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Grass, fire, kangaroos and cattle: The nexus between fire and herbivory in northern Australia

by

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Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

University of Tasmania, November 2019

The tropical savannas of northern Australia are a dynamic system where humans, wildlife, forage and fire interact to create habitat mosaics suitable for large herbivores.

Statements and declarations

Declaration of originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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Signed:

Date:
15 November 2019

Statement of co-authorship

The following people and institutions contributed to the publication of work undertaken as part of this thesis as specified at the start of each chapter.

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Abstract

Australian mammals have exhibited exceptionally high rates of decline since European settlement 230 years ago, especially in arid and semi-arid regions. In recent decades there has been increasing concern over the current declines of small mammals in northern tropical savannas. In these systems, little scientific attention has been given to the suite of large macropods, family Macropodidae, (common wallaroo [*Osphranter robustus*], antilopine wallaroo [*O. antilopinus*] and agile wallaby [*Notamacropus agilis*]), some thought to be declining by Aboriginal Traditional Owners. These species may be impacted by feral herbivores and contemporary fire regimes, threats that are both linked to small mammal decline and impact forage quantity and quality. A multi-scale approach – from landscape- to local-scales – was utilized with the overall objectives of exploring the nexus between fire, forage and herbivory in two regions of northern Australia and examining the applicability of the concept of pyricherbivory, the spatial and temporal interactions of fire and grazing, to Australian savannas. The North Kimberley bioregion in Western Australia and Arnhem Land in the Northern Territory are regions of largely intact tropical savanna, each with well-established feral herbivores and active Indigenous fire management. Arnhem Land, where water buffalo (*Bubalus bubalis*) is the dominant feral herbivore, has a continual history of Aboriginal fire management, in contrast to the North Kimberley, where fire management was disrupted by European colonial activity and with a more recent establishment of the dominant feral herbivore, cattle (*Bos* spp.). Arnhem Land has also been the focus of several feral herbivore surveys in the recent past, unlike the North Kimberley.

My thesis begins by using aerial surveys, road transects and remote camera trapping to examine the effects of feral cattle and fire on the distribution and abundance of large macropods in the North Kimberley. Density and biomass of feral cattle exceeded that of macropods regardless of survey technique utilised. Density estimates for cattle were up to 125 times higher (0.3-10.0 km^{-2}) than estimates for macropods (0.08-0.49 km^{-2}). Cattle biomass, based on the aerial surveys (corrected for perception bias), were 15 and 95 times higher than macropods for infertile (279 versus 19 kg km^{-2}) and fertile savannas (518 versus 5 kg km^{-2}), respectively. Proximity to the nearest pastoral property was a significant predictor of the aerial sightings of feral cattle, suggesting cattle are continuing to expand throughout the area from adjacent pastoral lands. Abundance and foraging activity of cattle were positively associated with recently burnt areas. In contrast, camera trapping showed agile wallaby and wallaroo occurrence and foraging behaviour were associated with unburnt areas. Agile wallabies and wallaroos were negatively associated with cattle and showed substantial diurnal and seasonal separation consistent with an antagonistic interspecific interaction. These multi-scale surveys suggest that recent landscape changes such as altered fire regimes and introduced herbivores have negatively impacted large grazing macropod species.

Isotopic analysis of faecal samples was conducted in the North Kimberley to evaluate how macropods and feral cattle utilise such variable forage resources throughout the dry season. Feral cattle, wallaroos and agile wallaby utilised forage resources differently, consistent with previous related studies comparing buffalo and macropods in Arnhem Land. The contribution of grass to the diet of the agile wallaby was unrelated to substrate fertility, fire or dry season period (early, mid-, late dry season) which aligns with their known status as a mixed feeder. Wallaroos had the highest contribution of grass to their diet, compared to cattle and agile wallaby, with higher proportions of grass consumed on fertile substrates, regardless of fire or dry season period. Cattle diets incorporated more grass in burnt, fertile areas and in the early and late dry season, with a decrease in grass utilisation during mid-dry season, most likely related to the availability of alternative food resources. Cattle diets were highly variable in response to forage quality, ranging from 0-91% grass compared to wallaroos, ranging from 36-100% grass. Diets of wallaroos and cattle were correlated with live forage fibre content (R^2 = 0.41 and 0.56, respectively). As fibre content increased with herbaceous biomass curing, grass intake decreased, precipitously so for cattle, demonstrating their diet flexibility.

To understand the underlying mechanisms of local-scale competition in both the North Kimberley and Arnhem Land, we used remote camera trapping and grazing exclosures to examine how herbivory, fire, seasonality, and soil fertility affect forage quantity and quality, in turn affecting herbivore distribution. We found that, even at low herbivore densities, grazing reduced forage quantity (live, dead and total standing herbaceous biomass) and increased forage quality (crude protein content of live herbaceous biomass). Fibre content of live herbaceous biomass was significantly lower in burnt vs. unburnt sites and fertile vs. infertile sites. There was no significant distinction between early and late dry season fires. However, sites burnt in the late dry season had the highest crude protein content of live biomass, highlighting the importance of heterogeneous fire regimes in providing high-quality forage throughout the dry season. Field sites in Arnhem Land had lower measures of overall forage quality (lower crude protein and higher fibre contents of live biomass) but supported more feral herbivores and wallaroos than sites in the North Kimberley. One possible explanation is that water buffalo and feral cattle may exert different levels of competitive pressure on native herbivores. Results suggest that pyricherbivory strongly influences the feeding behaviour of feral herbivores and some native herbivores.

In summary, I found that the biomass of introduced feral herbivores far outweighs that of native herbivores at the two study locations in Australia’s northern savannas. Macropods are not behaving as predicted by the theory of pyricherbivory, which contends that herbivores are drawn to, and utilise, recently burnt, highly nutritious forage. Macropod foraging was associated with unburnt areas of low forage quality, in contrast to both historical and contemporary records of Traditional Ecological Knowledge regarding burning for macropod management. This discrepancy is possibly due to competition with feral herbivores for limited high-quality forage. Feral cattle and water buffalo have a wider dietary breadth than large macropods in the savannas and are thus better able to cope with forage of lower quality by varying their relative intake of grass and browse. The largest native grazing herbivores, wallaroos, are less capable of such dietary plasticity. Collectively, my results point to the importance of ongoing control of large feral herbivores in conservation areas and the incorporation of more late dry season fires in addition to early dry season burning to maintain forage quality for macropods throughout the dry season, more closely replicating the historical Indigenous fire regime. Further surveys of grazing macropods elsewhere in the tropical savannas of Australia are necessary to confirm regional population declines and advance our understanding of the complex relationships between native and feral herbivores, forage, fire and Indigenous wildlife management.

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Chapter 1

General introduction

1.1 SAVANNA DYNAMICS: FIRE AND HERBIVORY

Fire is a natural process in many ecosystems across the globe (Bond and Keeley, 2005) where it influences nutrient cycling, distribution, abundance and vigour of wildlife, livestock, and vegetation, and affects human use of landscapes. Likewise, grazing by herbivores, large herbivores especially, can alter fire regimes, as well as nutrient cycling, vegetation structure and species composition (Chaneton *et al*., 1996; Ash and McIvor, 1998b; Asner *et al*., 2009). Both fire and grazing are strongly influenced by human activity. Humans can alter the seasonality, frequency and size of fires, both by lighting and suppressing fires (Bowman *et al*., 2011; Archibald, 2016), while hunting of native herbivores and the introduction of exotic herbivores and pastoralism alters the abundance, diversity and distribution of herbivores across the landscape.

Savannas are a dynamic laboratory in which to study interactions between fire and grazing as they are one of the primary ecosystems in the world where large herbivores and fire occur in abundance. Fire has been likened to a global herbivore and both fire and herbivores are able to exert consumer control over ecosystems (Bond and Keeley, 2005), but although fire may compete with herbivores for plant biomass it can also provide benefits to competing herbivores. In grass dominated ecosystems, such as grasslands and savannas, fire consumes poor-quality dry forage and replaces it with high-quality forage. Pyricherbivory describes this process; herbivores follow nutritious grasses resprouting after fire (known as ‘green pick’) resulting in a fine-scaled patch mosaic of vegetation caused by the differential grazing pressure (Fig. 1.1; Fuhlendorf and Engle, 2001). Grazing pressure regulates fire on the landscape as different patches vary in flammability creating a feedback between herbivores, vegetation and fire; this feedback is thought to increase ecosystem productivity and biodiversity (Fuhlendorf and Engle, 2001; Fuhlendorf *et al*., 2009). Similarly, the pyrodiversity hypothesis proposes that spatial heterogeneity of landscape fire leads to higher biodiversity (Martin and Sapsis, 1992). Pyricherbivory is just one example of how pyrodiversity operates to connect biodiversity with ecosystem processes and patterns via fire (Bowman *et al*., 2016).

Pyricherbivory and pyrodiversity have been most thoroughly examined within the North American grassland and African savanna ecosystems with ungulate herbivores. The interaction of fire and grazing supersedes either process working individually to shape grassland ecosystems in the North American Great Plains and operates similarly for native and introduced species (Allred *et al*., 2011a). This interaction has been linked to greater botanical and vegetation structural diversity (Fuhlendorf and Engle, 2004) and the shifting mosaic of habitat patches across the landscape in varying states of recovery from the forces of fire and herbivory can fulfil habitat needs for more species than a uniformly managed landscape (Fuhlendorf *et al*., 2006; Engle *et al*., 2008; Ricketts and Sandercock, 2016). Similarly, African grazing lawn distribution and persistence is explained by pyricherbivory (Archibald *et al*., 2005; Archibald, 2008) and in systems with a high diversity of large herbivores, such as African savannas, the scale and patchiness of fires can influence the selectivity by herbivores for years following a fire (Kimuyu *et al*., 2017). Australian savannas draw several parallels with other grass-dominated systems around the world including a long history of grazing and high fire frequencies, however, the relative low density of herbivores, marsupial herbivore guild and nutrient deficient soils may be important differences relating to how pyricherbivory and pyrodiversity function on the continent.

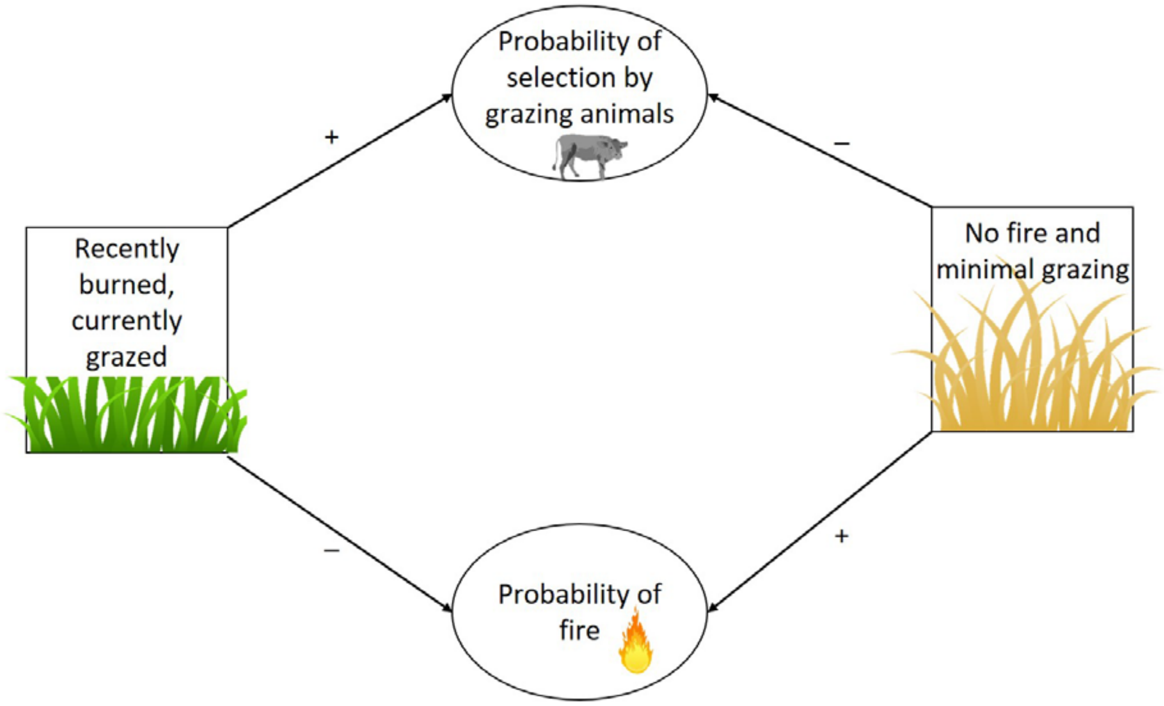

Figure 1.1 Conceptual model of the interacting consumer controls exerted by fire and herbivory. Adapted from (Fuhlendorf and Engle, 2004).

1.2 THE AUSTRALIAN CONTEXT: NORTHERN TROPICAL SAVANNAS IN FLUX

> “*Fire, grass, kangaroos and human inhabitants, seem all dependant on each other for existence in Australia; for any one of these being wanting, the others could no longer continue. Fire is necessary to burn the grass, and form those open forests, in which we find the large forest-kangaroo; the native applies that fire to the grass at certain seasons, in order that a young green crop may subsequently spring up, and so attract and enable him to kill or take kangaroo with nets*.”
>
> -Major Thomas Mitchell (Mitchell, 1848, p. 412)

Fire and herbivory remain integral to the formation and maintenance of ecosystems characterised by high fire frequency, such as tropical savannas, that account for approximately 22% of global land area (Ramankutty and Foley, 1999) and 26% of mainland Australia. Northern Australia’s tropical savannas have likely been experiencing and been shaped by frequent fires since the development of its monsoon climate in the late Tertiary (Bowman, 2002), receiving the majority of its rainfall during the austral summer wet season, December to April. Alternately, the remainder of the year is relatively dry. This wet–dry cycle allows for the rapid accumulation of forage (edible herbaceous biomass) during the wet season while plants have ample water resources followed by conditions that rapidly dry out the vegetation. This cycle both allows the landscape to support large-bodied grazing animals, such as macropods (i.e. members of the marsupial family Macropodidae, including kangaroos and wallabies) and extinct megafauna, and makes the landscape a ready fuel source for fires. The “boom–bust” nature of high-quality forage in these savannas in addition to a long history of both natural and Indigenous fire has led to an intricate web of relationships between vegetation, large herbivores, and fire that has evolved over millennia, complicated by the relatively recent introduction of feral grazing animals and changed fire regimes following European settlement.

1.2.1 ‘Fire-stick farming’: traditional Aboriginal fire use and contemporary fire regimes

Australia’s savannas have a long history of human occupation (beginning around 65,000 years ago; Clarkson *et al.*, 2017) and subsequent Aboriginal fire use that changed the previous lightning fire regime and altered the landscape (Bowman, 1998). The traditional fire regime is characterized by frequent, small fires lit throughout the dry season with high spatial and temporal heterogeneity (Vigilante, 2001). Aboriginal fire use, coined ‘fire-stick farming’ (Jones, 1969), was utilized for many reasons including food gathering (foraging and hunting), protection of sacred sites and plant resources, and ease of travel (Lewis, 1989; Bowman *et al.*, 2001; Walsh and Cross, 2004). Though northern Australia would have had high fire frequencies in the absence of humans, due to lightning strike density and dry fuel sources, it is the Aboriginal inhabitants that have harnessed this tool for improved production of resources and the use of fire to provide high-quality forage for grazing macropods is well documented (Lewis, 1989; Saint and Russell-Smith, 1997; Bowman *et al.*, 2001).

Landscape fire changed drastically where Aboriginal populations were moved off country and into settlements (Russell-Smith, 2001; Vigilante, 2001; Edwards *et al.*, 2003; Fisher *et al.*, 2003; Russell-Smith *et al.*, 2003; Legge *et al.*, 2011b). The fire regime shifted to large, high intensity fires burning predominantly in the late dry season in unmanaged landscapes (Vigilante, 2001). In areas historically characterized by predominantly late dry season burning, there is evidence of a seasonal shift to early dry season burning as European management pre-emptively burnt landscapes in an attempt to eliminate late dry season wildfires (Bowman *et al.*, 2007a). Increased tree mortality, reduced production of fruit by trees, reduced fire patchiness, and damage to rainforest patches and populations of obligate-seeding trees and shrubs have all resulted from shifting fire regimes (McKenzie and Belbin, 1991; Russell-Smith and Bowman, 1992; Bowman and Panton, 1993; Williams, 1995; Setterfield, 1997; Williams, 1997; Legge *et al.*, 2015; Trauernicht *et al.*, 2015). In areas where Traditional Owners have been given back rights to their land (under the *Native Title Act 1993*) fire regimes have changed to smaller fires in the early dry season resulting in higher landscape heterogeneity (Legge *et al.*, 2015) than unmanaged lightning regimes (Bird *et al.*, 2008).

1.2.2 Marsupial herbivores: past and present

In prehistoric times, the savannas of Australia were inhabited by a diversity of megaherbivores, including giant kangaroos (e.g. *Procoptodon goliah* [c. 240 kg]) and the largest known marsupial herbivore weighing up to 2,700 kg *(Diprotodon optatum; Long et al., 2002).* However, by the Late Pleistocene, 26 herbivorous species larger than the biggest extant herbivore (*Macropus rufus* [c. 60 kg]) had become extinct (Flannery, 1990), linked by some to overhunting by humans (Johnson, 2006) and biased towards browsers (Bowman *et al.*, 2010b). Today, there is only a small suite of large herbivores with a range across the northern tropical savannas including the common wallaroo (*Osphranter robustus* [c. 40 kg]), antilopine wallaroo (*O. antilopinus* [c. 35 kg]), and agile wallaby (*Notamacropus agilis* [c. 20 kg]). These are some of Australia's largest extant native herbivores, occurring in varied assemblages with smaller macropods across the north, and are of importance to local Aboriginal populations as both a food source and spiritually/culturally (Altman, 1982). The common wallaroo, antilopine wallaroo and agile wallaby are all listed by the International Union of Conservation and Nature as species of least concern even though the antilopine wallaroo and agile wallaby populations are noted as declining with no known major threats listed for either species (IUCN 2018). There is anecdotal evidence to support this claim in the northern savannas (Ritchie, 2007; White *et al*., 2009; Roberts *et al*., 2016) where introduced grazers are well-established.

1.2.3 Niche vacancy and the introduction of domestic livestock

Australian tropical savannas were devoid of megaherbivores (> 100 kg) when European settlers introduced grazing animals starting in the 1820s (Letts, 1962). Subsequently, these ungulate herbivores (e.g. cattle [*Bos* spp.], water buffalo [*Bubalus bubalis*], horse [*Equus caballus*] and donkey [*E. asinus*]) established large feral populations and have resisted eradication despite extensive control attempts of some species (Freeland and Boulton, 1990). By 1985, the Top End of the Northern Territory had approximately 341,406 ± 22,693 buffalo, 355,963 ± 20,475 cattle (both domestic and feral) and 71,806 ± 6,114 horses and it was recommended that attempts at feral cattle and buffalo eradication be abandoned (Bayliss, 1985; Bayliss and Yeomans, 1989b). Indeed, feral herbivores in the northern savannas have become more populous in Australia than in their native habitat (Freeland, 1990) and some (cattle and water buffalo) have become a major source of protein for Aboriginal populations, making their extirpation undesirable (Altman, 1982; Bowman and Robinson, 2002; Robinson *et al*., 2005).

Cattle and water buffalo (450-1,200 kg), the largest and most numerous feral herbivores (Bayliss and Yeomans, 1989b), can affect existing native herbivores directly by introducing competition for forage, water and habitat or indirectly by manipulating the habitat through trampling/habitat degradation and changes to the fire regime (Taylor and Friend, 1984; Petty *et al*., 2007; Bowman *et al*., 2011; Eldridge *et al*., 2016). These feral ungulates are more generalised feeders compared to the relatively specialised native macropods. Specialists utilize their chosen resources more efficiently but are only favoured under optimal habitat conditions compared to generalists who can adjust to fluctuating or degraded habitats (Brown, 1996; Bowman *et al*., 2010b; Poisot *et al*., 2011).

1.2.4 The North Kimberley and Arnhem Land: analogous regions with divergent contemporary disturbances

Tropical savannas span the longitudinal range of Australia, comprising several biogeographical regions. The North Kimberley in northern Western Australia and Arnhem Land in the north-eastern Northern Territory are part of two of the three major sandstone regions of the northern tropical savannas and are considered to be sister bioregions (Fig. 1.2; Cracraft, 1991; Bowman *et al*., 2010a). Arnhem Land is dominated by infertile sandy soils (Aldrick, 1976) while the North Kimberley is a combination of infertile sands and relatively fertile volcanic soils though average herbaceous biomass in *Eucalytpus tetrodonta* habitats for the Kimberley and Arnhem Land are similar (1.30 and 1.14 t ha-1, respectively; Bowman *et al*., 2007b), while tall grass savannas have a higher grassy biomass. Both regions have a similar rainfall pattern, receiving over 90% of rain between November and April with comparable mean rainfall (approximately 1200 mm; Bureau of Meteorology 2018). Both regions share the same suite of large grazing macropods mentioned above (Table 1.1), except for the black wallaroo (*Osphranter bernardus*) endemic to Arnhem Land, and ethnographic evidence recorded from Traditional Owners in both regions confirms the traditional use of burning for production of forage for kangaroos (Bowman *et al*., 2001; Bowman and Vigilante, 2001).

Colonial activity in the North Kimberley and Arnhem Land starting in the late 1800’s led to movement of Aboriginal populations off country and into settlements and a subsequent shift in fire regime towards large, high-intensity fires predominantly in the late dry season on unmanaged landscapes (Russell-Smith, 2001; Vigilante, 2001; Edwards *et al*., 2003; Fisher *et al*., 2003; Russell-Smith *et al*., 2003; Legge *et al*., 2011b). Subsequently, lands under European management have been dominated by early dry season fires in an attempt to control the large late season fires previously dominating the landscape (Bowman *et al*., 2007a). However, Arnhem Land has an unbroken history of Aboriginal ownership and management and the outstation movement starting in the 1980s led to Aboriginal groups establishing small settlements back on homelands and a return to more traditional livelihoods which support customary burning practices (Yibarbuk *et al*., 2001). Aboriginal populations in the North Kimberley have been progressively confined to settlements off-country as their homelands were claimed by colonists, including pastoralists, and government. Native Title claims won in the North Kimberley in recent decades have allowed Traditional Owners to reclaim their traditional lands and establish fire management programs better replicating historical fire regimes (Vigilante *et al.*, 2004; Vigilante *et al.*, 2017) but the North Kimberley is still dominated by non-traditional ignition sources (e.g. aerial incendiaries) with fire ignitions concentrated in the early dry season compared to Arnhem Land with an even distribution of fires throughout the dry season (Petty and Bowman, 2007).

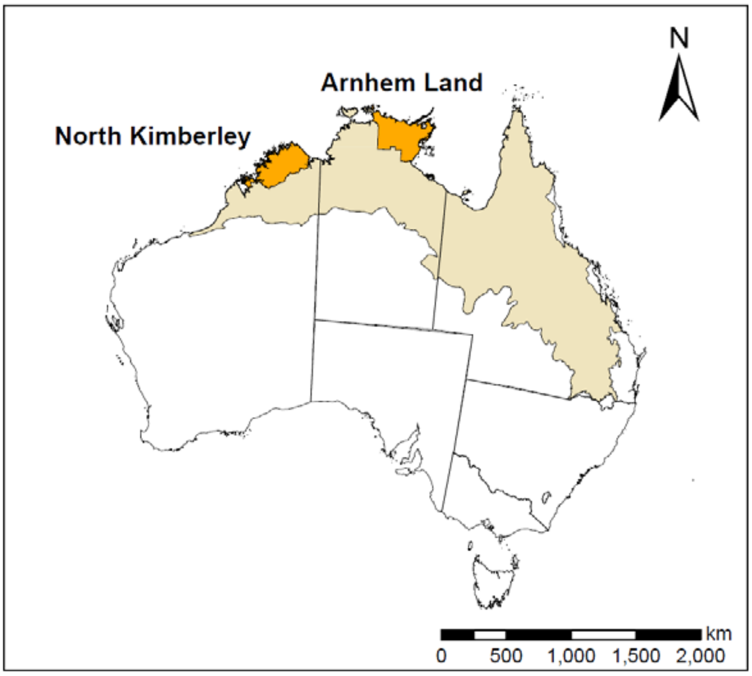

Figure 1.2 Location of the North Kimberley and Arnhem Land (shaded orange) within the greater context of the Australian tropical savannas (shaded beige).

The dominant feral herbivores in Arnhem Land (water buffalo) and the North Kimberley (cattle) are both bulk-feeding ruminants (Table 1.1), utilising fermentation during digestion to process large amounts of high-roughage forage, and of similar body size. However, Arnhem Land has a longer history of invasion by large feral herbivores than the North Kimberley. Water buffalo introductions started in the Northern Territory in the 1820s (Letts, 1962) compared to the North Kimberley where feral cattle dispersed from pastoral leases starting in the 1900s. Due to the proximity to the scientific base of the Northern Territory (Darwin), Arnhem Land has been more extensively surveyed for both feral and native herbivores (Bayliss and Yeomans, 1989b; Koenig *et al.*, 2003; Saalfeld, 2006; Ritchie *et al.*, 2008) including research on diet and habitat associations (Telfer and Bowman, 2006; Murphy and Bowman, 2007b; Telfer *et al.*, 2008; Bowman *et al.*, 2010b). There has been little published regarding feral cattle and large native macropod surveys and landscape distribution in the North Kimberley (Ritchie *et al*., 2008) owing to the distance from Perth, the main research base in Western Australia, and no studies in either region looking specifically at interactions between feral herbivores and native macropods.

1.3 CONCEPTUAL MODEL OF FACTORS AFFECTING MACROPOD ABUNDANCE

The nexus between vegetation, herbivore abundance, and fire in tropical savannas has been made more complex by recent changes to this long-evolved system. Potential factors relating to macropod decline are considered in a conceptual model (Fig. 1.3). The factors presented here are not exhaustive and were not all explored during this project (only factors in the shaded polygon were considered further), however, it is important to acknowledge other factors not dealt with here that may be contributing to changes in large macropod abundance in northern Australia's tropical savannas.

1.3.1 Factors affecting macropod abundance further considered in this project

Fire

Increased fire frequency, intensity and extent are often provided as reasons for widespread floral and faunal declines in the northern savannas (Woinarski *et al*., 2001; Pardon *et al*., 2003; Woinarski *et al*., 2004; Legge *et al*., 2008; Woinarski *et al*., 2010). Extensive research has been undertaken into impacts of altered fire regimes on small mammals, reptiles and birds (e.g. Pardon *et al*., 2003; Woinarski *et al*., 2004; Legge *et al*., 2008; Woinarski and Legge, 2013; Lawes *et al*., 2015) but macropods have been studied to a lesser extent. Across northern Australia, Ritchie *et al*. (2008) found antilopine wallaroos to be more abundant at sites burnt more than once by late dry season fires during the 3-year study period and common wallaroos to be less abundant on burnt sites. In contrast, Telfer *et al*. (2008) found common wallaroos in Arnhem Land to be marginally associated with recently burnt areas. Murphy and Bowman (2007b) found that the relationship to burnt areas was dependant on habitat and large macropods were more abundant on burnt areas only on moist sites whereas more infertile sites had a higher abundance in unburnt areas. Of the previous studies, Ritchie *et al*. (2008) was the only to incorporate sites outside Arnhem Land.

Competition with feral species

In concert, altered fire regimes and introduced large herbivores have reduced landscape productivity by reducing vegetative cover and habitat alteration (Burbidge and McKenzie, 1989) and studies suggest that the interactive effects of introduced grazers and changed fire regimes have been largely underestimated in regard to faunal declines across northern Australian savannas (Woinarski and Ash, 2002; Kutt and Woinarski, 2007; Legge *et al*., 2008; Legge *et al*., 2019). Similar to changed fire regimes, grazing impacts of large feral herbivores on small mammals have been examined (e.g. Legge *et al*., 2011a) but to a lesser degree on macropods which are likely to be negatively impacted by such introductions. Although Ritchie *et al*. (2008) found antilopine wallaroos were more abundant on cattle grazing sites than conservation lands on basaltic geology and no difference in abundance between sandstone conservation lands versus cattle grazing sites, the authors recognized that pastoral leases are typically in more productive parts of the landscape than conservation areas and provide access to artificial watering points so the association may be more directly related to substrate fertility and better water accessibility. Similarly, common wallaroos were more abundant on sites grazed by cattle than conservation area on granitic geology (Ritchie *et al*., 2008). Though this previous work in the tropics has examined the association between macropods and pastoral lands, it has not looked specifically at interspecific associations between feral and native herbivores.

Habitat requirements

Habitat requirements of the antilopine and common wallaroos and agile wallaby have been extensively studied in the tropical savannas. The antilopine wallaroo is found in woodlands and open forests in gently undulating terrain with perennial grass-dominated understoreys and avoid rocky areas (Croft, 1987; Ritchie, 2007). The antilopine wallaroo is associated with permanent water (Ritchie *et al*., 2008) because this species uses evaporative cooling (thus more water loss) and does not use rock shelters during the day (Dawson, 1995). The abundance and distribution of the common wallaroo are strongly influenced by climate with a weak positive correlation with water availability (Ritchie *et al*., 2008). The common wallaroo is associated with rockier habitats and the species uses boulders, rock outcrops and caves as a shelter resource for thermoregulation allowing less dependence on water sources (Croft, 1987; Dawson, 1995; Telfer and Garde, 2006). The agile wallaby utilises a range of habitats including upland undulating woodlands, valleys, alluvial plains and forests and are often associated with riverine habitats (Bell, 1973; Croft, 1987; Press, 1988; Stirrat, 2003).

Table 1.1 Dominant native and introduced herbivores in the North Kimberley and Arnhem Land.

Species	Weight (kg)	Habitat	Feeding	Behaviour
Native				
Common wallaroo *Osphranter robustus*	25-55	rocky ranges and plateaux in arid shrublands, grasslands and wet eucalypt forests	grazer - forages on grasses and forbs	nocturnal and crepuscular, rests during the day in cave or under rock overhang
Antilopine wallaroo *O. antilopinus*	20-49	tropical savannas with perennial grasses, usually on plains and low hills	grazer - forages on grasses	active throughout day and night in wet season and emerges from shelter in late afternoon in dry
Agile wallaby *Notamacropus agilis*	15-27	wide range of grassy forest and woodland communities, often in riverine habitats in tropical savannas	mixed - grazes and browses on wide variety of plants, also eats fallen fruit	shelters during the day under dense vegetation and emerges in late afternoon to feed
Introduced				
Water buffalo *Bubalis bubalis*	450-1,200	floodplains and adjacent slopes in the Top End of NT	grazer - aquatic vegetation during wet season; dry season includes terrestrial veg and browse	nocturnal and crepuscular, spends days in muddy wallow and nearby wooded country
Cattle *Bos taurus*	400-1,100	riverine habitats, plains and low hills	grazer - forages on grasses and forbs	crepuscular, shelters in rainforest patches, riverine habitat and rock overhangs

Cattle information gathered from local knowledge; all other entries from (McKenzie, 1981)

Forage

Macropods have been shown to vary their diet in relation to fluctuating forage quality and quantity, for example, eating a larger proportion of grass on burnt areas where nitrogen content is highest (Telfer and Bowman, 2006; Murphy and Bowman, 2007b). Forage quantity and quality can fluctuate greatly in tropical savannas due to dynamic processes such as fire and herbivory or more static underlying factors such as soils. However, it is unknown how these factors influence the diet of the largest macropods in the Kimberley region as previous diet studies have been conducted exclusively in the Northern Territory or subtropical regions. Previous studies have reported that the antilopine wallaroo only grazes grasses (Croft, 1987) while the diet of the common wallaroo includes large amounts of non-grass, such as woody browse and forbs, when grass is in limited supply (Dawson, 1995; Telfer and Bowman, 2006). The agile wallaby prefers grasses and legumes, but broadens its diet to include browse, leaf litter, fruits, flowers and roots when forage quality is low during the dry season (Stirrat, 2002).

1.3.2 Factors affecting macropod abundance not in the scope of this project

Hunting

Aboriginal hunting was most likely a more substantial pressure on abundance of large macropods in pre-European times with subsistence hunting and the Aboriginal population distributed across the northern savannas. Even so, research done in the deserts of northern Western Australia, south of the tropical savannas, found that benefits to the common wallaroo population from Aboriginal burning outweighed the negative effects of Aboriginal hunting (Codding *et al*., 2014).

Predation

In addition to bottom-up controls (forage), herbivore populations are affected by top-down controls (predators). Dingoes, considered the only major predator of large macropods (apart from humans; Robertshaw and Harden, 1989), are controlled over large areas of southern Australia and large macropod abundance is typically highest where dingoes are absent (Pople *et al*., 2000; Letnic *et al*., 2009). This is true in the tropical savannas as well, large macropods were more abundant on sites where dingo baiting occurred (Leo *et al*., 2019). While dingoes remain widespread and abundant throughout most of northern Australia (Ritchie *et al*., 2008), predation risk isn't necessarily dependent on predator density, but can be related to the presence of alternative prey (Nordberg and Schwarzkopf, 2019). Caughley *et al*. (1980) found this to be true in pastoral lands of southern Australia where large macropods were present at lower densities when preyed upon by dingoes with abundant alternative prey, in this case, rabbits. Croft (1987) suggests common wallaroos might escape predation by dingoes because they can outmanoeuvre them in rocky terrain where they typically are found. Alternately, antilopine wallaroos and agile wallabies may have a higher predation risk as they are more dependent on water, where predators focus hunting.

Disease

Monitoring and testing of a sentinel herd of cattle, an early detection system for biosecurity risks, at Kalumburu Mission in the North Kimberley starting in 1989 as part of the Northern Australia Quarantine Strategy program has not revealed evidence of disease outbreak and biosecurity officers have more recently (since 2013) been gathering community animal health reports from Indigenous ranger groups across northern Australia without any reports specifically relating to large macropod health concerns (Cassandra Wittwer, pers. comm., 2018). In addition, there have been no reported population crashes before 1989 for antilopine or common wallaroos or agile wallabies in the tropical savannas (Speare *et al*., 1989).

Climate change

Macropods in the northern savannas are well-adapted to harsh conditions with characteristics such as minimal water dependence, body heat management and reproductive control via embryonic diapause and seasonal anoestrous (Jackson and Vernes, 2010). However, as temperatures increase due to climate change, northern macropods may suffer range reductions. For example, the antilopine wallaroo is projected to have an 89% range contraction with a 2.0˚C increase in mean annual temperature (Ritchie and Bolitho, 2008). Additionally, suitable climatic conditions for both antilopine and common wallaroos are likely to disappear from the Northern Territory and Western Australia under warmer conditions, with a modest scenario (0.4˚C increase) leading to a 22% reduction in the core range of the antilopine wallaroo (Ritchie and Bolitho, 2008). Increases to mean annual temperature projected by 2070 are predicted to threaten the antilopine wallaroo with extinction and reduce the habitat of the four largest macropods by an average of 96% (Ritchie and Bolitho, 2008).

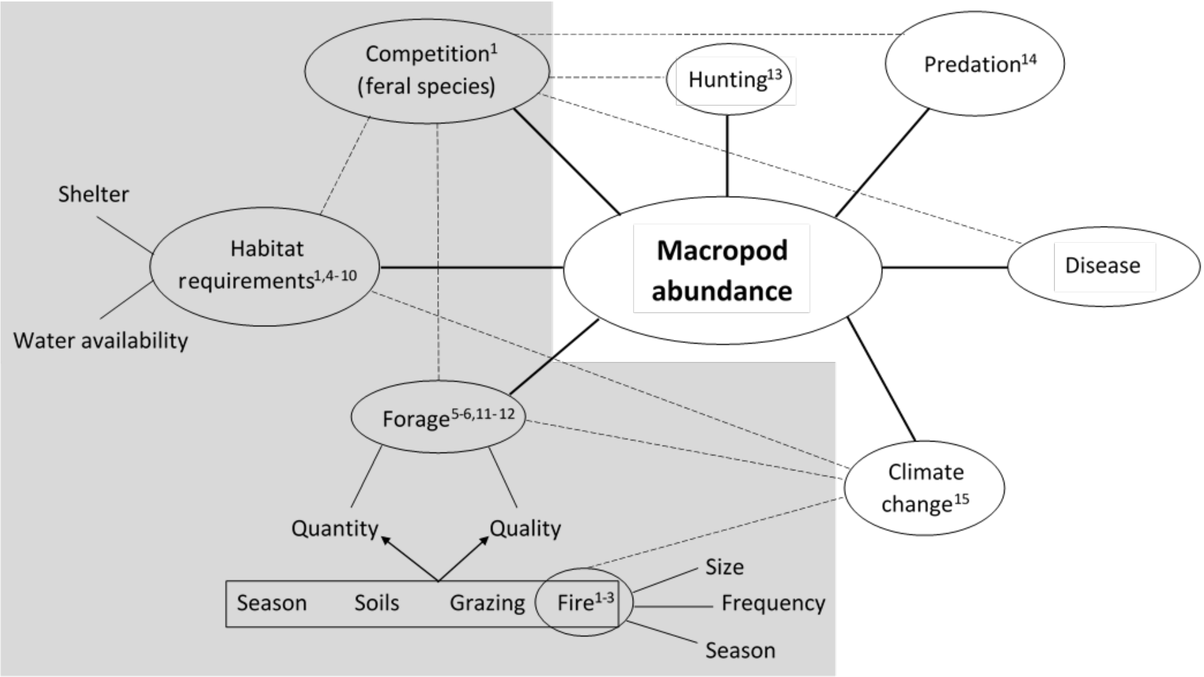

Figure 1.3 Conceptual model of factors affecting abundance of large macropods. Factors with a direct impact on population size are denoted with solid lines while indirect connections are denoted with dashed lines and are not exhaustive. This project focused on factors within the shaded polygon only. Previous research in the northern tropical savannas is denoted as superscript numerals as follows: 1 - (Ritchie *et al*., 2008); 2 - (Telfer *et al*., 2008); 3 - (Murphy and Bowman, 2007b); 4 - (Ritchie, 2007); 5 - (Croft, 1987); 6 - (Dawson, 1995); 7 - (Telfer and Garde, 2006); 8 - (Bell, 1973); 9 - (Stirrat, 2003); 10 - (Press, 1988); 11 - (Telfer and Bowman, 2006); 12 - (Stirrat, 2002); 13- (Codding *et al*., 2014); 14 - (Leo *et al*., 2019); 15 - (Ritchie and Bolitho, 2008).

1.4 THESIS OUTLINE

Arnhem Land has a longer history of feral megaherbivore establishment and a relatively uninterrupted traditional fire regime compared to the North Kimberley, two mechanisms that can create and maintain landscape mosaics. Paired studies in these regions can fill knowledge gaps regarding fire, forage and herbivory and place findings in the framework of a well-established scientific body of research. Additionally, comparison of similar geological substrates in the North Kimberley and Arnhem Land with slight variations in fire and differing dominant feral herbivores allows for interpretation of results over a broader geographical range and generalisation regarding the role of large feral herbivores. Past research has largely focused on feral herbivores and native macropods independently. However, there is a need to study both herbivore groups together in relation to savanna dynamics in northern Australia. It is in this context that I examine the complexity of associations between forage, fire and herbivory of the dominant species.

1.4.1 Thesis aims

My thesis explores the interrelationships between forage, fire and large native and introduced herbivores on lands under Aboriginal management by utilizing landscape ecology and targeted experiments to further the understanding of fire and grazing dynamics in tropical savannas. Specifically, the aims are to:

- Compare the density and biomass of native and feral large herbivores and investigate environmental factors affecting multi-scale herbivore distribution in Australian tropical savannas;
- Examine the dietary breadth of large herbivores and evaluate the implications for success of feral cattle and water buffalo;
- Explore the effects of fire and herbivory on forage quantity and quality and investigate the mediating role of forage between fire and herbivore distribution.

This research was undertaken in collaboration with Wunambal Gaambera Aboriginal Corporation (WGAC; covered under a cooperative research agreement) and the Uunguu Rangers in the North Kimberley, and Kune Traditional Owners in Arnhem Land. The WGAC, Uunguu Rangers and Kune Traditional Owners participated in the planning and implementation of fieldwork for this project and I relied heavily on their Traditional Ecological Knowledge (TEK) to provide baseline information about habitat and wildlife abundance on traditional lands. The TEK was an immeasurable resource regarding knowledge of local flora, fauna and ecosystem processes such as fire, and provided important information on changing environmental conditions that was otherwise unrecorded in the scientific literature.

1.4.2 Overview of chapters

My thesis consists of five chapters: experimental chapters (Chapters 2–4) are written in the style of peer-reviewed journal articles and will be submitted for publication. Chapter 2 has been submitted and is currently under review (Reid *et al.*, 2019a), Chapter 3 has been accepted for publication by *Austral Ecology* (Reid *et al.*, in press) and Chapter 4 is in preparation for submission (Reid *et al*., 2019b). In all cases I was the lead author and developed and conducted the research under guidance of my supervisory team. The articles have been reformatted (including figure and table numbering) for ease of reading and references have been collated into a single section at the end of the document.

Arnhem Land and the North Kimberley represent two large expanses of intact tropical savanna, currently under the management of Aboriginal Traditional Owners, with active fire management and populations of both native and feral large herbivores. Including both areas as study sites allows for examination of processes and patterns at a sub-continental scale (Table 1.2). Arnhem Land has a more comprehensive record of feral herbivore surveys than the North Kimberley due to its proximity to the scientific research base in Darwin, NT. In order to conduct a proper comparison of large herbivore density and distribution in the northern savannas, large-scale herbivore surveys were required in the North Kimberley. In Chapter 2, I describe a landscape-wide survey of feral and native large herbivores in the North Kimberley and examine multi-scale herbivore distribution in relation to biotic and abiotic variables including interspecific competition.

Anecdotal evidence from Traditional Owners and past research (Ritchie, 2007; White *et al*., 2009; Roberts *et al*., 2016) suggest a decline in some large macropod species in the northern tropical savannas. These declines coincide with the expansion of large feral herbivores in Australia and therefore may be driven by resource competition with the introduced species. In Chapter 3, I examine the proportion of C_4 grass consumption and dietary breadth of macropods and feral cattle throughout the dry season as it relates to fire and substrate fertility as a potential mechanism for the success of feral herbivores and to determine the level of overlap in utilisation of food resources.

Forage is the mediating factor between fire and herbivory in savanna ecosystems. Both fire and herbivores act as consumers of savanna vegetation and thus influence the quantity and quality of vegetation available for the other consumer. The complicated nature of these interactions as they relate to both native and introduced herbivores require further investigation. In Chapter 4, I utilise grazing exclosures to investigate the effects of fire, soil fertility, season and herbivory on forage quantity and quality. Additionally, I examine how forage quantity and quality alter herbivore distribution of native and feral species to explore potential management strategies beneficial to native herbivores.

Table 1.2 Multi-scale monitoring methods utilised in the Kimberley (K) and Arnhem Land (A) to obtain measurements regarding herbivore abundance, distribution, behaviour and diet and forage quantity and quality. Measurements obtained provide information on specific factors affecting macropod abundance as modelled in Fig. 1.3 as well as linkages between forage, fire and herbivory as outlined in Fig. 1.1. Data were often utilised in multiple chapters.

Scale	Monitoring Method	Region	Measurements obtained	Associated model factors	Chapters
Largest	Aerial Survey	K	Herbivore abundance	Baseline abundance data	2
			Joint species distribution	Habitat requirements, Competition	2
			Interspecific relationships	Competition	2
	Road Transects	K	Herbivore abundance	Baseline abundance data	2
	Remote Camera Trapping	K, A	Herbivore abundance	Baseline abundance data	2, 4
			Joint species distribution	Habitat requirements, Competition, Predation	2
			Activity patterns	Competition, Predation	2
	Scat surveys	K	Dietary range	Competition	3
Smallest	Grazing exclosures	K, A	Forage biomass	Forage	3, 4
			Forage crude protein and fibre	Forage	3, 4

Chapter 2

Distribution and abundance of large herbivores in a northern Australian tropical savanna: a multi-scale approach

Chapter 2

Title:

Distribution and abundance of large herbivores in a northern Australian tropical savanna: a multi-scale approach

Authors:

Angela M. Reid, Brett P. Murphy, Tom Vigilante, Wunambal Gaambera Aboriginal Corporation, and David M.J.S. Bowman

Status:

Under review (submitted 9 May 2019)

Author roles:

Author	**Contribution**	**Signature**
AMR	Conceived, developed and designed the study; analyzed research data; wrote the manuscript	
BPM	Contributed to the conception and design of the study; provided input into the writing of the manuscript	
TV	Contributed to the conception and design of the study; provided input into the writing of the manuscript	
WGAC	Contributed to the conception and design of the study	
DMJSB	Contributed to the conception and design of the study; provided input into the writing of the manuscript	

2.1 ABSTRACT

Australian mammals have exhibited exceptionally high rates of decline since European settlement 230 years ago with much focus on small mammals in northern tropical savannas. In these systems, little scientific attention has been given to the suite of large herbivorous macropods, family Macropodidae, (common wallaroo [*Osphranter robustus*], antilopine wallaroo [*O. antilopinus*] and agile wallaby [*Notamacropus agilis*]) thought to be declining by traditional Aboriginal landowners. These species may be impacted by feral herbivores and contemporary fire regimes, two threats linked to small mammal decline. A multi-scale approach using aerial surveys, road transects and camera trapping was utilised to determine the effects of feral cattle and fire on the distribution and abundance of large macropods in the North Kimberley bioregion. Feral cattle density and biomass exceeded that of macropods regardless of survey technique utilised. Density estimates for cattle were up to 125 times higher (0.3-10.0 km^{-2}) than estimates for macropods (0.08-0.49 km^{-2}). Cattle biomass, based on the aerial survey estimates (corrected for perception bias), were 15 and 95 times higher than macropods for infertile (279 versus 19 kg km^{-2}) and fertile savannas (518 versus 5 kg km^{-2}), respectively. Proximity to the nearest pastoral station was a significant predictor of the aerial sightings of feral cattle. Abundance and foraging activity of cattle were positively associated with recently burnt areas. In contrast, camera trapping showed agile wallaby and wallaroo occurrence and foraging behaviour were associated with unburnt areas. Agile wallabies and wallaroos were negatively associated with cattle and showed substantial diurnal and seasonal separation consistent with an antagonistic interspecific interaction. Collectively, this study suggests that recent landscape changes such as altered fire regimes and introduced herbivores have negatively impacted large grazing macropod species.

2.2 INTRODUCTION

Australian mammals have exhibited an exceptionally high rate of decline comprising almost 30% of all the world's known mammal extinctions since 1600 AD (Baillie *et al.*, 1996; McKenzie *et al.*, 2007). Around 10% of Australian endemic mammal species have gone extinct since European colonisation 230 years ago (Woinarski *et al.*, 2015). Much of the recent focus has been on "critical weight range" mammals, marsupials and rodents with small body mass (35 – 5500g), in the northern tropical savannas where declines are linked to introduced predators, competition and habitat degradation by feral and domestic livestock, and the increased frequency, size and severity of landscape fires following the decline of Aboriginal patch burning (Woinarski *et al*., 2001; Pardon *et al*., 2003; Legge *et al*., 2008; Woinarski *et al*., 2010; Woinarski *et al*., 2014). Notably, land clearance, which is a threatening process for many species globally, is not implicated in the northern Australian small mammal declines, reflecting that most northern savannas remain free of agricultural development (Woinarski *et al*., 2007; Bradshaw, 2012).

Compared to the small mammal declines, little attention has been given to the conservation status of Australia's larger mammals (Ziembicki *et al*., 2015). Unlike the tropical savannas of Africa, the native Australian large herbivore assemblage now lacks megaherbivores (> 100 kg) and has few species > 20 kg. The large native herbivores with a widespread range across the savannas of northern Australia are all macropods (i.e. members of the marsupial family Macropodidae, including kangaroos and wallabies): common wallaroo (*Osphranter robustus*), antilopine wallaroo (*O. antilopinus*) and agile wallaby (*Notamacropus agilis*). These species occur in varied assemblages, with biogeographic patterns strongly controlled by terrain and climate (Ritchie and Bolitho, 2008; Ritchie *et al*., 2008), often with other smaller macropods (e.g. rock-wallabies [*Petrogale* spp.] and northern nail-tail wallaby [*Onychogalea unguifera*]). A suite of marsupial megaherbivores became extinct in the Late Pleistocene, coincident with human colonisation (Johnson, 2006; Johnson, 2016). European settlers introduced large ungulate grazing animals (e.g. cattle [*Bos* spp.], water buffalo [*Bubalus bubalis]*, wild horses [*Equus caballus]* and donkeys [*E. asinus*]), starting in the 1820s, at various places in northern Australia (Letts, 1962). These domesticated species subsequently established feral (wild) populations, rapidly expanding and achieving higher densities than in their native ranges and predictions from the body-size population density relationship (Freeland, 1990). Their success suggests that introduced herbivores are occupying an ecological niche that became vacant following the Pleistocene extinctions (Bowman *et al*., 2010b).

Compared to the largest northern grazing macropods (55kg), bovines are much larger (> 10 times), are generalist bulk-feeders, utilise both grass and browse, and have fundamentally different digestive systems (ruminant vs. non-ruminant foregut fermenters; Sanson, 1989; Bowman *et al*., 2010b). Hence the dietary breadth of bovines and macropods is different in terms of forage quantity and quality, whereby macropods can utilise phytomass more efficiently than bovines, which are better able to adjust to fluctuating forage quality (Brown, 1996; Bowman *et al*., 2010b; Poisot *et al*., 2011). In semi-arid and arid rangelands used for cattle and sheep production, the provision of water points, control of dingoes and promotion of pasture has led to population irruptions of red (*O. rufus)* and grey kangaroos (*Macropus fuliginosus, M. giganteus*) indicating that, in some settings, large populations of introduced and native herbivores can co-exist at high densities (Caughley *et al*., 1980; Calaby and Grigg, 1989). However, in tropical savannas introduced herbivores especially feral bovines (cattle and water buffalo) can negatively affect native herbivore abundance directly by competing for high-quality forage, water and habitat, or indirectly by degrading the habitat (Taylor and Friend, 1984; Petty *et al*., 2007; Bowman *et al*., 2011; Eldridge *et al*., 2016).

Surveys across Australia's tropical savannas suggest some macropods (antilopine wallaroo) are declining (Ritchie, 2007) although the ubiquity of this decline and drivers are poorly understood. Higher temperatures and more intense dry seasons associated with climate change may become a threatening process to large macropod populations in northern Australia in the future (Ritchie *et al*., 2008) but are unlikely to have seriously affected population dynamics in the recent past. Introduced predators that have been linked to small mammal declines, feral cat (*Felis catus*) and European red fox (*Vulpes vulpes*), are unlikely to impact large macropods. The range of the European red fox does not extend into the tropics and feral cats are not known to predate adult large macropods, although they are predated by the dingo (*Canis lupus dingo*) and wild dog (*C. lupus familiaris* and *C. lupus dingo* x *C. lupus familiaris*).

Similar to small mammal populations, changed fire regimes have been implicated in macropod declines in tropical savannas (Woinarski *et al*., 2014). The strongly seasonal rainfall pattern of the monsoon tropics leads to rapid production of tall grass during the wet season followed by desiccation during the dry season creating a high biomass of combustible grass with low nutritional quality. Aboriginal people used patch burning to provide nutritious 'green pick' for herbivores by setting numerous small fires throughout the dry season (Crawford, 1982; Braithwaite, 1991; Saint and Russell-Smith, 1997; Murphy and Bowman, 2007b). This management approach is a form of pyricherbivory, an ecological process whereby herbivores follow post-fire nutritious resprouting grasses resulting in a patch mosaic of vegetation caused by differential grazing pressure (Fuhlendorf and Engle, 2001). The Aboriginal socio-ecological tradition of patch burning drastically changed since European settlement (Russell-Smith, 2001; Vigilante, 2001; Edwards *et al.*, 2003; Fisher *et al*., 2003; Russell-Smith *et al*., 2003; Legge *et al.*, 2011b) shifting to large, high intensity fires burning predominantly in the late dry season in unmanaged landscapes (Vigilante, 2001).

Introduced large herbivores may also be a potential driver of macropod decline. Experiments have shown that cattle stocking can be increased via nutrient supplementation and strategic patch burning during the dry season (Mott *et al*., 1981; Winter, 1987). It is therefore possible that cattle and macropods compete for green pick, or that the combination of altered fire regimes and introduced large herbivores have reduced landscape productivity (Burbidge and McKenzie, 1989). Indeed, some Aboriginal Traditional Owners show growing concern over the negative impact of inappropriate fire regimes and feral species on populations of large macropods (Wunambal Gaambera Aboriginal Corporation, 2010).

The Uunguu Indigenous Protected Area (Uunguu IPA), in the North Kimberley bioregion of Western Australia, is an ideal location to study the interactions between macropods and feral bovines because it has never been used for pastoralism or experienced large-scale vegetation clearing, is little affected by economic development and has highly diverse savannas on both fertile and infertile substrates (Fig. 2.1). The feral herbivore assemblage is dominated by cattle, that have only recently spread from adjoining pastoral leases, with much smaller populations of wild horses and donkeys. Although modes of Aboriginal fire management were disrupted in the 1930s with the nearby establishment of Kalumburu Mission, Uunguu IPA is currently managed by its Aboriginal Traditional Owners in a way intended to replicate the historical fire regime. In this setting we used a variety of survey methods to address three linked questions:

1) How do the density and biomass of native and non-native herbivores (macropods and cattle, respectively) differ?
2) Do the occurrence and abundance of macropods and cattle have similar environmental correlates, especially relating to time since fire?
3) Do macropods and cattle show competitive exclusion in space and time?

These questions are approached using a range of different methods applied at varying spatial and temporal scales (Fig. 2.2). At the landscape-scale, aerial and vehicle-based censuses were used to provide snapshot estimates of herbivore density and examine environmental correlates impacting landscape distribution of herbivores. Camera traps were used to gauge site-level environmental correlates of herbivore diversity, abundance and foraging behaviour on fertile and infertile substrates and evidence of on-going interspecific associations. These methods allow us to evaluate the hypothesis that cattle and macropods occupy separate niches and examine how both groups are influenced by fire.

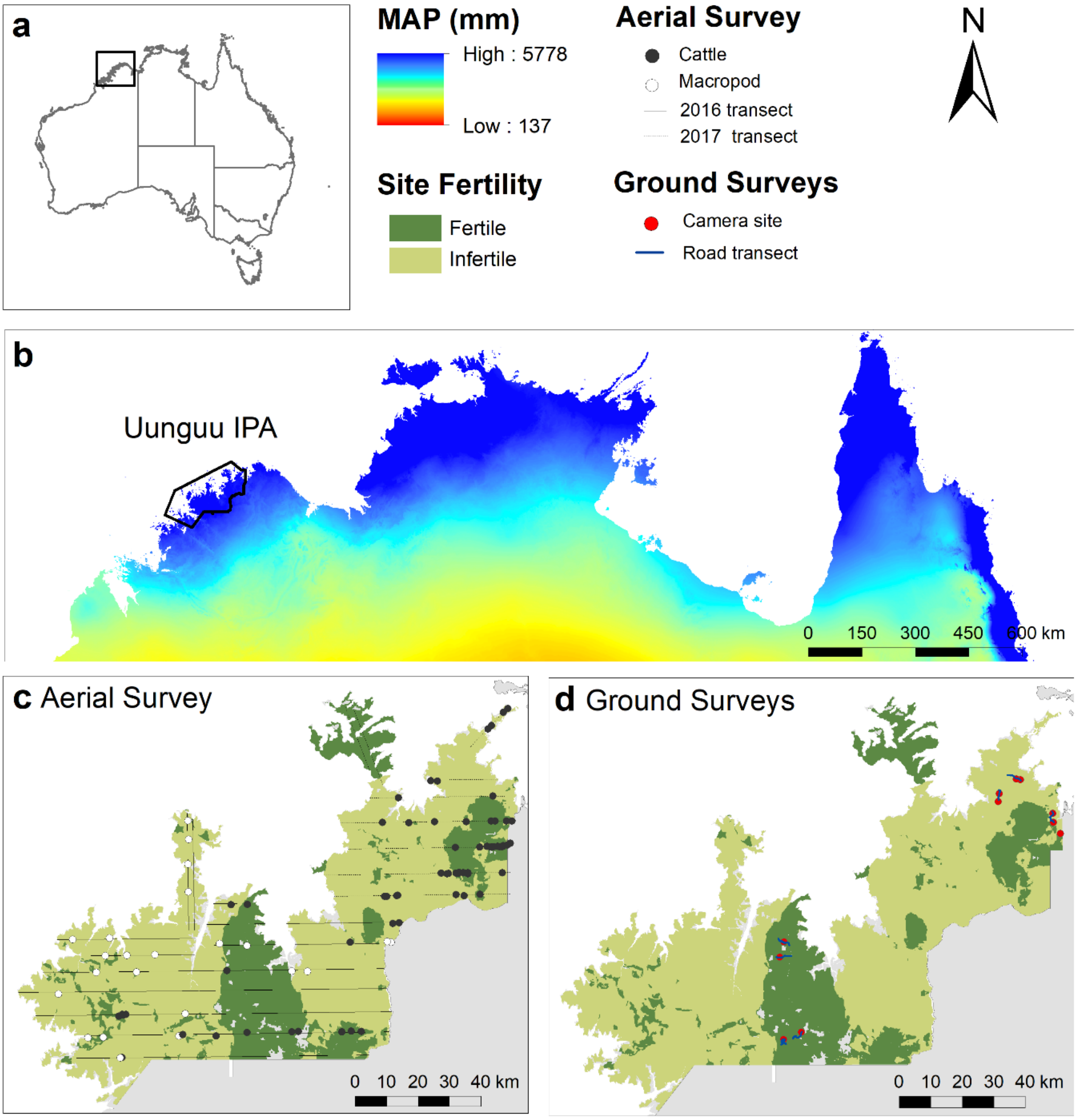

Figure 2.1 Geographic context of the study area (a) location of the Uunguu IPA, North Kimberley, Western Australia; (b) mean annual precipitation (MAP; mm) across the top end of Australia; (c) aerial survey 2016-2017 transects and macropod and cattle sightings; (d) fertile and infertile soil parent material with the location of monitoring sites and road transects. Data sources: MAP data modelled using methods from Hijmans *et al*. (2005) and data from BMA (2005); geology (used to determine site fertility) as classified by DMPWA (2010).

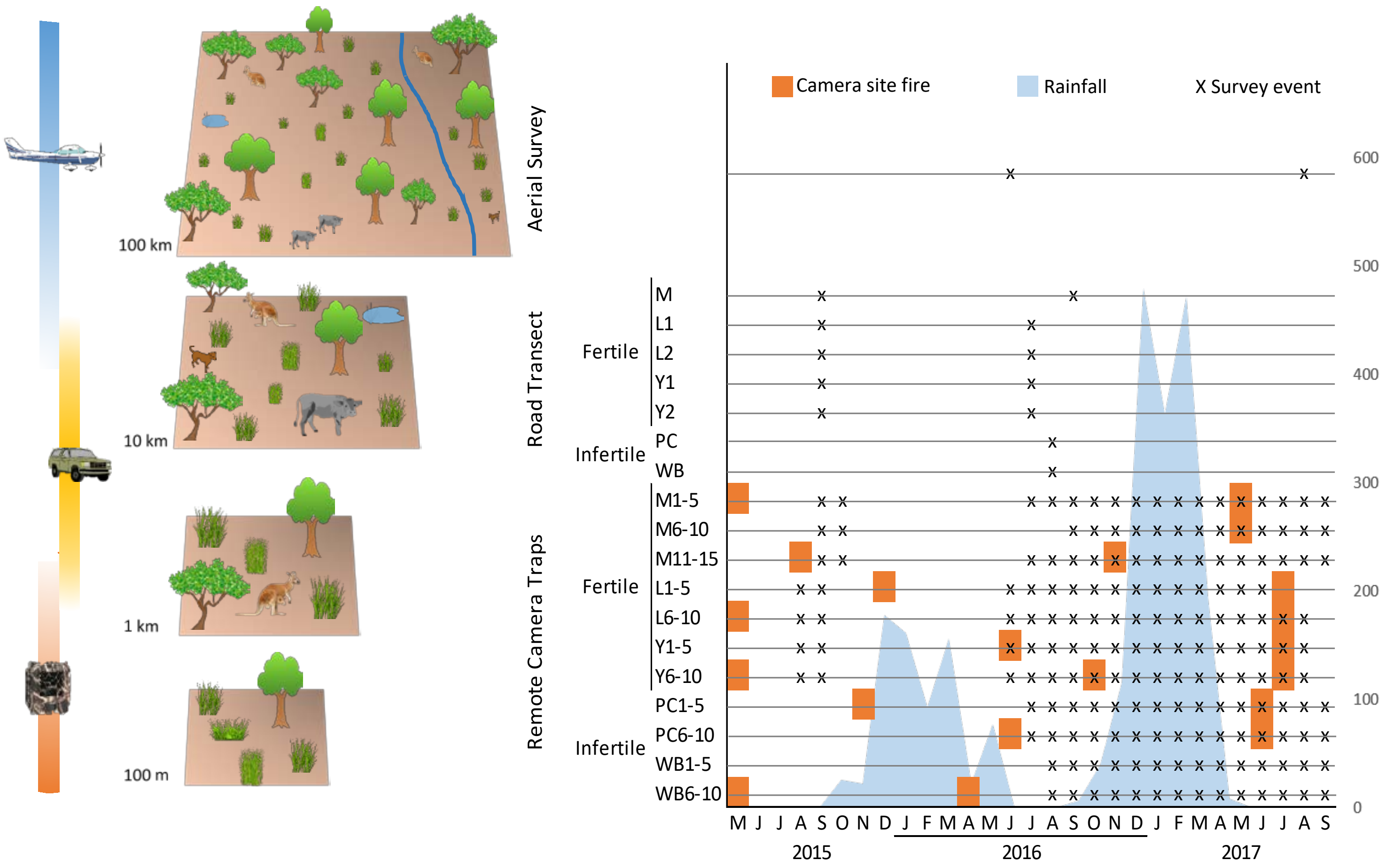

Figure 2.2 Survey schedule for aerial surveys, road transects and remote camera trapping on fertile and infertile savannas in the Uunguu IPA, North Kimberley, Western Australia from 2015-2017. Orange boxes designate a fire occurrence at a camera trap site; road transects were a mix of burnt and unburnt area, as were the aerial surveys. Annual wet season rainfall (mm) is recorded in light blue. An “x” designates each month the given survey type occurred.

2.3 METHODS

2.3.1 Study Area

This study was undertaken in the North Kimberley bioregion of Western Australia on the Uunguu Indigenous Protected Area (approximately 8,000 km^2), declared in 2011 and managed by the Wunambal Gaambera Aboriginal Corporation (WGAC, the Uunguu IPA is an IUCN category VI protected area; Fig. 2.1a). The vegetation is dominated by eucalypt (*Eucalyptus* and *Corymbia* spp.) savanna with a physiognomy of woodland and open forest with an understorey of hummock and tussock grasses on infertile soils and a mixture of perennial and annual tussock grasses on more fertile soils. The climate is defined by a monsoonal wet–dry seasonal cycle with mean annual rainfall of 1,100-1,600 mm across a steep latitudinal gradient (Fig. 1b; BMA, 2018). Approximately 90% of annual rainfall occurs during the 5-month wet season (December-April), greatly impacting the availability of fresh water throughout the middle of the year.

Much of the landscape burns each dry season. Most fire ignitions are anthropogenic but lightning storms concentrated in the transition between the dry and wet season (October-December) can ignite fires. The mean fire return interval for all of the Uunguu IPA is 2.5 years with 73% of fires occurring in the early dry season (before 1 August). Significant changes to the historical fire regime occurred around the mid-1900s because the Wunambal Gaambera people, the Aboriginal people of the region, had moved to nearby settlements and as a result traditional fire management ceased in most areas. A small community was re-established at Mitchell Plateau in the 1980s, but fire management was limited in scale (Vigilante *et al*., 2004). Historical fire regimes have been better replicated in recent decades with the establishment of Aboriginal fire management programs (Vigilante *et al*., 2004; Vigilante *et al*., 2017).

The large macropod populations known to occur on the Uunguu IPA are the antilopine wallaroo, common wallaroo and agile wallaby. Macropods are an important traditional food resource for Wunambal Gaambera people, and culturally significant animals. Fire is used to manage forage and habitat mosaics for macropods and, less commonly today, to facilitate hunting them (Vigilante *et al*., 2009). Pastoral leases adjacent to the Uunguu IPA were established in the 1900s and cattle grazing intensified in the 1950s and 1960s, such that these leases became a major source of feral cattle dispersal. Johnstone and Burbidge (1991) documented the arrival of cattle at Mitchell Plateau in 1976 while some coastal peninsulas have remained cattle free due to exclusion fencing and rugged terrain (McKenzie and Belbin, 1991). The Western Australian state government carried out an aerial shooting program at Mitchell Plateau from 2007 to 2017, initially targeting all cattle and subsequently only bulls (Corey *et al.*, 2013). Although annual culls of up to 30% of the total cattle population occurred within the Uunguu IPA during the study period, cattle have a high maximum population rate of increase (0.17; Bayliss and Yeomans, 1989b) resulting in only a modest potential population decline (13%). In addition, there is a high likelihood that cattle continue to migrate into the Uunguu IPA from surrounding properties. All cattle in the study area are considered feral.

2.3.2 Aerial Survey

Aerial surveys were conducted in June 2016 and August 2017 to determine macropod and cattle distribution and abundance across the Uunguu IPA in the dry season (Fig. 2.1c). The survey methodology was based on established aerial survey techniques for wildlife populations (Caughley and Grice, 1982, Bayliss and Yeomans, 1989b, Marsh and Sinclair, 1989). Overall there were 26 transects (17 in 2016 and 9 in 2017), on average 6.5 km apart and orientated east-west (except on peninsulas), with a mean length of 43 km, resulting in a coverage of 5.2% of the property. Surveys were conducted up to 3 h after sunrise or 3 h before sunset to capture daylight times of highest macropod activity.

A fixed-wing aircraft was flown at a mean altitude of 76 m (250 ft) above ground level and an average ground speed of 204 km h^{-1} (110 kn). Fiberglass rods were attached to aircraft wing struts to delineate a 200 m wide transect on each side. Each survey had three observers seated in the starboard middle and rear and port rear with each observer rotating through the seat positions such that all combinations of two observers sat on a side together for a portion of the survey allowing for correction of perception bias described by the double-count technique (Caughley and Grice, 1982). Two observers remained constant for the 2015 and 2016 surveys, but the third observer differed. Species, number of animals and transect zone (inside, low, high, outside as marked by wing struts) were recorded for each sighting on digital voice recorders. Flight paths were logged using a handheld global positioning system (GPS) recording latitude, longitude, and date and time every 30 s which was divided into six intervals to provide estimated location every 5 s. Sighting location was determined by matching the date and time from the observer log with the flight path log, and the midpoint of the recorded transect zone.

Error associated with sighting locations could be from estimated time lag between observation and nearest GPS record (up to 280 m, i.e. the distance travelled in 5 s at 204 km h^{-1}) and location within the transect zone (up to 50 m, i.e. the maximum distance from transect zone midpoint to edge of zone). Environmental data was collected at the start of each transect including air temperature at flying height, cloud cover percent and light conditions (bright or dull). Survey conditions averaged 28.7 ˚C, 8% cloud cover and 86% bright light conditions.

Population estimates

Perception bias correction factors for starboard and port side observations were 3.08 and 10.00 and 1.87 and 3.14, for macropod and cattle, respectively; these values were averaged across observers and habitats. Uncorrected and corrected (for perception bias only) population estimates were calculated using the ratio method for unequal transects in Caughley (1979b) following the method of Edwards *et al*. (2004) that was adapted from Caughley (1979a), Marsh and Sinclair (1989) and Caughley and Sinclair (1994). Observations outside the transect were removed for population estimates but included in the habitat association analysis. Validated correction factors for both macropods and cattle within the study region do not exist, therefore, no correction factors were applied for habitat or species. Densities were calculated based on transect area and herbivore biomass estimates were calculated using an average of 450 kg for cattle, the slaughter weight of shorthorn steers (DEDJTRV, 2018), and 32 kg for macropods, the average of female and male weight limits for antilopine wallaroo, common wallaroo and agile wallaby (Menkhorst and Knight, 2001).

Joint species distribution modelling

Aerial transect observations were further analysed with binomial Hierarchical Modelling of Species Communities (HMSC; Ovaskainen *et al*., 2017) to determine if herbivore groups (cattle, macropods) were associated with specific habitat characteristics and to examine species-to-species association. We used the 'HMSC' package in R (Blanchet, 2018) that provides significance of environmental correlates for each species as well as the amount of variation each correlate accounts for in species occurrence. This package is a Bayesian joint species distribution model that allows for the examination of signals of environmental filtering and biotic filtering and was chosen for its ability to handle both joint species and single species distribution modelling within a single package. Only 2016 data were used for joint species modelling (macropod and cattle) because no macropods were sighted in the 2017 survey and there was concern that it was due to the varying conditions between 2016 and 2017 surveys including moisture conditions and different observers. Data from both the 2016 and 2017 surveys were utilised to model cattle distribution.

Pseudo-absences were randomly generated (*n* = 1000) within the aerial transects and added to aerial sighting data for analyses. Using the location of each animal sighting or pseudo-absence, a GIS was used to associate time since fire, fertility, distance to perennial water and distance to nearest pastoral tenure. These variables were included in the model along with a species co-occurrence matrix (joint species on the 2016 survey) or cattle occurrence (cattle only from the 2016 and 2017 surveys). Convergence of parameters for all models was evaluated by visual inspection of the Markov chain Monte Carlo trace plots to ensure a representative sample from the posterior distribution before further evaluation of model outputs. The 95% central credible interval was used to assess the level of statistical relationship of cattle and macropods with a given environmental covariate. If the credible interval does not include zero, it can be concluded that this covariate relates positively or negatively (according to if the credible interval is above or below zero) to occurrence with this level of statistical support. ‘HMSC’ package outputs include significance between each species and environmental covariates, percent variability associated with each covariate and a species-to-species correlation matrix assessing associations amongst species after accounting for all environmental correlates.

2.3.3 Land system pasture potential

A pastoral potential classification map was obtained from the Department of Agriculture, based on CSIRO land system mapping assessments (Speck *et al*., 1960), and overlaid with the Uunguu IPA boundaries. Each of the five pasture potential categories had a range of carrying capacity densities (i.e. very low: 1 – 2.5 animal km^{-2}), the minimum density was used to calculate a weighted average pasture potential for the entirety of the Uunguu IPA.

2.3.4 Road Surveys

Seven transects were surveyed between 2015 and 2016 during the dry season months July-September following the approach of Ritchie *et al*. (2008) (Fig. 2.1d). Transects were selected along existing road networks and based on dominant savanna fertility, fertile (*n* = 5) and infertile (*n* = 2), fire management and proximity to camera trap monitoring sites. Repeat surveys for each 5 km transect were conducted at each sampling period between one to three consecutive days consisting of two morning surveys (05:30-07:30 hrs) and two afternoon surveys (17:00-18:30 hrs) with an average of 3.6 ± 1.1 repeat surveys. Surveys were conducted with a vehicle moving 10-15 km h^{-1} while three observers visually scanned the surrounding area. Species (cattle, antilopine wallaroo, common wallaroo, agile wallaby), group size, burn status and GPS location on each transect were recorded for each sighting. A laser rangefinder was used to estimate visibility every 1000 m on each side of the road; with an average visibility of 88.7 m ± 26.6 SE. Average density estimates were calculated using transect length and average visibility for width using the mean of repeat surveys at each sampling period. Herbivore biomass estimates were calculated as above. Joint species distribution modelling was not conducted on road survey data due to lack of macropod sightings.

2.3.5 Remote Camera Trapping

Site establishment and data acquisition

Monitoring sites (n = 11) were selected to span geological formations that yield comparatively fertile soils (n= 7; Carson Volcanics) and relatively infertile soils (n = 4; King Leopold Sandstone and Colluvium and Alluvium; Fig. 2.1d) based on geological classifications (Geoscience Australia, 2012, DMP, 2010). The fertile sites are characterized by gently undulating to hilly terrain with shallow stony soils dominated by a mixture of perennial and annual tussock tall grasses; infertile sites are characterized by gently undulating sandstone terrain with sandy soils of variable depth dominated by a mixture of hummock grasses in the endemic Australian genus *Triodia* and perennial and annual tussock grasses. Sites were selected based on fire management and utilization by both large macropods and feral cattle. Aboriginal Traditional Owners located sites in recently burnt and unburnt areas known to be historically good macropod habitat and areas were searched for macropod and cattle dung to confirm presence of both herbivore groups. Distance to nearest perennial freshwater source was calculated for each site (DLAWA, 2003, Crossman and Li, 2015). Fire history of each site for the duration of the project (2015-2017) and one-year previous (2014) was derived from observations and a satellite-derived (MODIS) fire history (NAFI, 2018). See Appendix A for detailed site descriptions.

Five cameras (RECONYX PC800 Hyperfire, RECONYX, Inc., Holmen, USA) were deployed at each site at various periods between 2015-2017 ranging from 31 to 294 trap nights (Fig. 2.1d). Areas around the cameras (~25 m^2) were cleared with a brush-cutter and cameras were attached to robust trees 1 m above the ground for fire protection and to reduce false triggers due to wind blowing the vegetation. Clipping the grass was necessary but likely to stimulate localized new growth if moisture conditions were suitable, however, we assume here that a small area within a larger unburnt area would not be drawing in animals that were not already in the vicinity. Cameras were set to trigger mode with motion sensor on medium/high sensitivity, three photos per trigger with a 1 s interval between photos and a 1 min quiet period between triggers.

Images were classified as containing cattle, dingo or macropod species (if identifiable), number of animals and behaviour. Due to the difficulty of positively identifying antilopine and common wallaroos in the night-time black and white photos these two large-bodied species were lumped together and are referred to as "wallaroos," agile wallabies were separate, and a further category for unknown macropods was created for macropods unidentifiable to species. Behaviour was defined as foraging if the animal was clearly chewing or had its head down to the forage below and all other activities lumped together as non-foraging. A measure of abundance of the top predator, the dingo, which may influence herbivore distribution was calculated per site based on monthly camera trap records. Date, time and temperature were automatically recorded for each photo. Temperature represents herbivore activity period as it is a continuous variable closely linked to time of day which was expected to show a divergent pattern for cattle and macropods; Julian date represents seasonal dryness. Distance to perennial water, site fertility, time since fire and a measure of dingo abundance (calculated as a monthly ratio of dingo photos to trap nights by site) were determined for each photo trigger.

Herbivore abundance

Across all sites, animal detections per trap night was compiled to provide an index of activity. Differences amongst species were tested using analysis of variance (ANOVA) and Tukey HSD for multiple comparisons where the overall ANOVA was significant ($p \leq 0.05$). Data were checked for normality and heteroscedasticity and log transformed prior to analysis.

The total number of individual animals detected for each species at each site during each 2-week period that cameras were deployed was determined. The midpoint of each 2-week period was used to establish time since fire and Julian date to model total individuals detected. We also determined presence or absence of agile wallabies, wallaroos, unidentified macropods and cattle to calculate the total (native and non-native combined) herbivore species richness in each

2-week period. Unidentified macropods were only included if no other macropod group had been counted so that total species present ranged from 0-3. Data were analysed using generalized linear mixed modelling to determine if effects of time since fire, site fertility, dingo abundance, and season on the total number of individuals of each species was similar to significant environmental correlates for basic detection data used in joint species modelling. This analysis was also utilised to examine a suspected interaction between substrate fertility and time since fire on herbivore abundance. Normal probability and residual plots were examined to determine appropriate distribution families. Total animals detected per species were modelled using a negative binomial distribution in the ‘glmmTMB’ package in R (Brooks *et al.*, 2017). Total trap nights per 2-week period per site was used as an offset for all models to account for incomplete 2-week periods and camera malfunction; site was included as a random variable.

Joint species distribution modelling

Camera trap detection/non-detection data were further analysed using binomial Hierarchical Modelling of Species Communities to determine environmental factors affecting presence (cattle, agile wallabies, wallaroos and dingo) and foraging behaviour (cattle, agile wallabies and wallaroos) and to examine species-to-species association and species-to-species effects on foraging behaviour. Model evaluation and interpretation as described in “Aerial Survey-Joint species distribution modelling” section.

Diurnal patterns of cattle, macropods and dingo

Diurnal activity profiles for cattle, agile wallaby, wallaroos and dingo were examined to determine the level of overlap in species at camera sites using the ‘overlap’ package in R to provide a non-parametric kernel density estimate using the default smoothing parameters recommended by Ridout and Linkie (2009).The coefficient of overlap, Δ, ranging from 0, no overlap, to 1, exact overlap, was calculated (Ridout and Linkie, 2009).

2.4 RESULTS

2.4.1 Density and biomass of native and non-native herbivores

Landscape-scale: aerial survey and pasture potential estimate

A total of 96 animal group sightings were recorded during the 2016 and 2017 aerial surveys (72 cattle groups and 24 macropod groups). Mean group size (± SE) for cattle and macropod sightings was 2.4 ± 0.26 and 1.4 ± 0.12, respectively. Only groups recorded inside the transects were used for density estimates: 140 cattle in 54 groups and 33 macropods in 23 groups. The corrected (for perception bias only) population estimates for the Uunguu IPA (7,815 km^2) were 6,096 ± 1, 603 for cattle and 3,845 ± 1,343 for macropods, yielding densities of 0.78 and 0.49 km^{-2}, respectively. Population estimates for cattle were 1.6 and 4.3 times higher than macropod population for corrected and uncorrected estimates with a precision of 24% and 26% for cattle (corrected and uncorrected estimates, respectively) and 27% and 35% for macropods. Cattle and macropod densities based on corrected population estimates were similar for infertile savannas (0.62 and 0.59 km^{-2}) but 6.8 times higher for cattle than macropods in fertile savannas (1.15 and 0.17 km^{-2}). Biomass estimates of cattle were 15 and 95 times higher than macropods for infertile and fertile savannas, respectively (Fig. 2.3). The pasture potential estimate based on land system mapping assessments for the Uunguu IPA was 1.45 km^{-2}.

Medium-scale: road survey

For all transects and sample periods there was only a single macropod sighting, two antilopine wallaroos, yielding an overall density estimate of 0.08 km^{-2}. Cattle were 125 times more abundant and had approximately 1800 times the biomass of macropods. A total of 164 cattle were sighted, yielding a density of 10.0 km^{-2} (Fig. 2.3).

Site-scale: remote camera trapping

Across all sites, a total of 3,703 triggers were recorded for cattle and macropods during 20,591 trap nights. Cattle had the highest total abundance (0.23 individuals night^{-1} vs. 0.07 and 0.08 night^{-1} for wallaroos and agile wallabies, respectively) as measured by detections per trap night ($p \leq 0.05$; Fig. 2.3).

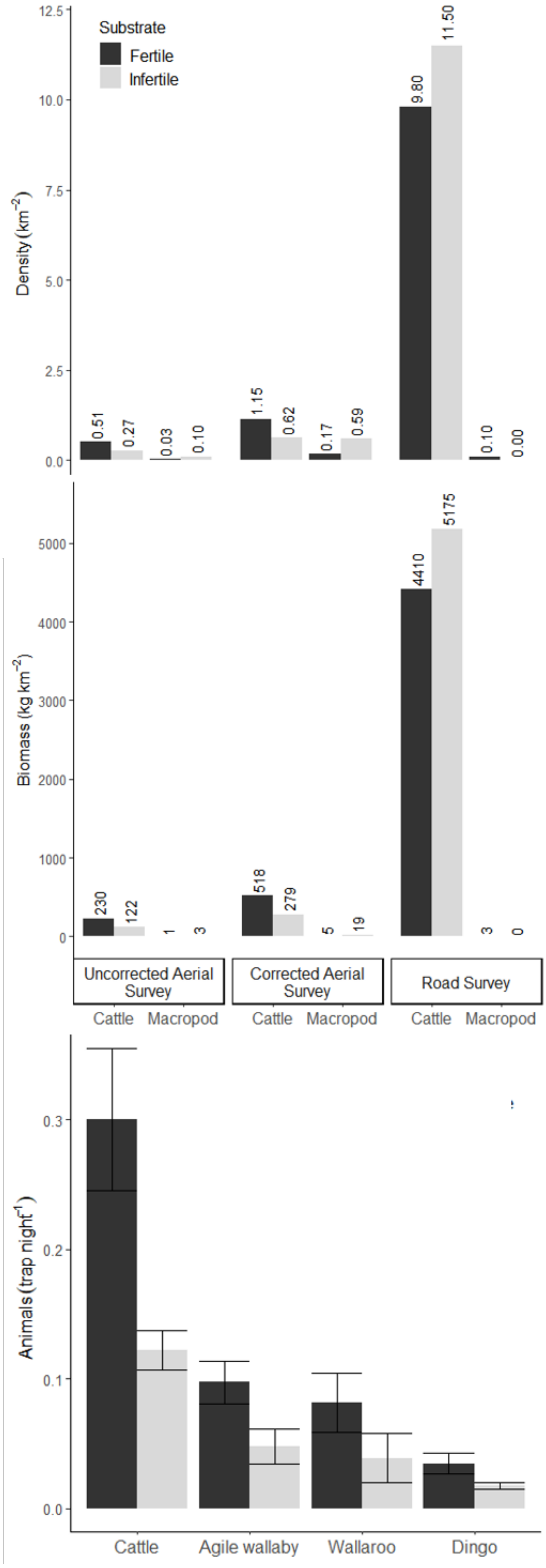

Figure 2.3 Density (km^{-2}) and biomass (kg km^{-2}) estimates for feral cattle and macropods based on property-wide aerial surveys (uncorrected and corrected for perception bias) and road surveys in savannas on fertile and infertile substrates. Abundance, as measured by individual animals per trap night, and standard error for feral cattle, agile wallaby, wallaroos (antilopine and common) and dingo on fertile and infertile substrates. Surveys were conducted during 2015-2017 in the Uunguu IPA, North Kimberley, Western Australia.

2.4.2 Environmental correlates of occurrence and foraging of large herbivores

Landscape-scale: aerial survey

The joint species distribution model using 2016 aerial survey data showed that the greatest variability (38%) in macropod occurrence was associated with substrate fertility with a significant ($p \leq 0.05$) association with infertile savanna. Macropods were significantly ($p \leq 0.05$) associated with greater distance to pastoral lease, accounting for an additional 30% of variability in occurrence (Table 2.1). Cattle occurrence was not significantly ($p > 0.05$) related to any of the correlates (substrate fertility, time since fire, distance to perennial water and nearest pastoral station).

The single species distribution model for cattle occurrence across all of the Uunguu IPA showed significant ($p \leq 0.05$) effects of proximity to pastoral stations, recently burnt areas and increased distance from perennial water, correlates explaining respectively 60%, 21% and 15% of the variation (Table 2.1).

Site-scale: remote camera trapping

Herbivore species occurrence and abundance

The joint species distribution model based on presence data of agile wallabies, wallaroos, cattle and dingoes showed that the random variable (site) accounted for approximately 50% of variation for all species except dingoes (Table 2.1). Agile wallaby occurrence was significantly ($p \leq 0.05$) associated with longer time since fire, cooler temperatures and the late dry season/early wet season ($R^2 = 0.22$). Wallaroo occurrence was significantly ($p \leq 0.05$) associated with longer time since fire, increased distance to water and cooler temperatures and had the best fit of all species in the model ($R^2 = 0.57$). Cattle occurrence was significantly ($p \leq 0.05$) associated with recently burnt areas, proximity to perennial water, warmer temperatures, late wet season/early dry season and low dingo abundance ($R^2 = 0.31$). Dingo occurrence was significantly ($p \leq 0.05$) associated with fertile savannas, proximity to water and cooler temperatures ($R^2 = 0.13$).

Large herbivore abundance (total number of individuals per species per bi-weekly camera trapping period) was examined with single species GLMMs and was positively related to seasonal dryness for all species ($p \leq 0.05$) meaning that total animals detected increased towards the end of dry season/beginning of wet season (Tables 2.2 and Appendix B). Agile wallaby

Table 2.1 Species distribution modelling results including variance partitioning and environmental correlate significance from four models: 1) landscape occurrence from 2016 aerial survey records for cattle and macropods, 2) landscape occurrence from 2016 and 2017 aerial survey records for cattle, 3) occurrence and 4) foraging behaviour from 2015-2017 camera trap records for cattle, agile wallabies, and a combined category for wallaroos (antilopine and common). Models 3 and 4 include site as a random variable. Values in the table represent the amount of variance each correlate accounts for in each model. Correlates with significant positive relationships are in bold and significant negative relationships are in bold italics for all models as determined by the 95% central credible intervals.

Scale	Method	Model	Species	Fertility	TSF	Water	Pastoral
Landscape	Aerial	1	Cattle	0.09	0.39	0.18	0.34
			Macropods	***0.38***	0.06	0.25	**0.32**
		2	Cattle only	0.04	***0.21***	**0.15**	***0.60***

Scale	Method		Species	Fertility	TSF	Water	Temp	Julian	Dingo	Site
Site	Camera-Occurrence	3	Cattle	0.10	***0.12***	***0.18***	**0.09**	***0.00***	***0.02***	0.49
			Agile	0.10	**0.16**	0.07	***0.17***	**0.02**	0.00	0.49
			Wallaroo	0.02	**0.33**	**0.10**	***0.03***	0.00	0.01	0.51
			Dingo	**0.11**	0.01	**0.44**	***0.04***	0.00	**0.28**	0.12
	Camera-Foraging	4	Cattle	0.05	***0.23***	0.07	**0.08**	***0.01***	0.00	0.56
			Agile	***0.24***	**0.16**	***0.12***	***0.35***	**0.01**	0.01	0.12
			Wallaroo	***0.10***	**0.26**	0.02	***0.02***	**0.00**	**0.02**	0.57

TSF: time since fire; Water: distance to perennial water; Pastoral: distance to nearest pastoral lease; Temp: temperature; Julian: Julian date; Dingo: dingo abundance index and cattle abundance were positively associated with dingo abundance in contrast to analyses using presence/absence data suggesting that higher dingo numbers are associated with areas with higher numbers of their potential prey species. The number of individual cattle was higher on recently burned areas whereas the number of agile wallabies increased in longer unburnt areas ($p < 0.05$) in agreement with joint species distribution analysis. An interaction between site fertility and time since fire was significant ($p < 0.05$) for the abundance of wallaroos. The abundance of wallaroos decreased with time since fire on infertile sites and increased with time since fire in fertile sites until approximately 1.5 years post-burn, then declined (Fig. 2.4).

Table 2.2 Model fit of generalized linear mixed models of total number of animals detected for agile wallabies, wallaroos, cattle and dingoes from camera traps established at 11 sites from 2015-2017 in the Uunguu IPA, North Kimberley, Western Australia. Correlates with significant ($p < 0.05$) positive relationships are in bold and significant negative relationships are in bold italics for all models.

Response variable	Model[a]	ΔAICc[b]	Explained deviance[c]
Total agile wallaby	~ SF + **TSF** + **DA** + **SD**	0.0	0.04
	~ 1	11.4	0.00
Total wallaroos	~ **SF * TSF** + DA + **SD**	0.0	0.03
	~ 1	3.0	0.00
Total cattle	~ SF + ***TSF*** **+ DA + SD**	0.0	0.01
	~ 1	16.2	0.00
Total dingo	~ SF + TSF + **SD**	0.0	0.02
	~ 1	4.4	0.00

[a] *SF* site fertility; *TSF* time since fire; *DA* dingo abundance; *SD* seasonal dryness. All models contained log(total trap nights/site/2 weeks) as an offset and site as a random variable.

[b] AICc second order Akaike's Information Criterion for large and small sample sizes; ΔAICc is the difference between the model's AICc value and the minimum AICc of all models in the candidate set. Models are ranked in ascending order of ΔAICc.

[c] Explained deviance is the proportional reduction in residual deviance, relative to the null model.

Foraging behaviour

Joint species distribution model results for wallaroo and cattle showed that site accounted for over 50% of variation in detection of foraging behaviour, with time since fire explaining approximately 25% (Table 2.1). Observed wallaroo foraging behaviour was significantly ($p \leq 0.05$) associated with infertile savannas, longer time since fire, cooler temperatures, late dry season/early wet season and higher dingo abundance and had the best fit of all species in the model ($R^2 = 0.51$). Observed cattle foraging behaviour was significantly ($p \leq 0.05$) associated with recently burnt areas, warmer temperatures and late wet season/early dry season ($R^2 = 0.17$). Variation in agile wallaby foraging behaviour was largely explained by temperature (35%) and site fertility (24%) and significantly associated ($p \leq 0.05$) with infertile savannas, longer time since fire, increased distance to perennial water, cooler temperatures and the late dry season/early wet season ($R^2 = 0.20$; Table 2.1).

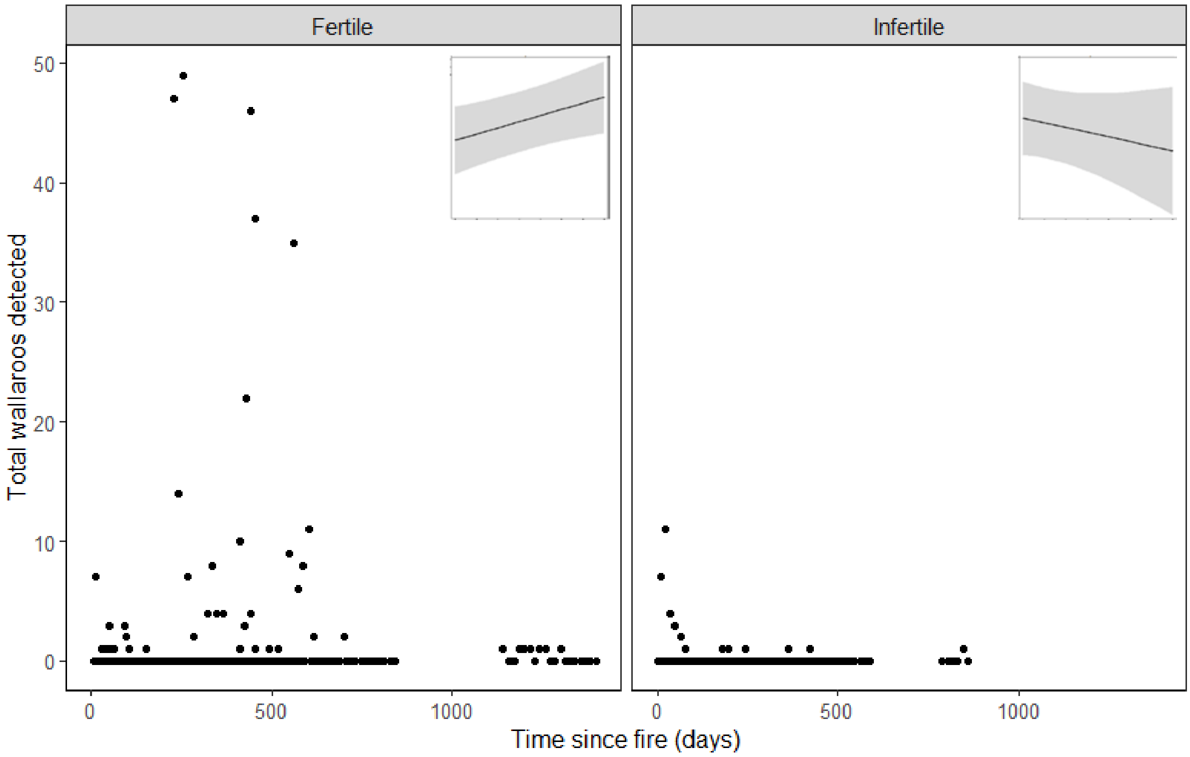

Figure 2.4 Total antilopine and common wallaroo fortnightly camera trap detections plotted with increasing time since fire between 2015-2017 pooled for fertile (n=7) and infertile (n=4) savanna sites in the Uunguu IPA, North Kimberley, Western Australia. Insets show contrary relationship between time since fire and total wallaroo abundance in fertile and infertile substrates representing the significant interaction term ($p < 0.05$) between time since fire and substrate fertility from generalized linear modelling.

2.4.3 Interspecific relationships

Landscape-scale: aerial survey

There was no significant association between macropods and cattle sightings detected by the aerial surveys.

Site-scale: remote camera trapping

After accounting for environmental covariates, both agile wallabies and wallaroos were negatively associated with cattle ($p \leq 0.05$; Fig. 2.5a). Dingoes and agile wallabies were positively associated ($p \leq 0.05$), and cattle and dingoes were negatively associated ($p \leq 0.05$). Only agile wallabies and wallaroos exhibited foraging behaviour together less often than expected after accounting for environmental covariates ($p \leq 0.05$; Fig. 2.5b).

Camera derived activity profiles show a distinct separation in activity period between species (Fig. 2.6). Cattle were active primarily during mid-afternoon and before sunrise. Agile wallabies were active during the night with peak activity before sunrise overlapping 73% with cattle while wallaroos were primarily active from before sunset and throughout the night without a distinct peak and a 57% overlap with cattle. The dingo activity profile was similar to agile wallabies with 78% overlap during a 24-hour period.

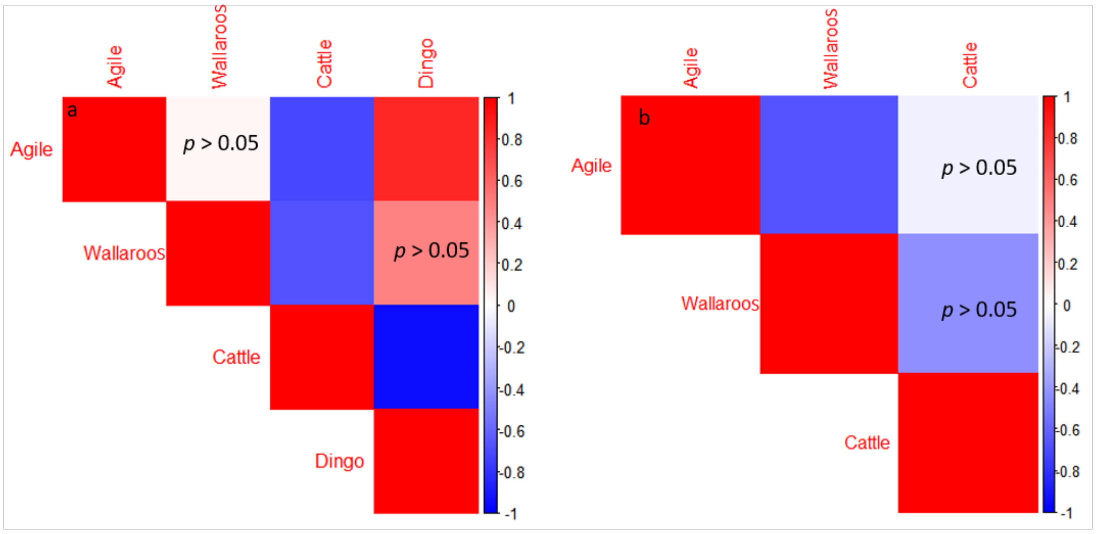

Figure 2.5 Species-to-species association matrix for (a) presence and (b) foraging behaviour for agile wallaby (agile), antilopine and common wallaroos combined (wallaroo), cattle and dingo using 2015-2017 camera trap data in the Uunguu IPA, North Kimberley, Western Australia. Blue colours are negative associations and red are positive associations as shown by the colour scale; non-significant relationships ($p > 0.05$) are noted.

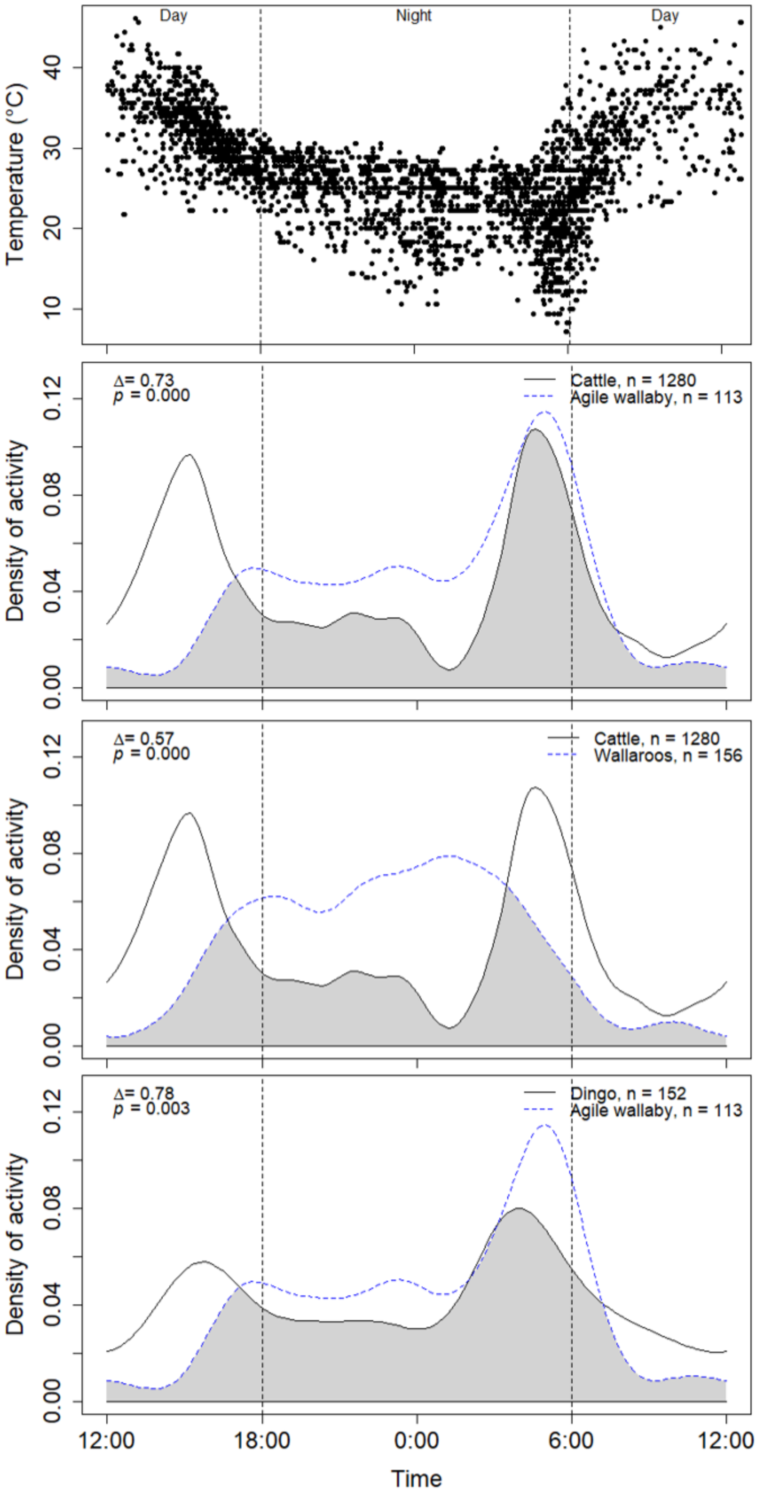

Figure 2.6 Relationship between time and temperature and activity overlap for feral cattle and agile wallabies, cattle and wallaroos, and dingoes and agile wallabies for camera trap records in the Uunguu IPA, North Kimberley, Western Australia 2015-2017. Record times were converted to solar time to account for changing sunrise and sunset times throughout the year. Delta is the proportion of overlap in activity period between species and dashed lines denote sunset and sunrise.

2.5 DISCUSSION

This study was framed around three questions concerning (a) abundance (b) distribution and environmental controls, and (c) interspecific relationships of native and non-native large herbivores in a monsoonal eucalypt savanna using a range of methods that span local- to landscape-scale. We found that the density, abundance and biomass of feral cattle exceeded that of macropods, regardless of survey technique utilised (aerial survey, road transects, remote camera trapping). Cattle were most abundant near pastoral leases while macropods were more abundant further from pastoral leases and on infertile, sandstone substrates. As expected by the pyricherbivory model, cattle occurrence and observed grazing were significantly associated with recently burnt areas, yet, contrary to the model, agile wallaby and wallaroo occurrence and foraging were associated with longer unburnt areas. Consistent with competitive exclusion, joint species distribution models revealed that macropods occurred with cattle less frequently than expected by chance, and temporal separation is evident both diurnally and seasonally. Below we contextualise our findings in light of previous studies of cattle and macropod abundance and distribution, their responses to landscape fire and theories of herbivore niche separation.

2.5.1 Abundance of cattle and macropods

Our landscape-wide estimate of cattle density was 0.78 cattle km^{-2} (aerial survey corrected for observer bias) though differing between fertile and infertile substrates (1.15 and 0.62 km^{-2}). This density estimate is slightly lower than the cattle density of 1.38 km^{-2} (uncorrected for observer bias or habitat) reported by an aerial survey conducted in 2008 covering approximately 10% of the Uunguu IPA, centred on infertile substrates that abutted a large area of fertile savanna (Corey *et al.*, 2013). This is also similar to the minimum estimated cattle density (1.36 km^{-2}) derived from pasture potential based on land system mapping assessments for the same area (Speck *et al.*, 1960). Our density estimate based on the aerial survey is around half (54%) of the minimum pasture potential estimate (1.45 km^{-2}) for the Uunguu IPA. Our density estimate is also lower than the typical carrying capacity of 1-3 cattle units km^{-2} for northern Western Australian pastoral lands (DPIRDWA, 2018). This most likely reflects that the Uunguu IPA is not being managed for cattle production and that the feral cattle populations have been recently culled so are unlikely to have reached carrying capacity.

Our density estimates are broadly comparable to feral bovine densities recorded in other eucalypt savannas outside the study area using similar aerial and ground survey techniques, with ground surveys consistently producing higher estimates (Fig. 2.7; Ridpath *et al.*, 1983; Bayliss and Yeomans, 1989a; Koenig *et al.*, 2003; Bayliss *et al.*, 2006; Saalfeld, 2006; Gorman *et al.*, 2007; Australian Wildlife Services, 2010; Eldridge, 2012b). Our density estimates are similar to those available for introduced bovines of similar size (*Bos javanicus* and *Bubalus bubalis*) in their native habitats (Hoogerwerf, 1970; Eisenberg and Seidensticker, 1976). Cattle biomass, based on the corrected aerial survey estimates, was estimated to be 351 kg km^{-2}, less than half the previously reported ungulate biomass for northern Australian monsoon tallgrass by Mott *et al.* (1981) and an order of magnitude less than large herbivore biomass estimates for some African savannas (8427 kg km-2; Damuth, 1982). Collectively these observations support the view that the empty megaherbivore niche in Australian savannas can be effectively filled by introduced bovines (Freeland, 1990; Bowman *et al.*, 2010).

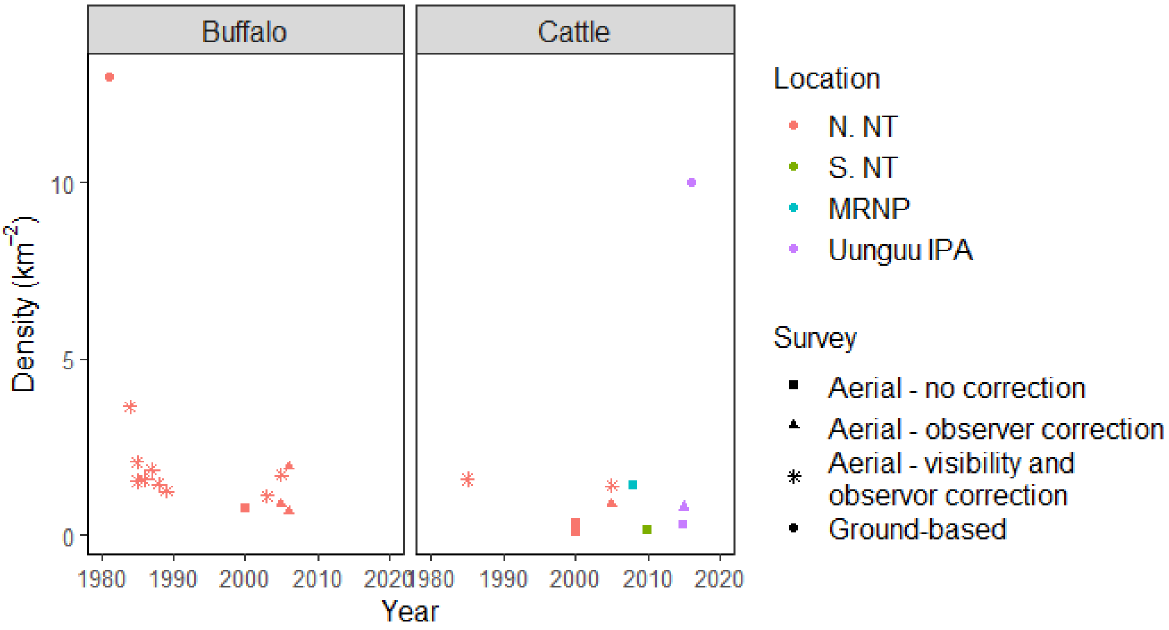

Figure 2.7 Published estimates of feral bovine densities for aerial (uncorrected, corrected for observer bias and corrected for visibility and observer bias) and ground-based surveys in Western Australia and the Northern Territory (Ridpath *et al*. 1983; Bayliss and Yeomans, 1989b; Koenig *et al.*, 2003; Bayliss *et al.*, 2006; Saalfeld, 2006; Gorman *et al.*, 2007; Australian Wildlife Services, 2010; Eldridge, 2012b; Corey *et al.*, 2013). N. NT = North Northern Territory; S. NT = South Northern Territory; MRNP = Mitchell River National Park located within Uunguu IPA; Uunguu = Uunguu IPA.

Macropod densities found in our study were much lower than those reported for pastoral landscapes in South Australia and central and southern Queensland (Caughley and Grigg, 1981; Caughley and Grigg, 1982; Caughley *et al*., 1985; Pople *et al*., 1998), where land management, including provision of artificial water points and dingo control, compensate for the competitive effects of high cattle densities (Fig. 8). Our macropod density estimates were also lower than less intensely managed tropical savannas in Western Australia, the Northern Territory and Queensland (Fig. 2.8; Croft, 1987; Ritchie *et al*., 2008; Ritchie *et al*., 2009). For instance, ground-based surveys in the mesic savannas of the Northern Territory in the early 1980s provided substantially higher densities (up to 325 times higher) than this study (Croft, 1987). One exception is the study of Koenig *et al*. (2003) that reported a very low (0.023 km^{-2}) uncorrected aerial survey macropod density (*Osphranter robustus*, *O. antilopinus, O. bernardus*) in Arnhem Land. Aside from land management, it is possible that soil infertility in the North Kimberley and Arnhem Land is the primary reason for macropod scarcity. However, there is some evidence that macropods are also declining. Ritchie (2007) provides anecdotal evidence of decline and road surveys during 2003-2005 in the North Kimberley, including our study area, reported a higher total density of antilopine wallaroos than this study (4 km-2 vs. 0.08 km-2; Ritchie *et al*., 2008) although whether this points to a trend in declining macropod densities in northern Australia's tropical savannas is unclear and highlights the need for further surveys. Such surveys must use a diversity of methods, as we have done, because of the variable sightability of macropods. For instance, using camera traps we found common wallaroos were abundant, yet this species was not sighted on our road surveys.

Regardless of the survey technique utilized (aerial survey, road transects, remote camera trapping) we have shown that the biomass of a large non-native herbivore (cattle) is much higher than the native herbivore biomass in the Uunguu IPA by 1 and 2 orders of magnitude (based on corrected aerial surveys) for infertile and fertile savannas, respectively. This pattern is even more pronounced in Arnhem Land where the biomass of non-native cattle and buffalo is 98 and 725 times higher than macropods, respectively (based on densities reported by Koenig *et al*. 2003). It is important to acknowledge that because habitat correction factors could not be applied for cattle and macropod density estimates, these differences may be exaggerated. Nonetheless, even when macropod densities are higher than cattle, the non-native herbivores still have a higher total landscape biomass. For example, on a pastoral lease in arid central Australia where the density of red kangaroos *(M. rufus;* 0.91 km^{-2}) is higher than cattle (cattle estimates were not corrected for visibility so represent a minimum population; Australian

Wildlife Services, 2010), non-native herbivore biomass is at least 1.2 times that of macropods. The vast difference in biomass between native and non-native large herbivores highlights the need to convert density measurements to have a more realistic understanding of feral herbivore abundance.

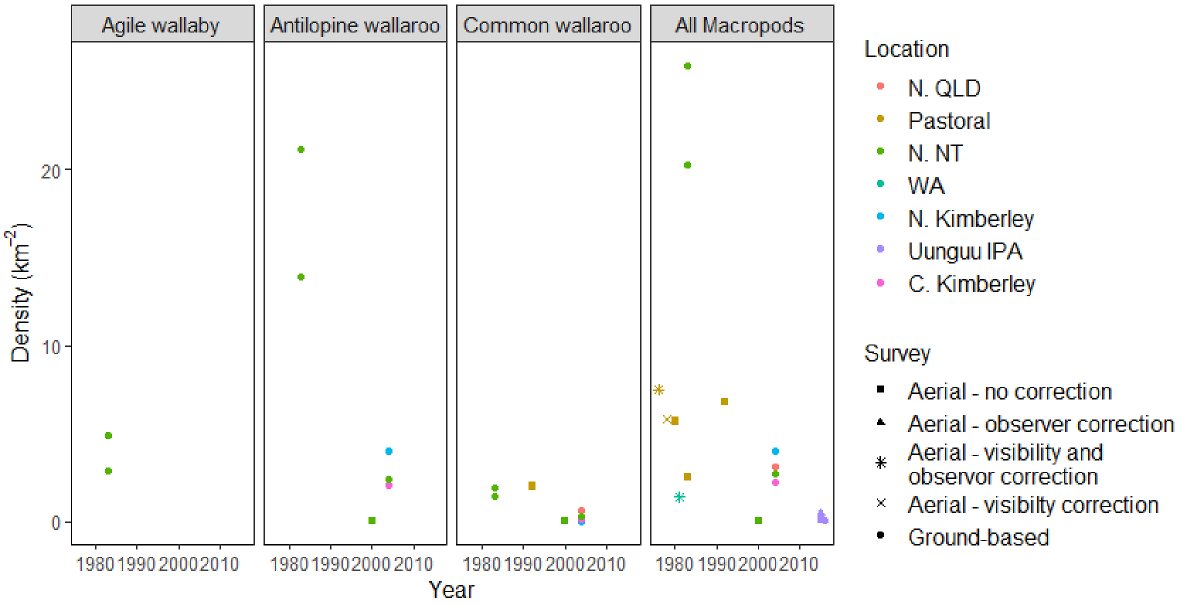

Figure 2.8 Published estimates of agile wallaby, antilopine wallaroo, common wallaroo and all large macropod species combined for aerial (uncorrected, corrected for observer bias only, corrected for visibility and observer bias and corrected for visibility only) and ground-based surveys across Northern Australia (Caughley and Grigg, 1982; Short *et al*., 1983; Caughley *et al*., 1985; Croft, 1987; Pople *et al*., 1998; Koenig *et al*., 2003; Ritchie *et al*., 2008; Ritchie *et al*., 2009). N. QLD = North Queensland, Pastoral = surveys conducted on pastoral country in Central and South Queensland and South Australia; N. NT = North Northern Territory; WA = Western Australia; N. Kimberley = North Kimberley; Uunguu = Uunguu IPA; C. Kimberley = Central Kimberley. WA was a state-wide survey except for the deserts and the Kimberley region. Areas outside the tropical north include densities of eastern grey, western grey and/or red kangaroo in their total macropod densities.

2.5.2 Distribution and environmental correlates

Cattle occurrence, abundance and foraging were influenced by both season and time of day (as represented by temperature). Cattle detections were less frequent at the camera trap sites towards the end of the dry season/beginning of wet season, but the number of total individuals detected was higher, suggesting larger group sizes later in the year possibly due to limited water resources towards the end of the dry season. Daily activity was associated with warmer temperatures and daylight hours, consistent with other studies (Borchard and Wright, 2010).

Landscape distribution of feral cattle was closely associated with pastoral leases and post-burn regrowth and inconsistently associated with water points. Importance of proximity to historical distribution points suggests that bovines are opportunistically expanding from pastoral properties that border the Uunguu IPA. Geographic complexity across the property such as rugged sandstone may impede northward movement especially in the west and distribution is periodically being altered by aerial shooting programs designed to limit the spread and density of feral cattle. Landscape-scale occurrence and site-scale occurrence, abundance and foraging behaviour of cattle were all significantly associated with recently burnt areas consistent with multi-scale pyricherbivory, whereby herbivores are attracted to the nutritious regrowth following a fire event (Fuhlendorf and Engle, 2001). Though it is well established that water points strongly influence bovine landscape distribution (Koenig *et al*., 2003; Allred *et al*., 2011a), our analyses did not reveal such clear-cut relationships, most likely because of the persistence of ephemeral water sources into the dry season. Site-scale cattle occurrence was linked to perennial water, but foraging behaviour was not, suggesting recently burnt areas are a stronger driving force (Allred *et al*., 2011a).

In contrast to cattle, the landscape-scale distribution of macropods was associated with greater distance to adjacent pastoral properties suggesting macropods may be geographically displaced northwards as feral cattle expand from the south into the Uunguu IPA. We also found substrate fertility affects the distribution and abundance of macropods. Camera trapping suggests common wallaroo are common in infertile sandstone habitats, possibly on fertile substrates as well, whereas antilopine wallaroos are more strongly associated with fertile substrates (Ritchie *et al*., 2008). We found wallaroos occurred further from perennial water bodies while agile wallaby foraging was associated with proximity to water, corroborating previous literature on differences in physiological tolerance of dryness between wallaroos and the agile wallaby (Ritchie *et al*., 2009; Stirrat, 2009). However, the ranges of the two wallaroo species are thought to be differentiated in part by their tolerance of water scarcity (Croft, 1981; Letnic *et al*., 2014) where antilopine wallaroos require access to permanent water (Ritchie *et al*., 2008; Ritchie *et al*., 2009). Our inability to reliably differentiate the two wallaroo species prevented us from identifying the environmental factors that differentiate these macropods across the study area.

Contrary to the pyricherbivory model, macropod occurrence, abundance and foraging were not uniformly associated with recently burnt areas and patterns varied between species. For the two wallaroos, we found an interaction between fertility and time since fire whereby abundance was highest on recently burnt areas in infertile savanna and abundance increased in fertile savanna sites up to approximately 1.5 years after a fire. Interactions between habitat and time since fire have been previously reported for both cattle and macropods (Vermeire *et al*., 2004; Murphy and Bowman, 2007b; Ritchie *et al*., 2008; Ritchie *et al*., 2009). The cause of this interaction could be related to avoidance of cattle on recently burnt fertile areas and the ability of macropods, with more selective feeding ecology, to utilize the smaller and more sparsely distributed amounts of green pick available on infertile substrates (Dawson, 1995). Common wallaroo abundance has been previously linked to low fire frequency but antilopine wallaroo abundance has been shown to increase with late dry season fires (Ritchie *et al*., 2008; Ritchie *et al*., 2009) highlighting the importance of maintaining or reintroducing the seasonal heterogeneity of the historical Aboriginal fire regime known to affect macropod abundance (Murphy and Bowman, 2007). Fire management programs in the North Kimberley in recent years have reduced late dry season fires by 50% (Corey *et al*., 2016) in efforts to better control late dry season wildfires and generate carbon credits with the abatement of greenhouse gas emissions. Current carbon credit programs provide economic incentives to participants for burning before 1 August encouraging fire management programs to focus on early dry season burning (Carbon Credits, 2018). Such a management regime of only early dry season burning may be disadvantaging the antilopine wallaroo whereas incorporating mid-dry season and late dry season burning, if moisture conditions are appropriate to allow for green pick emergence, could produce new forage throughout the dry season. The spatial pattern of fire is also likely an important influence on macropod species abundance. For instance, in arid central Australia Codding *et al*. (2014) found common wallaroo scat densities were higher in early seral (recently burnt) patches with emerging green pick and mid-seral patches with longer time since fire where fruits and herbaceous browse had recovered. Ritchie *et al*. (2008) and Telfer *et al*. (2008) also note the nexus between fire mosaics and the abundance of the common wallaroo.

Macropod activity was also linked to seasonal shifts and diurnal cycles. In contrast to cattle activity patterns, macropods were more abundant and foraging more frequently at study sites at the end of the dry season/beginning of the wet season and were detected and foraging more frequently in cooler temperatures linked to night-time or crepuscular activity, a result found previously for the common wallaroo and agile wallaby (Ealey, 1967; Kaufmann, 1974; Stirrat, 2004). Green-Barber and Old (2018) similarly found that macropod occurrence and behaviour were dictated by season and time of day with feeding occurring most often at night and early morning in the summer and early-morning to mid-afternoon in winter.

2.5.3 Interspecific relationships

Our findings of spatial and temporal partitioning of landscape resources between macropods and cattle may be a result of competition. Consistent with previous studies, we found cattle mostly foraged during the day while macropods foraged at night (Ealey, 1967; Kaufmann, 1974). Although we found no association between cattle and macropod presence with the aerial survey data, we did find a significant negative association at the site-level using camera trapping. Previous work across northern Australia has suggested cattle abundance was not an important factor for predicting wallaroo distribution (Ritchie *et al.*, 2008; Ritchie *et al.*, 2009). Elsewhere, competitive relationships between cattle and macropods is mixed and context-specific. Non-native and native herbivore interactions can be affected by habitat quality (Dudzinski *et al.*, 1982; Daskin and Pringle, 2016). For example, in Arnhem Land, feral herbivores are most strongly associated with more fertile habitat and native species with less fertile habitats (Koenig *et al.*, 2003). In less productive semi-arid ranglelands, cattle production can be adversely affected by large macropod abundance (Kutt *et al.*, 2012; Frank *et al.*, 2016) but on improved pastures, there can be a positive association between cattle and macropods (eastern grey kangaroos) with little evidence of competition (Payne and Jarman, 1999). Despite competition with higher densities of cattle, pastoral lands can sustain very high macropod populations in response to provision of water points and reduced predation by dingoes (Caughley *et al.*, 1985). Herbivorous species have a higher potential for competition when resources are limiting (Dudzinski *et al.*, 1982), especially with independent evolutionary histories (Davis *et al.*, 2017). Although much of Australia's tropical savannas have high pasture productivity associated with the wet season, by the end of the dry season they can become nutrient deserts if there have been no fires to initiate new growth. Thus, it is possible that the most intense competition between cattle and macropods occurs at the end of the dry season and is strongly influenced by fire, or lack thereof. In addition to competition for food resources, predation by dingoes may be more heavily skewed towards macropods than cattle given the positive association of dingoes and agile wallabies and negative association with cattle.

2.6 CONCLUSION

Using a multi-scale survey approach, we have found that feral cattle, a non-native herbivore, are more abundant in terms of density and biomass than the largest native herbivores in a little-modified Australian tropical savanna. Further, there is some evidence suggestive of population declines of macropods, which may be related to a contemporary fire regime of early season burning that has replaced the traditional Aboriginal practice of burning throughout the dry season, as well as competition with cattle for the highest quality forage resources. Multi-scale monitoring as applied in this study is essential to determine if large macropods are declining across northern Australia because camera trapping can record macropod species and behaviours that are often unidentifiable using aerial survey and road transects. The ecological cause of putative macropod declines, including the nexus of soil fertility and season of burning, warrants further investigation.

Chapter 3

Carbon isotope analysis shows introduced bovines have broader dietary range than the largest native herbivores in an Australian tropical savanna

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Title:

Carbon isotope analysis shows introduced bovines have broader dietary range than the largest native herbivores in an Australian tropical savanna

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Author roles:

Author	**Contribution**	**Signature**
AMR	Conceived, developed and designed the study; analyzed research data; wrote the manuscript	
BPM	Contributed to the conception and design of the study; provided input into the writing of the manuscript	
TV	Contributed to the conception and design of the study; provided input into the writing of the manuscript	
WGAC	Contributed to the conception and design of the study	
LAB	Conducted analyses and provided interpretation for carbon isotopes; provided input into the writing of the manuscript	
DMJSB	Contributed to the conception and design of the study; provided input into the writing of the manuscript	

3.1 ABSTRACT

Australian savannas lack native megaherbivores (> 1,000 kg body mass), but since the commencement of European colonisation in the 19th century bovine livestock, such as cattle (*Bos* spp.) and water buffalo (*Bubalus bubalis*), have established large feral populations that continue to geographically expand. The largest extant native herbivores are marsupials in the family Macropodidae (henceforth 'macropods': common wallaroo, *Osphranter robustus* [c. 40 kg]; antilopine wallaroo, *O. antilopinus* [c. 35 kg]; agile wallaby, *Notamacropus agilis* [c. 20 kg]) and occur at low densities, with evidence that some species are in decline, the cause of which remains uncertain. We tested the hypothesis that bovines and macropods compete for nutritious forage in the North Kimberley, Western Australia. To do so, we used carbon isotope analysis of feral cattle and native macropod dung (as a proxy for the relative contribution of C_4 grass to their diet) and nutrient analysis of standing herbaceous biomass. Grass consumption varied between macropod species, being highest in the two larger wallaroo species and lowest in the smaller agile wallaby reflecting its broader dietary range. Grass consumption by wallaroos was maximal on fertile sites and negatively correlated with fibre content of live biomass, which was lowest on fertile and burnt sites highlighting the importance of dry season burning to provide wallaroos with continuous access to high-quality, low-fibre forage. The relative abundance of grass in the diet of cattle was lowest in the middle of the dry season with an interaction between fire and substrate fertility where grass consumption was highest on fertile sites, particularly those recently burnt. Grass consumption by cattle was also negatively correlated with the fibre content of live biomass. Introduced bovines shift their diets to non-grasses as quality of herbaceous biomass declined with increasing fibre content, by contrast, the largest macropod herbivores do not have this dietary flexibility. We conclude a plausible mechanism for the success of bovines and the decline of large macropods in Australian savannas is competition for nutritious grass that is abundant immediately after landscape fire.

3.2 INTRODUCTION

Australia has no extant native megaherbivores with a body mass of > 100 kg, although European colonisation of northern Australia commencing around the 1820s established large feral populations of livestock (e.g. cattle [*Bos* sp.], water buffaloes [*Bubalus bubalis]*, horses [*Equus caballus]* and donkeys [*E. asinus*]) which continue to expand their geographic range (Letts, 1962; Freeland, 1990). The success of these feral herbivores in Australian savannas suggests that they may be occupying an ecological niche that became vacant following the extinction of native megafauna in the late Pleistocene (Bowman *et al*., 2010b).

In contrast to savannas elsewhere in the world, where both domesticated livestock and the large native herbivores are typically ungulates, Australia's native herbiovores are taxonomically and functionally distinct, being non-ruminant foregut feeding macropods (i.e. members of the marsupial family Macropodidae, including kangaroos and wallabies) including the antilopine wallaroo (*Osphranter antilopinus*), common wallaroo (*O. robustus*) and agile wallaby (*Notamacropus agilis*; Fig. 3.1). Suspected decline of some macropod species has been reported by Aboriginal Traditional Owners and past research (Ritchie, 2007; White *et al*., 2009; Roberts *et al*., 2016; Reid *et al*., 2019a), coincident with the introduction and expansion of large feral bovines such as cattle and water buffalo. While agile wallabies are considered intermediate feeders utilising both browsing and grazing strategies, common and antilopine wallaroos are thought to be more dependent on a grass diet (Sanson, 1989) but none have the gut capacity required to handle large amounts of poor-quality grass. The macropod declines may be caused by competition with feral bovines for food resources, which are generalist bulk-feeders. In Arnhem Land, water buffalo utilize a larger proportion of browse in their diet as the dry season progresses combating the nutritional decline of grasses (Bowman *et al*., 2010b). However, water buffalo are thought to have a broader diet and be better adapted to poor-quality grass than cattle (Eldridge, 2012a) so it is unknown if cattle exhibit the same dietary trends.

Tropical savannas are characterised by an annual cycle of weather extremes and frequent fire, conditions which greatly influence forage (herbaceous biomass consumed by herbivores) quantity and quality. The strongly seasonal rainfall pattern of the monsoon tropics leads to rapid production of tall grass during the wet season followed by desiccation during the dry season creating a high biomass of combustible grass with low nutritional quality and a 'boom-bust' cycle of forage quantity and quality (Mott *et al*., 1985). In northern Australian savannas, Australian Aboriginal people traditionally used patch burning to provide nutritious 'green pick' for herbivores by setting numerous small fires throughout the dry season (Crawford, 1982; Braithwaite, 1991; Saint and Russell-Smith, 1997; Murphy and Bowman, 2007b). This is because the fibre content of live forage is lower and crude protein content is higher in post-burn regrowth (Reid *et al*., 2019b) meaning that post-fire green pick is more digestible and nutritious. The Aboriginal socio-ecological tradition of patch burning has drastically changed since European settlement (Russell-Smith, 2001; Vigilante, 2001; Edwards *et al*., 2003; Fisher *et al*., 2003; Russell-Smith *et al*., 2003; Legge *et al*., 2011b) and altered fire regimes have been implicated in macropod declines in tropical savannas (Woinarski *et al*., 2014).

The Uunguu Indigenous Protected Area (Uunguu IPA), in the North Kimberley bioregion of Western Australia, is an ideal location to study the feeding ecology of macropods and feral cattle and how this is influenced by fire and soil fertility. This region has never been used for pastoralism or experienced large-scale vegetation clearing, is little affected by economic development, and represents a diversity of savannas on both fertile and infertile substrates (Fig. 3.2). In the Uunguu IPA, feral cattle are the dominant introduced herbivores and have only recently spread from adjoining pastoral leases, with rare populations of wild horses and donkeys. Although modes of Aboriginal fire management were disrupted in the 1930s with the nearby establishment of Kalumburu Mission, the Uunguu IPA is currently managed by its Aboriginal Traditional Owners in a way intended to replicate the historical fire regime. In this setting we used isotopic analysis of dung and forage nutrient analysis to address three linked questions:

1) Do macropods and feral cattle differ in their seasonal consumption of grass?
2) How do fire, substrate fertility and progression of dry season influence the proportion of grass in the diet?
3) What fire-influenced forage attributes affect the proportion of grass intake?

This study was designed to harmonise with previous projects conducted in Arnhem Land, Northern Territory, another large swath of relatively undisturbed tropical savanna (Fig. 3.2; (Telfer and Bowman, 2006; Murphy and Bowman, 2007b; Bowman *et al*., 2010b). The combination of results from this study and previous similar studies allows for the examination of savanna dynamics at a sub-continental scale.

Figure 3.1 The large herbivore assemblage in the Uunguu IPA consists of three native macropod species (a) agile wallaby (c. 20 kg), (b) antilopine wallaroo (c. 35 kg) and (c) common wallaroo (c. 40 kg) and has several introduced herbivores including feral horses and donkeys but are dominated by (d) feral cattle (c. 450–1,100 kg). The primary feral herbivore in Arnhem Land is the water buffalo (c. 450 – 1,200 kg). Photo credits: Fig. 1b – Sally Vigilante, Fig. 1c – Tom Vigilante.

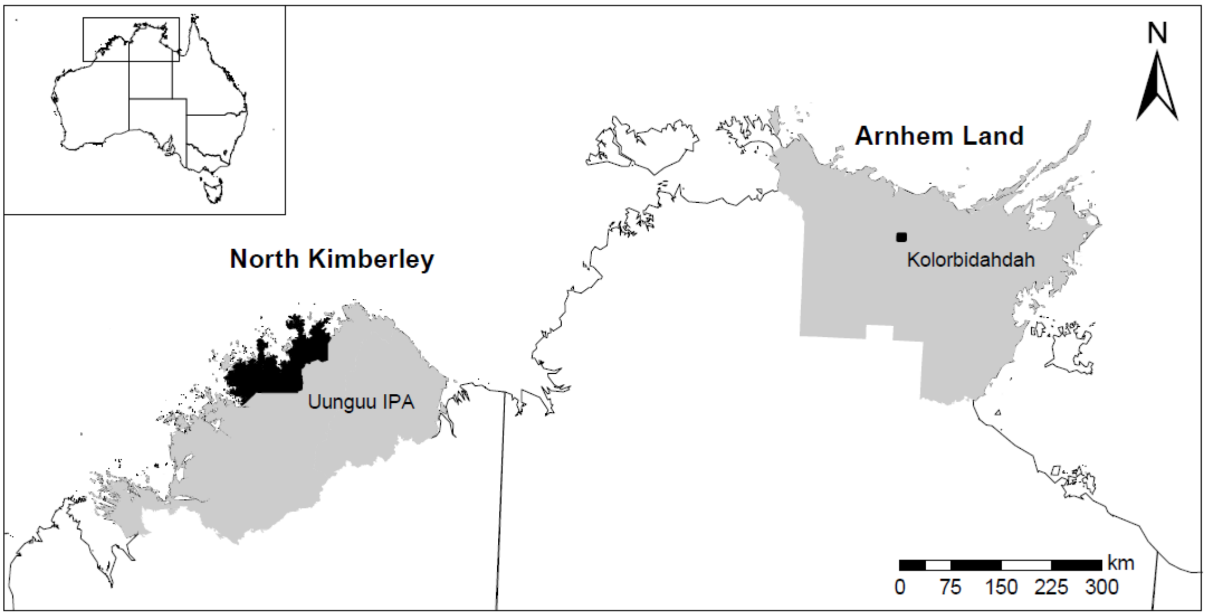

Figure 3.2 Location of the Uunguu IPA (black) within the North Kimberley bioregion, Western Australia where dung and forage samples were collected for this study and the location of previous macropod and feral bovine dietary studies at Kolorbidahdah, Arnhem Land, Northern Territory.

3.3 METHODS

3.3.1 Study Area

This study was undertaken in the North Kimberley bioregion, Western Australia in the Uunguu IPA (approximately 8,000 km^2) declared in 2011 and managed by Wunambal Gaambera Aboriginal Corporation (WGAC, Kalumburu, Australia). The vegetation is dominated by eucalypt (*Eucalyptus* and *Corymbia* spp.) savanna with a physiognomy of open forest and woodland with a grassy understorey. The climate is defined by a monsoonal wet–dry season cycle with mean annual rainfall of 1,100–1,600 mm across a steep latitudinal gradient, approximately 90% of which falls during the 5-month wet season (December-April; BMA, 2018).

Much of the landscape burns each dry season. Nearly all fires are intentionally ignited by humans, but lightning strikes concentrated in the transition between the dry and wet season (October to December) also ignite fires. The mean fire return interval for the Uunguu IPA during the project was 2.5 years with 73% of fires occurring in the early dry season (before 1

August). Significant changes to the historical fire regime occurred around the mid-1900s because the Wunambal Gaambera people, the Aboriginal people of the region, had moved to nearby settlements and, as a result, traditional fire management ceased in most areas. Historical fire regimes have been better replicated in recent decades with the establishment of Aboriginal fire management programs (Vigilante *et al.*, 2004; Vigilante *et al.*, 2017).

The large species of macropod (marsupial family: Macropodidae) known to occur in the Uunguu IPA are the agile wallaby, antilopine wallaroo and common wallaroo. Recent monitoring of large herbivores in the study area has shown large macropods collectively to be less abundant than feral cattle, and that the agile wallaby and common wallaroo are more common than the antilopine wallaroo which is rarely sighted (Reid *et al.*, 2019a). Pastoral leases adjacent to the Uunguu IPA were established in the 1900s and intensified in the 1950s and 1960s becoming a source of cattle (*Bos taurus*) dispersal, the most abundant introduced herbivore in the area.

3.3.2 Site establishment

Monitoring sites (*n* = 11; 3-5 ha each) were selected to span geological formations with relatively fertile soils (*n* = 7; Carson Volcanics) and infertile soils (*n* = 4; King Leopold Sandstone and Colluvium and Alluvium) based on geological maps (DMPWA, 2010; Geoscience Australia, 2012) and site-based observations. The fertile sites were characterized by gently undulating to hilly terrain with shallow stony soils dominated by a mixture of perennial and annual tussock tall grasses (e.g. *Sorghum* spp., *Themeda australis, Heteropogon contortus, Sehima nervosa, Chrysopogon fallax*); infertile sites were characterized by gently undulating sandstone terrain with sandy soils of variable depth dominated by a mixture of hummock grasses (*Triodia* spp.) and perennial and annual tussock grasses (e.g. *Sorghum* spp., *Eriachne sulcata*). Sites were selected based on fire history and utilization by both large macropods and feral cattle. In identifying study sites, we had guidance from Aboriginal Traditional Owners about areas known to be preferred macropod habitat. The identified areas were searched for macropod and cattle dung to confirm presence of both herbivore groups. Sites were either recently burnt or unburnt, defined by occurrence of fire in the dry season of measurement. In 2016, 8 sites were unburnt and 3 sites were burnt and in 2017, 3 sites were unburnt and 8 sites were burnt. Fire history of each site was constructed from field observations and satellite-derived (MODIS) burnt area records (NAFI, 2018). Five permanent 1-m^2 quadrats were established at each monitoring site for forage measurements, location of quadrats was selected to capture the characteristic grasses on fertile and infertile sites.

3.3.3 Isotopic analysis of dung

To evaluate whether grass intake differs between species, and whether it is related to fire history, substrate fertility and season, we collected fresh dung samples for isotopic analysis in the early dry season (EDS; May–June), mid-dry season (MDS; July–August) and late dry season (LDS; September–October) of 2016 and 2017. Fires occurring at monitoring sites during the course of this study ranged from approximately 500 to 11,000 ha, while home ranges for the species studied are significantly smaller, approximately 25 ha for the agile wallaby (Stirrat, 2003), 10 ha for common wallaroo, 76 ha for antilopine wallaroo (Croft, 1987) and 330 ha for cattle (Howery *et al*., 1996; Cowie *et al*., 2016). We therefore assume that dung collected at a monitoring site is from plant material consumed at that monitoring site or from nearby areas with analogous fertility and recent fire history. Dung samples were not collected during the wet season (November-April) due to access constraints. Macropod dung was considered fresh if it was without cracking or deterioration and retained an intact shiny black coating. Macropod dung in this condition is generally estimated to be less than 3 months old. Dung deteriorates faster during the wet season or when affected by fire in the dry season (Telfer *et al*., 2006), therefore fresh dung found during the early dry season when the first collections were made can reasonably be assumed to have been recently deposited. Cattle dung was considered fresh if it was in a recognizable pile and the interior of the dung was still moist or dark brown in colour. Cattle dung deterioration is assumed to be faster than macropod dung due to its higher moisture content and lack of hard exterior coating. Dung with any evidence of being burnt was not collected to ensure it was deposited after fires at the monitoring sites. Each sample was allocated to one of three categories: small to medium-sized macropod dung (< 18.5 mm wide; agile wallaby), large macropod dung (> 18.5 mm wide; antilopine and common wallaroo) and cattle dung. Macropod dung categories were based on average sizes found by Telfer *et al.* (2006). At each site, and on each sampling occasion, 0–10 individual dung samples were collected, based on dung availability, for each of the three categories by a thorough foot-based search of the site. In some instances, there were no fresh samples available. Samples were stored in plastic bags by category and subsequently oven-dried at 60˚C for 24–48 hours. The dimensions of the macropod dung samples were measured in the lab with callipers and a classification tree was used to separate samples into agile wallaby and wallaroos (Telfer *et al*., 2006). Antilopine and common wallaroo dung samples were not reliably differentiated based on the classification tree of Telfer *et al.* (2006) and these two species were pooled in further analyses and referred to collectively as “wallaroos,” as has been done in other studies (Murphy and Bowman, 2007b; Letnic *et al.*, 2014). Samples were pooled for each combination of dry season segment (early, mid, late), substrate fertility (fertile, infertile), fire history (burnt, unburnt), year (2016, 2017) and species (agile wallaby, wallaroo, cattle) and 1–3 replicates for each sent for isotopic analysis ($n = 180$). No late dry season fires occurred at monitoring sites during 2016-2017, so all fires were early dry season fires (before 1 August).

A 1 cm^3 subsample of each dung sample was ground to a fine powder with an electric mill then loaded into tin cups for analysis of carbon isotope abundances ($\delta^{13}C$) using a VarioMICRO Elemental Analyser (Elementar, Langenselbold, Germany) and Continuous-Flow Isotope Ratio Mass Spectrometer (IsoPrime, Cheadle, UK). The $\delta^{13}C$ data is reported in parts per thousand (‰) where $\delta^{13}C$ refers to the ratio of ^{13}C to ^{12}C relative to an internationally defined scale (V-PDB). The $\delta^{13}C$ results were normalised to an IAEA reference material, IAEA C8, with a consensus value of $\delta^{13}C_{V\text{-}PDB}$ = -18.31‰ (Gonfiantini *et al.*, 1995; Le Clercq *et al.*, 1997) and analysed with commercial reference standards from Elemental Microanalysis – ‘High Organic Sediment Standard OAS’ (CatNo. B2151) and ‘Protein Standard OAS’ (CatNo. B2155) as quality control references. All results are the mean of repeat measurements with the standard deviation of the replicate analyses less than or equal to ± 0.6.

Carbon isotope composition of dung samples was used as an estimate of seasonal variation in diet contributed by plants using the C_4 photosynthetic pathway (Jones *et al.*, 1979) which in northern Australia are primarily grasses, and nearly all grasses are C_4 (Bowman and Cook, 2002; Murphy and Bowman, 2007a). Therefore, we assume that the $\delta^{13}C$ value of a dung sample is equivalent to proportion of grasses in the diet. The relative contribution of grass to the diet was calculated as:

$$\%\text{ grass in diet} = \frac{\mu\delta^{13}C_{C3} - (\delta^{13}C_{sample} - \mathcal{E}^{*}_{diet\text{-}dung})}{\mu\delta^{13}C_{C3} - \mu\delta^{13}C_{C4}} \times 100$$

where $\mu\delta^{13}C_{C3}$ and $\mu\delta^{13}C_{C4}$ are the global means of $\delta^{13}C$ for C_3 (-26.5‰) and C_4 (-12.5‰) plants, respectively (Van der Merwe, 1982; Cerling *et al.*, 1997), and $\mathcal{E}^{*}_{diet\text{-}dung}$ is the average estimated ^{13}C enrichment which occurs between diet and dung (-0.8‰; Sponheimer *et al.*, 2003).

3.3.4 Forage quantity and quality

Biomass, crude protein and fibre content of live herbaceous biomass were measured at each monitoring site for each visit at which dung samples were collected for isotopic analysis to examine the relationship between forage attributes and grass intake.

Biomass

At each sampling occasion, average height and cover of live herbaceous vegetation were measured in the permanent quadrats. Live biomass was measured at the final sampling occasion each dry season by clipping all herbaceous vegetation inside permanent forage quadrats and separating live and dead biomass. Forage samples were dried in an oven at 60˚C for 48 hours and weighed. Live biomass measurements were significantly correlated ($p < 0.001$) with live forage volume (forage height multiplied by forage cover); thus, we were able to estimate live biomass for sampling occasions throughout the dry season.

Crude protein and fibre

To measure crude protein and fibre content, a minimum of 10 g live biomass representative of the dominant species of grass and herbs was clipped and placed into a sealed plastic bag at each sampling occasion. Samples were dried as above and milled to pass through a 1-mm sieve. Crude protein was determined by combustion (AOAC Official Method 990.03., 2005) with a CN628 Carbon/Nitrogen Determinator. To provide a measure of the fibrous bulk of the forage, amylase and sodium sulphite treated neutral detergent fibre (aNDF) content was assessed with ANKOM Technology Method 6 (ANKOM Technology, Macedon, NY, USA) using solutions as outlined in Van Soest *et al.* (1991). This measure is based on the amount of hemicellulose, cellulose and lignin following the removal of protein/starch contamination using addition of amylase and sodium sulphite.

3.3.5 Analysis

Ordinary least-squares linear modelling was used to examine the influence of species on percent grass in the diet by comparing the null model and a model with species as the predictor variable. The influence of fire, substrate fertility and dry season period on grass content of the diet of each species was also examined with ordinary least-squares linear modelling. A total of eight candidate models, representing all combinations of the three explanatory variables (fire, substrate fertility, season), were developed to explain variation in the grass content of herbivore diet. Models were compared using AIC*c*, the second-order form of Akaike's Information Criterion. Interaction terms between all predictor variables were also added to the best-supported model for each response variable, and AIC*c* used to assess whether the interaction(s) improved the model. Linear correlation was used to examine relationships between percent grass in the diet of each species and fire-influenced forage attributes (biomass and fibre and crude protein content of live biomass).

3.4 RESULTS

Agile wallabies, wallaroos and cattle all differed in the proportion of grass in their diet (Table 3.1a, Fig. 3.3). Wallaroos consumed the most grass and cattle consumed the least, albeit grass consumption by cattle was the most variable (ranging from 0–91%) thereby exhibiting greater dietary breadth compared to agile wallabies (32–91%) and wallaroos (36–100%). Agile wallaby grass consumption was unaffected by fire, substrate fertility or season, in line with the classification of mixed feeder utilising grass, forbs and browse throughout the year (Table 3.1b). Variation in the contribution of grass to wallaroo diet was best explained by substrate fertility, accounting for 42% of the deviance of the null model; wallaroos utilised more grass on fertile substrates (Table 3.1c; Fig. 3.4). By contrast, variation in the contribution of grass to cattle diet was more complex and best explained by dry season period and an interaction between fire and fertility (Table 3.1d; Fig. 3.5). Cattle ate a higher proportion of grass in the early and late dry season and less in the mid-dry season, possibly related to other food sources becoming available during that time such as fruiting or flowering of some browse species. Cattle ate the highest proportion of grass on burnt, fertile sites, and least on infertile sites and this was unaffected by fire.

Of live biomass, crude protein content and fibre (aNDF) content of live biomass, only fibre content was significantly correlated with the contribution of grass to the diet (Fig. 3.6). Both wallaroos and cattle ate a significantly lower proportion of grass when live herbaceous biomass had a high fibre content ($p < 0.001$; $R^2 = 0.41$ and $R^2 = 0.56$, respectively). Cattle severely reduced grass intake as fibre content increased (Fig. 3.7); on occasions where fibre content was at its highest (around 75–80%) almost no grass was consumed. Agile wallaby selection of grass was not correlated with any of the measured forage attributes consistent with their broad dietary range that includes forbs.

Table 3.1 Species linear models for dry season proportion of grass in diet, based on δ^{13}C levels of dung. When the best-supported model is not the null model, only models with ΔAIC*c* < 5 are shown. Significant predictor variables ($p \leq 0.05$) are in bold for the best models.

Response variable	Model	ΔAIC*c*[a]	Explained deviance (%)[b]
a) All species	~**Species**	0.00	22.15
b) Agile wallaby	~1	0.00	0.00
	~Fertility	0.88	2.50
	~Fire	1.97	0.51
c) Wallaroos	~**Fertility**	0.00	42.35
	~Fire + Fertility	2.25	42.36
	~Fertility + Season	3.92	42.92
d) Cattle	~**Fire** * **Fertility** + **Season**	0.00	71.48
	~Fire + Fertility + Season	4.86	67.72

[a] AIC*c* second order Akaike's Information Criterion for large and small sample sizes; ΔAIC*c* is the difference between the model's AIC*c* value and the minimum AIC*c* of all models in the candidate set. Models are ranked in ascending order of ΔAIC*c*.

[b] Explained deviance is the proportional reduction in residual deviance, relative to the null model.

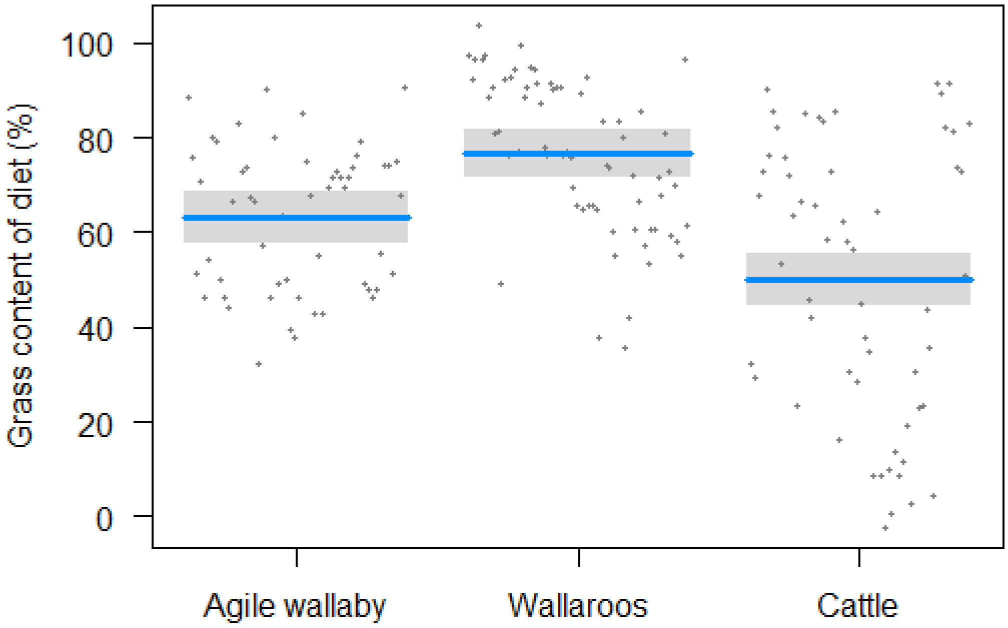

Figure 3.3 Predicted dry season contribution of grass to the diet of agile wallabies, wallaroos and feral cattle (based on δ^{13}C of dung) in the Uunguu IPA, North Kimberley, Western Australia. The grey shading indicates 95% confidence intervals and grey dots indicate partial residuals.

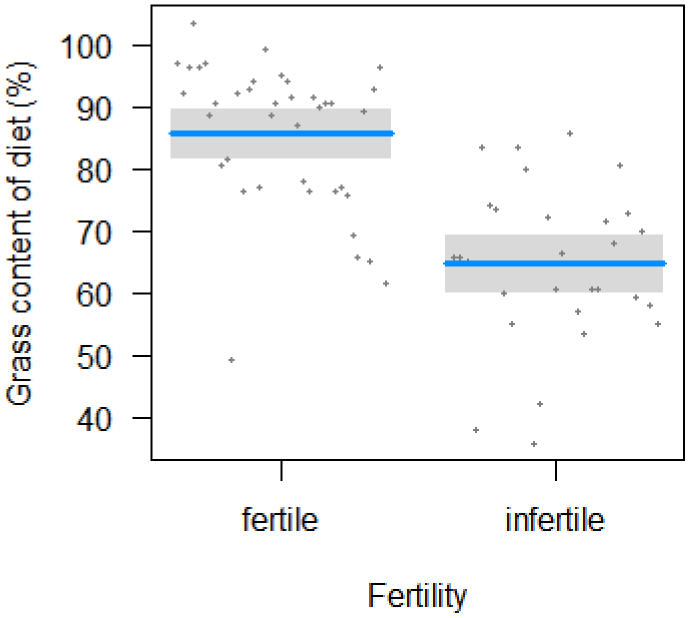

Figure 3.4 Predicted dry season contribution of grass to the diet of wallaroos (based on δ^{13}C of dung) on fertile and infertile soils in the Uunguu IPA, North Kimberley, Western Australia. The grey shading indicates 95% confidence intervals and grey dots indicate partial residuals.

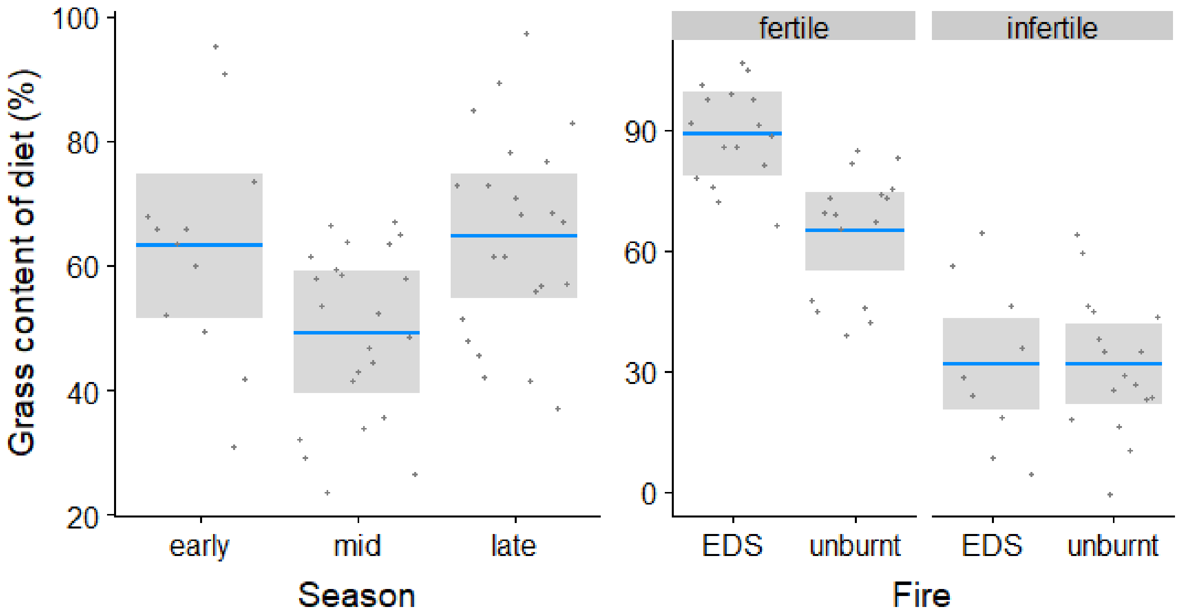

Figure 3.5. Predicted dry season contribution of grass to the diet of feral cattle (based on δ^{13}C of dung) by dry season period, substrate fertility and fire history in the Uunguu IPA, North Kimberley, Western Australia. The grey shading indicates 95% confidence intervals and grey dots indicate partial residuals.

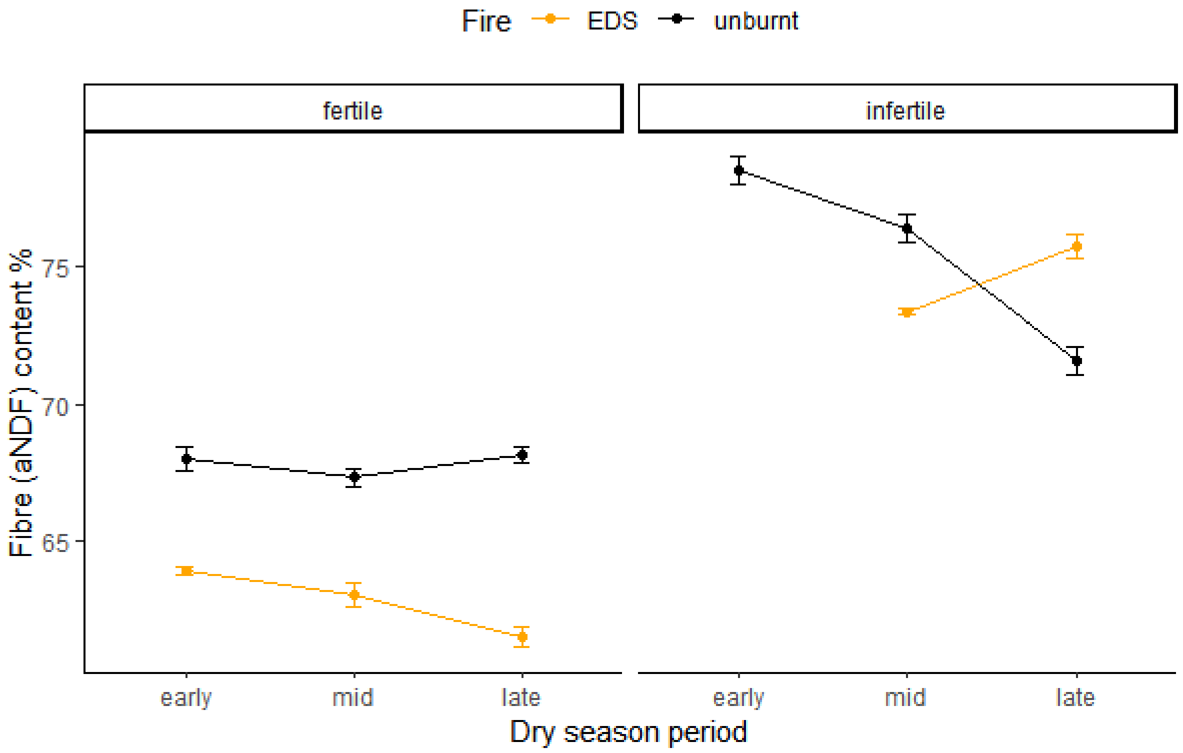

Figure 3.6 Seasonal variation in fibre content of live biomass (aNDF; ± SE) throughout the dry season in savannas burnt in the early dry season (EDS) and unburnt with relatively fertile and infertile underlying substrates.

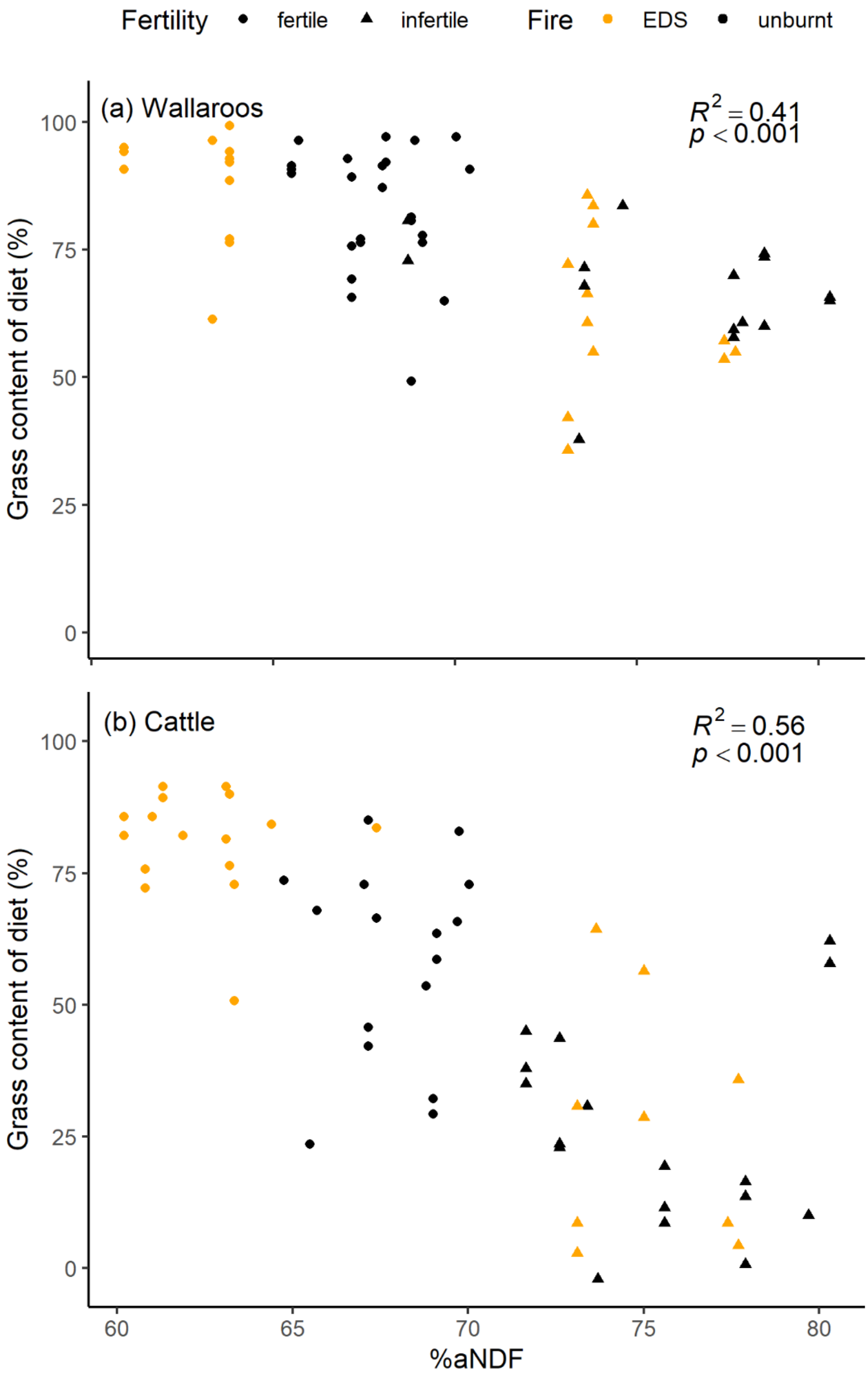

Figure 3.7 Proportion of grass in the diet of wallaroos and feral cattle on fertile and infertile savannas that have been burnt in the early dry season or unburnt in the Uunguu IPA, North Kimberley, Western Australia.

3.5 DISCUSSION

Our analysis of grass consumption by agile wallabies, wallaroos (antilopine and common wallaroo) and feral cattle in a north Australian tropical savanna highlights fundamentally different dietary breadth of these species. Macropods consume a higher proportion of grass and have a narrower dietary breadth than feral cattle. Thus, the large bulk feeding ungulates have substantial advantage over the macropods being able to tolerate the wide fluctuations in forage quality conditions that are characteristic of tropical savannas. Further, our analysis of forage quantity and quality showed that increasing fibre content of live biomass explained the decrease in grass consumption among both cattle and wallaroos, highlighting the importance of low fibre forage found on burnt, fertile sites for species more dependent on grazing, such as wallaroos.

The variability of the contribution of grass to macropod diets reported here is generally consistent with previous classifications of their feeding niche by their dentition: agile wallabies being defined as mixed feeders and wallaroo species as specialist grazers (Sanson, 1989). Consistent with a prior study (Murphy *et al.*, 2007), agile wallaby grass consumption showed the least variability and was unrelated to forage quantity and quality, fire activity, substrate fertility and dry season period highlighting their dependence on multiple food resources. Unlike wallaroos, this species is associated with moist riverine habitats where a wider variety of non-grass forage (herbs and browse) is available. When green grasses are available, agile wallabies prefer this resource but utilise a flexible foraging strategy to exploit a variety of resources including browse, leaf litter, fruits, flowers and roots when preferred foods are of poor quality (Stirrat, 2002). Nonetheless, previous work has shown that even though agile wallabies varied their dietary consumption to include higher protein foods when grasses had low nitrogen content, they were still unable to prevent loss of body condition with this feeding strategy (Stirrat, 2000; Stirrat, 2002) highlighting the potential importance to macropod health of resprouting grass following fire, especially in the late dry season.

Our results show broad dietary breadth of wallaroos (36–100% C4 grass), no doubt reflecting the pooling of wallaroo species. Previous work has shown a preference for grass in both species but that the common wallaroo consumes a lower proportion of grass than the antilopine wallaroo (Murphy *et al.*, 2007). Common wallaroos will target grass even when the abundance is low (Ellis *et al.*, 1977) and can continue to feed on grass of poor quality (high fibre and low nitrogen content; Freudenberger and Hume, 1992) and the antilopine wallaroo will exclusively consume grass if available (Croft, 1987; Murphy *et al*., 2007). However, the common wallaroo is associated with rocky habitats and escarpments, shown to have a greater vegetation species richness than the open plains providing access to more potential food resources (Freeland *et al.*, 1988). Variability of grass consumption by both wallaroo species could be explained by substrate fertility and forage quality: wallaroos ate more grass on fertile substrates and when fibre content of live biomass was low (i.e. grass forage was of high quality). The importance of substrate fertility likely reflects the effect on forage nutritional quality rather than quantity of forage. Forage quality, not quantity, has been shown to be the best predictor of macropod body condition (Croft, 1987; Shepherd, 1987). Freudenberger and Hume (1992) demonstrated that common wallaroos can digest grass with high fibre content with sufficient nitrogen supplementation. Nitrogen content in forage is highest in burnt areas (Murphy and Bowman, 2007b), particularly in new growth following a late dry season fire (Reid *et al*., 2019b), highlighting the importance of fire on the landscape to provide nitrogen when requirements are at their highest and can potentially increase intake and digestibility.

In contrast to previous studies, wallaroo grass intake did not vary seasonally or in response to early dry season fire activity. Common wallaroos and black wallaroos (*Osphranter bernardus*), endemic to Arnhem Land, have been shown to consume predominantly grass throughout the dry season (Telfer and Bowman, 2006). However, studies including year round measurements found antilopine and black wallaroos consumed a higher proportion of grasses during the wet season when high-quality forage was abundant with browse and forbs becoming a significant part of the diet during the late dry season when high-quality grass was limited (Fossan, 2005; Telfer and Bowman, 2006). Macropods have been shown to eat a larger proportion of grass on burnt areas (Telfer and Bowman, 2006; Murphy and Bowman, 2007b) although these studies did not differentiate between the responses of individual species.

The proportion of grass in the diet of macropod species is broadly comparable between the North Kimberley and Arnhem Land despite differences in substrate fertility and fire regimes (Fig. 3.8). The reported diet variability of common wallaroos in Arnhem Land (15-98%) was slightly greater than for common and antilopine wallaroos together in the North Kimberley. The mean grass consumption of all large macropods in Arnhem Land (antilopine, common and black wallaroos and agile wallaby) was lower than species in the North Kimberley (Murphy and Bowman, 2007b) signifying a regional difference in proportion of grass intake. The black wallaroo and agile wallaby had substantially lower mean grass intake than the other macropods consistent with the broader dietary breadth and diversity of resources in the habitats they occupy (rocky gorges and riverine respectively; Fig. 3.8).

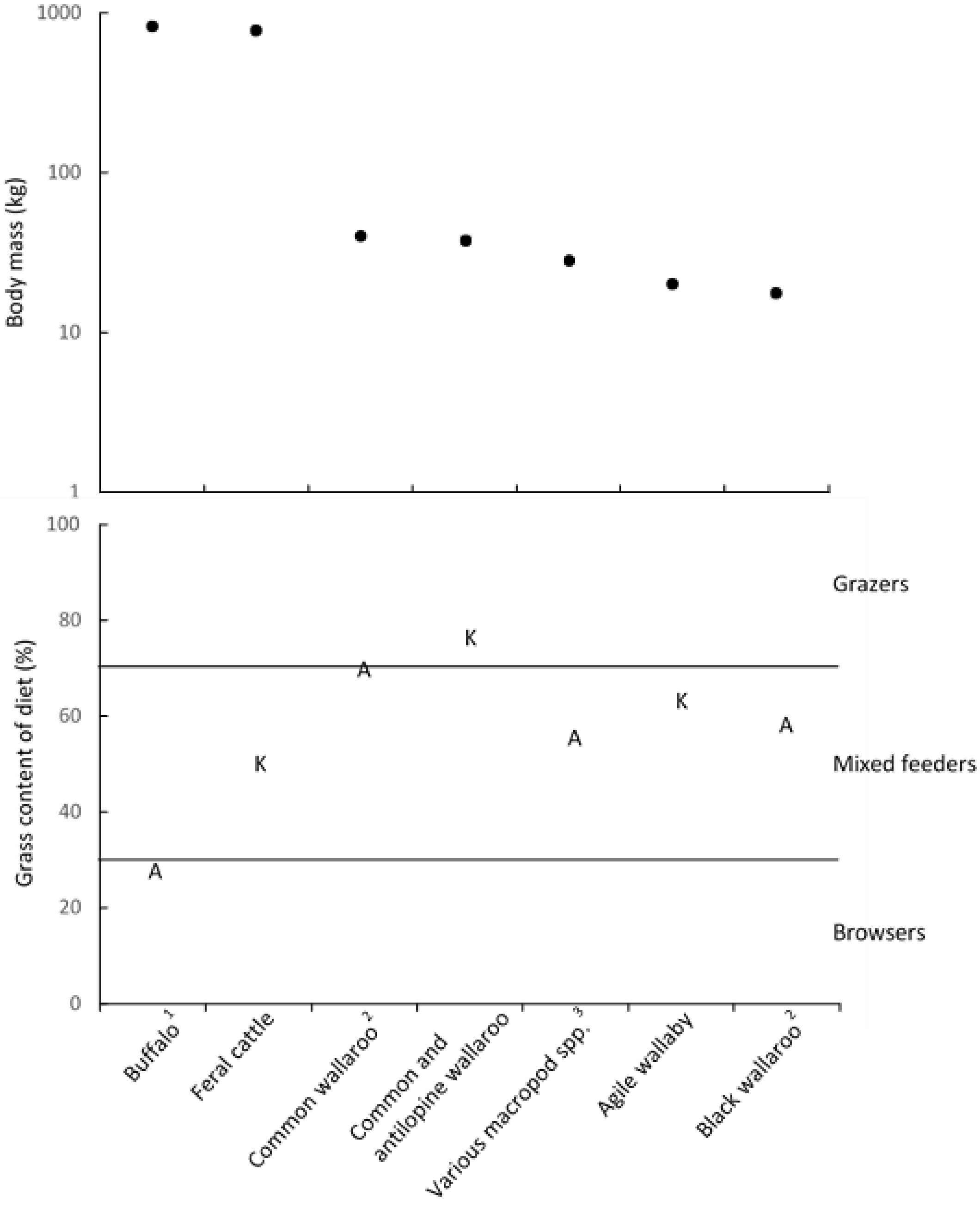

Figure 3.8 Proportion of grass consumed in the dry season by feral herbivores (water buffalo and cattle) and native macropod herbivores in Arnhem Land, Northern Territory (A) and the North Kimberley, Western Australia (N). “Various macropod spp.” includes agile wallaby and antilopine, common and black wallaroos combined. Superscript numbers indicate data sources (1, Bowman *et al*. 2010; 2, Telfer and Bowman 2006; 3, Murphy and Bowman 2007b). Body mass for each species is plotted in the top panel for comparison (Menkhorst and Knight, 2001).

Feral cattle had the greatest dietary flexibility compared to agile wallabies and wallaroos. We found grass consumption by feral cattle was related to substrate fertility, fire activity, forage quality and season. Grass consumption was highest on burnt, fertile sites but fire activity did not impact grass consumption on infertile sites likely due to lower fibre content of green forage on infertile sites, regardless of fire activity. Grass consumption by feral cattle was lowest during the mid-dry season possibly relating to other food resources coming available, such as flowering and leaf flushing on semi-deciduous trees. Cattle prefer sites closer to water and areas with woody vegetation for thermal refugia (Allred *et al*., 2011b; Allred *et al*., 2013; Reid *et al*., 2019a), a preference that may also provide access to a greater diversity of food resources such as riparian forbs and browse. The increase in grass consumption following the mid-dry season low may relate to new grass growth following sporadic rains at the end of the dry season.

There have been few other studies in Australia that have directly measured dietary niche separation between feral herbivores and macropods (as opposed to inference based on habitat use) and they have focused on the arid rangelands of southern Australia. Concurring with our findings from tropical savannas, in shrub rangeland the common wallaroo is a grazer with around 80% of the diet during severe drought made up of grass (Dawson and Ellis, 1996). By contrast, feral goats (*Capra hircus*) have broader diets with a strong preference for browse thereby potentially limiting competition with common wallaroos (Dawson and Ellis, 1996). In escarpment country of New South Wales, the yellow-footed rock wallaby (*Petrogale xanthopusin*) is a mixed feeder, like the agile wallaby, resulting in higher dietary overlap with feral herbivores (goats and rabbits [*Oryctolagus cuniculus*]) than is the case for the co-occurring obligate grazer, the common wallaroo (Dawson and Ellis, 1979). Studies conducted on dietary overlap between managed livestock and macropods are more prevalent than feral herbivores. A review of these studies from arid rangeland concluded there was minimal dietary overlap between large macropods (red kangaroo [*Macropus rufus*] and common wallaroo) and livestock (sheep and cattle) due to niche separation, but competition could intensify in times of limited resources (Squires, 1982). By contrast, Dawson *et al*. (1975) found that potential dietary overlap between the common wallaroo and sheep in rocky mulga and adjoining flat open country was greatest under good pasture conditions when they compete for nitrogen-rich grasses. Overall, introduced herbivores generally have wider dietary breadth than native species, and the intensity of overlap between them is modulated by habitat type and seasonal conditions.

In general, megaherbivores can consume lower quality forage due to longer gut retention time than smaller mass herbivores and are more generalised in their foraging habits (Owen-Smith, 1988) but high fibre concentrations can restrict cattle forage intake (Arelovich *et al*., 2008). Isotopic analysis of extinct Australian megaherbivores have shown they were opportunistic feeders adjusting dietary preference with environmental change (Gröcke, 1997), with a greater dietary range than extant large native herbivores and browsers were overrepresented in the suite of extinct marsupial megafauna (Bowman *et al*., 2010b). Their extinction left a vacant niche for large-bodied browsing and opportunistic feeders. Both feral cattle in the North Kimberly savannas (this study) and water buffalo in Arnhem Land (Bowman *et al*., 2010b) appear to have filled this niche given their greater dietary breadth than extant native herbivores switching from grazers under optimal conditions to browsers in the dry season as grasses lost nutritional value. This flexibility most likely gives both feral cattle and water buffalo an advantage over native herbivores during the highest stress time of the year.

Not only are feral herbivores in northern Australia much larger than native herbivores (Fig. 8), they represent a much greater proportion of the total herbivore biomass on the landscape (Reid *et al*., 2019a). Megaherbivores consume a greater relative fraction of landscape forage biomass (Owen-Smith, 1988) which is especially relevant when native and feral herbivores have a shared forage preference that is seasonally limited. The shift from grazing to browsing in both wallaroos and feral cattle appears to be driven by increasing fibre content of live biomass as opposed to decreasing crude protein content. Previous research has demonstrated that digestible dry matter intake declines in both ruminants and macropods as fibre content in feed increases (Freudenberger and Hume, 1992) which happens as grass cures (Terry and Tilley, 1964).

It has been suggested that Aboriginal burning has increased the abundance and geographic range of macropods by providing relatively constant high-quality forage (Codding *et al*., 2014). As Aboriginal fire was removed from the landscape in some areas, species' ranges may have contracted allowing feral herbivores to dominate the landscape. The provision of green pick by late dry season fires has been linked to abundance of antilopine wallaroos (Ritchie *et al*., 2008), one of the macropod species most dependant on grasses (Fig. 8). Areas that currently have a lower proportion of late dry season fires than in pre-European times may be limiting the ability of grass-dependant species to compete with feral herbivores and maintain historical levels of abundance. However, the role that fire plays in provision of late dry season forage resources and the importance of this to overall large macropod abundance requires further investigation.

3.6 CONCLUSION

Collectively, results suggest that forage quality but not quantity is the limitation in northern savannas, especially for macropods that have a narrower dietary breadth than feral herbivores. Results from the North Kimberley confirm previous work in Arnhem Land (Bowman *et al*., 2010b) showing that introduced megaherbivores occupy a feeding niche distinct from native herbivores, characterised by importance of browse and other non-grass resources in their diet and the flexibility to adjust to suboptimal forage conditions. Together, results from the North Kimberley and Arnhem Land are inconsistent with the notion that anthropogenic habitat change in the Late Pleistocene caused the megafauna extinctions (Johnson, 2016) because Australia's northern tropical savannas can still support large numbers of bulk feeding megaherbivores. We conclude a plausible mechanism for the success of bovines and the decline of large macropods in Australian savannas is competition for nutritious C_4 grass that is abundant immediately after landscape fire. We suspect competition between bovines and macropods may be particularly intense in areas of relative high productivity in the matrix of infertile sites (Braithwaite, 1990); patch burning mosaics may mitigate this effect but this conjecture requires further investigation.

Chapter 4

The nexus between forage, fire and herbivory in tropical savannas of northern Australia

Chapter 4

Title:

The nexus between forage, fire and herbivory in tropical savannas of northern Australia

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Status:

Manuscript in preparation

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Author	**Contribution**	**Signature**
AMR	Conceived, developed and designed the study; analyzed research data; wrote the manuscript	
BPM	Contributed to the conception and design of the study; provided input into the writing of the manuscript	
TV	Contributed to the conception and design of the study; provided input into the writing of the manuscript	
WGAC	Contributed to the conception and design of the study	
DMJSB	Contributed to the conception and design of the study; provided input into the writing of the manuscript	

4.1 ABSTRACT

Tropical savannas around the world support a diversity of large grazing herbivores that depend on a highly fluctuating resource, high-quality forage. Annual wet–dry cycles, fire activity and herbivory combine to influence forage quality and availability throughout the year. In the savannas of northern Australia, native marsupial herbivores (wallaroos [*Osphranter* spp.] and the agile wallaby [*Notamacropus agilis*]) compete for resources with introduced bovines (feral cattle [*Bos* spp.] and water buffalo [*Bubalus bubalis*]) that now dominate the landscape. Reports of population declines and negative impacts of introduced herbivores on large macropods indicate a need to better understand the complex relationship between forage, fire and abundance of native and introduced large herbivores. We used herbivore exclosures, forage biomass and nutrient analyses and motion-sensor camera-trapping to evaluate whether forage quantity and quality are impacted by herbivory, soil fertility, season and fire activity and determine which forage attributes most influence herbivore abundance. Forage quantity, as measured by live, dead and total herbaceous biomass and proportion of live biomass, was higher inside herbivore exclosures, even at relatively low densities of herbivores. Forage quality, as measured by fibre content, was not affected by herbivory, however, crude protein content of live herbaceous biomass was greater outside herbivore exclosures. Recent fire activity and study region (North Kimberley and Arnhem Land) were important predictors of all measures of forage quantity and quality. Recent fire occurrence decreased overall quantity (biomass) but increased quality (decreased fibre content and increased crude protein content); late dry season fires resulted in forage with the highest crude protein content. The Arnhem Land study sites, that have exclusively siliceous infertile soils, had lower quality forage but supported higher numbers of introduced bovines and wallaroos than the study sites in the North Kimberley, which also had soils derived from more fertile substrates. Potential explanations for this difference include reduced competition between wallaroos and water buffalo compared to cattle and the continuity of traditional Aboriginal fire management at the Arnhem Land study sites, characterised by finer scale and more even distribution of fire activity throughout the dry season. The predictions of the pyricherbivory conceptual model are consistent with the feeding behaviour of introduced bovines and some native macropods in northern Australian savannas.

4.2 INTRODUCTION

Savanna ecosystems occupy large areas of the tropics, representing approximately 22% of Earth's total land area (Ramankutty and Foley, 1999). Their formation and maintenance are based, in part, on highly fluctuating dynamics between fire and herbivory (Van Langevelde *et al*., 2003; Archibald *et al*., 2005; Bond and Keeley, 2005). Both fire and herbivory consume herbaceous biomass, thereby indirectly affecting each other. The interplay and feedbacks between fire and herbivory have been termed pyricherbivory (Fig. 4.1; Fuhlendorf and Engle, 2001). According to this conceptual model, consumption of herbaceous biomass by fire reduces the amount of available forage (edible herbaceous biomass) but increases the quality of regrowth, or 'green pick', attracting herbivores to the area. At the same time, the effects of herbivory on vegetation can be dependent on the intensity of grazing, thereby creating a feedback between fire, forage quality and subsequent focal grazing (Fuhlendorf and Engle, 2004; Archibald *et al*., 2005).

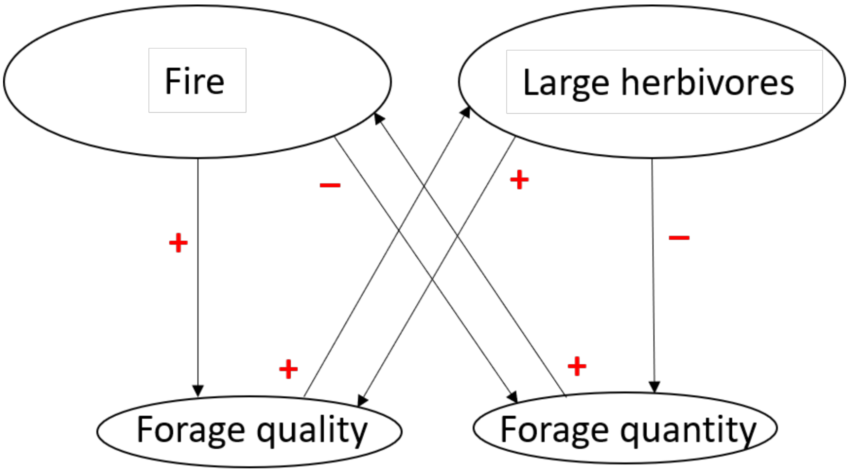

Figure 4.1 Conceptual model of direct relationships between forage, fire and large herbivores in tropical savannas. Fire and herbivory reduce the quantity of forage on the landscape and increase the quality of forage. Forage quantity impacts the likelihood of fire on the landscape while forage quality impacts the abundance of herbivores. Large herbivores and landscape fire indirectly influence each other, and their relationship is mediated by forage. Large herbivores can indirectly reduce fire frequency by reducing available fuel. However, in tropical savannas where the wet season resets forage biomass each year, densities of herbivores are unlikely to be high enough to affect this. Landscape fire improves the post-burn forage quality thus attracting more animals to the area.

In the tropical savannas of northern Australia, European colonists introduced domestic herds of a suite of large-bodied, bulk-feeding ruminant herbivores that, in turn, established feral populations. Immediately prior to the arrival of Europeans, these landscapes were occupied by a depauperate herbivore guild consisting entirely of macropods (i.e. members of the marsupial family Macropodidae, including kangaroos and wallabies) with more selective feeding strategies and completely lacked megaherbivores (all extant native species are < 100 kg). Previous research suggests that at least three of the feral herbivores, water buffalo (*Bubalus bubalis*), banteng (*Bos javanicus*) and cattle (*Bos taurus*), are filling a feeding niche left vacant by the Pleistocene extinction of the marsupial megafauna (Bowman *et al*., 2010b; Reid *et al*., in press), however, there is evidence of competition between introduced and native herbivores (Reid *et al*., 2019a). Both in Australia and elsewhere, competition between livestock and native herbivores is expected to intensify in the future, with trends in agricultural land-use showing a net redistribution towards the tropics (Mishra *et al*., 2002; Stewart *et al*., 2002; Young *et al*., 2005; Foley *et al*., 2011; Ogutu *et al*., 2011; Kutt *et al*., 2012), highlighting the importance of understanding how native and introduced herbivores respond to fluctuating forage conditions. This is especially true when native and introduced herbivores are dissimilar, as opposed to African and North American savannas where both groups are ungulates and have considerable functional similarities (Veblen *et al*., 2016).

The concept of pyricherbivory has been developed and tested in grass-dominated ecosystems of North America and Africa (Fuhlendorf and Engle, 2004; Archibald *et al*., 2005; Fuhlendorf *et al*., 2009; Allred *et al*., 2011a; Kimuyu *et al*., 2017), but fire is thought to have been used to manage forage nutrients and habitat mosaics for the maintenance of populations of macropods in tropical savannas by Australian Aborigines for thousands of years (Bowman *et al*., 2001; Vigilante *et al*., 2009). However, recent research has found an unexpected negative association between large macropods and recently burnt areas where feral cattle are well-established but remain at relatively low density compared to northern Australian commercial pastoral operations (Reid *et al*., 2019a). It is not clear if this relationship is present in areas dominated by other feral herbivores, but this finding suggests a possible change in feeding behaviour in response to competition for high-quality forage with introduced herbivores. Lack of high-quality food has been shown to impact feeding behaviour in agile wallaby leading to increased time spent foraging and distance travelled while foraging (Stirrat, 2004) while Favreau *et al*. (2018) found that food resources were the primary driver affecting feeding rate of eastern grey kangaroos (*Macropus giganteus*). Water buffalo and feral cattle have a broader diet, consuming significant quantities of both grass and browse, than the largest native herbivores providing a distinct advantage when high-quality grass forage is scarce (Bowman *et al.*, 2010b; Reid *et al.*, in press). The introduction of feral herbivores that overwhelm native species both in number and biomass (Koenig *et al.*, 2003; Reid *et al.*, 2019a) may result in changes to feeding strategy in order to better exploit forage resources and maximize energy intake. For example, macropods may be better able to utilise and choose to focus grazing in areas with smaller amounts of high-quality forage, such as burnt infertile sites with a smaller flush of green pick or unburnt areas, due to their smaller mouths and more selective feeding than bulk feeders (Fig. 4.2).

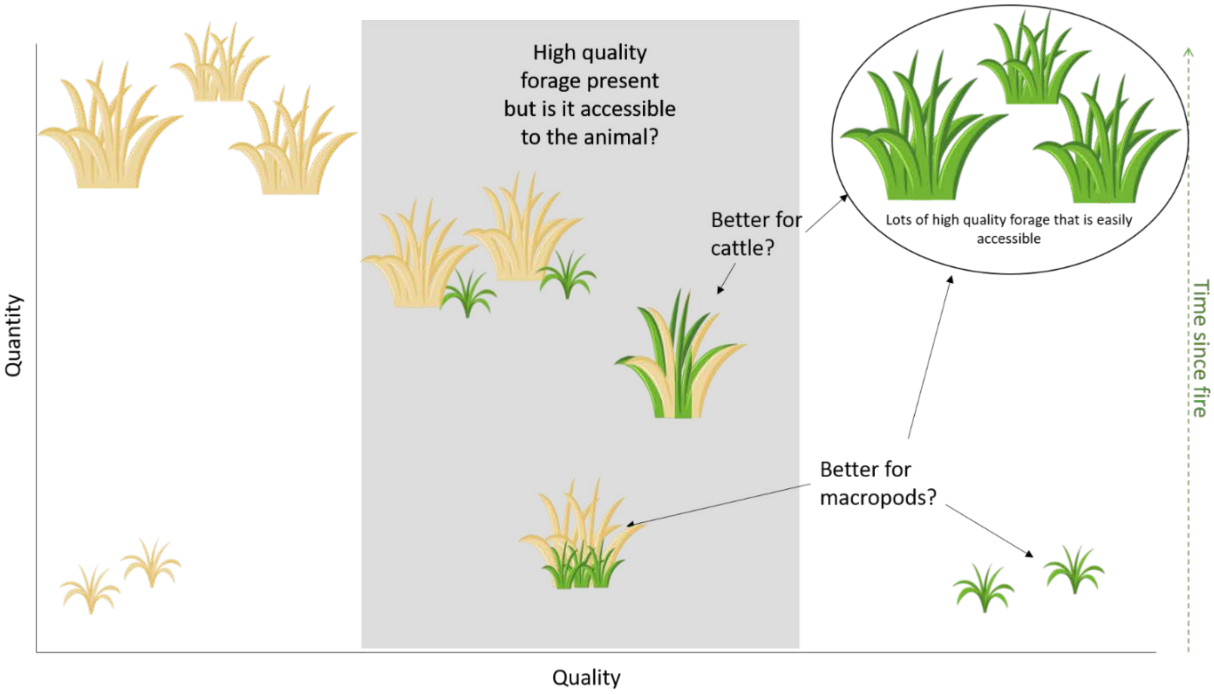

Figure 4.2 Conceptual model relating forage quantity and quality to herbivore utilization. The ideal situation for an herbivore is expected to be a large quantity of high-quality forage that is easily accessible. However, due to different feeding ecology of introduced and native herbivores accessibility of high-quality forage may vary. Bulk feeders that take large bites and consume a large quantity of forage might prefer grazing areas where there are large quantities of green grass regardless of whether it is mixed within a matrix of dead forage whereas a macropod might prefer smaller amounts of forage that is primarily green as they are more selective feeders. Grass image from Freepik.com.

In comparison to tropical savannas elsewhere in the world, Australia has lower diversity and biomass of large herbivores, nutrient-poor soils and introduced herbivores that are evolutionarily distinct from the native herbivores (eutherian vs. metatherian; Mott *et al.*, 1985).

There has been substantial research on relationships between forage quantity and quality, fire and large herbivores in tropical savanna landscapes elsewhere in the world but the unique context of northern Australia and recent studies suggesting competition between native and introduced large herbivores necessitates further investigation. To understand the nexus between forage, fire and herbivory and the applicability of the pyricherbivory model in Australian tropical savannas we addressed two key questions: (1) How do herbivory, fire, soil fertility and season impact forage quantity and quality? (2) How does forage quantity and quality impact feral and native herbivore abundance? We combined methods from the fields of plant and wildlife ecology –herbivore exclosures, forage chemical analyses and remote camera trapping – to answer these questions at two study sites in Australia’s tropical savannas.

4.3 METHODS

4.3.1 Study Area

This study was undertaken in the tropical savannas of northern Australia with field sites in two regions: (1) North Kimberley bioregion, Western Australia; and (2) north-central Arnhem Land, Northern Territory.

The North Kimberley

The North Kimberley (NK) sites were in the Uunguu Indigenous Protected Area (Uunguu IPA; approximately 8,000 km^2), declared in 2011 and managed by Wunambal Gaambera Aboriginal Corporation (WGAC, Kalumburu, Australia; Fig. 4.3a), encompassing diverse savannas overlaying both fertile and infertile substrates, primarily derived from volcanic materials and sands, respectively. The climate is defined by a monsoonal wet–dry cycle with mean annual rainfall of 1,100–1,600 mm across a steep latitudinal gradient, approximately 90% of which falls during the 5-month wet season (December-April; Bureau of Meteorology 2018).

The mean fire return interval during the project (2014–2017) was 2.5 years with 73% of fires occurring in the early dry season (before 1 August) based on a satellite-derived (MODIS) fire history (NAFI 2018). Significant changes to the historical fire regime occurred around the mid-1900s in what is now the Uunguu IPA because the Wunambal Gaambera people, the Aboriginal people of the region, moved to nearby settlements and, as a result, traditional fire management ceased in most areas. Historical fire regimes have been better replicated in recent decades with the establishment of Aboriginal fire management programs (Vigilante *et al*., 2004; Vigilante *et al*., 2017).

The large grazing macropods present at the North Kimberley study sites are the common wallaroo (*Osphranter robustus*), antilopine wallaroo (*O. antilopinus*) and agile wallaby (*Notamacropus agilis*). Pastoral leases adjacent to the Uunguu IPA were established in the 1900s, becoming a source of feral cattle (*Bos taurus*) dispersal, which have now reached higher densities than native macropod herbivores (Reid *et al*., 2019a).

Arnhem Land

Arnhem Land (AL) covers a large region overlaying mainly sandy, infertile substrates (c. 97,000 km^2) in the north-eastern corner of the Northern Territory and was declared an Aboriginal reserve in the 1930s, subsequently owned and managed by an Aboriginal land trust. Field sites were located near Kolorbidahdah on the Cadell River, an isolated Aboriginal outstation, with a continuous history of Indigenous occupation, except for a few years in the 1950s (Yibarbuk *et al*., 2001). Mean annual rainfall is 1080 mm, with approximately 90% falling during the 5-month wet season (December-April; Bureau of Meteorology 2018).

The mean fire return interval was 2.7 years with 48% early dry season fires for the 100 km^2 area surrounding Kolorbidahdah (Fig. 4.3b-c; NAFI 2018). Kolorbidahdah is managed in a traditional manner with small patches being ignited by hand throughout the dry season, mainly by the extended Aboriginal family residing at the outstation. The suite of grazing macropods in Arnhem Land is the same as in the North Kimberley with the addition of the black wallaroo (*O. bernardus*), which is endemic to Arnhem Land. The main feral herbivore is the water buffalo (*Bubalus bubalis*), originally introduced to the Northern Territory mainland in 1827, dominating the sub-coastal plains across the Northern Territory since the 1880s (Letts, 1962).

4.3.2 Site establishment

Monitoring sites (n = 14; Fig. 4.3d-e) were selected to span geological formations that yield comparatively fertile soils (n= 7; Carson Volcanics) and relatively infertile soils (n = 7; King Leopold Sandstone and Colluvium and Alluvium in the North Kimberley and Marlgowa Sandstone in Arnhem Land) based on geological classifications (DMPWA, 2010, Geoscience Australia, 2012). Vegetation at the field sites is dominated by eucalypt (*Eucalyptus* and

Corymbia spp.) savanna with a physiognomy of woodland and open forest. The fertile sites are characterized by gently undulating to hilly terrain with shallow stony soils dominated by a mixture of perennial and annual tussock tall grasses; infertile sites are characterized by gently undulating sandstone terrain with sandy soils of variable depth dominated by a mixture of hummock grasses in the endemic Australian genus *Triodia* and perennial and annual tussock grasses (DAFWA, Undated, DENRNT, 2000). Sites were selected based on fire management and utilization by both large macropods and feral bovids. Aboriginal Traditional Owners located sites in recently burnt and unburnt areas known to be historically good macropod habitat and areas were searched for macropod and bovine dung to confirm presence of both herbivore groups. Dingo abundance at monitoring sites, as measured by dingoes per camera trap night, was similar for both regions (0.011 ± 0.003 SE at Arnhem Land sites and 0.008 ± 0.001 SE at North Kimberley sites).

4.3.3 Forage quantity and quality

Five pairs of permanent 1 m^2 quadrats spaced 2 m apart were established at each monitoring site. Quadrat pairs were visually assessed for approximately equivalent vegetation biomass and species composition and an exclosure (1.5 x 1.5 x 2.4 m) built around one quadrat in each set (one site had 10 quadrat pairs; $n = 150$ quadrats). Exclosures were made with steel reinforcing mesh and 180 cm fencing posts with steel wire netting (1 mm diameter, 5 cm hex aperture) installed around the bottom 90 cm to keep out large and small herbivores (Fig. 4.3f).

Forage sampling occurred during the dry seasons of 2015 and 2016 in Arnhem Land and 2015-2017 in the North Kimberley. Forage cover, height, moisture, crude protein (CP) and fibre (aNDF) were measured at each sampling occasion for both standing dead and live herbaceous biomass (Table 4.1). Standing biomass was measured at the final sampling occasion each dry season by clipping all herbaceous vegetation inside each quadrat and separating dead and live biomass. Standing biomass measurements were significantly correlated ($p < 0.001$) with forage volume (forage height multiplied by forage cover) thus we were able to estimate standing biomass for sampling occasions throughout the dry season. Annual production, proportion of live biomass and an index of dead to live herbaceous biomass were calculated (Table 4.1).

Forage moisture and nutrients (CP and aNDF) were sampled from the areas directly surrounding quadrat sets throughout the dry season. A minimum of 10 g each of standing dead and live forage were clipped and placed separately into sealed plastic bags per monitoring site to represent the species of grass and herbs inside the quadrats. At the end of each dry season, a subsample from biomass clippings was kept for moisture and nutrient measurements. Samples were weighed in the field to provide wet weights and later dried in an oven at 60 ˚C for 48 hours then reweighed. Dried samples were milled to pass through a 1 mm sieve. Crude protein was determined by combustion (AOAC Official Method 990.03., 2005) with a CN628 Carbon/Nitrogen Determinator. To provide a measure of the fibrous bulk of the forage, amylase and sodium sulphite treated neutral detergent fibre (aNDF) was assessed with ANKOM Technology Method 6 (ANKOM Technology, Macedon, NY, USA) using solutions as in Van Soest *et al*. (1991). Forage samples collected in 2015 were also analysed for phosphorus (CEM, Undated) but it was found to be significantly correlated with crude protein ($r = 0.84$, $p < 0.05$) and only crude protein was analysed going forward.

4.3.4 Remote Camera Trapping

Remote camera traps were used as an indication of herbivore abundance at monitoring sites in the time surrounding sampling occasions. Five RECONYX PC800 Hyperfire cameras (RECONYX, Inc.) were deployed at each monitoring site at various periods between 2015-2017 ranging from 31 to 294 trap nights (Fig. 4.1d-e). Approximately 25 m^2 areas around the cameras were cleared with a whipper snipper and cameras were attached to robust trees 1m off the ground for fire protection and to reduce false triggers due to wind. Clipping the grass was necessary but likely to stimulate localized new growth if moisture conditions were suitable, however, we assume that a small area within a larger unburnt area would not be drawing in animals that were not already in the vicinity. Cameras were set to trigger mode with motion sensor on, medium/high sensitivity, 3 photos per trigger with a 1 s interval between photos and a 1 m quiet period between triggers. Images were classified by species (cattle, water buffalo, agile wallaby, wallaroo) and number of animals. Due to the difficulty of positively identifying antilopine, common and black wallaroos in the night-time black and white photos these large-bodied species were lumped together and are referred to as “wallaroos.”

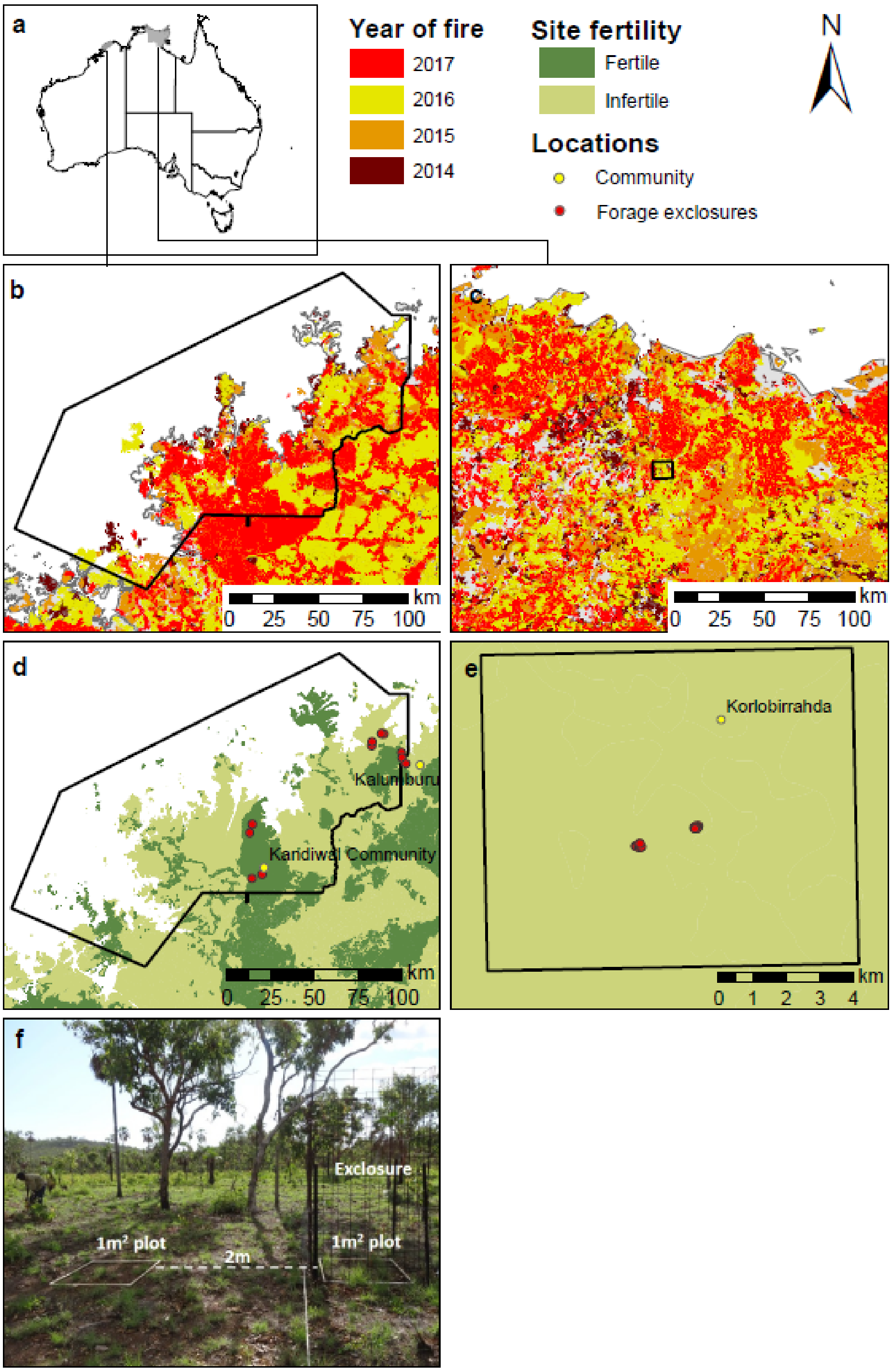

Figure 4.3 Geographic context of the study region (a) location of the Uunguu IPA, North Kimberley, Western Australia and Arnhem Land, Northern Territory; fire history from 2014-2017 for (b) the Uunguu IPA and (c) north-central Arnhem Land; substrate fertility for (d) the Uunguu IPA and (e) 100 km^2 area surrounding Arnhem Land field sites; **(**f) permanent forage plot design in the North Kimberley and Arnhem Land, photo taken in the Uunguu IPA. Data sources: geology (used to determine site fertility) as classified by Geoscience Australia (2012) and DMPWA (2010).

Table 4.1 Variables measured for live and dead standing herbaceous biomass.

Variable	Description/Calculation	Units
Forage height	average height of standing biomass in 1 m quadrat	cm
Forage cover	visual estimate of area covered by vegetation within 1 m quadrat	%
Forage moisture	$\frac{\text{weight of wet sample} - \text{weight of dry sample}}{\text{weight of wet sample}} \times 100$	%
Crude protein	true protein and non-protein nitrogen, required on a daily basis for maintenance, lactation, growth and reproduction.	%
Amylase neutral detergent fibre	hemicellulose, cellulose and lignin representing the fibrous bulk of forage	%
Standing biomass	dry weight of standing forage within 1 m quadrat	t ha^{-2}
Annual production	$\frac{\text{total standing biomass}}{\text{years since the quadrat was previously denuded (by fire or clipping)}}$	t ha^{-2}
Proportion of live biomass	$\frac{\text{live biomass}}{\text{total biomass}} \times 100$	%
Index of dead to live biomass	$\frac{\text{dead biomass}}{\text{live biomass}}$	na

4.3.5 Analysis

Herbivory and forage attributes

Generalized linear mixed modelling (GLMM) was used to evaluate the effect of herbivory on measures of forage quantity (live, dead and total standing biomass, proportion of live biomass) and quality (live and dead forage moisture, CP, aNDF). Forage measurements were modelled by plot location (inside or outside exclosure) and compared to null models; models contained exclosure as a random variable. Model fit was evaluated using second order Akaike's Information Criterion for large and small sample sizes (AICc). Model sets where the null model had the lowest AICc or were within two units of each other were considered to have equal support and interpreted as no effect of herbivory.

Environment and forage attributes

Linear modelling was used to evaluate the influence of substrate fertility, seasonality (time since end of wet season), fire (time since fire and fire season) and savanna region on forage quantity and quality. Fire season was categorized into early dry season fire (before 1 August), late dry season fire and unburnt in dry season of sampling. The end of wet season was determined by the date 95% of annual rainfall was received following the previous dry season. Forage measurements were averaged by monitoring site for each sampling occasion and principal components analysis (PCA) was conducted to determine uncorrelated forage quantity and quality variables. Total annual production (t ha^{-2}) and proportion of live biomass were selected as measures of forage quantity and CP (%) and aNDF (%) of live biomass for forage quality. Since forage quality measures required destructive sampling, our forage nutrient dataset (CP and aNDF) only contains full dry season records for forage outside the exclosures. However, due to the previously mentioned relationship between forage volume and biomass, our data set has complete records of forage quantity from protected quadrats and we were able to evaluate quantity in the absence of herbivory utilising only inside quadrat data. Dependant variables were transformed as needed to achieve a normal distribution of residuals. Model fit was evaluated using AICc and models within two units of each other were considered to have equal support for the best model in the set and effects from the simplest model presented. Model visualization graphs were produced with 'visreg' package in R (Breheny and Burchett 2017).

Large herbivore abundance and forage attributes

The number of bovines, wallaroos and agile wallabies recorded by camera trap for the 10 days before and after each forage sampling date were calculated as a measure of herbivore abundance. A PCA was conducted to determine uncorrelated forage quantity and quality attributes to include in herbivore abundance models. We selected total standing biomass and the dead:live forage index as measures of quantity. In contrast to the models above where annual production and proportion of live biomass were modelled, the attributes selected here are focused on what would attract large herbivores. As such, it is the total standing biomass at time of sampling versus annual production that would be more likely to influence herbivore abundance. Similarly, dead:live index was used instead of proportion of live biomass because it gives a better measure of the disparity between dead and live. Crude protein was significantly correlated with dead:live index ($p < 0.05$) so live forage moisture (significantly correlated with crude protein of live biomass but not dead:live index) was used alternatively along with aNDF of live biomass to represent forage quality. Region was included, and in the case of bovine camera trap records, reflects the difference in species, as cattle occur only at North Kimberley sites and water buffalo only at Arnhem Land sites. The best-supported bovine abundance model was used to test for significant interactions between region (representing bovine species) and all other significant variables to determine if cattle and water buffalo had different relationships with forage attributes in the model. The same was done for the best supported macropod abundance models to determine if there were any behavioural differences present between regions that may be related to the difference in dominant feral herbivore. The log of camera trap days was used as an offset in zero-inflated Poisson models to account for camera traps that malfunctioned during the 20 days surrounding forage measurements.

4.4 RESULTS

4.4.1 Herbivory and forage attributes

Dead, live and total standing herbaceous biomass and the proportion of live biomass were higher in protected than unprotected quadrats (Table 4.2; Fig. 4.4). Forage quality at the end of the dry season, as measured by forage moisture and fibre content of live and dead biomass, were best explained by the null model, showing no effect of herbivory. Mean estimates for aNDF content of live (71.0% ± 0.6 SE) and dead biomass (71.3% ± 0.5 SE) were high and almost identical by the end of the dry season while moisture contents of live (53.1% ± 1.2 SE) was still much greater than dead biomass (6.3% ± 0.9 SE). However, crude protein content of live biomass was higher in unprotected (7.4% ± 0.2 SE) than protected plots (7.0% ± 0.2 SE; Table 2; Fig. 4) while there was no effect of herbivory on crude protein content of dead biomass, which was much lower (3.0% ± 0.1 SE).

Table 4.2 Model fit of linear models comparing measures of forage quantity and quality in paired plots, protected and unprotected from herbivory, from 2015-2017 in the Uunguu IPA, North Kimberley, Western Australia and near Kolorbidahdah, Arnhem Land, Northern Territory. Models including plot protection were compared to the null model and only those models where the saturated model was the best-supported are shown.

Model	ΔAIC*c*[a]
Live herbaceous biomass ~ plot protection	105.8
Dead herbaceous biomass ~ plot protection	30.2
Total herbaceous biomass ~ plot protection	81.5
Proportion of live biomass ~ plot protection	18.3
Crude protein content of live biomass~ plot protection	14.5

[a]AIC*c* is the second order Akaike's Information Criterion for large and small sample sizes; ΔAIC*c* is the difference between the model's AIC*c* value and null model.

4.4.2 Environment and forage attributes

All measures of forage quantity and quality varied by fire season and savanna region with seasonality and site fertility occasionally associated (Table 4.3, Fig. 4.5). Burnt sites had the lowest annual production but the highest proportion of live biomass, with no distinction between early and late dry season fires (Table 4.3a, Fig. 4.5.a,e). Infertile sites in Arnhem Land had higher annual production than North Kimberley infertile sites, but fertile sites (all in the North Kimberley) had the highest overall annual production (Table 4.3a., Fig. 4.5b-c). Similarly, the proportion of live biomass was highest at Arnhem Land sites, and immediately following the wet season, declining throughout the dry season with changing climatic conditions (Table 4.3a, Fig. 4.5d,f). Fibre content of live biomass was lower in burnt and fertile sites than unburnt and infertile sites with no distinction between early and late dry season fires (Table 4.3b, Fig. 4.5g-h). However, sites with late dry season fires had the highest crude protein content of live biomass and unburnt sites had the lowest (Fig. 4.5j). The Arnhem Land sites were characterised by lower quality forage with higher fibre and lower crude protein content of live biomass than the North Kimberley sites (Fig. 4.5i,k).

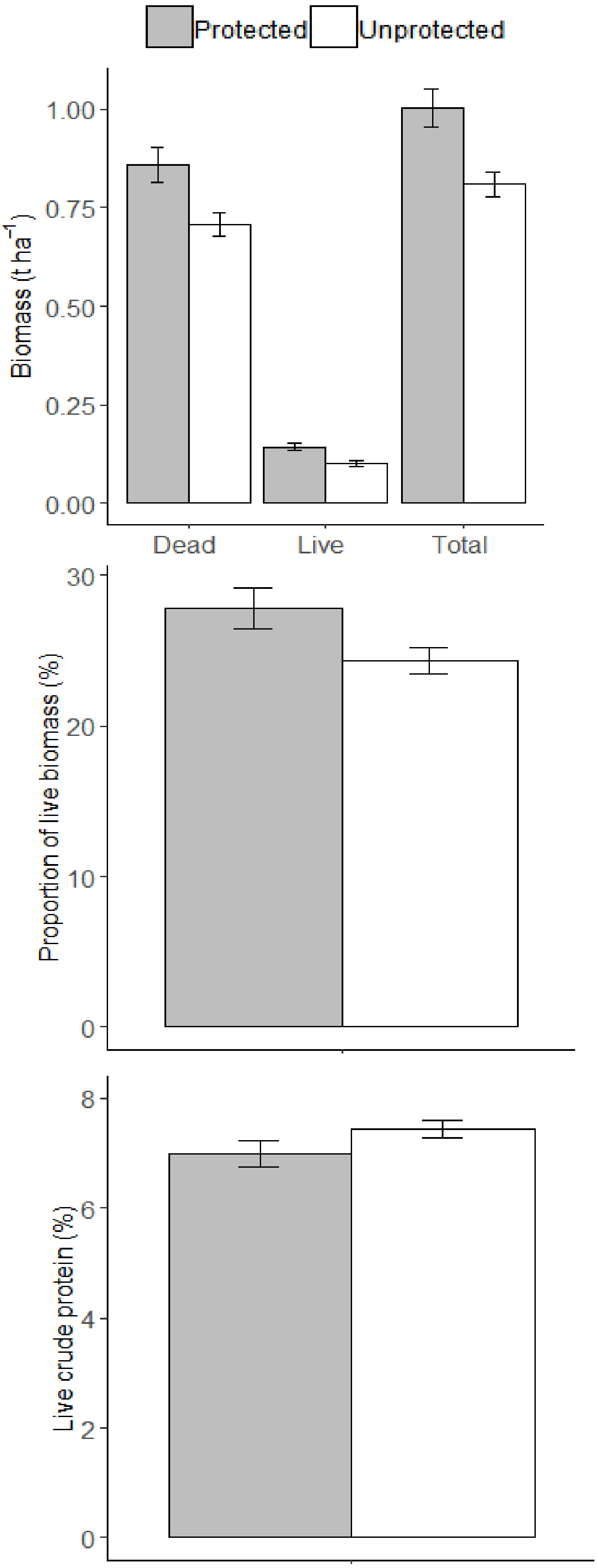

Figure 4.4 Predicted dead, live and total herbaceous biomass (t ha^{-1}), proportion of live biomass (%) and live crude protein content (%) ± standard error in quadrats protected (grey) and unprotected (white) from vertebrate herbivores across fertile and infertile savanna substrates in the Uunguu IPA, North Kimberley and Kolorbidahdah, Arnhem Land, Northern Territory.

Table 4.3 Model fit of liner models for forage and quality and generalized linear models for bovine and macropod abundance (wallaroo and agile wallaby) based on number of animals recorded by remote camera traps at 14 sites from 2015-2017 in the Uunguu IPA, North Kimberley, Western Australia and near Kolorbidahdah, Arnhem Land, Northern Territory. Independent variables that were significant ($p < 0.05$) in the best-supported model are denoted with bold text and only models < 4 ΔAIC*c* from the best-supported model are shown.

Model	ΔAIC*c*
a) Forage quantity	
Annual production	
Fire Season + **Fertility** + **Region**	0.00
TSF+ Fire Season + Fertility + Region	0.35
TSEWS + Fire Season + Fertility + Region	2.40
TSF + TSEWS + Fire Season + Fertility + Region	2.76
Proportion of live biomass	
TSEWS + **Fire Season** + **Region**	0.00
TSEWS + Fire Season + Fertility + Region	0.72
TSF + TSEWS + Fire Season + Region	1.59
TSF + TSEWS + Fire Season + Fertility + Region	2.60
b) Forage quality	
aNeutral Detergent Fibre (aNDF) of live biomass	
Fire Season + **Fertility** + **Region**	0.00
TSF + Fire Season + Fertility + Region	2.03
TSEWS + Fire Season+ Fertility + Region	2.23
Crude Protein of live biomass	
Fire Season + **Region**	0.00
TSF + Fire Season + Region	1.36
TSEWS + Fire Season + Region	1.93
Fire Season + Fertility + Region	2.11
Fire Season	2.56
TSF + TSEWS + Fire Season + Region	2.75
c) Herbivore abundance	
Bovine camera count	
Live aNDF + **Live moisture** + **Total standing biomass** + **Dead:live Index** + **Region**	0.00
Wallaroo camera count	
Live aNDF + **Live moisture** + **Total standing biomass** + **Dead:live Index** + **Region**	0.00
Live aNDF + Live moisture + Total standing biomass + Region	2.27
Live aNDF + Live moisture + Total standing biomass + Dead:live Index	3.06
Agile wallaby camera count	
Live aNDF + **Total standing biomass** + **Region**	0.00
Live aNDF + Live moisture + Total standing biomass + Region	3.13
Live aNDF + Total standing biomass	3.20

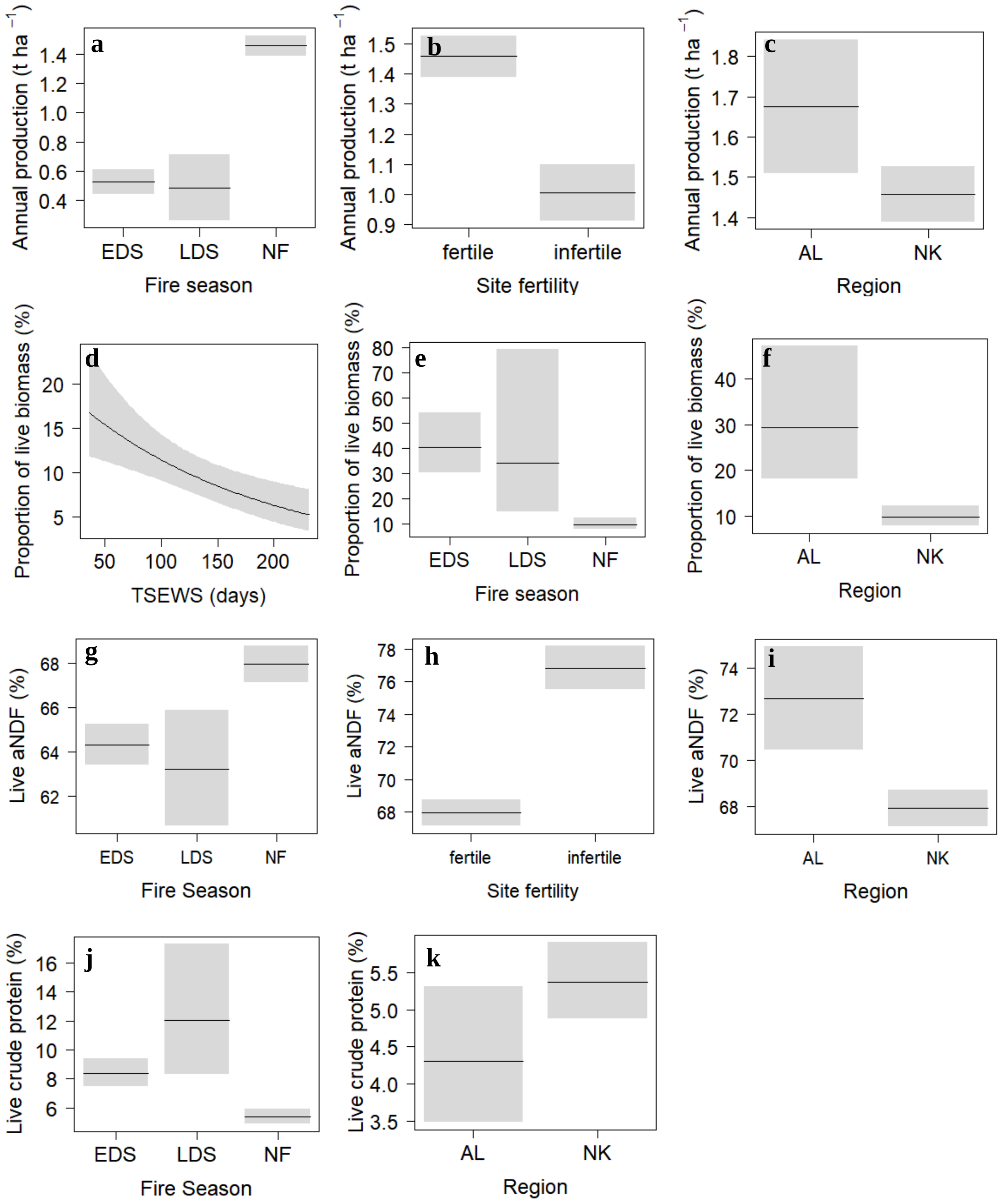

Figure 4.5 Predicted relationships for environmental correlates affecting measures of forage quantity and quality including annual forage production, proportion of live biomass, percent amylase neutral detergent fibre (aNDF) and percent crude protein (CP) in live biomass for forage plots in the Uunguu IPA, North Kimberley and Kolorbidahdah, Arnhem Land, Northern Territory. Plots show mean prediction and 95% confidence bands (shaded grey).

4.4.3 Large herbivore abundance and forage attributes

The influence of forage attributes on large herbivore abundance is complex, as indicated by the best-supported models for both bovine and wallaroo abundance including all predictor variables: fibre and moisture of live biomass; total standing biomass; dead:live index; and region (Table 4.3c, Fig. 4.6). The number of bovines (cattle at the North Kimberley sites and water buffalo at the Arnhem Land sites) was highest at sites with forage of low fibre content, low standing biomass and high forage moisture (correlated with crude protein), all attributes of forage burnt in the dry season (Fig. 4.6a-c). There was also a positive relationship with dead:live index which could relate to patchily burnt areas with remaining dead forage or unburnt areas with bulk forage (Fig. 4.6d). Bovine abundance was higher at Arnhem Land sites (Fig. 4.6e). We introduced an interaction term to the best-supported model for bovine abundance between region (which represents the difference in bovine species) and all other predictor variables. None of the introduced interaction terms improved model fit or were significant in the model suggesting that water buffalo and cattle have similar relationships to the forage attributes tested.

Similar to bovines although with weaker relationships, wallaroo abundance was higher in areas with low fibre, high moisture content of live biomass and at Arnhem Land sites but in contrast, wallaroos were associated with higher total standing biomass and negatively related to dead:live index (Table 4.3c, Fig. 4.6f-j). However, when interaction terms between region and all other variables in the best-supported model were introduced, an interaction between region and total standing biomass improved the model by 10.9 AIC units showing wallaroos at Arnhem Land sites to be more abundant in areas with low standing biomass and wallaroos at the North Kimberley sites more abundant in areas with high standing biomass (Fig. 4.7). Agile wallaby abundance was best described by a single variable, total standing biomass, with higher abundance at sites with greater total biomass, consistent with wallaroos at the North Kimberley sites. However, in contrast to both bovines and wallaroos, agile wallabies were more abundant at the North Kimberley sites.

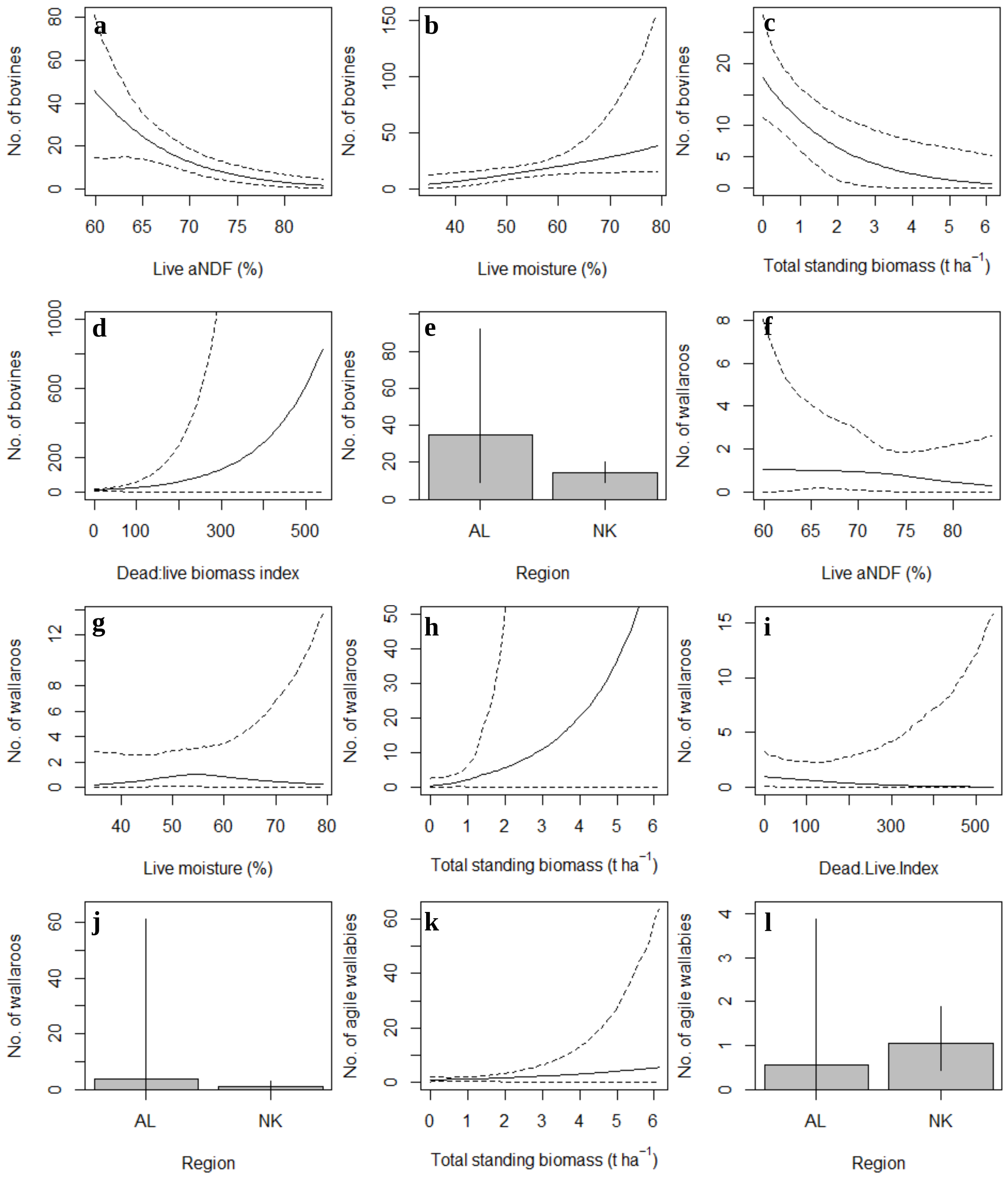

Figure 6. Predicted relationships for forage attributes affecting abundance of bovines (cattle on the Uunguu IPA and water buffalo in Arnhem Land), wallaroos, and agile wallabies based on number of animals recorded by remote camera traps in the Uunguu IPA, North Kimberley and Kolorbidahdah, Arnhem Land, Northern Territory. Plots show predicted relationship (solid line) and 95% confidence interval generated by bootstrapping (dashed lines).

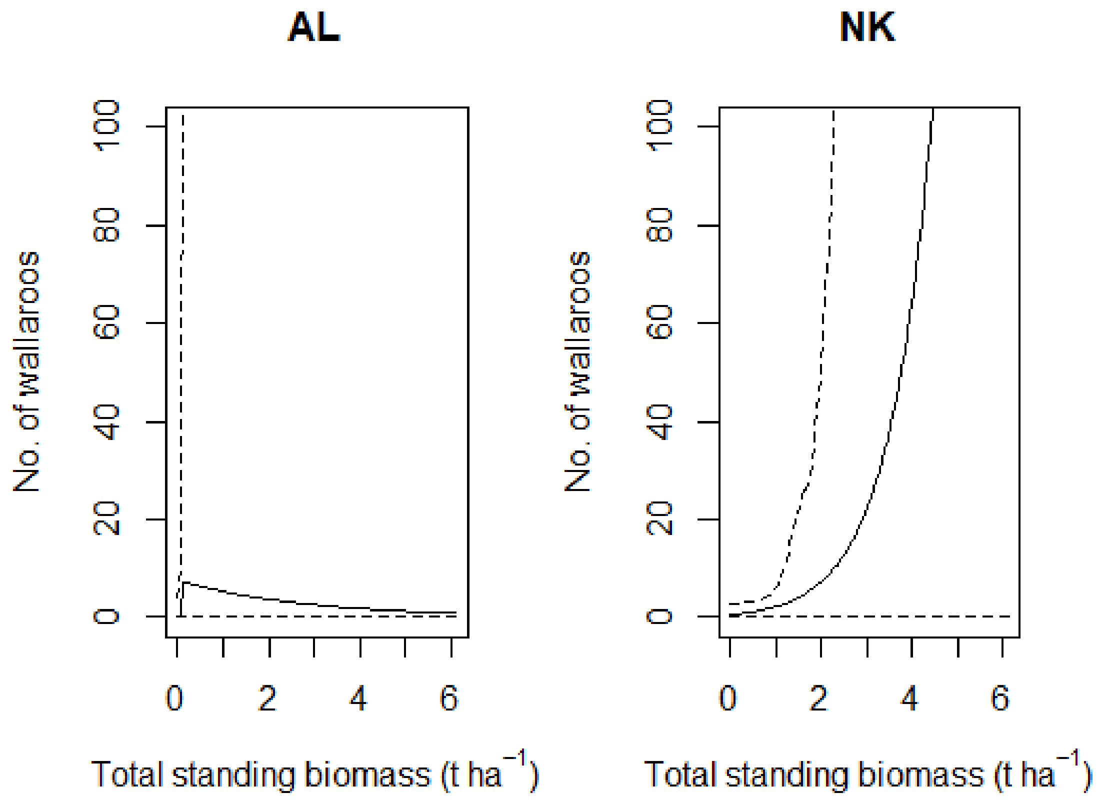

Figure 4.7 Predicted relationship between wallaroo abundance and total standing biomass in in the Uunguu IPA, North Kimberley (NK) and Kolorbidahdah, Arnhem Land, Northern Territory (AL). Plots show predicted relationship (solid line) and 95% confidence interval generated by bootstrapping (dashed lines).

4.5 DISCUSSION

Despite Australian savannas having relatively low herbivore biomass, large herbivores significantly impacted forage quantity (negatively) and quality (positively). Fluctuations in forage quantity and quality were closely related to fire activity but forage attributes did not entirely account for herbivore abundance. Forage quality was higher on recently burnt areas, with post-burn regrowth being lower in fibre and higher in crude protein than unburnt sites. The highest crude protein content of live biomass was found at sites following late dry season fires. This highlights the importance of maintaining temporally heterogeneous fire regimes under appropriate moisture conditions to provide high-quality green pick throughout the dry season, most likely similar to pre-European fire regimes in Australian tropical savannas (Lewis, 1985; Bowman *et al*., 2001). Field sites in Arnhem Land had lower measures of overall forage quality (lower crude protein and higher fibre contents of live biomass) but supported more introduced bovines and wallaroos than sites in the North Kimberley. One possible explanation is that water buffalo and feral cattle may exert different levels of competitive pressure on native herbivores. Our results suggest that pyricherbivory strongly influences the feeding behaviour of feral herbivores and some native herbivores in northern Australian savannas, like in savannas elsewhere in the tropics.

Grazing by herbivores, even at low densities, significantly reduced herbaceous biomass and increased crude protein content of live biomass. Grazing of tropical tussock grasses by bovines during the early wet season reduces grass productivity, only partially compensating for plant tissue lost to herbivory (Ash and McIvor, 1998a). Hence, the differences detected at the end of dry season could be a residual effect of grazing earlier in the year as well as differential grazing pressure during the dry season relating to fire activity (Fuhlendorf and Engle, 2004). The crude protein content of live biomass was greater in grazed quadrats, consistent with other studies where nutrient uptake by roots in grazed grasses was higher (Chaneton *et al*., 1996; Mbatha and Ward, 2010), but fibre content was unaffected by herbivory.

Recent fires reduced overall forage availability but improved the quality of forage (via resprouting). Resprouting grasses had lower fibre content, which is inversely related to forage intake (Freudenberger and Hume, 1992), and higher crude protein content, which is required daily for maintenance, lactation, growth and reproduction. These results represent the mechanism underpinning pyricherbivory and align with previous research showing the increased quality of forage post-fire (Murphy and Bowman, 2007b; Allred *et al*., 2011a; Powell *et al*., 2018). An undesirably high fibre content of live herbaceous biomass has been linked to the shift away from consumption of grasses, to forbs and/or browse, by both wallaroos and feral cattle (Reid *et al*., in press), highlighting the importance of fire in prolonging the availability of preferred forage for herbivores. Desirable high-protein grass has been linked to high densities of the common wallaroo (Taylor, 1984) and crude protein content was found to be highest in regrowth following late dry season fires suggesting a disproportionate importance of late dry season fires for providing high-quality forage on an otherwise dry and cured vegetative landscape. However, late dry season fires represented a small portion of data in this study and post-fire regrowth after late season fires is highly dependent on moisture conditions at the time of and following the fire so there is a need for further investigation regarding late dry season post-fire regrowth.

Our results show that the abundance of introduced bovines (water buffalo and feral cattle) is associated with low forage quantity (i.e. grass biomass) but high forage quality (i.e. low fibre content, high moisture content (correlated with crude protein content). These attributes are characteristic of recently burnt areas. In contrast, macropods were generally associated with the opposite forage quantity attributes (i.e. high quantity) and similar forage quality attributes but with much weaker relationships. These findings support a recent landscape-scale analysis of the distribution of feral cattle and macropods in the North Kimberley, that showed that cattle are more abundant in recently burnt areas and large macropods are more abundant in unburnt areas (Reid *et al.*, 2019a). These findings suggest that pyricherbivory applies to introduced bovines but not necessarily native macropods and aligns with previous research showing fire-focused grazing by bovines (Archibald and Bond, 2004; Fuhlendorf and Engle, 2004; Allred *et al.*, 2011a; Allred *et al.*, 2011b) and ungulates more broadly (Wilsey, 1996; Archibald *et al.*, 2005; Kimuyu *et al.*, 2017) in North American and African savannas. However, our findings appear to run counter to previous research and traditional Aboriginal knowledge regarding macropods in the tropics which suggests that they exhibit focal grazing in recently burnt areas (Bowman *et al.*, 2001; Bowman and Vigilante, 2001; Yibarbuk *et al.*, 2001; Murphy and Bowman, 2007b; Telfer *et al.*, 2008).

Upon closer examination, we found that the positive relationship between wallaroos and standing biomass was limited to the North Kimberley field sites, and wallaroos at Arnhem Land field sites may be more abundant in areas with less standing biomass, characteristic of burnt sites. Reasons for the lower wallaroo abundance and unexpected relationship with standing biomass in the North Kimberley may be due to differences in the dominant feral herbivore and fire activity. While both cattle and water buffalo have greater dietary flexibility in response to low-quality forage than native herbivores, the mean proportion of grass in the diet of cattle is greater (Bowman *et al.*, 2010b; Reid *et al.*, in press). Alternatively, wallaroos are dependent on high-quality forage and at times consume exclusively grass (Ellis *et al.*, 1977; Croft, 1987; Telfer and Bowman, 2006; Murphy *et al.*, 2007; Reid *et al.*, in press). Therefore, it is possible that wallaroos are experiencing greater competition for preferred resources in the North Kimberley against feral cattle than water buffalo in Arnhem Land.

During this study, Arnhem Land field sites were characterised by a finer-scale fire mosaic and a more even distribution of fire throughout the dry season, with more fire in the late dry season than the North Kimberley field sites. A more even distribution of fire could be responsible for providing a constant source of forage to wallaroos throughout the dry season. Similarly, the agile wallaby was more abundant in the North Kimberley and its diet as a mixed feeder (Stirrat, 2002; Reid *et al*., in press) aligns more closely with that of the water buffalo and thus potentially experiences more competition for food resources in Arnhem Land. The positive relationship between agile wallaby and standing biomass was independent of region and likely related to their association with wetter habitats (Menkhorst and Knight, 2001). Large macropod abundance is unlikely to be related to dingo abundance in this case, as it was similar at both sites and macropod abundance did not reflect an overall tendency favouring one region or the other (wallaroos were more abundant at Arnhem Land sites and agile wallaby more abundant at North Kimberley sites).

Competition between introduced and native herbivores means that native macropods may be forced to rely, to a greater extent than in the past, upon sub-optimal food resources. Wallaroo abundance in relation to recent fire at field sites in the North Kimberley was found to be related to savanna substrate fertility with wallaroos more abundant on unburnt fertile sites and infertile burnt sites (Reid *et al*., 2019a) possibly reflecting the ability of small-mouthed, selective feeding macropods to better utilise the limited green pick on infertile savannas. In contrast, fertile sites with a greater flush of post-fire vegetation may be dominated by bulk-feeding bovines. Our results show that wallaroo abundance was highest when the proportion of live biomass was higher or equal to dead biomass, suggesting that live biomass must be present in a high proportion in the vegetation matrix even when the live biomass represents more mature live forage of lower quality than post-fire green pick. Alternatively, bovine abundance was high in burnt areas with a high proportion of dead to live biomass likely reflecting patchily burnt sites. Because cattle and water buffalo are large bulk feeders, they cannot survive on small amounts of green pick alone and would benefit from access to areas that have both highly nutritious green pick and bulk dry forage, reflective of the style of burning practised by Australian pastoralists who burn earlier in the dry season to achieve patchier fire mosaics (Lewis, 1985). Similarly, Wilsey (1996) suggested that larger ungulate species in Africa try to maximize energy intake by feeding on both burned sites with low quantity but high-quality forage and unburned sites with high forage biomass but poor quality.

Abundance of introduced bovines and large macropods, wallaroos specifically, is affected by a contrasting set of forage attributes characteristic of burnt areas for bovines and unburnt areas for macropods. Competition for limited high-quality food resources may be altering feeding behaviour of native herbivores, especially when introduced herbivores have similar food preferences. Fire activity that is spread throughout the dry season (rather than concentrated at the start) is be important for providing continual access to low-fibre, high-protein forage for macropods, and late dry season fires, under appropriate weather and moisture conditions, may be of greater relative importance. These findings contribute to our understanding of the underlying ecological principles of traditional Aboriginal burning/patch mosaic burning, provide insights into whether fire management can sustain high-quality forage throughout the dry season and reflect upon the pyricherbivory conceptual models and its applicability to Australian savannas.

Chapter 5

General discussion and conclusions

5.1 SYNTHESIS

My research has filled a series of knowledge gaps regarding feral and native large herbivores in the tropical savannas of northern Australia. These include the drivers of the distribution and spatial interactions and dietary breadth of feral cattle and large macropods and drivers of key forage attributes in the Uunguu IPA (North Kimberley bioregion, Western Australia) and Arnhem Land (Northern Territory). Previous work has focused primarily on impacts of managed cattle herds (e.g. on pastoral land) on native species. There has been a notable lack of research on the impacts of unmanaged, feral populations of cattle. Similarly, there has been a lack of research on the impact of livestock on the larger macropods despite anecdotal evidence of declines in the northern savannas. My research adds important knowledge and raises questions to guide ongoing research regarding the interaction of introduced and native herbivores in the northern savannas.

Feral species dominate the herbivore assemblages of northern Australia, with potential negative implications for native species. Biomass of feral cattle was much greater than biomass of large macropods across the Uunguu IPA (Ch 2), similar to the pattern found during earlier work in Arnhem Land by Koenig *et al*. (2003). During an aerial survey in 2000, they noted that 78% of herbivore sightings were of water buffalo with native large macropods making up less than 8%. Additionally, feral herbivores were concentrated in recently burnt areas and along waterways, representing high quality foraging areas (Ch2; Bayliss and Yeomans, 1989b; Koenig *et al*., 2003), while native macropods were unexpectedly associated with less fertile, unburnt areas (Ch 2 & 4). Native macropod concentration on poorer quality habitat and a negative association between large macropods and feral cattle, demonstrated by joint species distribution modelling and activity budget analyses (Ch2), suggests that both exploitation (the reduction of resources) and interference (exclusion from access to resources) competition may be occurring (Petren and Case, 1996; Amarasekare, 2002). When competing herbivores use the same resource (herbaceous forage), the inferior competitor may be forced to change activity patterns (Chesson, 2000), a form of interference competition, as seen by the contrasting periods of activity between feral cattle and wallaroos (Ch 2). Additionally, there may be little 'top-down' control (i.e. due to predation) of the new dominant herbivores as dingoes avoided cattle (Ch 2). Hence, macropods may be experiencing competition for forage resources but the same level of predation because adult cattle are not an alternative prey source for dingoes. Although, local pastoralists bait for dingoes, as they claim dingoes kill calves, this predation is likely limited to calving season.

The dominance of feral herbivores across the landscape can be explained, in part, by higher dietary flexibility amid fluctuating forage conditions. Feral cattle had the greatest dietary breadth compared to large macropods (Ch 3), similar to water buffalo in Arnhem Land (Bowman *et al*., 2010b). Feral herbivores are thought to have a similar diet to extinct megaherbivores and may therefore be filling a vacant ecological niche (Bowman *et al*., 2010b) demonstrating that the ecosystem can sustain large-bodied mixed feeders. However, my results still suggest competition between native and introduced herbivores as grass may be the preferred food, especially for cattle, and a move to other resources was triggered in both cattle and wallaroos, to a lesser extent, by reduced forage quality, specifically high dietary fibre of live herbaceous biomass. Wallaroos appear to be more affected by lack of high-quality grass than agile wallabies, known to utilise a wider variety of food resources (Stirrat, 2002).

Forage quantity and quality were largely influenced by fire activity, but pyricherbivory incompletely described herbivore abundance (Ch 4). Dry season fires reduced the overall quantity but greatly improved the quality of available forage by reducing fibre content (inversely related to intake) and increasing crude protein content (necessary for daily maintenance, growth and reproduction) in live biomass. The highest crude protein content was found in green pick emerging after late dry season fires, suggesting fires at this time of year might be necessary for maintaining body condition in obligate grazing species such as the antilopine wallaroo, especially given that grass other than post-fire regrowth would have lower crude protein content at this time of year. Forage quality was higher at sites in the North Kimberley on both fertile and infertile substrates, but abundance of feral herbivores and wallaroos was highest at Arnhem Land field sites. Abundance data confirmed that feral bovine herbivores were associated with recently burnt areas that have forage attributes characterised by low biomass, high protein and low fibre while macropods were associated with areas of poorer quality forage (Ch 4). Pyricherbivory explained the feeding behaviour of bovine herbivores but not large macropods in contrast to previous research and Traditional Ecological Knowledge (Lewis, 1989; Saint and Russell-Smith, 1997; Bowman *et al*., 2001; Yibarbuk *et al*., 2001; Murphy and Bowman, 2007b; Telfer *et al*., 2008). The unexpected association between wallaroo abundance and increased standing herbaceous biomass at North Kimberley but not Arnhem Land field sites led to a consideration of the major differences between the regions, the dominant feral herbivore and fire regime. Browsers were more likely to go extinct amongst the suite of marsupial megafauna (Bowman et al., 2010b) suggesting that introduced herbivores that fill that niche might have lower competitive pressure on extant herbivores. Although water buffalo and cattle are both considered bulk-feeding grazers, water buffalo consume a lower overall proportion of grasses (Fig 3.8) likely leading to reduced competition with large macropods for green pick. Additionally, the high density of feral herbivores on the landscape compared to the extinct megafauna may increase the level of competition.

In recent times, Arnhem Land, and Korlobidahdah in particular, has experienced a continuity of stewardship by Traditional Owners unseen in the majority of the North Kimberley. As it relates to this project, that means smaller-scale fires lit with a more even distribution across the dry season. More mid- and late dry season fires in Arnhem Land result in a higher proportion of the landscape with available green pick towards the end of the dry season when high-quality forage is otherwise most scare (Fig. 5.1). However, when fires are temporally constrained to the early dry season, as is common in areas participating in carbon credit programs that provide an economic incentive to burn early in the dry season thus minimising carbon emissions, a less constant supply of green pick is produced. Importantly, traditional patch burning isn't ubiquitously applied across Arnhem Land, most of central and western Arnhem Land is unoccupied and unmanaged (Yibarbuk *et al.*, 2001) and contemporary savanna burning methodology originated in western Arnhem Land due to concerns from Traditional Owners regarding devastating fires in inaccessible areas, which is analogous to the situation in the North Kimberley where people were displaced from more distant country.

A fire regime dominated by early dry season fires produces green pick for the first portion of the dry season but then does not provide any additional resources towards the end of the dry season. Currently, carbon credit programs use the date of 1 August to distinguish between early dry season and late dry season fires providing economic incentive to have an early dry season dominated fire regime. It is important to differentiate between mid- and late dry season fires set under appropriate moisture conditions that will produce green pick and large uncontrolled, high-severity wildfires that may not. While carbon credit programs have had an overall benefit to areas that in pre-program years were dominated by late dry season wildfires, an arbitrary date that does not incorporate natural variability may have led to unforeseen negative impacts. Fine-grained mosaics have been linked to large macropod abundance in more arid systems (Codding *et al.*, 2014) but it is important to recognize that there are many constraints including monetary and time constraints to setting small-scale mosaic fires when Traditional Owners live off-country (e.g. in the North Kimberley) *versus* living on-country in outstations (e.g. in Arnhem Land), where burning is part of day to day life. Additionally, government policy and legislation limit the ability to burn in the mid- and late dry season. Obtaining permits to burn under the *Bush Fires Act 1954* (WA), for example, becomes increasingly difficult after June and fire weather warnings become more prevalent once 100% curing of herbaceous biomass occurs. Aboriginal people with Native Title and customary rights to burn must still comply with local government oversight. Lastly, there are issues of insurance and liability if fires impact neighbours or other interest holders. Groups that are more remote are less affected by some of these factors, but Traditional Owners in Arnhem Land must still contend with some of these constraints including the *Bushfires Management Act 2016* (NT). Results from this study suggest that pyrodiversity may be positively influencing large macropod abundance but the role of a spatially and temporally heterogenous fire regime in mitigating competition between introduced and native herbivores warrants further investigation.

Savanna systems are inherently dynamic on both an intra- and interannual basis and because some of the processes that maintain savannas, fire and herbivory, are unevenly applied across the landscape it limits the conclusions that can be definitively drawn after a short-term study. However, the Kimberley and Arnhem Land provide important regional ‘replication’ of pattern and process as they are similar but not the identical, especially with respect to climate and fire. This provides some confidence in any broad inference from a short-term study. Additionally, using both traditional methods (aerial and road transects) and new methods (remote camera trapping) emergent patterns were evident, though ongoing data collection to incorporate more natural variation is important. It was also determined during this study that methods of aerial and road surveys that have been used to estimate macropod populations in the past, may no longer be ideal once densities are low, making it important to utilise a suite of methods over multiple scales. The use of camera traps, though time-consuming to process the data, provided a much finer-scale resolution of both herbivore activity and relative abundance. Lastly, the complexity of relationships addressed in this project between introduced and native herbivores, forage and fire and to a much lesser degree, predator-prey interactions, are nearly impossible to tease apart in a large-scale natural experiment. This is especially true when there have been recent changes to the historical fire regime, suite of herbivores and predators and a changing climate. It is within these constraints, that I developed a conceptual model of relationships between native and introduced large herbivores, fire and forage (Fig. 5.1) to guide future targeted research.

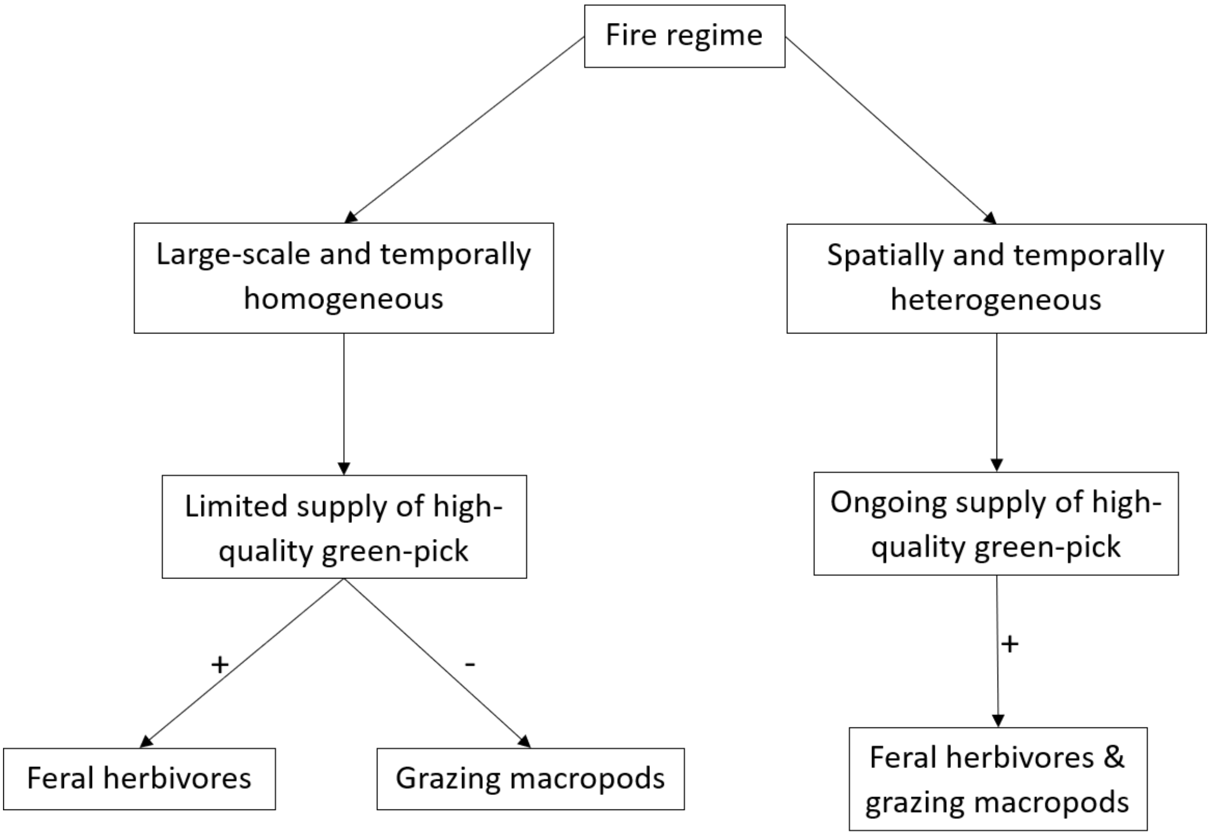

Figure 5.1 Simplified conceptual model of hypothesized relationships between fire, forage and large introduced and native herbivores in the tropical savannas of northern Australia.

5.2 TRADITIONAL ECOLOGICAL KNOWLEDGE

Traditional Ecological Knowledge (TEK) was relied on heavily throughout this study to provide baseline information about habitat and wildlife abundance on traditional lands. Specifically, Traditional Owners were first to notice declines of native herbivore species and provided knowledge regarding areas of past macropod abundance which aided in locating appropriate areas to monitor the target species. Additionally, concerns from Traditional Owners in the Kimberley relating to feral cattle impacts, fire management and native species (Wunambal Gaambera Aboriginal Corporation, 2010) played a large role in initiating this project to answer key questions and fill information gaps. This project represents some of the first research on feral cattle in Australian tropical savannas. Traditional Owners have played a major role in past research aimed at understanding the nexus between fire and macropods as well (Bowman et al., 2001; Telfer et al., 2008). Indigenous ranger groups and Traditional Owners provide an immeasurable resource when it comes to knowledge of local flora, fauna and ecosystem processes such as fire, including recent changes. In fact, in remote areas with limited basic or long-term ecological information, a local community with a long history of resource utilization may be the only source of information on changing environmental conditions (Johannes *et al*., 2000). Lewis (1989) summarises prior research regarding Aboriginal fire management in the northern savannas as “derived from understandings of how fires influence the distribution and relative abundance of plant and animal resources.” This is the fundamental basis of pyroherbivory and pyrodiversity and it is important to credit such knowledge and understanding appropriately. Though TEK has not always been fully utilised in the past, there is growing recognition of its importance and the need to incorporate it into official natural resource management policy (Horstman and Wightman, 2001). Using TEK in concert with scientific methodology to provide both the ecological context and data is essential for contemporary research. To better integrate TEK and western science, the first step of all future research projects should be consultation with the relevant Traditional Owners.

5.3 FUTURE RESEARCH

As with all research, my study culminates with more questions than answers. Though it has provided critical information about the nexus between forage, fire and herbivory in the tropical savannas of northern Australia, particularly the relationship between introduced and native herbivores, it also highlights several avenues of future research. The apparent importance of mid- to late dry season fires, under appropriate conditions, needs to be further investigated as there were few late dry season fires included in this study. Further, the implications of current carbon credit programs with rigid cut-off dates distinguishing early and late dry season fires, applied across all of northern Australia's monsoon tropics, need to be explored. Though these programs as a whole have been beneficial to the North Kimberley by reducing high-intensity late dry season wildfires (Vigilante, 2001; Legge *et al*., 2015), in areas such as Arnhem Land with a more diverse fire regime, the program encourages an early dry season dominated fire regime, and thus may reduce heterogeneity of the fire regime. New models utilising fire severity, as indicated by relative scorch height, are currently being developed and will replace the use of 1 August differentiating early and late dry season fire (Andrew Edwards, pers. comm.). This would allow for the application of low-severity fires in the late dry season when conditions permit. A suite of constraints currently limit the ability to apply a full range of fire to the landscape including economic, time, government oversight and insurance even though traditional fire regimes were quite diverse (Vigilante, 2001; Yibarbuk *et al*., 2001), reinforcing the need for further research on managed late dry season fires.

My research only tangentially touched on predation of herbivores with the use of joint species distribution modelling which suggested that adult cattle were not an alternate prey source for dingoes during the dry season (Ch 2). Instead, dingoes were most closely associated with the agile wallaby, the smallest species and likely the most common prey out of the macropods studied. The wallaroo group (antilopine and common) was uncorrelated with dingo abundance, yet these two species may have different predation risk. The common wallaroo may escape predation due to their superior ability to move across rocky terrain (Croft, 1987) while the antilopine wallaroo, similar to the agile wallaby, is more dependent on water, where predators focus hunting, thus incurring a higher predation risk. There is a need to undertake more specific research on predation risk on each macropod species as well as investigation of whether predation accounts, in part, for the higher abundance of macropods at sites in Arnhem Land than the North Kimberley, though similar regional dingo abundance estimates from camera traps found in my study suggest it does not.

Large macropods living in more rugged habitats may have a lower predation risk and may also incur a lesser likelihood of competition with introduced herbivores. Landscape-scale macropod distribution on the Uunguu IPA was skewed towards the western block, containing large amounts of rugged terrain, where cattle are unlikely to inhabit (Ch 2). It is due to this ruggedness that this study was unable to incorporate ground-based methods (road surveys and remote camera traps) to confirm a higher site-scale macropod abundance. The further study of macropod abundance in more rugged terrain is necessary as it may be acting as a refuge against predation and competition for species such as the common wallaroo and a barrier to migration of large feral herbivores.

The potential causes of population decline are especially relevant to one species, the antilopine wallaroo. It was definitively recorded only once during either the road surveys or remote-camera trapping. This species is possibly the most sensitive to environmental changes related to introduced herbivores, increased predation and lack of late dry season fire. The antilopine wallaroo inhabits plains and hills, not rocky areas like the common wallaroo (Menkhorst and Knight, 2001), putting them in direct competition for grassy forage with introduced herbivores. Habitats near rocky escarpments are also higher in plant species richness and productivity, providing greater food resources for the common wallaroo than habitats of the antilopine wallaroo (Freeland *et al*., 1988). The antilopine wallaroo is also more water-dependent, putting it at a higher risk of predation by dingoes. Lastly, the antilopine wallaroo is the most dependent of all the large macropods on grass (Croft, 1987; Murphy *et al*., 2007) and a lack of late dry season fire may eliminate an important nutrient influx during the end of the dry season. This study was unable to separate the abundance and distribution patterns of antilopine and common wallaroos, as the two species were indistinguishable in black and white night-time photographs, therefore any further research on this species done with camera trapping should utilise white-flash remote cameras that allow for night-time colour photography. Results from this study have triggered targeted monitoring of this species on the Uunguu IPA to better evaluate its abundance and distribution (Tom Vigilante, pers. comm.). Previous research (Ritchie, 2007) and accounts from Traditional Owners (White *et al*., 2009) have called attention to likely declines of the antilopine wallaroo and this study supports this assertion with a further recommendation to evaluate the abundance and distribution of this species across its range to confirm the status and bring attention to the native herbivores that have largely gone unstudied in relation to contemporary changes in fire regimes and introduced feral species.

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Appendices

Appendix A

The diversity, basal area (BA) and canopy cover of tree layer at these sites was described adapting the point-centred quarter method of Cottam and Curtis (1956). We sampled 6 points spaced 30 m apart on a 180m transects where we recorded the distance to the closest tree ≥ 4cm diameter at breast height (DBH) in each of 4 quadrants, DBH, species identity, tree canopy cover length and width, and height. Vegetation structure was classified according to Specht (1970) by converting canopy area to leaf projected area by 50% (Walker and Hopkins 1990).

Site ID	Geology[a]	Fertility	Vegetation class[b]	Specht classification[c]	Tree density (stems ha^{-1})	% *Eucalyptus* stems	Total BA (m^2 ha^{-1})	% *Eucalyptus* BA	Species count	*Eucalyptus* species count	Mean tree height (m)	% Foliage Cover	Distance to perennial water (km)[d]	Distance to non-perennial water (km)[d]
Yalgi 1-5	Carson Volcanics	Fertile	EWMF	low open-woodland	147	29	2.5	46	7	4	7.3	6	2.8	0.8
Yalgi 6-10	Carson Volcanics	Fertile	EWMF	low woodland	490	25	8.0	16	5	1	6.3	21	0.7	0.1
Lone Dingo 1-5	Carson Volcanics	Fertile	EWF	low-open forest	280	79	7.6	84	4	2	9.1	41	1.9	0.1
Lone Dingo 6-10	Carson Volcanics	Fertile	EWF	open-forest	245	96	5.0	98	6	5	11.3	46	3.2	0.3
Monger 1-5	Carson Volcanics	Fertile	EWF	low woodland	192	75	4.9	73	4	2	9.0	18	0.9	0.1
Monger 6-10	Carson Volcanics	Fertile	EWF	low open-woodland	183	42	2.2	49	8	2	7.6	8	1.2	0.5
Monger 11-15	Carson Volcanics	Fertile	EWF	low woodland	165	71	3.6	96	5	3	8.5	15	2.7	0.2
Wobinbeyi 1-5	King Leopold Sandstone	Infertile	EWMI	low woodland	205	79	6.9	92	7	3	8.2	25	1.8	0.3
Wobinbeyi 6-10	Colluvium/Alluvium	Infertile	EWMI	low woodland	356	29	2.3	26	7	2	7.4	18	1.2	0.3
Pauline Creek 1-5	Colluvium/Alluvium	Infertile	EWH	woodland	144	88	4.1	97	5	2	10.5	20	2.9	0.7
Pauline Creek 6-10	King Leopold Sandstone	Infertile	EWH	low woodland	204	71	5.5	91	8	4	9.0	24	5.3	0.5

[a] Department of Mines and Petroleum 2010

[b] Adapted from Carbon Credits (Carbon Farming Initiative—Emissions Abatement through Savanna Fire Management) Methodology Determination 2015 (Austl.).

[c] Specht 1970

[d] Department of Land Administration, Western Australia 2003

Site descriptions

Yalgi 1-5

The site is on gently undulating basalt plains with laterite soils. The vegetation was low (7.3m) open-woodland (6 % foliage cover). The tree layer was dominated by *Eucalyptus* spp. (*E. tectifica, E. tetrodonta, E. confertifolia*), and *Corymbia* spp. (*C. latifolia, Corymbia* sp.) that combined accounted for 46% of the 2.5 m^2 ha^{-1} site basal area. Fan palms (*Livistona eastonii)* and broadleaf tree species (*Planchonia careya, Grevillea mimosoides)* made up the remainder of the tree layer. The herbaceous layer was dominated by tall tropical perennial grasses *Sorghum plumosum, Themeda australis* and *Sehima nervosa*. The site was burnt 3 times from 2014-2017 in the early to mid-dry season (May-July).

Yalgi 6-10

The site is on basalt hills and lowlands with laterite soils near an ephemeral watercourse. The vegetation was low (6.3m) woodland (21% foliage cover) dominated by the fan palm *L. eastonii* and *E. confertiflora,* with subdominant broadleaf tree species (*Erythrophleum chlorostachys, Terminalia canescens).* Although the site had a comparatively high total basal area (8.0 m^2 ha^{-1}) it had the lowest proportion of eucalypts (16%). The herbaceous layer was dominated by tall tropical perennial grasses *S. plumosum*, *S. nervosa*, *Heteropogon contortus* and *Mnesithea rottboelliodes.* The site partially burnt in 2014 and fully burnt every year from 2015-2017 in the dry season (May-October).

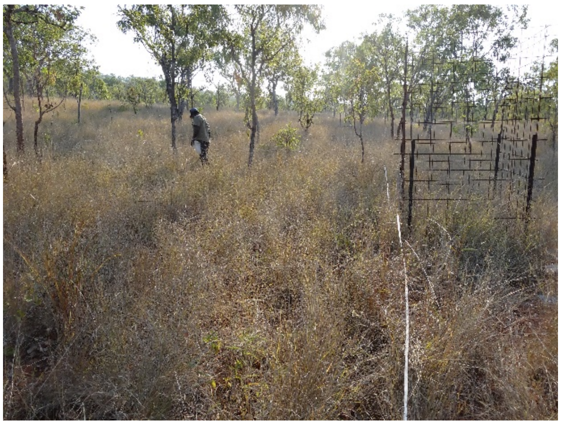
Lone Dingo 1-5

The site is on hilly basalt country near an ephemeral watercourse. The vegetation was low (9.1m) open-forest (41% foliage cover) dominated by *Eucalyptus* and *Corymbia* spp. (*E. tectifica, E. tetrodonta, C. latifolia)* accounting for 84% of total basal area (7.6 m^2 ha^{-1}), with subdominant broadleaf tree species (*P. careya, Antidesma ghaesembilla*). The herbaceous layer was dominated by tall tropical perennial grasses *T. australis, S. plumosum, S. nervosa and H. contortus*. The site burnt 2 times from 2014-2017 in the mid- and late dry season (July-November).

Lone Dingo 6-10

The site is on hilly basalt country with open-forest (11.3m tall, 46% foliage cover) vegetation dominated by *Eucalyptus* and *Corymbia* spp. (*E. miniata, E. confertiflora, E. tectifica, E. tetrodonta, C. latifolia, C. nesophila)* accounting for 98% of the 5.0 m^2 ha^{-1} basal area, with subdominant broadleaf tree species (*P. careya*). It has the highest foliage cover of all the sites. The herbaceous layer was dominated by tall tropical perennial grasses *H. contortus, T. australis, S. plumosum, S.* nervosa and *M. rottboelliodes*. The site burnt 2 times from 2014-2017 in the early to mid-dry season (May-July).

Monger Creek 1-5



The site is on hilly basalt country with low (9.0m) woodland (18% foliage cover) vegetation dominated by *Eucalyptus* and *Corymbia* spp. (*E. tectifica, C. latifolia)* accounting for 73% of total basal area (4.9 m^2 ha^{-1}), with subdominant broadleaf tree species (*T. canescens*, *Gardenia* sp.) The herbaceous layer was dominated by tall tropical perennial grasses *S. plumosum* and *S. nervosa*. The site burnt 3 times from 2014-2017 in the early dry season (May-June).

Monger Creek 6-10

The site is on hilly basalt country near an ephemeral watercourse. The vegetation was low (7.6m) open-woodland (8% foliage cover) dominated by *Eucalyptus* and *Corymbia* spp. (*E. tectifica, C. latifolia)* accounting for 49% of total basal area (2.2 m^2 ha^{-1}), with subdominant broadleaf tree species (*G. mimosoides*, *Chochlospermum fraseri*, *T. canescens*, *E. chlorostachys*, *Gardenia* sp., *Acacia* sp.). The herbaceous layer was dominated by tall tropical perennial grasses *S. nervosa*, *S. plumosum*, *Chrysopogon fallax* and *H. contortus*. The site burnt once from 2014-2017 in May.

Monger Creek 11-15

The site is on hilly basalt country with low (8.5m) woodland (15% foliage cover) vegetation dominated by *Eucalyptus* and *Corymbia* spp. (*E. tectifica*, *Eucalyptus* sp.,*C. latifolia)* accounting for 96% of total basal area (3.6 m^2 ha^{-1}), with subdominant broadleaf tree species (*G. mimosoides*, *T. canescens*). The herbaceous layer was dominated by tall tropical perennial grasses

S. nervosa, *S. plumosum* and *H. contortus*. The site burnt twice from 2014-2017 in the mid- to late dry season (August-November).

Wobinbeyi 1-5

The site is on gently undulating sandstone country with rock outcrops in close proximity to an ephemeral watercourse. The vegetation was low (8.2m) woodland (25% foliage cover) dominated by *Eucalytpus* spp. (*E. miniata, E. tetrodonta)* with subdominant broadleaf tree species (*C. latifolia*, *Buchanania obovata*, *Syzygium eucalyptoides*, *Terminalia cunninghammi*, *Acacia platycarpa*). The total basal area of 6.9 m^2 ha^{-1} was 92% eucalypts. The herbaceous layer was dominated by tropical perennial grasses *Eriachne sulcata*, *S. plumosum*, *S. stipodium*, *Triodia* sp., *C. fallax*, *Chrysopogon* sp. and graminoid *Xyris complanata*. The site burnt twice from 2014-2017 in the mid- to late dry season (July-November).

Wobinbeyi 6-10

The site is on gently undulating sandstone country with rock outcrops in close proximity to an ephemeral watercourse. The vegetation was low (7.4m) woodland (18% foliage cover) dominated by *Eucalyptus* spp. (*E. tetrodonta*, *Eucalyptus* sp.), Grevillea *pteridifolia*, and *A. platycarpa*, with subdominant broadleaf tree species (*Persoonia falcata*, S. *eucalyptoides*, *Verticordia cuninghamii*). Total basal area was 2.3 m^2 ha^{-1} with eucalypts accounting for 26%. The herbaceous layer was dominated by tall tropical perennial grasses *E. sulcata*, *Sorghum stipodium*, *C. fallax*, *Chrysopogon* sp., hummock grasses *Triodia* sp., and graminoid *X. complanata*. The site burnt twice from 2014-2017 in the early dry season (April-May).

Pauline Creek 1-5

The site is on gently undulating sandstone country with rock outcrops. The vegetation was woodland (10.5m tall, 20% foliage cover) dominated by *Eucalyptus* spp. (*E. miniata*, *E. tetrodonta)* accounting for 98% of total basal area (4.1 m^2 ha^{-1}), with subdominant broadleaf tree species (*Acacia retinervis, Petalostigma pubescens, Grevillea* sp.). The herbaceous layer was dominated by tall tropical perennial grasses E. *sulcata, S. plumosum, S. stipodium, Eriachne* sp. and hummock grasses *Triodia* sp. The site burnt twice from 2014-2017 in the dry season (June-November).

Pauline Creek 6-10

The site is on gently undulating sandstone country with rock outcrops. The vegetation was low (9.0m) woodland (24% foliage cover) dominated by *Eucalyptus* and *Corymbia* spp. (*E. tetrodonta*, *E. miniata, C. latifolia, Corymbia polycarpa)* accounting for 91% of total basal area (5.5 m^2 ha^{-1}), with subdominant broadleaf tree species (*P. falcata, T. cuninghamii, G. pteridifolia, A. platycarpa*). The herbaceous layer was dominated by tall tropical perennial grasses *S. stipodium*, hummock grasses *Triodia* sp., and graminiods *Lomandra tropica*, and *Xyris complanata*. The site burnt 3 times from 2014-2017 in the early dry season (April-June).

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Appendix B

Results of generalized linear mixed models for total animals detected for agile wallabies, wallaroos, cattle and dingos from camera traps established at 11 sites from 2015-2017 in Uunguu IPA, north Kimberley, Western Australia. Significant *p*-values of the predictor variables are bolded. Refer to Table 2 for model selection results.

Response variable	Predictor variables	Estimate	SE	*p*-value
Total agile wallaby	Site fertility	1.50	1.38	0.28
	Time since fire	0.49	0.16	**0.00**
	Dingo abundance	0.34	0.17	**0.04**
	Seasonal dryness	0.30	0.12	**0.01**
	Site fertility*Time since fire	-0.18	0.37	0.63
Total wallaroos	Site fertility	0.25	2.09	0.91
	Time since fire	0.86	0.36	**0.02**
	Dingo abundance	0.47	0.29	0.11
	Seasonal dryness	0.40	0.20	**0.04**
	Site fertility*Time since fire	-1.50	0.74	**0.04**
Total cattle	Site fertility	0.21	0.41	0.61
	Time since fire	-0.33	0.09	**0.00**
	Dingo abundance	0.13	0.06	**0.03**
	Seasonal dryness	0.13	0.07	**0.04**
	Site fertility*Time since fire	0.08	0.20	0.67
Total dingo	Site fertility	-0.20	0.47	0.67
	Time since fire	-0.09	0.16	0.56
	Seasonal dryness	0.39	0.12	**0.00**
	Site fertility*Time since fire	-0.18	0.39	0.64