 2018 started fires which affected 6 study sites. However, an equal number of fenced and unfenced sites were impacted.

Data collection

Field work was conducted from April to October in 2018 and March to August in 2019. Study sites were sampled on a 5-week rotation (4 waterholes per week) from the beginning of the dry season, until each waterhole dried out. The order in which sites were sampled was based on accessibility at the start of the dry season; however, once sampling order was established, it was maintained throughout each season. Paired sites were typically sampled at the same time. However, this was not always logistically possible due to poor condition of 4WD tracks within the park, which prolonged travelling times between some paired sites. To limit the potential for non-simultaneous sampling of some pairs to affect the fencing experiment, an approximately equal number of fenced and unfenced sites were sampled first each time.

Reconyx Hyperfire HC600 motion triggered wildlife cameras (“camera traps”) were used to sample animal presence at waterholes. Camera traps were set up around each waterhole for 5 continuous day/night cycles and were set to take 3 photos at 1-s intervals when triggered by movement or body heat (key settings used; trigger: sensitive, night mode: max range, quiet period: no delay). Cameras were set up using two different sampling methods to maximise detection likelihood: 3 cameras were mounted to trees around each waterhole and positioned to capture as much of the waterline as possible, and a further 2 cameras were placed in the surrounding savanna within each study plot (i.e., < 75 m from water), mounted to horizon tree branches and positioned facing directly downwards above a staked cork-tile baited with a mixture of linseed and tuna oils. Waterhole facing cameras were mounted at approximately 1.3 m above the ground to minimise false triggers from ground vegetation, while downward facing cameras were mounted approximately 1.8 m above ground (wherever possible) to standardise camera field of view. Both types of camera trapping method were used in each study plot at the same time and for the same duration within a given sample rotation (i.e., 5 day/night cycles). Photos from waterline cameras were pooled with baited camera photos to compile presence/absence data for animals visiting each study plot (i.e., the waterhole and its immediate surrounds). This prevented double counts of animals which entered the field of view of multiple cameras during a visit to a waterhole and/or a baited cork-tile in the surrounding savanna. In total, cameras were deployed at sites across the duration of the study for 740 trap nights.

Data processing

Photos taken by cameras were examined, their meta-data collated (i.e., date and time of photo capture) and the species present identified using the database program, CPW Photo Warehouse version 4.3.0.5 (Newkirk 2016). Given the geographic location of the study area, sunrise and sunset times did not fluctuate by > 1 h over the data collection period and were defined as follows: sunrise (6 am–7 am), sunset (6 pm–7 pm). It was not possible to record data blind because characteristics which identified each study waterhole were visible in photos which the observer had to process.

The response variable for our analysis was the presence or absence of a species at a site within any given hour of sampling. Hence, each time a target species was detected at a study waterhole, we recorded the hour of day the detection occurred within that 24-h period (i.e., hour 0–23). As the variable is presence/absence rather than a count of visitation events, multiple visits within a given hour still only represented a single data point. This method was then applied over the entire period cameras were deployed at each site over each season and then pooled to create a 24-h representation of temporal activity for each species studied.

We included several predictor variables in our analysis: fencing treatment (i.e., fenced or unfenced), number of days since the dry season started (as a continuous variable), year, and moon phase. Fencing treatment was included as a fixed factor for macropod, pig, and dingo models only, because they were present in both treatments. Fencing was not included as a variable in cattle and buffalo models, because they could not access fenced sites. Although we observed waterholes for a total of 17,761 h, the different species studied here (i.e., ungulates, macropods, and dingos) rarely visited waterholes simultaneously. There were only 81 instances in which more than one species visited the same waterhole within the same hour, and the number of instances in which specific competitors visited waterholes at the same time (e.g., macropods and cattle) is an even smaller fraction of this number. Hence, the inclusion of presence/absence of heterospecifics as covariates in our modelling was not possible, as the amount of zero inflation prevented model convergence.

Due to differences in the amount and date that rainfall fell across the 2017/2018 and 2018/2019 wet seasons, the date the dry season started differed between years. Given that researchers lived on site and could begin sampling as soon as rains ceased and tracks became accessible, the date sampling began was taken as the start of the dry season. Year
and moon phase were also included as fixed factors. Moon phase was classified into 3 categories: waxing/waning moon, no moon, and full moon. To assess whether the activity of species changed in response to moonlight intensity, we used activity in the wax/wane phase as a baseline to compare activity during the no moon and full moon phases. The dates considered as no moon and full moon were taken as the day of the phase ± 3 days (following Coulson 1982), and all days between were classified as waxing/waning days. Data was collected during the dry season when cloud cover is absent. Study site was included as a random effect to account for repeated sampling of sites. See Table 1 for a summary of the number of trap nights cameras sampled each variable.

All n values reported are the total number of hours a given species was detected in (i.e., hours present). As we were interested in whether macropods as a family were affected by the presence of feral ungulates and dingoes around savanna waterholes, data from all macropod species detected by cameras was pooled into a single dataset.

**Data analyses**

Generalised additive mixed-effect models (GAMMs) were used to analyse temporal activity data. This approach was taken because this type of regression is able to model non-linear relationships (Wood 2006), which was necessary given temporal dynamics of species over the diel cycle are often highly non-linear. Additionally, GAMMs allow the effects of multiple covariates on the response variable to be modelled at the same time (unlike pairwise comparisons). A binomial distribution with a logit link function was used because our response variable was a vector of ones and zeroes (i.e., species present = 1, species absent = 0 within a given hour of day). We used GAMMs to model the probability of presence of each species against time of day, to the nearest hour, specified as a smoothed term fitted to a cyclic cubic regression spline (Wood and Scheipl 2020). We used a cyclic spline so that there would be no discontinuity between first and last hours of the day (i.e., over the cusp of midnight), allowing us to produce curves which illustrate the temporal activity patterns for each species (see Cunningham et al. 2019).

To determine whether the temporal activity patterns of macropods, pigs, and dingoes differed between fenced and unfenced sites, fencing treatment was included as a categorical variable with two levels: fenced and unfenced. We compared the base model for each of these species with a variable co-efficient GAMM that included an interaction between treatment and time of day using the “by” function (Wood and Scheipl 2020). This allowed the generation of a separate smoothed term for fenced and unfenced sites (see Wood 2006; Zuur et al. 2009) so we could compare whether the temporal activity patterns of species differed between fencing treatments. We also determined whether the inclusion of an additional smoothed term was required to model the relationship between species presence and dry season progression, as the data indicated this relationship may have been non-linear for some species. Akaike’s Information Criterion (AIC; Akaike 1973) was calculated to compare models with and without the interaction and smooth terms to determine which model was most parsimonious.

To investigate how dry season progression affected temporal activity patterns we divided the data for each species into three stages of the dry season: start, middle, and end. Sub-setting the data in this manner allowed us to create separate temporal activity curves for each species in each treatment (where possible) during each stage of the dry season. We followed the same model selection process as outlined above for the base models to determine whether the temporal activity patterns of macropods, pigs, and dingoes differed in fenced and unfenced sites at different stages of the dry season. We accounted for variation between years in the number of days sites were sampled over the dry season due to study waterholes drying out at slightly different times (n 2018 = 173 days, n 2019 = 150 days). It is important to note that our definition of the end of the dry season is based on the drying of ephemeral waterholes in the study area, rather than the true end of the season per se (i.e., when first storms begin). See Table 1 for a summary of the number of trap nights cameras sampled each subset category of the dry season.

All models were created using the “gamm4” package (Wood and Scheipl 2020) in statistical program, R (R Core Team 2020). Figures were then generated with R by using these models to calculate predicted hourly presence values using the “ggeffects”

**Table 1** The number of trap nights sampled for each variable used in analyses

<table>
<thead>
<tr>
<th></th>
<th>Number of trap nights sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Both fence treatments*</td>
</tr>
<tr>
<td><strong>Year</strong></td>
<td></td>
</tr>
<tr>
<td>2018</td>
<td>446</td>
</tr>
<tr>
<td>2019</td>
<td>294</td>
</tr>
<tr>
<td><strong>Moon phase</strong></td>
<td></td>
</tr>
<tr>
<td>Wax/wane</td>
<td>394</td>
</tr>
<tr>
<td>No moon</td>
<td>171</td>
</tr>
<tr>
<td>Full moon</td>
<td>175</td>
</tr>
<tr>
<td><strong>Subset dry season</strong></td>
<td></td>
</tr>
<tr>
<td>Start</td>
<td>294</td>
</tr>
<tr>
<td>Middle</td>
<td>262</td>
</tr>
<tr>
<td>End</td>
<td>184</td>
</tr>
<tr>
<td><strong>Total sampling effort</strong></td>
<td>740</td>
</tr>
</tbody>
</table>

*Denotes data used for macropod, pig, and dingo models
^Denotes data used for cow and buffalo models
and plotted with “ggplot2” (Wickham 2016).

Results

General waterhole use

Buffalo and cattle were present around waterholes approximately twice as much as the other species studied \( n_{\text{buffalo}} = 162 \, \text{h}, n_{\text{cow}} = 149 \, \text{h}; \) where \( n \) is the number of hour-long sample blocks during which the species was detected). Dingoes were detected more often than macropods \( n_{\text{dingo}} = 81 \, \text{h}, n_{\text{macropod}} = 70 \, \text{h} \), while pigs were detected least often \( n_{\text{pig}} = 65 \, \text{h} \). Macropod species detected on camera included primarily northern nailtail wallaby \( \text{(Onychogalea unguifera,} n = 27 \, \text{h}) \) and antilopine kangaroo \( \text{(Macropus antilopinus,} n = 18 \, \text{h}) \), although agile wallabies \( \text{(M. agilis,} n = 3 \, \text{h}) \) were also detected in very low numbers. Macropods which could not be identified to the species level were detected in a further 22 hours, although most of these were likely antilopine kangaroos based on their size.

We found that the general activity of all species (across the entire dry season) varied significantly with time of day (Table 2). Macropods were active at night, with peak activity occurring around 11 pm (Fig. 3a). Pigs were most active in the early morning, with a peak in activity just before dawn (Fig. 3b). Cattle were active during daylight hours, with their activity rising steadily from dawn and peaking in the late afternoon before dropping quickly around dusk (Fig. 3c). Buffalo activity had two distinct peaks around dawn and dusk, but they were more active around dusk (Fig. 3d). Dingo activity was similar to that of buffalo, with two distinct peaks around dawn and dusk, but they were most active around dawn (Fig. 3e).

<table>
<thead>
<tr>
<th>Species</th>
<th>Macropod</th>
<th>Pig</th>
<th>Cow</th>
<th>Buffalo</th>
<th>Dingo</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total n</td>
<td>70</td>
<td>65</td>
<td>149</td>
<td>162</td>
<td>81</td>
</tr>
<tr>
<td>Smoothed term (time) edf</td>
<td>3.014</td>
<td>2.707</td>
<td>3.486</td>
<td>3.072</td>
<td>3.191</td>
</tr>
<tr>
<td>Chi-sq</td>
<td>37.17</td>
<td>26.74</td>
<td>52.91</td>
<td>9.521</td>
<td>15.62</td>
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<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.0173</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Fencing treatment n (f, unf)</td>
<td>37, 33</td>
<td>28, 37</td>
<td>-</td>
<td>-</td>
<td>36, 45</td>
</tr>
<tr>
<td>St. error</td>
<td>0.7764</td>
<td>0.7259</td>
<td>-</td>
<td>-</td>
<td>0.2912</td>
</tr>
<tr>
<td>z</td>
<td>-1.142</td>
<td>0.359</td>
<td>-</td>
<td>-</td>
<td>0.449</td>
</tr>
<tr>
<td>p</td>
<td>0.2533</td>
<td>0.7197</td>
<td>-</td>
<td>-</td>
<td>0.6531</td>
</tr>
<tr>
<td>Year n (2018, 2019)</td>
<td>30, 40</td>
<td>43, 106</td>
<td>43, 106</td>
<td>76, 86</td>
<td>46, 35</td>
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<tr>
<td>St. error</td>
<td>0.3509</td>
<td>0.2971</td>
<td>0.1903</td>
<td>0.1623</td>
<td>0.2367</td>
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<tr>
<td>z</td>
<td>3.814</td>
<td>3.68</td>
<td>6.484</td>
<td>2.572</td>
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<tr>
<td>p</td>
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<td>&lt;0.001</td>
<td>0.0101</td>
<td>0.3735</td>
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<tr>
<td>Smoothed term (days since dry season began) edf</td>
<td>5.286</td>
<td>4.077</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Chi-sq</td>
<td>49.67</td>
<td>18.55</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>p</td>
<td>&lt;0.001</td>
<td>0.0011</td>
<td>-</td>
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<tr>
<td>Dry season progression (overall) St. error</td>
<td>-</td>
<td>-</td>
<td>2.833</td>
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<td>z</td>
<td>-</td>
<td>-</td>
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<td>-</td>
<td>-</td>
<td>0.1892</td>
<td>0.0798</td>
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</tr>
<tr>
<td>No moon n (no, wax)</td>
<td>18, 38</td>
<td>31, 75</td>
<td>21, 80</td>
<td>30, 39</td>
<td>-</td>
</tr>
<tr>
<td>St. error</td>
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<td>0.4269</td>
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<td>0.1836</td>
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<td>0.05198</td>
<td>0.0213</td>
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<td>Full moon n (full, wax)</td>
<td>14, 38</td>
<td>43, 75</td>
<td>61, 80</td>
<td>12, 39</td>
<td>-</td>
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<tr>
<td>St. error</td>
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<td>p</td>
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<td>0.4501</td>
<td>0.00552</td>
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<tr>
<td>Adj. r^2 (%)</td>
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<td>0.549</td>
<td>1.53</td>
<td>0.384</td>
<td>0.161</td>
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</tbody>
</table>

Significant \( p \) values (<0.05) are displayed in bold; hyphens denote variables not included in models. Total \( n \) is the number of hours a species was detected in. Smoothed term describes the deviation of predicted presence from zero. For \( n \) values, (f, unf) denotes (fenced, unfenced); (no, wax, full) denote moon phases.
Fencing treatment

We found no significant difference in the predicted hourly presence of macropods, pigs, and dingoes in fenced and unfenced sites (Table 2). The addition of an interaction term (a by factor) between fencing treatment and time of day resulted in a less parsimonious model for all species (i.e., higher AIC, see online supplementary material Table S1), indicating that the temporal activity patterns of macropods, pigs, and dingoes did not differ substantially between fenced and unfenced sites over the entire dry season.
When we considered the dry season as three stages, we found that macropods, pigs, and dingoes did not use fenced sites significantly more than unfenced ones (see online supplementary material Table S2). In addition, the temporal activity patterns of dingoes did not differ significantly between fencing treatments during different stages (i.e., Δ AIC for all models ≥ 2, and model with by factor removed was the most favourable; Table S2). This was also the case for macropods and pigs during the start and end of the dry season (Table S2). However, the temporal activity of macropods and pigs did differ significantly between fencing treatments during the middle of the season when the presence of both species peaked (see Table 3 for significance of smooth results), although the model without by factor for fencing was still the most parsimonious in both cases (Table S2). Macropod presence at fenced sites during the middle of the dry season was greater than at unfenced sites (although not significantly so—Table 4), and their temporal activity patterns (Fig. 4a) were similar to those observed overall (Fig. 3a). At unfenced sites in the middle of the dry season, macropods did not have well-defined temporal patterns (Fig. 4a), although their activity peaked at ~2 am as opposed to ~9 pm in fenced sites. This may have been due to low macropod visitation to unfenced sites during this stage (n = 9), which is supported by the lack of difference seen in the temporal activity patterns of macropods in different fencing treatments at the end of the dry season (when macropods visited unfenced sites more, n = 24). Pig activity patterns in fenced and unfenced sites during the middle of the dry season (Fig. 4b) were more consistent with those observed overall (Fig. 3b); however, their activity at unfenced sites peaked a few hours earlier (~1 am) than at fenced sites (~4 am) (Fig. 4b).

### Water scarcity

Overall, the predicted presence of cattle and dingoes increased in a linear pattern as the dry season progressed (cattle: Fig. 5c, dingoes: online supplementary material Fig. S2); however, this increase was only significant for cattle (Table 2). Buffalo presence declined in a linear pattern as the dry season progressed and was not significant (Fig. S2, Table 2). In contrast, macropod and pig presence had a non-linear relationship with dry season progression (Fig. 5a, b respectively). The visitation of both species increased gradually before peaking in the middle of the dry season and then declining sharply towards the end of the dry season. In 2018, there were zero macropod detections in the last 34 days of sampling, and in 2019 there were only 2 detections in the last 40 days of sampling. Pigs followed a similar pattern, with zero detections in the last 52 days of sampling in 2018, and only 3 detections in the last 40 days of sampling in 2019.

Year had a significant effect on the predicted presence of all species, except dingoes (Table 2; Fig. 6). The mean hourly presences of macropods, pigs, cattle, and buffalo were significantly higher in 2019 (drought year) than in 2018, and this response was greatest in cattle.

### Moon phase

The presence of dingoes increased significantly during the no moon compared to the wax/wane phase, whereas there was no significant difference detected for macropods, pigs, cattle, and buffalo (Table 2, Fig. 7). During the full moon, buffalo presence was significantly greater than in the wax/wane phase.
while the presence of macropods, pigs, cattle, and dingoes was not affected significantly (Table 2, Fig. 7).

Discussion

Water scarcity and interspecific competition

The presence of herbivores which are larger in size and/or behaviourally dominant can affect the visitation behaviour of competitively inferior species at waterholes (Ostermann-Kelm et al. 2008; Valeix et al. 2009; Hall et al. 2018). We assessed native macropod visitation to savanna waterholes and found they did not preferentially use sites where large feral ungulates were excluded, even when resources became scarce. We also found no significant difference in their overall temporal activity patterns (i.e., over the entire dry season) across the two fencing treatments. As our fencing experiment prevented buffalo and cattle from accessing fenced sites, we could not model their direct impact on the temporal behaviour of species which could access both fencing treatments (e.g., macropods) due to complete separation of the data. However, when we considered macropod behaviour during different stages of the dry season, we found that their temporal activity patterns differed significantly between fencing treatments during the middle of the dry season, when macropod presence at sites was greatest (but not at the start or end of the season). Compared to fenced sites, macropods visiting unfenced sites in the middle of the dry season had less defined activity patterns, and their peak activity occurred later at night. This may be explained by
lower macropod attendance to unfenced sites during this stage, which may have confounded our results. In addition, the model which assumed macropods did not vary their temporal activity between fencing treatments was found to be the more favourable of the two supported models, and the temporal activity patterns of macropods did not differ across fencing treatments at the end of the dry season (when macropods visited unfenced sites most). However, as the model which assumed macropod temporal activity patterns did vary with fencing treatment during this stage was also supported, we cannot discount the possibility that competition from large ungulates may affect macropod behaviour. This may explain why macropod activity peaked at unfenced sites later at night, when cattle activity was lower. As resource scarcity can intensify interspecific competition and force species to adjust their temporal niche (Valeix et al. 2007; Hasui et al. 2009), our findings suggest that macropods may temporally avoid cattle as water scarcity increases. In addition, at the end of the dry season, macropod presence around waterholes declined rapidly in both years, while cattle presence continued to increase. Hence, when water scarcity peaks, macropods may not just temporally, but also spatially avoid waterholes in areas utilised by cattle due to interference competition, as has been demonstrated with feral horses (Equus caballus) (Ostermann-Kelm et al. 2008; Hall et al. 2018). While we acknowledge that not including direct interactions between heterospecifics in our modelling (due to zero inflation and complete separation of the data) may have lessened our ability to demonstrate clear impacts of ungulate presences on macropods, we believe that our fencing experiment and observed differences in temporal visitation patterns to waterholes provide insights into potential interference competition between native and introduced species for access to limited water resources.

exploitative competition for food resources may also explain our results, as increasing cattle presence may have depleted green vegetation resources (e.g., riparian grasses, forbs, and sedges) which establish around waterhole peripheries as the dry season progresses. Macropods may be sensitive to this type of competition because they have narrower feeding niches than introduced ungulates (Reid et al. 2020).

<table>
<thead>
<tr>
<th>Dry season stage</th>
<th>Species</th>
<th>Model terms</th>
<th>St. error</th>
<th>z</th>
<th>p</th>
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<tr>
<td>Start Macropod</td>
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<td>8179</td>
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<td>-</td>
<td>-</td>
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<td></td>
</tr>
<tr>
<td>Base model</td>
<td>By factor for fencing treatment included</td>
<td>-</td>
<td>-</td>
<td></td>
<td></td>
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<tr>
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<td>0.774</td>
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<td>-</td>
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<tr>
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<td>-</td>
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</table>

Table 4: GAMM results for influence of fencing treatment on predicted presence of macropods, pigs, and dingoes over different stages of the dry season (start, middle, and end). Models presented are the most favourable based on AIC values (see online supplementary material Table S2). Where Δ AIC < 2, results for both models are presented.
This is of concern because the competitive exclusion of native species by introduced competitors has potential fitness consequences, such as decreased growth and fecundity (Harris et al. 2006; Ayala et al. 2007). However, as macropod presence also declined rapidly at fenced waterholes at the end of the dry season, their response may be related to other seasonal factors not studied here (e.g., changes in food availability in the wider savanna, breeding cycles). Overall, our results suggest that small scale exclusion fencing may not affect macropod visitation to waterholes in areas where feral ungulates are present (at least not over short time spans), but more research is required.

In contrast to cattle, the presence of buffalo at study waterholes was not significantly affected by dry season progression. Buffalo have fewer sweat glands than other ungulates (e.g., cattle, sheep), forcing them to wallow regularly to thermoregulate (Tulloch and Litchfield 1981; Bracke 2011; Collier and Gebremedhin 2015). Hence, the progression of the dry season may have had little effect on their overall water requirements. We also found that the temporal activity patterns of pigs differed between fencing treatments during the middle of the dry season, with their activity peaking at unfenced sites several hours earlier than at fenced sites. This
difference in pig behaviour could be explained by temporal avoidance of buffalo at unfenced sites, which are known interference competitors of pigs (Corbett 1995a; Finlayson et al. 1999). However, as with macropods, the model which assumed pig temporal activity did not vary between fencing treatments was the more favourable of the two supported models, and low pig visitation could have confounded our results. Pig activity also declined rapidly at the end of the dry season. However, as pigs forage on benthic vegetation (e.g., tubers of spike rushes and water lilies) at this time of year (Ridpath 1991), this response is likely due to declining food availability as study waterholes dried out, rather than competition.

Drought also affected animal visitation to savanna waterholes, resulting in significantly higher presences of macropods, pigs, and cattle. Buffalo presence also increased significantly during the drought, despite dry season progression having no effect on their behaviour. Ephemeral rainfall-fed water sources (such as the waterholes studied here) are sensitive to climatic variation and can dry faster in low rainfall years (Redfern 2002; Chamaillé-Jammes et al. 2007). Hence, the water demands of buffalo may have increased during the drought (but not necessarily over the dry season) due to reduced water availability across the landscape in that year. Our findings closely mirror those of a similar 2-year study in African savanna (Valeix 2011) and suggest that competition between feral ungulates and native wildlife for waterhole access may progressively intensify with increasing water scarcity. However, we acknowledge that the measures of water scarcity used here are coarse (i.e., days since the dry season began, year), and the availability of water at alternative waterpoints surrounding our study sites may have affected our results.

**Predator and prey responses to water scarcity and moon phase**

The threat of predation is not uniform in natural systems but varies both spatially and temporally due to changes in environmental conditions (Penteriani et al. 2013; Palmer et al. 2017). We found that both seasonal and interannual bottlenecks in water availability corresponded with increased prey presence (i.e., macropods, pigs, cattle, and buffalo) at savanna waterholes, similar to previous findings from Africa (Thrash et al. 1995). However, this did not correspond with increased dingo presence around waterholes, despite overlap in their temporal activity with all of the prey species studied. This could indicate that dingoes are not using waterholes as primary hunting grounds in this system, unlike in more arid parts of Australia (Shepherd 1981). Alternatively, dingoes may favour other prey during the dry season which are more prevalent in the surrounding savanna, such as reptiles, insects, and ground dwelling birds. Dingoes may also focus their hunting activity around larger, more permanent waterbodies than those studied here (e.g., large billabongs, wetlands) where prey visitation may be more consistent throughout the year. The drought could also have provided scavenging opportunities for dingoes away from waterpoints.

Predation threat can also vary with changes in night-time illumination (Harmsen et al. 2011; Penteriani et al. 2011, 2013; Palmer et al. 2017). We found that dingo activity around waterholes increased on moonless nights, suggesting that dingo hunting success may improve under low light conditions, as has been shown for other savanna predators (e.g., lions: Funston et al. 2001; Packer et al. 2011). This is because prey may find detection or defence against dingoes more difficult on moonless nights, particularly when young are present. In support of this theory, we observed two dingo predation attempts at waterholes during this study and both were targeted on ungulates with calves on moonless nights. Furthermore, while not significant, buffalo showed reduced activity on moonless nights compared to other moon phases. During the full moon, buffalo activity increased significantly compared to the wax/wane phase. However, as this did not correspond with a decline in dingo activity, the response of buffalo may not necessarily reflect changes in predation risk. Buffalo are primarily crepuscular; hence, they may utilise higher illumination levels during full moons for increased movement or foraging. In contrast, cattle are primarily diurnal, and pigs are most active during pre-dawn hours. Hence, moon phase may not provide them the same advantages and disadvantages as for buffalo, which may explain why no response to moon phase was observed in cattle and pigs.

Surprisingly, macropods did not shift their visitation behaviour in response to moon phase. However, macropod activity peaked during the night-time lull in dingo activity, which may be an antipredator response to limit their exposure to dingoes. Alternatively, macropods may increase their vigilance during moonless nights when predation risk is highest, rather than altering their overall visitation behaviour. Considering dingoes are the apex terrestrial predator in Australian ecosystems and have a reputation as a threat to livestock (Letnic et al. 2012), more studies which investigate how water scarcity and moon phase affect their hunting behaviour are needed.

Due to rising temperatures, climate change is predicted to increase evaporation in northern Australia (Dai et al. 2018; NESP Earth Systems and Climate Change Hub 2020), which will likely reduce surface water availability for savanna wildlife (Ritchie and Bolitho 2008). Advances in geospatial technologies may allow future studies to evaluate in detail how changing availability of water sources in savanna ecosystems drives the spatial—temporal distributions of both native wildlife and introduced ungulates. As pastoralism is a major land use in the region (Holmes 2010) and continuing to intensify due to recent
improvements in remote cattle management technologies that allow increased stocking of remote areas (Hunt et al. 2013, 2014), competition between wildlife and ungulates (both feral and domestic) for access to water resources in Australian savannas is likely to intensify in the future. Our study highlights that feral ungulates may not only affect native wildlife communities indirectly (e.g., through changes to habitat structure and quality from vegetation grazing and trampling) but can also have direct impacts on the behaviour of native species. More research is needed to understand how the presence of introduced ungulates at water points impacts native wildlife communities in Australian savannas as availability of surface water sources may become more limited in space and time.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-022-03134-4.

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Author contribution All authors conceived and designed the study; HM conducted the field experiment and data collation; HM and DGN conducted the statistical analysis; all authors contributed to the writing and editing of the manuscript.

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Data availability All data analysed during this study are available in the supplementary material.

Code availability The modelling used for the statistical analysis is described in detail in the text, including the “R” packages used.

Declarations

Ethics approval Approval to conduct this study was granted by the Animal Care and Ethics Committee of Charles Sturt University (approved protocol number A17035) and the Parks and Wildlife Commission of the Northern Territory (permit number 61071). All field data collection adhered to the standards outlined in the Australian Code for the care and use of animals for scientific purposes and the Territory Parks and Wildlife Conservation Act 1976.

Consent for publication The authors consent to the publication of this manuscript in Behavioural Ecology and Sociobiology.

Conflict of interest The authors declare no competing interests.

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Reid AM, Murphy BP, Vigilante T, Corporation WGA, Barry LA, Bowman DM (2020) Carbon isotope analysis shows introduced bovines have broader dietary range than the largest native herbivores in an Australian tropical savanna. Austral Ecol 45:109–121

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Chapter 5: Effects of ungulate exclusion and water scarcity on the plant communities and bird assemblages of tropical savanna waterholes

This chapter has been prepared as a paper for submission to a peer-reviewed journal. It contains all references as part of the chapter.
Effects of ungulate exclusion and water scarcity on the plant communities and bird assemblages of tropical savanna waterholes

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Abstract

Savannas are one of the most degraded biomes in the world. Over 50% of savanna habitats have been converted for agricultural purposes and are now used for cropping or as pasture for domestic ungulates. In northern Australian savannas, several introduced ungulate species have established substantial feral populations, including within conservation areas. As Australian flora and fauna species evolved in the absence of hooved mammals, savanna ecosystems are particularly vulnerable to damage from introduced ungulates, especially during periods of low rainfall. Ungulates have high water requirements, and thus congregate around limited water resources. These areas also provide important resources for native plant and bird communities, particularly during periods of water scarcity. In this study, we quantified how ungulate presence around savanna waterholes impacts plant and bird communities during seasonal and interannual water scarcity events. We conducted a fencing experiment; whereby large ungulates were excluded from ten out of twenty savanna waterholes in Limmen National Park over three consecutive years. Rainfall varied greatly seasonally and interannually over the study period. We found that bird diversity was significantly lower as the dry season progressed and there was more bare ground surrounding waterholes accessible to ungulates, compared to fenced waterholes. Drought caused mass dieback of perennial grasses, which allowed forbs and annual grasses to increase in cover. Depending on their diet, birds responded differently to changes in plant cover. Our results illustrate that even highly mobile species suffer negative impacts from ungulate activity around important shared resources. The provision of ungulate-free refugia for...
native wildlife during water scarcity events will become increasingly important with climate change and pastoral intensification in northern Australia.

**Key words:** feral ungulate, bird, species richness, savanna, water scarcity, drought

**Introduction**

Savanna ecosystems dominate much of the tropical and sub-tropical latitudes, accounting for approximately 20% of the Earth’s land surface (Whitley et al. 2017; Pennington et al. 2018). However, savannas are one of the world’s most degraded biomes (de Lima et al. 2018), and by the year 2000, an estimated total of 49.7% of savanna habitats had been converted to pasture and crop lands (Ramankutty et al. 2008). As pastoralism has continued to intensify, particularly in South America (Williams and Anderson 2020), it is likely that additional savanna habitat has been lost over the last ~20 years. Increasing pastoralism in savannas has been accompanied by the replacement of native herbivores with domestic livestock. Human management provides livestock with protection against disease, predation, and resource bottlenecks, which enables them to survive at higher densities within savannas than native herbivores (Oesterheld et al. 1992). As a result, the conversion of native savannas to pastureland has been accompanied by drastic increases in grazing pressure from domestic ungulates (Sankaran 2019).

Rainfall is highly seasonal in savannas, whereby most of the rain received each year is concentrated over several months (wet season) and is followed by ~5-7 months (dry season) of little or no rain (Solbrig et al. 1996). To withstand these prolonged periods without rainfall, native plants have evolved mechanisms to cope with water stress (Vicente-Serrano et al. 2013), but their recovery following dry conditions can be slow (Schwalm et al. 2017). Hence, vegetation communities in savannas can be particularly susceptible to sustained grazing pressure from introduced ungulates, especially during drought (Sankaran 2019). Plant communities around waterpoints are particularly vulnerable to ungulate disturbance because the high water requirements of ungulates leads to their congregation around waterpoints (Tomkins and O’Reagain 2007; Graz et al. 2012). Increased ungulate trampling and grazing pressure around waterpoints causes declines in the species richness and structural complexity of plant communities (Ludwig et al. 1999; Landsberg et al. 2003; Petty et al. 2007) in a phenomenon known as the ‘piosphere effect’ (Thrash and Derry 1999; Illius and O’Connor 2000). Some important savanna plant species are more vulnerable to ungulate disturbance and water scarcity than others. For example, perennial grasses form dense tussocks which provide habitat and food resources for a range of native fauna, including birds (Radford and Andersen 2012). However, they can be particularly sensitive to ungulate grazing due to their higher palatability and longer life cycle compared to annual grasses (Diaz et al. 2007). In addition, perennial grasses can be...
slow to recover following drought if recruitment does not counterbalance mature plant deaths from grazing, which can occur even under moderate grazing pressure (Orr and O’Reagain 2011).

Northern Australia supports one of the largest savannas on Earth, which is home to a rich diversity of fauna (Woinarski et al. 2007). However, pastoralism has become a major land use in the region over the last ~200 years (Woinarski et al. 2007). In 2006, a total of 57.3% of Australia’s tropical savannas were under private pastoral tenure (Holmes 2010). Domestic cattle (Bos taurus, B. indicus) in northern Australia are rarely confined to fenced paddocks, but instead roam vast areas of native savanna until mustering (Hunt et al. 2013; Hunt et al. 2014; Chilcott et al. 2020). This allows domestic cattle to impact native ecosystems over extensive areas and to establish feral populations outside of pastoral zones. Several other ungulate species have also established large feral populations across northern Australia, including Asian water buffalo (Bubalus bubalis), pigs (Sus scrofa), horses (Equus caballus), and donkeys (E. asinus) (see Mihailou and Massaro 2021 for further details on introductions). Feral ungulate populations are spreading into national parks and conservation reserves (Bayliss and Yeomans 1989; Saalfeld 2014; Management 2016), where they threaten native flora and fauna communities. However, the removal of feral ungulates from such areas is often highly contentious due to their value to pastoralists, tourism operators, and as a food source for Aboriginal landowners (Robinson et al. 2005; Spear and Chown 2009; Ens et al. 2016; Sloane et al. 2021).

As Australian savanna plant species evolved in the absence of hooved mammals, they are thought to be particularly prone to disturbance from introduced ungulates (Freeland 1990; Sharp and Whittaker 2003; Scogings and Sankaran 2019). In recent years many native bird and mammal species have experienced rapid declines in their range and abundance (Woinarski et al. 2001; Franklin et al. 2005; Woinarski et al. 2011). While exotic predators and inappropriate fire-regimes have contributed to these losses, recent studies have demonstrated that feral ungulates exacerbate these declines through their negative effects on habitat (Legge et al. 2011; McGregor et al. 2014; Legge et al. 2019). Savanna waterholes are important habitat areas which act as natural hubs for animal activity where the abundance and diversity of species is more concentrated than in the surrounding landscape (Thrash et al. 1995; Redfern et al. 2003; Valeix 2011). This is because the monsoonal wet-dry cycle of rainfall in savannas limits the availability of surface water both seasonally and interannually (i.e., across the dry season, and during years of low rainfall) (Woinarski et al. 2007). Birds need regular access to water for bathing and drinking, particularly when conditions are hot or dry (Ambrose et al. 1996; Nicolson and Fleming 2003; Lee et al. 2017). Hence, during periods of water scarcity, waterholes in Australian savannas are important habitat areas for birds which provide access to limited water resources (Woinarski et al. 2007; Votto et al. 2020). However, because ungulates also need to drink frequently, and thus, rarely distribute themselves more than 5km from a water source (Tomkins and O’Reagain 2007; Graz et al. 2012), their impacts on vegetation communities
surrounding waterpoints can be exacerbated when water becomes scarce (Harrington et al. 1984; Pettit et al. 2012; Mihailou et al. 2022a). Ungulate damage to vegetation communities can have flow on effects for native bird communities through changes to habitat complexity and food availability. For example, the removal of understory vegetation by ungulates may reduce nesting substrate available for riparian bird species (Hunt et al. 2013; Neilly and Schwarzkopf 2019). Furthermore, grazing can reduce habitat quality for the prey of insectivorous bird species (Bromham et al. 1999; Ludwig et al. 1999; Woinarski et al. 2002) and can decrease the availability of grass seed for granivorous bird species (Crowley and Garnett 2001). During drought, overgrazing by ungulates can also exacerbate already poor grass-seed yields and lead to the local extinction of sensitive granivorous species (Barnard and Barvard 1925; Banko et al. 2013). Despite considerable potential for overlapping resource use by feral ungulates and birds, few studies have quantified how increasing ungulate activity around waterholes impacts bird communities in Australian savannas during seasonal and interannual water scarcity events.

In this study, we measured changes in plant and bird communities at 20 ephemeral savanna waterholes over three years in Limmen National Park, in northern Australia. To investigate the effects of feral ungulate presence on plant and bird communities, we fenced 10 waterholes to prevent ungulate access. As rainfall varied considerably over the study period, our aim was to investigate whether plant and bird communities were affected by the presence of feral ungulates, water scarcity, and the interaction of these two factors. We expected the percent cover of perennial grasses in the savanna, and of all vegetation classes in the receding water zones (i.e., closest to the water edge) would be lower at sites accessible to ungulates. We also expected bird species richness and abundance would be lower at sites accessible to ungulates, particularly as water scarcity increased. In addition, we hypothesised that the abundance of granivorous and insectivorous birds would be greatest at sites with higher perennial grass cover, while nectarivorous species would be most abundant at sites with high shrub/tree cover.

**Methods**

**Study area**

This study was conducted in Limmen National Park, which protects over a million hectares of mixed savanna woodland in the Gulf of Carpentaria region of the Northern Territory, Australia. The park has an annual rainfall average of 853mm (as measured at Nathan River Ranger Station, Bureau of Meteorology 2022), which mostly falls throughout the ‘wet season’ (October-April), while little to no rain is received throughout the ‘dry season’ (May-September). Ephemeral waterholes within the park are typically small clay basins, which dry completely by the end of the dry season and are refilled at the start of each wet season. Rainfall varied considerably in the region over the sampling period,
Site selection and experimental design

All waterholes studied here were ephemeral clay basins located in predominately clay soils with open mixed savanna woodland in the surrounding area (see Fig. 1a for an example). To limit differences in waterhole hydrology and surrounding vegetation, we excluded rocky and sandy basin waterholes, and waterholes located at the base of ridgelines or within 1 kilometre of larger watercourses (e.g., rivers, large permanent billabongs). The 20 waterholes selected were similar in size, depth, surrounding vegetation, and soil type. We then used a paired experimental design where we assigned the most similar waterholes into pairs based on their physical properties (as outlined above), estimated ungulate disturbance (e.g., determined from foot pugging, dung pats, tracks, wallows), and estimated density of alternate water sources in the surrounding area. All study waterholes were located within 1-2 kilometres of an alternative water source to minimise the likelihood that fencing would affect animal visitation to unfenced study waterholes. From each pair of waterholes, we then randomly selected one as a control (unfenced) and the other as a treatment site (fenced). The fencing design used is pictured in Fig. 1b and the locations of fenced and unfenced waterholes are shown in Fig. 2.

Fig. 1: An aerial view of a typical savanna waterhole accessible to feral ungulates in Limmen National Park in the mid dry season (a), and the four-wire fencing design used in this study (b).
Fig. 2: The locations of fenced (red circles) and unfenced (yellow circles) study waterholes within Limmen National Park.

Fences were erected in September 2017 to prevent waterhole access by cattle and buffalo, as well as horses (*Equus caballus*) and donkeys (*E. asinus*), which occur locally at very low densities (unpublished: Clancy and Vincent 2021). We were not able to exclude pigs from fenced sites because the use of meshed, pig-proof fencing would have also hindered the access of native wildlife (e.g., macropods, dingoes, etc). Fences excluded large ungulates from an area of 150 x 150 metres and were positioned so that the waterhole was in the centre of the fenced area. Fencing design was a standard four-strand, star picket fence, with barbed wire at approximately 120 centimetres and 60 centimetres above the ground (top and third line of fence) and galvanised plain wire in between (see Fig. 1b). Fences were reinforced against ungulate damage by spacing pickets at 7-meter intervals (10 to 12-
metre spacing is typically used) and including a steel dropper between pickets to help maintain tension under stress. Regular fence checks and maintenance were carried out at roughly 4-week intervals and fences re-stretched as necessary. Controlled, early season burns were used to create fire breaks (>1 kilometre away) so sites were protected from fire as much as possible over the duration of the study. Despite these precautions, lightning strikes in December 2018 started fires which affected 6 study sites. However, an equal number of fenced and unfenced sites were impacted.

Vegetation data
Vegetation was sampled using several different survey methods at the beginning of each field season when species identification is optimal (i.e., because detection of annual species and identification of perennial species declines as the dry season progresses). Permanent vegetation transects in study plots were established in early 2018 using a random selection process. The high-water line, which is characterised by vegetation change from inundation tolerant species to savanna species and visually distinguished by a ring of trees (Fig. 1) was used to delineate two zones: the receding water zone (area within the maximum high-water line) and the savanna zone (area outside the high-water line). A total of 3 vegetation transects were established in the receding water zone, and a further 5 transects in the savanna zone of each study plot. More transects were established in the savanna than in the receding water zones so that sampling effort was approximately proportional to the size of each zone within the plots. Transects measured 1 meter squared and were sampled using a frame with 16 equally distributed measurement points. The observer then used a 3-millimetre diameter pin to sample the presence or absence of each plant lifeform class at each measurement point (following Goodall 1952). Pins which were not contacted by any lifeforms were recorded as bare ground (both zones). Plant species were separated into several different lifeform classes: forbs (both zones), perennial grass (both zones), annual grass (savanna only), and shrubs/trees (savanna only).

Drone data
A DJI Phantom 3 Advanced drone was used to collect percentage cover data for shrubs and trees at the beginning of each field season. The drone was programmed using the Litchi mission hub application (Litchi 2021) to run autonomous flights over each of the 20 study plots (150 x 150 metres) while taking photographs at 2 second intervals with the camera facing directly downwards (gimbal position 90°). The white-balance was set to ‘sunny’ to adjust for low cloud cover over the sampling period. Photos were taken over a grid of 15 transect lines which were separated by 12 metres to allow ~50% overlap between photos. Transect lines extended 15 metres beyond the dimensions of the study plot in all directions to ensure the entirety of the plot was photographed. Drone flight lines were
mapped out for each site using Google Earth Pro (Earth 2021) and then exported into Litchi. The drone was programmed to fly at an altitude of 30m and a speed of 15 km/hr.

**Bird data**

Due to differences in waterhole drying times, bird surveys were conducted from April to October in 2018 (189 days), March to August in 2019 (143 days), and April to July in 2020 (107 days). Study sites were sampled on a 5-week rotation (4 waterholes per week) from the beginning of the dry season, until each waterhole dried out. The order in which sites were sampled was based on accessibility at the start of the dry season. Once established, sampling order was maintained throughout each season. Surveys were confined to the sample plots only (150 x 150 metres), which were delineated either by an enclosed fence line (fenced sites) or by a coloured star picket in each corner of the plot (unfenced sites). This ensured that the same area was sampled at the treatment and control sites and was easily distinguishable by the observer.

Each waterhole was surveyed once in the early morning and again in the late afternoon to account for the activity preferences of different bird species. For example, some Australian granivorous bird species can be more active (and thus more likely to be detected) in the morning than in the afternoon in hot climates (Fisher et al. 1972, Cooper et al. 2019). Abundance and species richness was assessed in study plots using two different survey methods: a 20-minute stationary point count (following Birdlife Australia’s standardised 2ha fixed point search methodology; Birdlife Australia 2022), and a 30-minute standardised search (following Watson 2003). Birds flying over or through the site were excluded, unless they were actively hawking for insects (e.g., woodswallows: *Artamus spp.*) or hunting (e.g., raptors). A total of 348 point counts (n = 145 in 2018, 100 in 2019, and 103 in 2020) and 351 standardised searches (n = 145 in 2018, 102 in 2019, and 104 in 2020) were conducted in total. To minimise disturbance from observer arrival and reduce recounting errors between surveys, a 10-minute buffer period was applied at the beginning of each survey (following Pascoe et al. 2019). Birds were identified to the species level either visually (using binoculars) or by call (when observer was certain the call originated within the survey plot). All surveys were conducted by the same observer, who wore plain, natural coloured clothing and either sat (point count) or walked quietly (standardised search) while conducting surveys. As point count data was used to assess abundance, only the minimum number of individuals (of a given species) detected within a plot was counted (following method described in Sullivan 2012) to reduce accidental recounting of moving individuals (i.e., if 3 moving individuals were detected in the middle of the plot and 12-minutes later, 5 individuals were detected in the corner of the plot, only a total of 5 individuals were recorded). The standardised search was used as the primary method for assessing species richness within plots because it allows the observer to walk freely around a search area (Watson...
increasing the likelihood of detecting cryptic savanna species, such as brown quail (*Coturnixypsiloaphora*).

**Response and predictor variables**

We calculated the proportional cover of a range of plant lifeform groups. Proportions were based on the number of pins in contact with a given lifeform (presence) and number of pins which the lifeform did not contact (absence) within each transect. Bare ground was also included in the analyses (i.e., no lifeforms in contact with a given pin). Response variables included the proportional cover of perennial grass, annual grass, forbs, shrubs/trees, and bare ground in the savanna zone, and perennial grass, forbs, and bare ground in the receding water zone. Other plant lifeforms, including sedges and weeds in both zones, and annual grasses in the receding water zone, were not modelled due to low coverage.

To determine the cover of shrubs and trees, drone photos were stitched together to create orthomosaic images for each site and year (a total of 60) using Agisoft Metashape version 1.6 (Agisoft LLC 2020). Due to very sunny conditions on some sampling days, the program MATLAB (The MathWorks Inc 2019) was used to correct while-balance where necessary. Each orthomosaic was compiled from ~400 photos at a resolution of 1cm per image. Orthomosaic images were trimmed to the plot dimensions (i.e., to remove the 15-meter buffer applied during sampling), and then divided into two zones: the receding water zone and the savanna zone, which was delineated visually by vegetation and/or soil colour differences at the transition point between the zones using ArcGIS Pro version 2.6 (Esri Inc 2020). Data from inside the transition line (i.e., in the receding water zone) was excluded to prevent aquatic vegetation from being included in the dataset. We then used ArcGIS Pro to perform an object-based classification workflow. Each orthomosaic was segmented, then an unsupervised ISO cluster classification was applied to each segmented image to determine the percentage cover of shrubs/trees in each plot. We then calculated the proportion of the plot covered by shrubs/trees.

To test how different factors affected birds with shared dietary preferences, species were pooled based on their feeding guilds (Table S1). These included granivores, insectivores, nectarivores, omnivores, frugivores, carnivores, nocturnal, and water foragers. The total community species richness was compiled from standardised search and point count surveys. The abundance of birds in different feeding guilds was determined from point counts only. We restricted our analysis to the three most common guilds recorded in surveys: insectivores, granivores, and nectarivores. Hence bird response variables included: total species richness, insectivore count, granivore count, and nectarivore count. As we wanted to determine whether dry season progression affected bird assemblages, data was compiled on a per survey basis.

To investigate whether the percentage cover of different plants affected bird assemblages around savanna waterholes, bird data was also compiled on a yearly scale (because plant data was...
only available on a yearly scale). To account for an unequal number of bird surveys at different sites due to differences in waterhole drying rate, we calculated the average species richness and counts for each guild variable as a function of the number of surveys conducted at a given site.

Data analyses

We used generalised linear mixed-effects models (GLMMs) for the analyses because they are well suited for modelling binomial and count data correlated by repeated sampling of study sites (Bolker et al. 2009; Bolker 2015). For plant data, GLMMs modelled each response variable against two fixed factors: fencing treatment, and year. To account for variation in bird assemblages over each season, bird GLMMs included an additional fixed factor: days since the dry season started (as a continuous variable). For each response variable (for both plant and bird datasets), we created a global model, which included all fixed factors and their interactions. To account for repeated sampling and variation between sites, we included site and pair as random effects. We then used the ‘dredge’ function from the ‘MuMin’ package (Barton and Barton 2015) to rank all possible models using Akaike’s information criterion (AIC; Akaike 1973). If more than one model was supported (i.e., ΔAIC ≤ 2, Akaike weight of most parsimonious model < 0.9), we produced a model which included all the variables (and their interactions) which were contained in the set of supported models (following Haslem et al. 2015; model details provided in Table S4 in supplementary information). For plant and bird data, we used function ‘emmeans’ from the ‘emmeans’ package (Lenth et al. 2019) to conduct full pairwise comparisons between different years and fencing treatments as required. For bird models where the full interaction between fencing, year and dry season progression was supported, we divided the data into years to compare how the dry season affected response variables across different fencing treatments (i.e., to compare curves). Plant data were modelled using a binomial family with a logit-link, while bird data were modelled using either a poisson or quasi-poisson family with a log-link. The quasi-poisson family was used for some variables to account for high variance (Wedderburn 1974; Ver Hoef and Boveng 2007) and an observation level random effect was included to include the dispersion of poisson models where necessary (Harrison 2014).

To investigate the importance of different plant lifeform groups on bird assemblages, we calculated the percent cover of each plant lifeform group and bare ground in the receding water and savanna zone of each plot. We then checked for correlated variables in each zone using the ‘chart.Correlation’ function from the ‘PerformanceAnalytics’ package (Peterson et al. 2018). In both zones, bare ground and perennial grass cover were correlated (i.e., correlation coefficients > 0.7). Hence, we used model selection to identify the most appropriate of the correlated variables to include in the global model for each bird predictor variable. We then used the ‘dredge’ function from the ‘MuMin’ package (Barton and Barton 2015) to rank models based on their AIC values. As with the
other analyses, where multiple models had support, we produced a model which included all variables (and their interactions) contained in the set of supported models (see Table S2 in supplementary information for details). Site, pair, and year were included as random effects. We used a Conway-Maxwell Poisson distribution to model the relationship between bird response variables and plant predictor variables due to its flexibility in dealing with both under- and over-dispersed count data (Sellers et al. 2012).

All data was analysed using the statistical program, ‘R’ (R Core Team 2020), with library ‘glmmTMB’ (Brooks et al. 2017). Model dispersion was checked using the ‘testDispersion’ and ‘simulateResiduals’ functions from the ‘DHARMa’ package (Hartig 2020). To estimate the proportion of variance explained by predictor variables and random effects (Nakagawa and Schielzeth 2013; Nakagawa et al. 2017), marginal and conditional r-squared values were calculated using the ‘r2’ function from the ‘performance’ package (Lüdecke et al. 2021). Figures were created by using models to calculate predicted values for each response variable using the ‘ggeffect’ function from library ‘ggeffects’ (Lüdecke 2018) and plotted with ‘ggplot2’ (Wickham 2016).

Results
Vegetation in the savanna zone
Forb cover in the savanna significantly declined from 2018 to 2019 (Fig. 3), and cover was significantly lower in unfenced sites than fenced sites (Table 1, Fig. 4). The interaction between year and fencing treatment was also important, as forbs in fenced sites declined significantly between 2018 and 2019, while the decline in unfenced sites between those years was not significant (Table 1, Fig. 4). Unfenced sites had lower coverage in 2018 compared to fenced sites, so their potential for decline was lower (Fig. 4).

The cover of all other savanna plants (shrubs/trees, annual and perennial grasses) and bare ground did not change due to fencing treatment alone. However, there was a significant interaction between year and fencing for bare ground and annual grass cover (Table 1). The amount of bare ground significantly increased in both fenced and unfenced sites following the onset of drought in 2019 (Table 1). However, unfenced sites had significantly more bare ground in 2020 than in 2018 (Fig. 4), indicating that vegetation recovery after the drought in 2019 was poorer at unfenced sites than at fenced sites (which showed no significant difference between 2018 and 2020; Table 1). Both annual and perennial grass cover declined over all fencing treatments from 2018 to 2019, but this decline was much more marked for perennials (Fig. 3). Following this initial decline, annual grass cover increased significantly from 2019 to 2020, however this recovery was better in fenced sites (Fig. 4). In contrast, perennial grasses did not show any significant recovery and continued to decline from 2019 to 2020 (although not significantly; Fig. 3). Shrub/tree cover increased significantly from
2018 to 2019, but then declined in 2020. Overall, there was no significant change in shrub/tree cover during this study (Fig. 3).

Table 1: Response of different plant lifeforms to year and fencing treatment in the savanna zone surrounding waterholes. Significant factors are presented in bold (p<0.05).

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Predictor variable(s)</th>
<th>Estimate</th>
<th>Odds ratio</th>
<th>Std. error</th>
<th>z value</th>
<th>t ratio</th>
<th>P value</th>
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<td>Shrub/tree</td>
<td>(Intercept)</td>
<td>36.65</td>
<td>-1.512</td>
<td>24.25</td>
<td>-</td>
<td>-</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2018 v 2019</td>
<td>6.201</td>
<td>-2.13</td>
<td>2.911</td>
<td>-</td>
<td>-</td>
<td>0.0036</td>
</tr>
<tr>
<td></td>
<td>2018 v 2020</td>
<td>0.3962</td>
<td>-2.13</td>
<td>0.186</td>
<td>-</td>
<td>0.8524</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2019 v 2020</td>
<td>-0.239</td>
<td>-0.09035</td>
<td>-2.645</td>
<td>-</td>
<td>0.00818</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 3: Effect of year on bare ground and plant cover in the savanna and receding water zones surrounding waterholes. Bars denote average percent cover, while error bars represent upper and lower confidence intervals. Letters (a-c) above error bars for each variable denote significance at the 5% confidence level (i.e., a common letter indicates that the difference between the mean count for different years is not statistically significant for a given variable).
Vegetation in the receding water zone

There was significantly more bare ground in the receding water zone at unfenced sites than fenced sites, but fencing treatment alone had no effect on forb and perennial grass cover (Table 2). However, there was a significant interaction between year and fencing on forb and perennial grass cover (Table 2). While forbs showed the same pattern as in the savanna (i.e., decline from 2018 to 2019, followed by an increase from 2019 to 2020), the recovery at fenced sites was greater than at unfenced sites (Fig. 5), although not significantly so (Table 2).

As observed in the savanna, perennial grasses in the receding water zone suffered significant decline between 2018 and 2020 (Table 2, Fig. 3). However, their decline in the receding water zone between 2018 and 2019 was not significant (Fig. 3). Perennial grass cover also declined significantly at fenced sites between 2019 and 2020 (Table 2), but fenced sites had more cover in 2019 overall, so had more potential for decline than unfenced sites (Fig. 5).
Table 2: Response of different plant lifeforms to year and fencing treatment in the receding water zone of savanna waterholes. Significant factors are presented in bold (p<0.05).

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Predictor variable(s)</th>
<th>Estimate</th>
<th>Odds ratio</th>
<th>Std. error</th>
<th>z value</th>
<th>t ratio</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare Ground</td>
<td>(Intercept)</td>
<td>-1.017</td>
<td>-0.4732</td>
<td>-2.149</td>
<td>-</td>
<td>0.03166</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td>2018 v 2019</td>
<td>1.301</td>
<td>0.2136</td>
<td>6.093</td>
<td>-</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2018 v 2020</td>
<td>-0.0215</td>
<td>0.2131</td>
<td>-0.101</td>
<td>-</td>
<td>0.9196</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2019 v 2020</td>
<td>-1.323</td>
<td>0.2133</td>
<td>-6.202</td>
<td>-</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Fencing</td>
<td>1.252</td>
<td>0.4407</td>
<td>2.841</td>
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<td></td>
</tr>
<tr>
<td>Perrenial grass</td>
<td>(Intercept)</td>
<td>-0.6265</td>
<td>-0.8567</td>
<td>-0.731</td>
<td>-</td>
<td>0.4646</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td>2018 v 2019</td>
<td>-0.217</td>
<td>0.3833</td>
<td>-0.566</td>
<td>-</td>
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<td></td>
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<td>2018 v 2020</td>
<td>-1.871</td>
<td>0.4033</td>
<td>-4.64</td>
<td>-</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
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<td>2019 v 2020</td>
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<td>1.837</td>
<td>-</td>
<td>0.0662</td>
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<tr>
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<td>-1.647</td>
<td>-</td>
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<tr>
<td></td>
<td>Fencing * Year</td>
<td>F 2018 v UNF 2018</td>
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<td>0.5675</td>
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<td></td>
<td></td>
<td>F 2019 v UNF 2019</td>
<td>6.56</td>
<td>6.266</td>
<td>1.969</td>
<td>0.3615</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>F 2020 v UNF 2020</td>
<td>2.356</td>
<td>2.28</td>
<td>0.886</td>
<td>0.9499</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>F 2018 v F 2019</td>
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<td>0.476</td>
<td>0.566</td>
<td>0.9931</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>F 2018 v F 2020</td>
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<td></td>
<td></td>
<td>F 2019 v F 2020</td>
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<tr>
<td></td>
<td></td>
<td>UNF 2018 v UNF 2019</td>
<td>1.679</td>
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<td>1.343</td>
<td>0.7606</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>UNF 2018 v UNF 2020</td>
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<td>1.256</td>
<td>2.884</td>
<td>0.0468</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>UNF 2019 v UNF 2020</td>
<td>1.878</td>
<td>0.741</td>
<td>1.598</td>
<td>0.6001</td>
<td></td>
</tr>
<tr>
<td>Forbs</td>
<td>(Intercept)</td>
<td>-3.335</td>
<td>-0.4559</td>
<td>-7.315</td>
<td>-</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td>2018 v 2019</td>
<td>-3.127</td>
<td>0.4824</td>
<td>-6.481</td>
<td>-</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2018 v 2020</td>
<td>2.328</td>
<td>0.333</td>
<td>6.991</td>
<td>-</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2019 v 2020</td>
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<td>0.6122</td>
<td>-3.092</td>
<td>-</td>
<td>0.00199</td>
</tr>
<tr>
<td></td>
<td>Fencing</td>
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<td>0.6319</td>
<td>0.436</td>
<td>-</td>
<td>0.6625</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fencing * Year</td>
<td>F 2018 v UNF 2018</td>
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<td>0.4796</td>
<td>-0.436</td>
<td>0.998</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>F 2019 v UNF 2019</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>F 2020 v UNF 2020</td>
<td>2.519</td>
<td>1.542</td>
<td>1.51</td>
<td>0.6582</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>F 2018 v F 2019</td>
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<td>11</td>
<td>6.481</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>F 2018 v F 2020</td>
<td>0.09745</td>
<td>0.03246</td>
<td>-6.991</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>F 2019 v F 2020</td>
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<td>0.00206</td>
<td>-11.31</td>
<td>0.0001</td>
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<tr>
<td></td>
<td></td>
<td>UNF 2018 v UNF 2019</td>
<td>11.4</td>
<td>4.686</td>
<td>5.918</td>
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<tr>
<td></td>
<td></td>
<td>UNF 2018 v UNF 2020</td>
<td>0.3235</td>
<td>0.106</td>
<td>-3.445</td>
<td>0.0008</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>UNF 2019 v UNF 2020</td>
<td>0.02839</td>
<td>0.01159</td>
<td>-8.721</td>
<td>0.0001</td>
<td></td>
</tr>
</tbody>
</table>
**Fig. 5:** Percent cover of perennial grasses and forbs in the receding water zone of waterholes in different years and fencing treatments. Bars denote average percent cover, while error bars represent upper and lower confidence intervals. Letters (a-c) above error bars for each variable and fencing treatment denote significance at the 5% confidence level.

**Bird assemblages**
A total of 103 species were detected in surveys. Bird species were primarily granivores (17 species, 40.4% of total count), insectivores (27 species, 29.1% of total count), and nectarivores (15 species, 19.8% of total count). The remaining guilds (i.e., omnivores, frugivores, carnivores, nocturnal, and water foragers) represented 44 species in total, but were not analysed individually due to their low collective abundance in study plots (10.7% of total count).

The total species richness of bird communities around savanna waterholes was significantly lower at unfenced sites as the dry season progressed, compared to fenced sites (Table 3). When year was also considered, there were significantly fewer species in unfenced sites as the dry season progressed in 2018, and although not significant, this trend was also observed in 2020 (Fig. 6, Table 3). In 2019, species richness declined in both fenced and unfenced sites as the dry season progressed (Fig. 6), but there was no significant difference between treatments (Table 3). Although species richness was significantly lower during the drought in 2019, there was no significant difference in species richness between 2018 and 2020 (Fig. 7).
Table 3: Response of birds to year, fencing treatment, and dry season progression around savanna waterholes. Significant factors are presented in bold (p<0.05). Dry season variables compare the dry season slopes between years and fencing treatments.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Predictor variable(s)</th>
<th>Estimate</th>
<th>Odds ratio</th>
<th>Std. error</th>
<th>z value</th>
<th>t ratio</th>
<th>P value</th>
</tr>
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<tbody>
<tr>
<td>Total species richness</td>
<td>(Intercept)</td>
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<td>-</td>
<td>0.0934</td>
<td>22.34</td>
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</tr>
<tr>
<td>Year</td>
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<td>0.07172</td>
<td>-6.202</td>
<td>-</td>
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</tr>
<tr>
<td></td>
<td>2018 v 2020</td>
<td>0.05876</td>
<td>-</td>
<td>0.06126</td>
<td>0.959</td>
<td>-</td>
<td>0.3375</td>
</tr>
<tr>
<td></td>
<td>2019 v 2020</td>
<td>0.5036</td>
<td>-</td>
<td>0.07637</td>
<td>6.594</td>
<td>-</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Fencing</td>
<td>2018 v UNF 2018</td>
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<td>-</td>
<td>0.1149</td>
<td>-0.261</td>
<td>-</td>
<td>0.7941</td>
</tr>
<tr>
<td>Fencing * Year</td>
<td>F 2018 v F 2019</td>
<td>-0.10342</td>
<td>-</td>
<td>0.1184</td>
<td>-6.202</td>
<td>-</td>
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</tr>
<tr>
<td></td>
<td>F 2018 v UNF 2018</td>
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<td>-</td>
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<td>F 2018 v F 2020</td>
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</tr>
<tr>
<td>Dry season</td>
<td>F 2019 v F 2020</td>
<td>-0.13546</td>
<td>-</td>
<td>0.10465</td>
<td>-3.361</td>
<td>-</td>
<td>0.000776</td>
</tr>
<tr>
<td>Dry season * Year</td>
<td>F 2019 v UNF 2019</td>
<td>-0.11939</td>
<td>-</td>
<td>0.07637</td>
<td>-1.56</td>
<td>-</td>
<td>0.1152</td>
</tr>
<tr>
<td></td>
<td>F 2018 v F 2020</td>
<td>0.0473</td>
<td>-</td>
<td>0.08814</td>
<td>0.537</td>
<td>-</td>
<td>0.592</td>
</tr>
<tr>
<td>Insectivore count</td>
<td>(Intercept)</td>
<td>1.564</td>
<td>-</td>
<td>0.09126</td>
<td>17.14</td>
<td>-</td>
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</tr>
<tr>
<td>Year</td>
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</tr>
<tr>
<td>Year</td>
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<td>-0.9237</td>
<td>-</td>
<td>0.1709</td>
<td>-5.405</td>
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</tr>
<tr>
<td></td>
<td>2018 v 2020</td>
<td>0.0385</td>
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<td>0.1602</td>
<td>3.361</td>
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<tr>
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<td>2019 v 2020</td>
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<tr>
<td>Fencing</td>
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<td>-</td>
<td>0.3049</td>
<td>-0.446</td>
<td>-</td>
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<tr>
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<td>-</td>
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<td>-</td>
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</tr>
<tr>
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<td>2018 v 2019</td>
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<td>-</td>
<td>0.1842</td>
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<td>-</td>
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</tr>
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<tr>
<td>Year</td>
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<tr>
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<td>0.163195</td>
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<td>-</td>
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<tr>
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<td>-</td>
<td>0.111712</td>
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<td>Dry season * Year</td>
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<td>-3.611</td>
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<td>-0.433985</td>
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<td>0.006745</td>
</tr>
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<td>2019 v 2020</td>
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<td>0.193017</td>
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<td>-</td>
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<td>Fencing * Dry season</td>
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<td>0.113693</td>
<td>-1.737</td>
<td>-</td>
<td>0.082461</td>
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</tr>
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</table>
Fig. 6: Species richness of bird communities around savanna waterholes in different years and with increasing days since the dry season began. Solid lines represent predicted mean values, shaded areas represent upper and lower confidence intervals.

The number of insectivores per survey was not affected significantly by dry season progression or fencing treatment, although there was a trend of lower counts at unfenced sites. Insectivore counts declined significantly between 2018 and 2019, but recovered in 2020 (i.e., no significant difference between 2018 and 2020; Table 3, Fig. 7).

Fencing treatment did not significantly affect granivore numbers, although there was a trend of lower counts at unfenced sites. There was a significant decline in granivores between 2018 and 2019, but then their numbers rose significantly in 2020 to above those recorded in 2018 (Table 3, Fig. 7). Granivore numbers were also affected by dry season progression, with significantly greater counts at the end of the dry season in 2020 compared to 2018 (Table 3).

Nectarivore counts were not significantly affected by year or fencing treatment alone (Table 3, Fig. 7). However, nectarivore abundances increased significantly as the dry season progressed in 2018 but declined during the drought (2019 and 2020; Table 3, Fig. S2).
Fig. 7: Effect of year on the predicted species richness, and counts of insectivores, granivores, and nectarivores per survey. Points denote average predicted counts per survey, while bars represent upper and lower confidence intervals. Letters (a-c) above bars for each variable denote significance at the 5% confidence level.

Effects of vegetation cover on bird communities

Model selection identified multiple models with support (i.e., ΔAIC≤2, Akaike weight of most parsimonious model <0.9) for each bird variable we investigated. Plant cover did not significantly affect bird species richness around savanna waterholes. However, model selection indicated that perennial grass, annual grass, and shrub/tree cover in the savanna, and forb cover in the receding water zone were still important factors that affected species richness around savanna waterholes (Table 4). Insectivore abundance increased significantly with increasing perennial grass cover in the savanna zone, but annual grass, and shrub/tree cover in the savanna zone were also identified as important factors affecting abundance (Table 4). Granivore abundance significantly decreased with increasing perennial grass cover, but significantly increased with increasing forb cover in the savanna zone (Table 4). However, perennial grass and forb cover in the receding water zone were also identified as important factors affecting granivore abundances around waterholes. Nectarivore counts were significantly higher with increasing annual grass cover in the savanna, but forb cover in the savanna, as well as perennial grass and forb cover in the receding water zone were also important factors affecting their abundance (Table 4).
Table 4: The effects of plant cover in the savanna and receding water zones of waterholes on the diversity (total species richness) and abundance of birds (insectivore, granivore and nectarivore count). Significant factors are presented in bold (p<0.05).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Predictor variable(s) in model including all hypotheses with substantial support</th>
<th>Zone</th>
<th>Estimate</th>
<th>Std. error</th>
<th>z value</th>
<th>P value</th>
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</thead>
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<td>0.2579</td>
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<td>0.002579</td>
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<td>0.00881</td>
<td></td>
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<tr>
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<td>-1.789</td>
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Discussion

Ungulate impacts on plant and bird communities

In the water limited savannas of northern Australia, waterholes provide important resources for native birds during seasonal and interannual periods of water scarcity (Woinarski et al. 2007; Votto et al. 2020). Feral ungulates in Australian savannas also aggregate around waterholes as water scarcity increases (unpublished: Mihailou et al. 2022b), but no previous research has investigated the impacts this may have on native birds. In this study, we demonstrate that seasonal water scarcity exacerbates feral ungulate impacts on savanna bird communities. As the dry season progressed and water became scarcer, the species richness of bird assemblages in Limmen National Park was significantly lower at waterholes accessible to feral ungulates, compared to those where ungulates had been excluded. Ungulate activity decreased the structural complexity of vegetation communities closest to water (i.e., more bare ground at unfenced sites), potentially reducing the suitability of these areas for water dependant bird species which prefer denser foraging habitats, such as brown quail (Legge et al. 2008) and common bronzewing (Phaps chalcoptera; Tassicker et al. 2006). Damage to these vegetation communities would have intensified as the dry season progressed due to increasing ungulate aggregation around remaining water sources (Thrash and Derry 1999; Illius and O'Connor 2000; unpublished: Mihailou et al. 2022b). Hence, as water scarcity increases, negative impacts of ungulates on vegetation communities
may limit the suitability of habitats surrounding waterholes for some bird species, decreasing overall species richness. Several other studies have similarly found that the structural simplification of savanna habitats is associated with species richness declines in bird communities (Tassicker et al. 2006; Hannah et al. 2007; Kutt and Fisher 2011). The importance of vegetation structure surrounding savanna waterholes is further exemplified by the decline in bird diversity that we observed after the drought caused a mass dieback of perennial grasses. Contrary to our findings, other studies in Australian savannas have found no correlation between bird diversity and ungulate grazing pressure (e.g., Woinarski and Ash 2002; Kutt and Woinarski 2007; Kutt et al. 2012). However, these studies did not account for seasonal fluctuations in water availability. Hence, our results demonstrate that feral ungulate impacts on savanna bird diversity may only become apparent when studied in the context of water scarcity.

We detected significant negative impacts of feral ungulates on native plant and bird communities in Limmen National Park, despite ungulates occurring at the very low density of <1 ungulate/km² (unpublished: Clancy and Vincent 2021). By comparison, some pastoralists in northern Australian savannas consider 11 cattle/km² as a ‘safe’ carrying capacity (Walsh and Cowley 2014). Given our findings, one can only imagine the detrimental impacts domestic cattle may be having on savanna ecosystems across northern Australia at such densities. Furthermore, pastoralism continues to intensify in the region and new technologies are allowing cattle management in increasingly remote areas (Hunt et al. 2013; Hunt et al. 2014). This highlights the importance of providing ungulate-free refuge areas for native species, particularly in water limited habitats. However, feral ungulates persist in national parks and conservation areas due to conflicting stakeholder values (Robinson et al. 2005; Spear and Chown 2009; Sloane et al. 2021), and the expense and public controversy surrounding aerial culling programs (see seminal paper by Nimmo and Miller 2007). As a result, the problem is often disregarded, and there have been no large-scale surveys of feral ungulate populations in northern Australia since the 1980’s (Bayliss and Yeomans 1989), despite evidence that local populations are expanding in size and distribution (Saalfeld 2014). While ungulate removal from conservation areas is the ultimate goal, this study demonstrates that the use of small-scale fences to exclude large feral ungulate species from waterholes is an effective, inexpensive way to protect the diversity of savanna bird communities. The provision of fenced ungulate-free refuges may be particularly important in areas home to threatened bird species reliant on riparian vegetation (e.g., purple-crowned fairy-wren: *Malurus coronatus*) or for those requiring regular access to water (e.g., granivores).

**Drought, plant cover, and bird assemblages**

Drought had a significant effect on vegetation communities surrounding savanna waterholes, causing the dieback of perennial grasses and creating space for forbs and annual grasses to colonise. While other studies in Australian savannas have recorded perennial grass recovery under reduced ungulate stocking rates (Foran and Bastin 1984; Skeat et al. 1996; Kutt et al. 2012), we found no significant change in cover following fencing. Furthermore, perennial grasses can be sensitive to the interaction between drought and grazing (Orr
and O’Reagain 2011), yet, we saw no such effect. However, the timing of grazing is important, as grazing during the dry season (when most grasses are senescent) can have minimal effects on savanna vegetation productivity (Ash and McIvor 1998). Instead, perennial grasses are most susceptible to damage during the late wet season (Ash and McIvor 1998). In this study, wet season grazing pressure was likely minimal because study sites were located on black soil plains which cattle typically avoid when wet. This may explain the lack of significant recovery of perennial grasses following ungulate exclusion. In addition, ungulate densities may not have been high enough before fencing to mediate significant change beyond the receding water zone and the severity of the drought may have impaired vegetation recovery at fenced sites. Nevertheless, our results highlight the complex interactive effects that grazing and water availability can have on savanna vegetation.

Depending on their diet, birds responded differently to changes in savanna plant cover and water scarcity events. Insectivorous bird abundances increased significantly with higher perennial grass cover in the savanna. Local perennial grass species form dense tussocks (e.g., Chrysopogon latifolius, C. fallax, Eulalia aurea, Aristida latifolia) which may provide better habitat for insect prey (Radford and Andersen 2012) than the sparser local annual species (e.g., Schizachyrium fragile, Sporobolus australasicus, Thaumastochloa pubescens). Conversely, granivore abundances declined with increasing perennial grass cover, which was strongly correlated with bare ground (i.e., more perennial grass = less bare ground). Hence, granivores may benefit from having more bare ground to forage for dropped seed. This illustrates that ungulate disturbance around waterholes may be beneficial for some bird groups but detrimental for others. Granivore abundances also increased significantly with higher forb cover in the savanna zone. Peaceful doves (Geopelia striata), the most common granivore detected, primarily feed on grass seeds but also eat seed from several locally common forbs whose cover increased during the drought, including Desmodium, Phyllanthus, and Spermacoce species (see Frith et al. 1976; Higgins and Davies 1996). Grasses can have reduced seed yields following periods of water stress (Peleg et al. 2011; Menezes et al. 2015), hence the positive association between granivore abundance and forb cover may be because granivores switched their diet to forb seeds during the drought.

Nectarivore abundances increased as the dry season progressed in 2018 but decreased during the drought years. Flowering in the region typically peaks in the mid dry season (Woinarski et al. 2000). Hence, increasing nectar availability likely resulted in greater nectarivore abundances as the dry season progressed in 2018. By contrast, decreasing nectarivore abundance as the dry season progressed during the drought may be due to reduced flowering of nectar producing trees following poor rainfall (Law et al. 2000; Mac Nally et al. 2009). As climate change is predicted to increase rainfall variability in northern Australia (Dai et al. 2018; NESP Earth Systems and Climate Change Hub 2020), further research is needed to assess how the different habitat preferences of savanna bird species affect their tolerance of drought, particularly under high ungulate stocking rates.
Conclusions
Overall, our results illustrate that even highly mobile fauna, such as birds, can be negatively impacted by ungulate aggregation around important water resources, particularly when water is scarce. We demonstrate that the use of small-scale fencing to exclude feral ungulates from water resources can provide important dry season refugia for bird communities in savanna environments. Considering feral ungulate densities are low within Limmen National Park, this study highlights that management of ungulates at a landscape scale may not provide adequate protection for native fauna species in water limited environments. The importance of ungulate-free refugia for wildlife will likely increase as climate change further limits water availability across northern Australia. Hence, additional research is needed to determine the optimum size and distance between refugia sites to protect bird assemblages in areas with differing water availability and ungulate densities. Ecologists, conservation land managers, and pastoralists need to work collaboratively to provide appropriate refuge either by physically restricting ungulate access to waterholes or through destocking/spelling practices, so that native bird communities have adequate protection before sensitive species are lost.

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Declarations
Funding
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Conflicts of interest
The authors declare no competing interests.

Code availability
The modelling used for the statistical analysis is described in detail in the text and supplementary material, including the “R” packages used.
Authors’ Contributions

All authors conceived and designed the study; MM and HM secured funding for the project; HM and JV conducted the field experiment and data collation; HM and DN conducted the statistical analysis; DD conducted the ISO cluster classification; HM and MM wrote the manuscript, and all authors contributed to editing of the manuscript.

Ethics Approval

Approval to conduct this study was granted by the Animal Care and Ethics Committee of Charles Sturt University (Approved protocol numbers A17035 and A20056).

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Chapter 6: General Discussion

Throughout this thesis I have shown that water scarcity has significant effects on feral ungulate behaviour and waterhole use in northern Australia. Ungulate access to waterholes had significant negative effects on the vegetation communities closest to water, even though ungulate densities were very low at the landscape scale (<1 ungulate/km²). Increased waterhole use by ungulates during periods of water stress also had significant negative flow-on effects for native mammal and bird communities. Macropods avoided waterholes during periods of peak cattle visitation and fewer bird species visited waterholes accessible to ungulates during periods of seasonal water scarcity.

6.1: Effects of water scarcity on feral ungulate behaviours

All three ungulate species studied here visited waterholes more during the drought, but cattle visitation increased most dramatically. Cattle visited waterholes approximately 3 times more often, spent 6 times longer at waterholes per visit, and 6 times more cattle attended waterholes per visit during the drought than in a normal rainfall year. In Africa, ungulates were also found to use waterholes more intensively and in greater numbers during a drought (Valeix 2011). In addition, African ungulates which are primarily grazers have greater water reliance during drought than browsing species (Valeix et al. 2008). As buffalo typically browse more than cattle (Reid et al. 2020a), this may explain why, in my study, cattle used waterholes considerably more than buffalo during the drought. Cattle in northern Australia can consume between 40-80 litres of water per day (Hunt et al. 2013; Bray et al. 2015), thus there is potential for them to prematurely deplete water sources, restricting availability for other species. The largest group of cattle detected visiting a single waterhole contained 29 individuals during the drought, compared to 12 cattle during a year of normal rainfall. Hence, during the drought, cattle potentially drank ~1100-2300 litres of water from a single waterhole in just one day. This considerable daily consumption of water by cattle likely contributes to the early depletion of waterholes (Fig. 1), especially during drought conditions. Additionally, feral ungulates often stand in waterholes while drinking (Fig. 1a), and faecal contamination can increase nutrient loads of water sources and lead to algal blooms which decrease water quality (Ridpath 1991; Pettit et al. 2012). Thus, if high cattle visitation is sustained over long periods, it may result in significant water losses and contamination of ephemeral waterholes, limiting water availability and quality for native species. Overall, these findings are highly concerning, as cattle are the most abundant feral ungulate species in Limmen National Park (unpublished: Clancy and Vincent 2021), and many of the cattle I
detected visiting waterholes during the drought were branded animals from neighbouring pastoral properties. Hence, not only are feral cattle impacts within the park exacerbated by drought, but there appears to be increased immigration of domestic animals into the park during years of high water scarcity. This exemplifies that the definition of ‘feral cattle’ needs to be reassessed in order to give land managers more control over the removal of cattle from national parks and conservation areas. This will increase the responsibility placed on pastoralists to prevent their animals from straying into national parks, as currently there are no significant repercussions for allowing such incursions.

![Water loss at a savanna waterhole in Limmen National Park over 3 weeks during a drought: (a) late May 2019, (b) mid June 2019. This waterhole received the highest feral ungulate visitation during this study and had dried completely by the mid dry season (June) in 2019.](image)
6.2: Effects of feral ungulates and water scarcity on plant communities

Australian plants evolved in the absence of grazing pressure from hooved mammals (Skarpe 1991; Scogings and Sankaran 2019) and hence, are thought to be particularly prone to disturbance from feral ungulates (Freeland 1990; Ash and Mclvor 1998; Sharp and Whittaker 2003). In water limited environments such as the savannas of northern Australia, ungulate impacts on vegetation communities are not uniform in time and space but vary both seasonally and interannually based on the distribution and availability of water (Illius and O’Connor 2000; Valeix et al. 2008). During the wet season, when water is plentiful and the distance between waterpoints is low, ungulate impacts are dispersed across the landscape (Thrash et al. 1995). However, as the dry season progresses, and water becomes scarcer, ungulate impacts become increasingly more concentrated around remaining water sources (Zvidzai et al. 2013). This aggregation of ungulates at remaining waterholes is further exacerbated during periods of drought, which compounds pressure on flora and fauna communities surrounding waterpoints as the dry season progresses (Illius and O’Connor 2000; Valeix 2011). Hence, how plants are spatially distributed throughout landscapes can affect their vulnerability to ungulate disturbance, as plant communities closest to waterpoints suffer the highest grazing and trampling pressures (Ludwig et al. 1999; Hunt et al. 2013). In this study, there was significantly more bare ground in the receding water zone of waterholes accessible to ungulates, than around those which had been fenced. I also detected a trend of better recolonisation of bare ground in the receding water zone of fenced sites compared to unfenced sites. Vegetation data for this study were collected at the beginning of the dry season each year before plants had started to senesce and were still identifiable to species level. Hence, any fencing effects I detected were likely to have been further exacerbated as the dry season progressed each year. Due to the porosity of studies in xeric Australian savanna habitats, more research into the seasonal exacerbation of ungulate impacts on vegetation communities close to water points is needed.

The vulnerability of different plants to ungulate disturbance can also vary because many ungulates selectively graze species based on their palatability (Ash and Corfield 1998). In addition, the physical form of plants can affect their vulnerability to ungulate grazing, as prostrate species are less susceptible to disturbance than erect species (Diaz et al. 2007). Hence, palatable erect plant species which grow close to water are most at risk of ungulate disturbance in savanna systems. During this study, I observed feral ungulates selectively grazing erect forb species in the receding water zone of unfenced waterholes, particularly the tall native pea, *Aeschynomene indica*. The fence line photo (Fig. 2) illustrates how intensive grazing from ungulates can completely remove palatable erect species in
areas where ungulates aggregate near water. The timing of such grazing is also important, as recurring selective grazing of plants before they have dropped viable seed can lead to local extinction once the soil seed bank has been exhausted (Walker et al. 1997).

**Fig. 2:** A fence line comparison photo taken in 2020 in Limmen National Park shows the impact of intensive grazing by feral ungulates on a native riparian pea species (*Aeschynomene indica*). The pea can be seen growing within the fenced area (dark green vegetation in mid zone of photo on the left of the fence) but has been almost completely grazed out (some bare stalks still visible) in the area ungulates could still access (right).

While I detected some positive plant responses following ungulate exclusion from waterholes, drought had the most significant effect on plant communities. Perennial grasses suffered mass dieback in both the receding water zone and surrounding savanna of waterholes following the onset of the drought in 2019 which continued into 2020. This dieback may have masked the effects of ungulate grazing on perennial grass cover, explaining why I did not detect any significant difference in cover between fencing treatments. Yet, perennial grasses are known to be sensitive to ungulate grazing due to their higher palatability and longer life cycle compared to annual grasses (Diaz et al. 2007). Perennial grasses can also be slow to recover following drought if recruitment is not high enough to counterbalance mature plant deaths from grazing, which can occur even under moderate grazing regimes (Orr and O'Reagain 2011). Hence, the capacity for perennial grasses to recover post-drought in areas where ungulate grazing pressure fluctuates seasonally and interannually, such as around savanna waterpoints, requires further study. This may be of particular importance in areas occupied by endangered granivorous bird species, as localised extinctions and severe declines have been attributed to overgrazing.
and its effects on seed availability during droughts (e.g., Barnard and Barvard 1925; Banko et al. 2013).

6.3: Effects of feral ungulates and water scarcity on native macropods

Due to the high water requirements of ungulates there is potential for them to act as both exploitative and interference competitors of native species in water limited environments, affecting the accessibility, availability, and quality of shared water resources. Limited resource availability concentrates ungulate activity spatially and temporally in important areas, such as around waterholes (Valeix et al. 2007; Valeix 2011). Due to their large size, ungulates have the potential to outcompete native wildlife for access to these resources. This has been demonstrated in North America, where native fauna spatially or temporally avoided waterholes visited by feral horses (Equus caballus; Ostermann-Kelm et al. 2008; Perry et al. 2015; Hall et al. 2018). In this study, daily cattle activity at waterholes peaked in the late afternoon, which is approximately the same time of day when macropods started to become active. Hence, the large number of cattle present at waterholes during the driest months of the year may limit macropod access to water. The potential for competitive interactions between cattle and macropods may be further exacerbated following poor wet season rainfall, as both visited waterholes significantly more during the drought.

The concentration of seasonally important food resources around waterholes, such as green vegetation which becomes available in the receding water zone as waterholes dry out, creates additional potential for competition between feral and native herbivores. As grasses dry, their fibre content increases, making them more difficult to digest than green vegetation (Terry and Tilley 1964). As the dry season progresses and the nutritional value of grasses declines, green vegetation (e.g., riparian forbs) becomes an increasingly important food source for both macropods and ungulates (Fossan 2005; Telfer and Bowman 2006; Reid et al. 2020a). During this study, macropods, cattle, and buffalo increasingly grazed green vegetation in the receding water zone of waterholes as the dry season progressed. Dietary isotope analysis has found significant overlap in the dietary niches of macropods and feral ungulates in Australian savannas (Reid et al. 2020a). As cattle densities can be as much as 125 times higher than native macropod densities in Australian savanna habitats (Reid et al. 2020b), there is significant potential for exploitative competition between feral and native herbivores for access to seasonally important food resources. Growing competition may explain why macropods abruptly left the study area towards the end of the dry season when increasing water scarcity resulted in a sharp rise in cattle activity around waterholes. Furthermore, species which have a size advantage are usually
competitively superior to smaller species (Peters and Peters 1986; Nakayama and Fuiman 2010), hence native macropods may face competitive exclusion from savanna habitats where ungulate densities around waterholes are high. Further research is needed to understand the complexity of competitive interactions between feral and native herbivores in Australian savannas.

6.4: Effects of feral ungulates and water scarcity on savanna bird communities

Ungulate activity around waterholes had significant effects on bird species richness. As the dry season progressed, bird diversity increased at fenced sites, but decreased at unfenced sites. Increasing ungulate activity around waterholes (i.e., grazing and trampling) as the dry season progressed likely reduced habitat suitability for savanna bird species. Ungulate access to waterholes can result in severe degradation to surrounding vegetation in the late dry season (Fig. 3a). However, sites protected from ungulate access showed substantial recovery of this vegetation within 3 years (Fig. 3b). Ungulate disturbance to vegetation surrounding waterholes reduces resources available for birds, including food resources (i.e., seeds: Crowley and Garnett 2001), foraging and nesting substrate (e.g., grasses: Hunt et al. 2013; Neilly and Schwarzkopf 2019), and habitat for prey (e.g., insects: Bromham et al. 1999; Ludwig et al. 1999; Woinarski et al. 2002). Buffalo can dramatically decrease the standing biomass of vegetation communities (Werner 2005) and concentrate their seasonal movements around core areas, revisiting favourable sites frequently (Campbell et al. 2020).

Hence, even small-scale fencing projects around savanna waterholes can create important refugia sites for species dependant on riparian vegetation in areas with high ungulate visitation. For example, during this study I observed a large number (>20 individuals) of typically uncommon golden-headed cisticolas (*Cisticola exilis*) at a fenced waterhole, where the tall native annual grass, *Oryza australiensis*, had recovered to a dense stand following ungulate exclusion (Fig. 4). As this area covered by *Oryza* was only about half an acre in size, the density of cisticolas using the grass as a nesting and foraging substrate was extremely high. The heavy grazing and resultant loss of vegetation biomass outside this fenced plot (Fig. 4) was likely caused by buffalo, as a resident group of ~15 individuals regularly visit the area where this waterhole is located. This example highlights that small-scale exclusion fencing may provide important refugia sites for bird species dependant on riparian vegetation. This may be particularly important in areas utilised by threatened riparian species which have shown negative responses to grazing in northern Australia, such as the purple-crowned fairy-wren (*Malurus coronatus*; van Doorn et al. 2015).
Fig. 3: Vegetation recovery at one of the fenced savanna waterholes. Both photos were taken in the late dry season: (a) was taken prior to fencing in 2017, while (b) was taken in 2020 after 3 years of ungulate exclusion.
Birds were affected by the percent cover of different types of vegetation surrounding waterholes. But interestingly, birds of different foraging guilds were affected differently by the amount of perennial grass cover in the savanna. Insectivore abundance increased with perennial grass cover, while granivore abundance decreased. This illustrates that ungulate disturbance around waterholes may provide benefits for some bird groups but can be disadvantageous for others. Granivorous birds are often associated with disturbed habitats, because a more open understory generally provides better foraging opportunities for dropped seeds (Chettri et al. 2005; Gray et al. 2007) and increases their ability to detect and evade predators (Devereux et al. 2006). However, as pastoralism has increased in Australia’s northern savannas over the last ~170 years, approximately a third of all granivorous bird species have declined in abundance or range (Franklin 1999). This decline has been attributed to the combined negative effects of ungulate grazing and inappropriate burning regimes on the grassy understory (Franklin 1999; Franklin et al. 2005). While this appears somewhat contradictory given the general benefits which open habitats provide for granivores, their abundance in grazed areas may be skewed by the presence of common and widely distributed species, such as the peaceful dove (Geopelia striata; Franklin 1999). Such species occupy wide ecological niches and hence, are likely more resilient to disturbance than other granivores which prefer denser habitats, such as common bronzewing (Phaps chalcoptera). Hence, while the abundance of some granivore species may increase with pastoralism, the diversity of granivores may decline as grazing sensitive species are lost. Furthermore, many Australian granivore species are capable of rapidly
increasing in abundance when conditions are favourable, particularly following high rainfall (Pascoe et al. 2021). This can be due to enhanced local breeding success or an influx of immigrants from surrounding areas in response to rain-induced resource pulses (Burbidge and Fuller 2007; Tischler et al. 2013; Pascoe et al. 2021). Opportunistic nomadic behaviour in granivore species, such as the diamond dove (G. cuneata), can also lead to rapid decreases in abundance once resource availability declines and the birds move elsewhere (Tischler et al. 2013). Hence, care should be taken in assessing the relationship between grazing and granivore abundance, as numbers may fluctuate greatly on a seasonal or interannual basis. Future studies should consider changes in the species composition of different feeding guilds to ensure responses to different grazing pressures are not skewed by increased abundances of common, irruptive, or nomadic species.

Ungulate impacts on vegetation may also increase predation risk for birds. Studies of habitat selection by feral cats (Felis catus) in Australia have found cats prefer areas grazed by introduced ungulates (McGregor et al. 2014; Stobo-Wilson et al. 2020), because their hunting efficacy is greater in areas with an open understory (McGregor et al. 2015). Daytime cat activity is also higher in grazed areas than in ungrazed areas (McGregor et al. 2014), hence, ungulate disturbance around waterholes may increase the predation risk for diurnal, ground dwelling bird species with high water requirements, such as brown quail (Coturnix ypsilophora). During this study, I observed cats hunting around unfenced waterholes during the day on several occasions, although they appear uncommon in Limmen National Park (i.e., 8 individuals detected by static and baited camera traps at 20 sites over 2 years). Granivore abundances tended to be lower at sites with more perennial grass cover in the receding water zone. As most of the granivores studied (e.g., peaceful dove, diamond dove) had short tarsi, thick mats of Pseudoraphis spinescens surrounding waterholes often appeared to entangle their legs, making walking difficult. As a result, they preferred to fly over dense patches of this grass, rather than walk on it. Occasionally, I also observed collared sparrowhawks (Accipiter cirrocephalus) hunting doves and brown quails as they visited waterholes to drink. Hence, granivores may prefer sites with less perennial grass cover in the receding water zone as it could limit their ability to detect and escape both aerial and terrestrial predators around waterhole edges.

6.5: Implications for conservation management
6.5.1: Feral ungulates in water limited environments
While northern Australia is home to many feral ungulate species, my results indicate that cattle have the greatest impacts on savanna waterholes in Limmen National Park. This is
due to their higher dependency on water, tendency to form large herds as water scarcity increases, and higher densities than other ungulate species present in the park. In the context of conservation land management, this is highly concerning due to the prevalence of feral cattle across northern Australia and the pervasiveness of pastoralism in the region. While pastoralists adapt cattle stocking rates based on rainfall in order to protect native pastures from overgrazing (Walsh and Cowley 2014), cattle impacts surrounding waterpoints are rarely considered. In savanna ecosystems where water is a limited resource, the loss of plant cover due to piosphere creation may reduce the suitability of riparian habitats for water dependant native species. In addition, the presence of cattle and their tendency to rest around waterpoints when water becomes scarce (Fig. 1b) can lead to the behavioural avoidance of waterpoints by native fauna, even when cattle densities are low at a landscape scale. This highlights the importance of providing ungulate-free refugia for native wildlife in northern Australia, particularly in the more xeric savannas where water is especially limited. This study has demonstrated that the exclusion of ungulates, even from small wetland areas and their surrounds, can have significant positive outcomes for native flora and fauna communities, including vegetation recovery and increases in bird diversity. Due to the high dependency of introduced ungulate species on water, strategic restriction of waterhole access could be used as a control method by land managers to reduce the carrying capacity of feral populations in northern Australia. However, the success of this approach would be highly dependent on the distribution of alternative water sources within the wider landscape. While the initial cost of installing such small fences is low, maintenance of fences needs to be consistent, particularly in areas where water buffalo are present, as they tend to damage fences more than other ungulate species (pers. obs.). Fences also need to be appropriately designed and flagged to ensure larger native species, such as macropods and dingoes (Canis lupus dingo) are still provided access while maintaining a low risk of fence entanglement. This research also highlights that feral ungulate culling programs in northern Australia should consider species specific differences in waterhole use under different environmental conditions. Cattle are best targeted around waterholes in the late dry season, buffalo during low rainfall years, and pigs when water scarcity is most extreme (i.e., late dry season during drought).

Rather than physically excluding ungulates from areas to provide refugia, researchers studying ungulate impacts in more arid parts of Australia have proposed the use of water remote areas (i.e., where distance between water points is >6km in the dry season) to conserve native ecosystems sensitive to grazing (e.g., James et al. 1999; Fensham and Fairfax 2008). This approach has been applied in African savannas to reduce
the homogeneity of grazed landscapes and provide refugia areas where more mobile and less water dependant herbivore species can access fodder (Smit et al. 2007; Smit et al. 2020). However, such approaches may only be effective in areas where the number of natural waterpoints which still contain water late in the dry season does not fluctuate interannually or spatially. Furthermore, the use of water remoteness as a conservation measure does not minimise ungulate impacts around waterpoints, hence affording no benefits for water dependant or riparian native species. As this study has demonstrated, even mobile species (e.g., birds, macropods) which still need to access waterpoints regularly to drink, are negatively affected by feral ungulate activity. Hence, the efficacy of landscape scale management approaches may be limited if they do not account for ungulate aggregation in wetland areas. Additionally, climate change will likely further exacerbate ungulate impacts in northern Australia, as rainfall is predicted to become more variable and increased temperatures will reduce surface water availability (Dai et al. 2018; NESP Earth Systems and Climate Change Hub 2020). Several native macropod species are predicted to suffer severe range contractions over northern Australia with climate change, particularly the antilopine kangaroo (*Macropus antilopinus*), whose extinction probability will dramatically increase with rising temperatures (Ritchie and Bolitho 2008). The endangered golden-shouldered parrot (*Psephotus chrysopterygius*), a granivore endemic to Australia’s northern savannas, has also been identified as highly vulnerable to climate change (Reside et al. 2016) and grazing impacts (Garnett and Crowley 1997; Crowley et al. 2004). This highlights the need for more research into the importance of waterholes in savanna landscapes and effective methods to exclude feral ungulates from important resource areas to provide refugia for native wildlife under stressful environmental conditions.

6.5.2: **Conflicting opinions**

Although there is still much more research needed to understand ungulate impacts on northern Australian flora and fauna communities, encouragingly, this area has begun to receive more research attention in the last 5-10 years. Collaborative projects between scientists and indigenous ranger groups (e.g., Ens et al. 2016; Reid et al. 2020a; Russell and Ens 2021) are becoming increasingly more common and illustrate that there is much that western and traditional approaches to conservation can contribute to practical land management. However, one of the most important issues complicating the management of feral ungulates in northern Australia has been the conflicting interests between land managers and different stakeholders. Pastoralists have obvious motivations in opposing the removal of domestic and feral cattle from native rangelands, but there has also been
opposition to buffalo control from tourism operators and indigenous landowners due to their value for trophy hunting and as a ‘self-sustaining’ food resource (Skeat et al. 1996; Robinson et al. 2005; Ens et al. 2016). Horses and donkeys (E. a sinus) are also looked upon favourably as ‘bush pets’ by some stakeholders, and thus evade control measures (Robinson et al. 2005).

Opposition to aerial culling programs from animal welfare groups, such as PETA (People for the Ethical Treatment of Animals), has also complicated management of feral ungulates in recent years, particularly horses (see seminal paper by Nimmo and Miller 2007), but also feral camels in central Australia (Gabbatt 2009). While such opposition is understandable and, in some cases, warranted, it nevertheless overlooks the ongoing detrimental impacts which ungulate species have on sensitive native ecosystems and the fauna which inhabit them. While the delay of ungulate culling and management programs may eventually result in ‘better’ control methods for feral species (e.g., sterilisation programs), in the meantime the welfare of native animals is ignored. The hypocrisy of this situation often compounds frustration for conservation land managers and highlights the importance of educating the public on the more insidious impacts ungulates have on native ecosystems. This thesis adds to the increasing evidence that the persistence of feral ungulate populations has significant negative impacts on native flora and fauna communities which may be irreversible under some circumstances (e.g., Sharp and Whittaker 2003). While ungulates may inspire empathy due to their familiarity and magnificence, the conservation of irreplaceable native Australian fauna and their habitats should be paramount. Hence, consilience between academics from a variety of disciplines, together with land managers, pastoralists, and the general public, is urgently needed to find practical, scientifically informed solutions to control feral ungulate species before it is too late for vulnerable native species.
References


Scogings PF, Sankaran M. 2019. Savanna woody plants and large herbivores. West Sussex, UK: John Wiley & Sons Ltd.


**Appendices**

**Appendix 1: Supplementary Material for Chapter 3**

**Table S1: Most parsimonious models determined through model selection for each species and response variable using AIC values.** Factors included in model are represented by a “+”, while those not included are represented with a “-”.

<table>
<thead>
<tr>
<th>Variable tested</th>
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<th>Zero-inflated model</th>
<th>AIC</th>
<th>Model family</th>
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<td>Year * Dry season progression</td>
<td>Year</td>
<td>Year + Dry season progression</td>
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<tr>
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<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Cow</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Buffalo</td>
<td>+</td>
<td>-</td>
<td>-</td>
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<td>+</td>
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<td>+</td>
</tr>
<tr>
<td></td>
<td>Cow</td>
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<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Buffalo</td>
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<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
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<td>Time spent wallowing</td>
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Table S2: Results of most parsimonious GLMMs for number of visits per sampling day by pigs, cattle, and buffalo. Zero-inflation model components are shown where applicable. Significance levels: *** (p < 0.001), ** (p < 0.01), * (p < 0.05), n.s (not significant, p > 0.05).

<table>
<thead>
<tr>
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<th>P value</th>
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Table S3: Results of most parsimonious GLMMs for the duration of visits per sampling day by pigs, cattle, and buffalo. Zero-inflation model components are shown where applicable. Significance levels: *** (p < 0.001), ** (p < 0.01), * (p < 0.05), n.s (not significant, p > 0.05).

<table>
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<tr>
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Table S4: Results of most parsimonious GLMMs for number of individual pigs, cattle, and buffalo attending waterholes per sampling day. Zero-inflation model components are shown where applicable. Significance levels: *** (p < 0.001), ** (p < 0.01), * (p < 0.05), n.s (not significant, p > 0.05).

<table>
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Table S5: Results of most parsimonious GLMMs for time cattle and buffalo spent drinking per sampling day. Zero-inflation model components are shown where applicable. Significance levels: *** (p < 0.001), ** (p < 0.01), * (p < 0.05), n.s (not significant, p > 0.05).

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<th>Std. Error</th>
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<th>P value</th>
<th>Sig. level</th>
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<td>(Intercept)</td>
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<td>-4.98</td>
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<tr>
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<td>(Intercept)</td>
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<td>0.121</td>
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<td>(Intercept)</td>
<td>-2.19062</td>
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<td>-3.948</td>
<td>7.89E-05</td>
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<td>Dry season progression</td>
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<td>0.992</td>
<td>0.3213</td>
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Table S6: Results of most parsimonious GLMMs for time pigs, cattle, and buffalo spent foraging per sampling day. Zero-inflation model components are shown where applicable. Significance levels: *** (p < 0.001), ** (p < 0.01), * (p < 0.05), n.s (not significant, p > 0.05).

<table>
<thead>
<tr>
<th>Species</th>
<th>Model component</th>
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<th>Estimate</th>
<th>Std. Error</th>
<th>z value</th>
<th>P value</th>
<th>Sig. level</th>
</tr>
</thead>
<tbody>
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<td>(Intercept)</td>
<td>-7.9404</td>
<td>1.9409</td>
<td>-4.091</td>
<td>4.30E-05</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Year</td>
<td>-0.9810</td>
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<td>-0.573</td>
<td>0.5669</td>
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<td>Dry season progression</td>
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<td>0.0152</td>
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<td>0.3172</td>
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<td>0.0242</td>
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<td>(Intercept)</td>
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<td>0.284</td>
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<td>0.8407</td>
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<td>0.2555</td>
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<td>Dry season progression</td>
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<td>0.0055</td>
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<td>0.0261</td>
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<td>(Intercept)</td>
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<td>0.3741</td>
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<td>(Intercept)</td>
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<tr>
<td></td>
<td></td>
<td>Dry season progression</td>
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<td>0.0029</td>
<td>-1.605</td>
<td>0.109</td>
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</table>

Table S7: Results of most parsimonious GLMM for time buffalo spent wallowing per sampling day. Significance levels: *** (p < 0.001), ** (p < 0.01), * (p < 0.05), n.s (not significant, p > 0.05).

<table>
<thead>
<tr>
<th>Species</th>
<th>Model component</th>
<th>Factor</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>z value</th>
<th>P value</th>
<th>Sig. level</th>
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</thead>
<tbody>
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<td>(Intercept)</td>
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<td>0.000245</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Year</td>
<td>1.0448</td>
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<td>2.793</td>
<td>0.0052</td>
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<td>-0.0012</td>
<td>0.0043</td>
<td>-0.294</td>
<td>0.7689</td>
<td>n.s</td>
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</table>
Appendix 2: Supplementary Material for Chapter 4

Table S1: AIC values used to determine whether the addition of a smoothed term on dry season progression (i.e., if there was a linear or non-linear relationship with presence) and/or fencing treatment as a by factor (i.e., if temporal activity varied between fencing treatments) to the base model provided the best model fit for each species. A by factor was not included in cow and buffalo model selection because they could only access unfenced sites. Models with the most support are displayed in bold. Where $\Delta$ AIC is <2, both models are considered favourable. See methods for a description of variables included in base models.

<table>
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<th>AIC</th>
<th>$\Delta$ AIC</th>
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<tr>
<td>Macropod</td>
<td>Base model</td>
<td>710.76</td>
<td>29.03</td>
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<td>Smooth term on dry season progression included</td>
<td>681.73</td>
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<td>By factor for fencing treatment included</td>
<td>719.23</td>
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<td>Both smooth term and by factor included</td>
<td>690.30</td>
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<tr>
<td>Pig</td>
<td>Base model</td>
<td>769.22</td>
<td>6.08</td>
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<td>Smooth term on dry season progression included</td>
<td>759.54</td>
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<tr>
<td></td>
<td>By factor for fencing treatment included</td>
<td>773.02</td>
<td>13.48</td>
</tr>
<tr>
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<td>Both smooth term and by factor included</td>
<td>763.31</td>
<td>3.77</td>
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<tr>
<td>Cow</td>
<td>Base model</td>
<td><strong>1379.43</strong></td>
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<td>Smooth term on dry season progression included</td>
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<td>Base model</td>
<td><strong>1607.11</strong></td>
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<td>Smooth term on dry season progression included</td>
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<td>Both smooth term and by factor included</td>
<td>1034.60</td>
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Table S2: AIC values used to determine whether the addition of fencing treatment as a by factor (i.e., if temporal activity varied between fencing treatments) to the base model provided the best model fit for species in both fencing treatments during different stages of the dry season. Models with the most support are displayed in bold. Where Δ AIC is <2, both models are considered favourable. See methods for a description of variables included in base models.

<table>
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<th>Δ AIC</th>
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<td>Base model</td>
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<td></td>
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<td>By factor for fencing treatment included</td>
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<tr>
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Table S3: Full GAMLSS results for dry season stage models. Models presented are the most favourable based on AIC values (see Table 4). Where Δ AIC < 2, results for both models are presented. Hyphens denote variables which were not included in base models. See methods for a description of base models for each species.

<table>
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<td>z</td>
<td>p</td>
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<td>0.6488</td>
<td>0.303</td>
<td>0.7622</td>
<td>0.4676</td>
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</table>
Fig. S2: Relationship between predicted hourly presence and days since the dry season began for buffalo (a), and dingoes (b) around waterholes in Limmen National Park. Mean presence values are shown as lines, while grey areas display upper and lower confidence intervals.
Fig. S1: Distribution of monthly rainfall over the wet season (~October to April) of each year sampled. Rainfall data obtained from Bureau of Meteorology (2022).
Table S1: Generalised feeding guilds of bird species detected during surveys of savanna waterholes. Note: Buttonquails were included as a group because they were typically too fast moving when flushed to identify to the species level reliably.

**Granivores**
- Bar-shouldered Dove (*Geopelia humeralis*)
- Brown Quail (*Coturnix ypsilophora*)
- Budgerigar (*Melopsittacus undulatus*)
- Buttonquail spp. (*Turnix spp.*)
- Cockatiel (*Nymphicus hollandicus*)
- Common Bronzewing (*Phaps chalcoptera*)
- Diamond Dove (*Geopelia cuneata*)
- Double-barred Finch (*Taeniopygia bichenovii*)
- Galah (*Cacatua roseicapilla*)
- Gouldian Finch (*Erythrura gouldiae*)
- Long-tailed Finch (*Poephila acuticauda*)
- Masked Finch (*Poephila personata*)
- Northern Rosella (*Platycercus venustus*)
- Peaceful Dove (*Geopelia striata*)
- Pictorella Mannikin (*Heteromunia pectoralis*)
- Red-tailed Black Cockatoo (*Calyptorhynchus banksii*)
- Sulphur-crested Cockatoo (*Cacatua galerita*)

**Insectivores**
- Black-faced Cuckoo-Shrike (*Coracina novaehollandiae*)
- Black-faced Woodswallow (*Artamus cinereus*)
- Brush Cuckoo (*Cacomantis variolosus*)
- Dollarbird (*Eurystomus orientalis*)
- Fairy Martin (*Petrochelidon ariel*)
- Golden-headed Cisticola (*Cisticola exilis*)
- Grey Fantail (*Rhipidura fuliginosa*)
- Horsfield's Bronze-Cuckoo (*Chrysococcyx basalis*)
- Jacky Winter (*Microeca fascinans*)
- Leaden Flycatcher (*Myiagra rubecula*)
- Little Woodswallow (*Artamus minor*)
- Magpie Lark (*Grallina cyanoleuca*)
- Masked Woodswallow (*Artamus personatus*)
- Pallid Cuckoo (*Cuculus pallidus*)
- Paperbark Flycatcher (*Myiagra nana*)
- Rainbow Bee-eater (*Merops ornatus*)
- Red-backed Fairy-wren (*Malurus melanocephalus*)
- Rufous Whistler (*Pachycephala rufiventris*)
- Varied Sittella (*Daphoenositta chrysoptera*)
- Striated Pardalote (*Pardalotus striatus*)
- Varied Wittler (*Dicaeum hirundinaceum*)
- Olive-backed Oriole (*Oriolus sagittatus*)
- Weebill (*Smicromis breviprostis*)
- Willie Wagtail (*Rhipidura leucophrys*)
- White-bellied Cuckoo-Shrike (*Coracina papuensis*)
- White-breasted Woodswallow (*Artamus leucorynchus*)
- White-browed Woodswallow (*Artamus superciliosus*)
- White-throated Gerygone (*Gerygone olivacea*)
- White-winged Triller (*Lalage sueurii*)

**Nectarivores**
- Little Friarbird (*Philemon citreogularis*)
- Banded Honeyeater (*Certhionyx pectoralis*)
- Bar-breasted Honeyeater (*Ramsayornis fasciatus*)
- Blue-faced Honeyeater (*Entomyzon cyanotis*)
- Brown Honeyeater (*Lichmera indistincta*)
- Grey-fronted Honeyeater (*Lichenostomus plumulus*)
- Grey-headed Honeyeater (*Lichenostomus heartlandi*)
- Red-collared Lorikeet (*Trichoglossus rubritorquis*)
- Rufous-throated Honeyeater (*Conopophila rufogularis*)
- Singing Honeyeater (*Lichenostomus virescens*)
- Silver-crowned Friarbird (*Philemon argenticeps*)
- Varied Lorikeet (*Psitteuteles versicolor*)
- White-gaped Honeyeater (*Lichenostomus unicolor*)
- White-throated Honeyeater (*Melithreptus albogularis*)
- Yellow-tinted Honeyeater (*Ptilotula flavescens*)

**Frugivores**
- Mistletoebird (*Dicaeum hirundinaceum*)
- Olive-backed Oriole (*Oriolus sagittatus*)
Omnivores
Australasian Pipit (*Anthus novaeseelandiae*)
Australasian Pratincole (*Stiltia isabella*)
Blue-winged Kookaburra (*Dacelo leachii*)
Brolga (*Grus rubicunda*)
Great Bowerbird (*Chlamydera nuchalis*)
Grey-crowned Babbler (*Pomatostomus temporali*)
Grey Shrike-thrush (*Colluricincla harmonica*)
Little Shrike-thrush (*Colluricincla megarhyncha*)
Masked Lapwing (*Vanellus miles*)
Pheasant Coucal (*Centropus phasianinus*)
Pied Butcherbird (*Cracticus nigrogularis*)
Red-backed Kingfisher (*Todiramphus pyrrhopygia*)
Red-winged Parrot (*Aprosmictus erythropterus*)
Sacred Kingfisher (*Todiramphus sanctus*)
Torresian Crow (*Corvus orru*)

Water foragers
Black-fronted Dotterel (*Elseyomis melanops*)
Black-necked Stork (*Ephippiorhynchus asiaticus*)
Black-winged Stilt (*Himantopus himantopus*)
Buff-banded Rail (*Gallirallus philippensis*)
Dusky Moorhen (*Gallinula tenebrosa*)
Intermediate Egret (*Ardea intermedia*)
Nankeen Night Heron (*Nycticorax caledonicus*)
Radjah Shelduck (*Radjah radjah*)
Red-kneed Dotterel (*Erythrogonys cinctus*)
White-faced Heron (*Egretta novaehollandiae*)
White-necked Heron (*Ardea pacifica*)

Nocturnal foragers
Australian Owlet-Nightjar (*Aegotheles cristatus*)
Southern Boobook (*Ninox boobook*)
Tawny Frogmouth (*Podargus strigoides*)

Carnivores
Australian Hobby (*Falco longipennis*)
Black-breasted Buzzard (*Hamirostra melanosternon*)
Black-shouldered Kite (*Elanus axillaris*)
Black Kite (*Milvus migrans*)
Brown Falcon (*Falco berigora*)
Brown Goshawk (*Accipiter fasciatus*)
Collared Sparrowhawk (*Accipiter cirrhocephalus*)
Nankeen Kestrel (*Falco cenchroides*)
Spotted Harrier (*Circus assimilis*)
Wedge-tailed Eagle (*Aquila audax*)
Whistling Kite (*Haliastur sphenurus*)

Compiled using references:
Fig. S2: Nectarivore count per survey as the dry season progressed in different years. Solid lines represent predicted mean values, shaded areas represent upper and lower confidence intervals.
Table S2: Summary table of GLMMs used in plant, bird, and interaction (bird vs plant) models, including the AIC of the best model, number of supported models (with a Δ≤2), and the r-squared values of the model including all hypotheses with substantial support.

<table>
<thead>
<tr>
<th>Model type</th>
<th>Response variable</th>
<th>AIC weight of best model</th>
<th>Number of supported models (ΔAIC≤2)</th>
<th>R-squared of model including all hypotheses with substantial support</th>
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<td>Marginal</td>
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<td>Plants</td>
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<td>Annual grass (savanna)</td>
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<td>Shrubs/trees (savanna)</td>
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<td>Bare ground (receding)</td>
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<td>Perennial grass (receding)</td>
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<td>Nectarivore count</td>
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