# Deer for the Tiger

## managing subtropical monsoon grasslands for preserving a flagship species

Shyam Kumar Thapa

**Propositions**

1. The present-day existence of grasslands in the Asian humid subtropics is a legacy effect of historic human activities (this thesis).
2. If viable wildlife populations are to be conserved in small areas, then wildlife conservation requires intensive management (this thesis).
3. Artificial intelligence (AI) is a double-edged sword when it comes to innovation.
4. Political actions are important to transfer insights from science to policy.
5. A sandwich PhD journey is like straddling two boats with a foot in each.
6. Conservation of flagship species is a political agenda.
7. Involvement of local communities in development planning promotes effective solutions to socio-economic challenges.

Propositions belong to the thesis, entitled
Deer for the Tiger: managing subtropical monsoon grasslands for preserving a flagship species

Shyam Kumar Thapa
Wageningen, 6 December 2023

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Shyam Kumar Thapa

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# CHAPTER

# 1

# Introduction

# Introduction

Tropical savannas and grasslands are among the world's most widespread terrestrial biome that covers nearly half of the area of Africa, Australia, and South America, and ~10% of South and South-East Asia (Ratnam et al., 2019). These grass-dominated systems have important ecological and economic implications as they can support high levels of biodiversity, serve as a source of forage for domestic livestock and wild mammalian herbivores, and have climate regulation functions (Bengtsson et al., 2019; Murphy et al., 2016; O'Mara, 2012). However, savannas and grasslands all over the world face numerous challenges that impact their health and functionality, including land use conversion, biological invasion, and overgrazing (Banerjee et al., 2023; Baudena et al., 2015). Furthermore, with increasing temperature and $CO_2$ concentration, modified rainfall patterns, and fire regimes, these tropical savannas and grasslands are expected to undergo significant changes in the future (Bardgett et al., 2021; Baudena et al., 2015; Reich et al., 2018). The recent increase in woody cover observed in savannas and grasslands worldwide (Buitenwerf et al., 2012; Staver et al., 2011; Stevens et al., 2017) further emphasises the dynamic nature of these ecosystems and poses an enormous threat to human wellbeing and globally significant wildlife.

## Subtropical monsoon grasslands of Asia

Subtropical monsoon grasslands in Asia represent a globally important ecoregion called 'Terai-Duar Savanna and Grasslands' (Olson and Dinerstein, 2002). These subtropical monsoon grasslands of Asia exhibit high variation in forage quality and availability for herbivores with respect to seasons (Ahrestani et al., 2011). One of the remarkable features of these subtropical monsoon grasslands is their capacity to support mammalian herbivores assemblages of different body sizes ranging from hispid hare (*Caprolagus hispidus*) to Wild Asian Elephant (*Elaphus maximus*) and with different feeding modes (grazers, browsers, and mixed feeders) in a small area compared to African Savannas and grasslands (Ahrestani and Sankaran, 2016). At present, only African and Asian savannas are characterised by the presence of megaherbivores (Ratnam et al., 2019; Ripple et al., 2015). However, the problem with the subtropical monsoon grasslands is the large-scale habitat destruction and land-use change. Over the past century, the region lost nearly 50% of its forest cover and the current rates of deforestation are considered to be the highest among the world's major tropical regions (Ripple et al., 2015). Worryingly, a fraction of these important savannas and grasslands are currently under protection within protected area systems (Wikramanayake et al., 2010) within Terai Arc Landscape, unlike Africa where a sizable fraction of savannas and grasslands are under protection (e.g., Serengeti - 14,763 $km^2$ and Kruger - 19,500 $km^2$ National Parks). A drastic decline in population and range reduction of megaherbivores especially wild Asian elephants (Ram et al., 2021), greater one-horned rhinoceros (*Rhinoceros unicornis*), and other herbivores like gaur (*Bos gaurus*), wild water buffalo (*Bubalus arnee*), and nilgai (*Boselaphus tragocamelus*) are witnessed (Jhala et al., 2021) due to accelerated human-induced land-use changes and overexploitation of resources including poaching in the subtropical region of Asia. At present, these mega and large herbivores are thriving in a low density in a few isolated protected areas within the subtropical region of Asia where there is the existence of the remnant of subtropical monsoon grasslands.

With mega and large herbivores functionally extinct from the grasslands and alteration in flooding regimes and human activities *viz.*, grass harvesting, livestock grazing, and fire, current Asian subtropical monsoon grasslands are typically in a fire-dominated state with high biomass and tall grasses (Ratnam et al., 2019, 2016) that are fairly indigestible for the existing assemblage of mesoherbivores (Ahrestani et al., 2016). Large herbivores are able to consume and digest nutrient-poor tall grasses (Illius and Gordon, 1992; Prins and Olff, 1998). The indiscriminate consumption of tall grasses by large herbivores creates openings that stimulate the regrowth of short nutritious grasses. This process results in the availability of high-quality forage for mesoherbivores (e.g., van Langevelde et al., 2008). In the past, grazing by mega and large herbivores together with annual flooding and human disturbances could have played a crucial role in maintaining the quality and quantity of herbaceous biomass by creating mosaics of tall and short grassland patches within the grasslands of the region that are suitable for both large and small body sized herbivores. However, with the current spatial extent and composition of the Asian subtropical monsoon grasslands, it remains challenging to meet the nutritional requirements of the existing assemblage of mesoherbivores (Ahrestani et al., 2011; Thapa et al., 2021). This applies, in particular, to the assemblage of chital (*Axis axis*), swamp deer (*Rucervus duvaucelii*), and hog deer (*Axis porcinus*) which are frequent users of the monsoon grasslands (Moe and Wegge, 1994; Wegge et al., 2006). The digestive physiology and higher body-mass energy requirements of the mesoherbivores make them particularly dependent on high-quality forage (Prins and Olff, 1998; Prins and Van Langevelde, 2008; van Langevelde et al., 2008) and are thus affected by the dearth of nutrient availability. These mesoherbivores are important from a wildlife conservation viewpoint as they are the major prey base of the endangered tigers in the region (Thapa and Kelly, 2017; Upadhyaya et al., 2018).

The subtropical monsoon grasslands of Asia support one of the highest recorded densities of tigers in the world (DNPWC and DFSC, 2022; Jhala et al., 2018). Larger body-sized prey, the preferred prey species of tigers (Karanth and Sunquist, 1995), especially wild water buffalo, gaur, nilgai, and sambar (*Rusa unicolor*), are either locally extinct or exist in relatively low densities in the protected areas that have tigers (DNPWC and DFSC, 2022; Jhala et al., 2018). As a result, tigers are relying on smaller body-sized prey (Ramesh et al., 2009; Upadhyaya et al., 2018) such as chital, hog deer, swamp deer, wild boar (*Sus* *scrofa*), and langur (*Semnopithecus hector*). These chital and alike mesoherbivores strive to acquire forage of higher quality in terms of digestibility, and nutrient content because of their body size and physiological requirements. Therefore, it is increasingly necessary for protected area managers of the region to manage highly productive grasslands to meet the nutritional requirement of the existing mesoherbivores assemblages so as to provide sufficient food for the tiger population.

### Subtropical monsoon grasslands and forage quality

The amount of energy obtained by an individual herbivore is determined by factors like animal's body size and digestive system (Gordon and Illius, 1996), parts of the plant consumed (Drescher et al., 2006a; Prins and Beekman, 1989), the nutritional value of the consumed forage in terms of nutrient and digestible energy content (Van Soest, 1982), and the quantity of the quality parts consumed (Thapa et al., 2021). In highly productive grasslands such as subtropical monsoon grasslands of Asia that exhibit high seasonal variation in forage availability and quality (Ahrestani et al., 2012), herbivores are continuously struggling to acquire quality forage to meet their nutritional requirement for various physiological functions like growth, reproduction, and lactation.

Forage quality for herbivores in grazing systems is determined by physical and chemical properties such as vegetation height, biomass, proportion of leaves over stem, and proportion of green parts over dry, and nutrient and digestible energy content of a forage respectively. Subtropical monsoon grasslands of Asia are characterised by tall grasses (> 2 m) with high biomass (Lehmkuhl, 1994; Peet et al., 1999a; Ratnam et al., 2019). The quality of grasses in terms of nutrient concentration and digestibility decreases with grass height and biomass (Thapa et al., 2022) and hence the availability of quality forage is negatively related to overall forage availability (van Langevelde et al., 2008). Therefore, herbivores strive to acquire high-quality forage from tall grasslands which requires searching for high-quality forage parts (Drescher et al., 2006a). This possibly results in a reduced rate of forage intake (Shipley et al., 1994; Spalinger and Hobbs, 1992). However, herbivores adjust their constraints related to forage intake rate by choosing grazing patches *viz.,* grazing lawns that contain high-quality forage (Fryxell, 1991; McNaughton, 1984; Raynor et al., 2016; Thapa et al., 2021). While all herbivores are not adapted to make efficient use of grazing lawns, mixed feeders with narrow muzzles such as chital, and swamp deer have the capacity to crop high-quality short grasses from the lawns.

Grazing lawns are important foraging areas from where herbivores can maximise their rate of intake of high-quality forage (Mayengo et al., 2020; Thapa et al., 2021; Verweij et al., 2006). Grazing lawns contain short grasses that have a higher proportion of quality forge parts (higher level of leaf-to-stem ratio), higher bulk density and lower biomass compared to tall grasslands (Donaldson et al., 2018; Hempson et al., 2015; McNaughton, 1984; Thapa et al., 2021). In addition, grazing lawns have grasses that have a higher concentration of nitrogen and phosphorus and lower fiber content hence higher digestibility (Thapa et al., 2021). A higher proportion of green leaves in grazing lawns ensures that each bite taken from the lawns contains a higher quantity of green leaf materials, leading to increased rates of energy gain. Green leaf contains a higher concentration of nitrogen compared to stem (Prins, 1996; Thapa et al., 2021). Likewise, the improved leaf quality metrics (higher nitrogen and phosphorus, and lower percentage of NDF – neutral detergent fibre and ADF – acid detergent fibre) of grazing lawns (Thapa et al., 2021) ensure higher digestibility and nutrient intake. Hence, grazing lawns are important nutrient sources from where herbivores can maximise the concentration of protein and phosphorus in their diet.

A large body of literature from Africa and other regions highlights that grazing lawns are animal driven and the persistence of grazing lawns depends on the intensity of grazing pressure (e.g., Cromsigt et al., 2017; Donaldson et al., 2018; Hempson et al., 2015; McNaughton, 1984). Experimental studies in South African savannas demonstrated that grazing lawns can be established when management interventions promote frequent grazing (Cromsigt and Olff, 2008). Studies on grazing lawns from African savannas do not yield comprehensive insight to fully understand the grazing lawn formation processes in Asian subtropical monsoon grasslands. Subtropical monsoon grasslands in Asia are highly productive and receive over 1200 mm of rainfall annually (Ratnam et al., 2019, 2016). The very high growth rate and fast production of combustible materials (Ahrestani et al., 2011) due to the hot and humid growing season characterised by monsoon-influenced humid subtropical climate (referred to as Cwa-climate in the Köppen-classification; (Chen and Chen, 2013) make these grasslands fundamentally different from savanna grasslands in arid and semi-arid ecosystems (Ratnam et al., 2019, 2016; Sankaran et al., 2005).

### Grazing lawns in the subtropical monsoon grasslands in Asia

Most present-day subtropical monsoon grasslands in Asia consist of two spatially separated types – riverine grasslands and grassland-forest mosaic - with the former dominating in floodplains and the latter in drier, and more disturbed sites (Lehmkuhl, 1994; Peet et al., 1999a; Thapa et al., 2021). The annual floods as a result of heavy rainfall during monsoon and subsequent changes in the alluvial deposition and water flow intensity are the most striking components for changing the extent and composition of floodplain grasslands (Biswas, 2010; Biswas et al., 2014; Lehmkuhl, 1994). These grasslands would develop into the forest if periodic flooding or river dynamics is changed which is likely because of development interventions in the Anthropocene. Likewise, grasslands interspersed within the forested mosaic were derived from forests resulting from human use (Ratnam et al., 2016, 2011) and maintained either by grass harvesting, grazing, fire or a combination of these three factors (Lehmkuhl, 1994; Peet et al., 1999a; Ratnam et al., 2011). Both these grassland types (riverine floodplain grasslands and grasslands interspersed within the forest) are experiencing reduced natural (flooding, and grazing by large herbivores) and anthropogenic (harvesting, livestock grazing, and fire) disturbances which have favoured tall grasses, woody shrubs, and invasive weeds to colonise in the existing grasslands leading into the spatial and compositional changes (Bijlmakers et al., 2023) along with the change in the quality and quantity of herbaceous biomass.

For instance, grasslands interspersed within a forest in Bardia National Park (Bardia NP) that lies in the subtropical region of Nepal carry a legacy of intensive human use. Until the 1970s i.e., before the establishment of Bardia National Park, there used to be agricultural fields in what are now the grasslands. Domestic livestock used to graze inside the parks along with wild herbivores (Dinerstein, 1979). In 1975, biomass of livestock was 15 – 17 times higher than biomass of wild ungulates in the park (Dinerstein, 1980). More importantly, a large volume of grasses was taken out of the system through thatch harvesting (Brown, 1997). In the 1990s more than 30,000 people entered the park to harvest thatch for 14 days per year but at present, only about 10,000 people enter the park and harvest thatch for three days per year (Thapa et al., 2021). Livestock grazing together with thatch grass harvesting could have facilitated the formation of mosaics of tall and short grassland patches within the subtropical monsoon grasslands in Bardia NP (Figure 1.1). More importantly, localised grazing pressure exerted by mesoherbivores in short grassland patches created through thatch harvesting and livestock grazing likely influenced the nutrient mineralisation process (Augustine and Frank, 2011; van der Waal et al., 2011) through the addition of manures via dung and urination (Moe and Wegge, 2008), and soil moisture content through trampling (van der Waal et al., 2011) and facilitated in formation of grazing lawns. Frequent and repeated grazing by mesoherbivores facilitated the maintenance of grazing lawns in the productive monsoon grasslands.

**Figure 1.1:** Local people harvesting thatch from the national park. Annually, the park administration grants permission for local communities to harvest thatch grass during a designated three-day period.

However, settlements were removed from the core area of the park, and livestock grazing inside the park was prohibited after the establishment of national parks in the 1970s. This sudden removal of settlements and domestic livestock from the park likely reduced the scale of interventions needed to maintain the grasslands (Figure 1.2). As a result, it caused the regeneration of tall grasses, woody shrubs, and invasive weeds (van Lunenburg et al., 2017; Wegge et al., 2009). Furthermore, forest areas increased at the expense of grasslands, leading to a decrease in the extent and abundance of grassland patches (Bijlmakers et al., 2023). This shift has adverse implication for the forage availability of mesoherbivores.

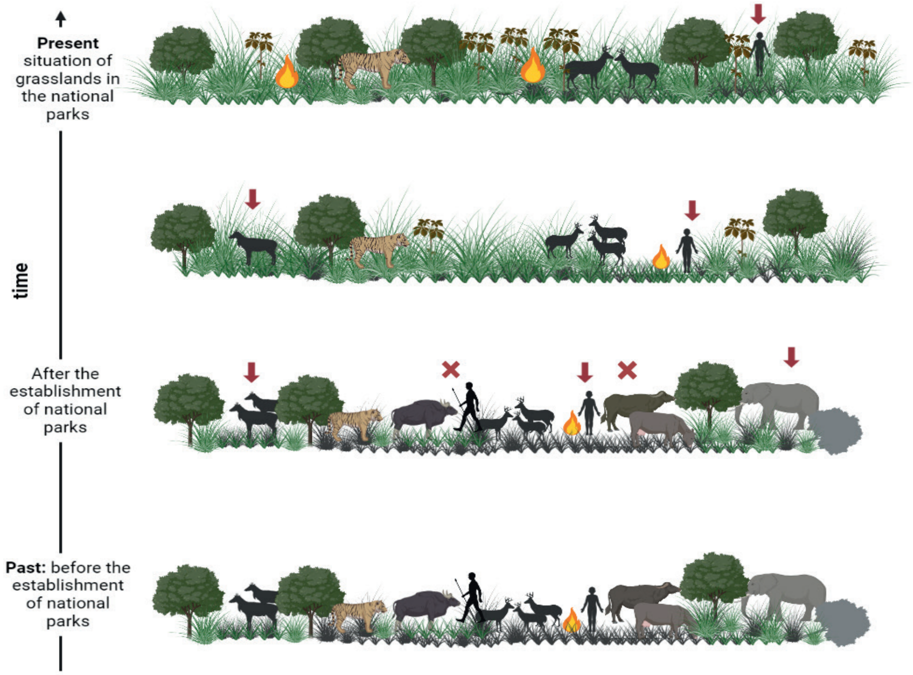


**Figure 1.2:** Changes in grassland ecosystems following the establishment of national parks. The 'x' marks indicate the elimination of specific factors, while the downward arrows symbolise the diminished status of those factors. For example, following the establishment of national parks, activities such as livestock grazing and hunting were prohibited. Similarly, human use (thatch harvesting) showed a decrease over time.
Created with BioRender.com

A large proportion of grasslands is burned every year in the subtropical region of Asia, a practice that has long been an important element of grasslands in the region (Ahrestani and Sankaran, 2016; Dinerstein, 1979; Ratnam et al., 2016, 2011; Sankaran, 2005). Protected area managers of subtropical Asia considered fire as a cost-effective method for grassland management with an aim to provide quality forage for herbivores during the dry season (Thapa et al., 2022). On one hand, fire plays an important role in the maintenance of grasslands by suppressing woody plant colonisation (Sankaran et al., 2005; Staver et al., 2011; Van Langevelde et al., 2003), but result in the production of high biomass (Sankaran, 2005). On the other hand, large-scale fires in grasslands disperse grazers throughout the burned areas (Donaldson et al., 2018; Moe and Wegge, 1997; Van de Vijver et al., 1999) resulting in a reduced grazing intensity (Archibald et al., 2005).

Existing grassland management practices in protected areas that have tigers in Terai Arc Landscape tend to create a homogeneous landscape either by burning or cutting.

It may benefit mesoherbivores as they aggregate to forage in such an open homogeneous landscape where they can exploit nutritious forage (le Roux et al., 2018; Moe and Wegge, 1997; Thapa et al., 2022). Perhaps, feeling safe (from predation) in an open homogeneous landscape could be the driving force for such aggregation (Epperly et al., 2021; le Roux et al., 2018). However, such open homogeneous large open grasslands might disrupt tigers hunting success rate (Karanth and Sunquist, 2000; Sunquist, 2010), and may have consequences on many aspects of tiger ecology including, territory size, energy expenditures, and their survival. It is because tigers employ a stalking strategy using vegetation cover as a tool to ambush the prey (Sunquist, 2010). The creation of homogeneous large open areas will disperse grazers and diminish grazing pressure due to the availability of nutritious re-sprout (Archibald et al., 2005; Thapa et al., 2022). This allows grasses to escape herbivory and establishes a feedback loop that facilitates the production of tall grasses and increases the risk of future fire (Van Langevelde et al., 2003). Subsequently, as grazing pressure is reduced, grasses start to grow fast and attain height and biomass, resulting in the disappearance of grazing lawns (Karki et al., 2000; Veldhuis et al., 2016).

It is not possible nor desirable to revive all the historical components (e.g., agricultural practices and cattle grazing) again inside the protected areas for the management of grasslands. But it is possible to create similar effects in grassland systems through management interventions like mowing tall grasses and creating openings for megaherbivores to graze (Figure 1.3). It has been proven that the formation and persistence of grazing lawns largely depend on the frequency and intensity of grazing (Cromsigt and Olff, 2008; Hempson et al., 2015; McNaughton, 1984; Veldhuis et al., 2014; Voysey et al., 2021). Therefore, grassland management interventions should create an environment to initiate a positive cycle of grazing where grazing shapes the structure and composition of grasslands (De Knegt et al., 2008; Hempson et al., 2015).

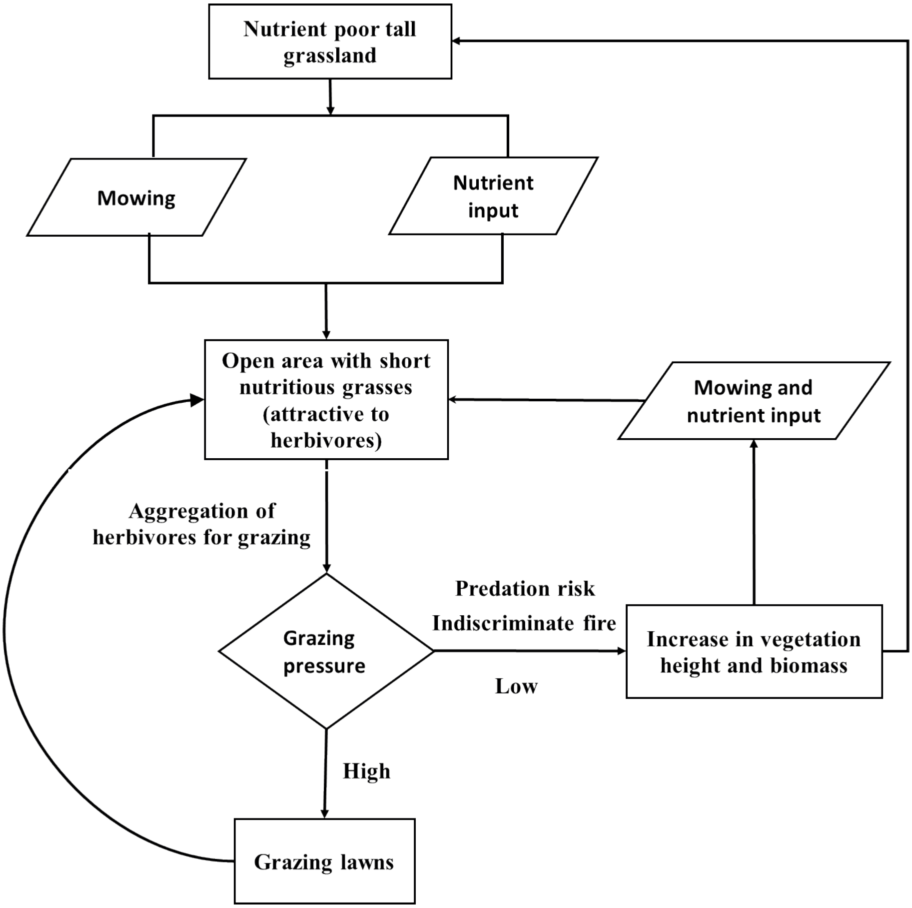


**Figure 1.3:** Conceptual framework illustrating initiation of grazing lawns in subtropical monsoon grasslands. The process involves the removal of tall grasses through mowing and the addition of artificial fertilisers, which increases the quality of forage. This increased forage quality attracts herbivores for grazing. The resulting grazing pressure initiate grazing lawns within the highly subtropical monsoon grasslands.

While most studies on grasslands and grazing lawns are from African savannas (e.g., Cromsigt et al., 2017; Donaldson et al., 2018; Hempson et al., 2015; McNaughton, 1984), studies on the nutritional quality of the different grassland states (grazing lawns and tall grasslands) and its implication on grazing herbivores are almost non-existent for the subtropical monsoon grasslands in Asia. Furthermore, fewer studies have focused on the impact of grassland management interventions on forage quality for herbivores from subtropical monsoon grasslands of Asia (e.g., Moe and Wegge, 1997; Peet et al., 1999b). Therefore, I aim to fill this knowledge gap by conducting experiment in the remaining remnant of subtropical monsoon grasslands within protected areas that house a sizable population of tigers. I will answer the question whether intensive grassland management interventions such as mowing and artificial fertilisation can initiate grazing lawns in a highly productive monsoon grassland which results in the higher production of mesoherbivores. I conduct this study in the grasslands of Bardia National Park that are interspersed within a forest and have a legacy of human use. In addition, the park holds the highest density of tigers that are entirely relying on mesoherbivores (chital, hog deer and swamp deer) and wild boar (DNPWC and DFSC, 2022). It, therefore, provides a unique opportunity to investigate the impact of management interventions on the forage quality and resulting foraging behaviour of mesoherbivores which is highly relevant to the conservation of endangered tigers and ecosystem functioning of highly productive subtropical monsoon grasslands.

**Study area**

Bardia National Park (Bardia NP) lies within the subtropical region in the western part of the Terai Arc Landscape of Nepal (centre of the park at 28$^0$23′ N, 81$^0$30′ E, elevation 100 to 200 m a.s.l., Figure 1.4). The park is home to both megaherbivores (e.g., rhinoceros and wild Asian elephant) and mesoherbivores (e.g., chital, swamp deer, sambar, hog deer, and muntjac - *Muntiacus vaginalis*). These mesoherbivores are important prey of the tigers in the park (Upadhyaya et al., 2018). The park holds the highest density of tigers in Nepal with an estimated density of ~7 individuals.100 km$^{-2}$ (DNPWC and DFSC, 2022).

The area has three distinct seasons: the monsoon (June to September), the dry winter (October to February) and the hot dry summer (March to May). The monthly mean temperature of the area ranges between 10 $^0$C in January and 45 $^0$C in June and the park receives a mean annual rainfall of ~1800 mm. According to the Köppen-Geigen climate classification, the area falls within a Cwa climate: monsoon-influenced humid subtropical climate (Chen and Chen, 2013).

The park consists of subtropical vegetation with riverine forest, riverine floodplain grasslands (Figure 1.5) along the two major rivers (Karnali and Babai Rivers), and *sal* (*Shorea robusta*) forest with interspersed grasslands (Figure 1.6). Assemblages of *Imperata cylindrica* (L.), *Saccharum spontaneum* (L.), *Vetiveria zizanioides* (L.), *Saccharum bengalense* (Retz.) and *Narenga porphyrocoma* (Hance ex Trin.) Bor. are reported from the grasslands that are interspersed within *sal* forest (Peet et al., 1999a; Thapa et al., 2021). Riverine floodplain grasslands and grasslands interspersed within the forest are the remaining remnant of an important global ecoregion known as 'Terai-Duar Savanna and Grasslands' and thus have global conservation significance.

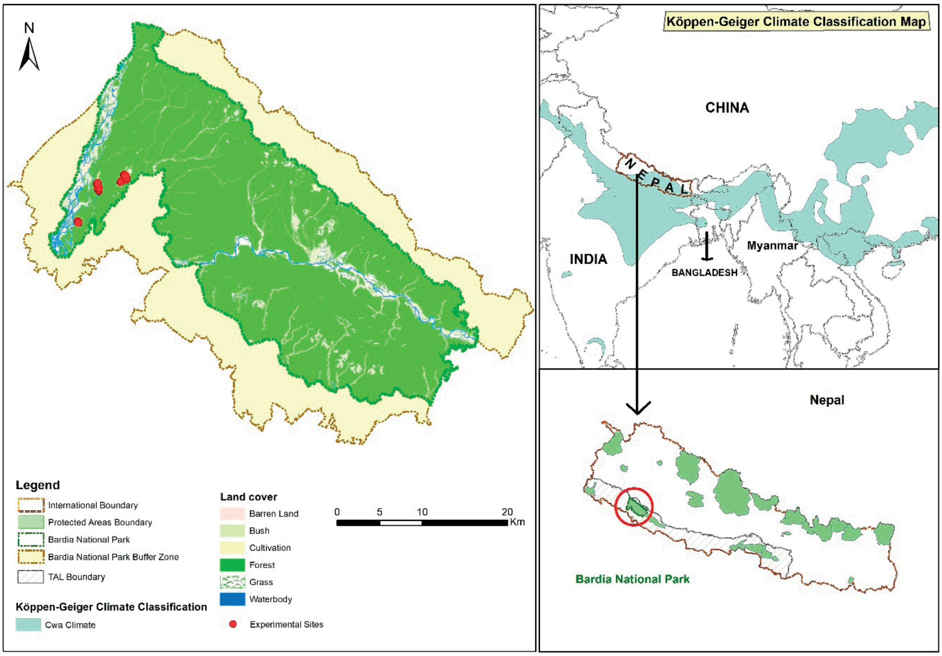


**Figure 1.4:** Experimental sites within Bardia National Park, Nepal. The park harbours one of the most significant tiger populations within the Terai Arc Landscape of Nepal. The park lies within Cwa climate, indicating a monsoon-influenced humid subtropical climate under the Köppen classification (light blue area on the top-right inset map).

**Figure 1.5:** Riverine floodplain grasslands in Bardia National Park.

**Figure 1.6:** Grassland interspersed within sal (*shorea robusta*) forest in Bardia National Park.

**Thesis outline**

To address the main research question, in my thesis I bring together five chapters which are outlined as follows:

In Chapter 2, I examined and compared the physical and chemical characteristics of existing grazing lawns with tall grasslands. In this paper, I showed that grazing lawns, like in African savannas, are important foraging ground within subtropical monsoon grasslands from where mesoherbivores obtain their required nutrients, especially nitrogen and phosphorus for maintenance and reproduction.

In Chapter 3, I investigated the effect of fire on forage quality and resulting pyric herbivory. Fire is considered as a cost-effective method for grassland management that aims to provide quality forage for herbivores, especially during the dry season.

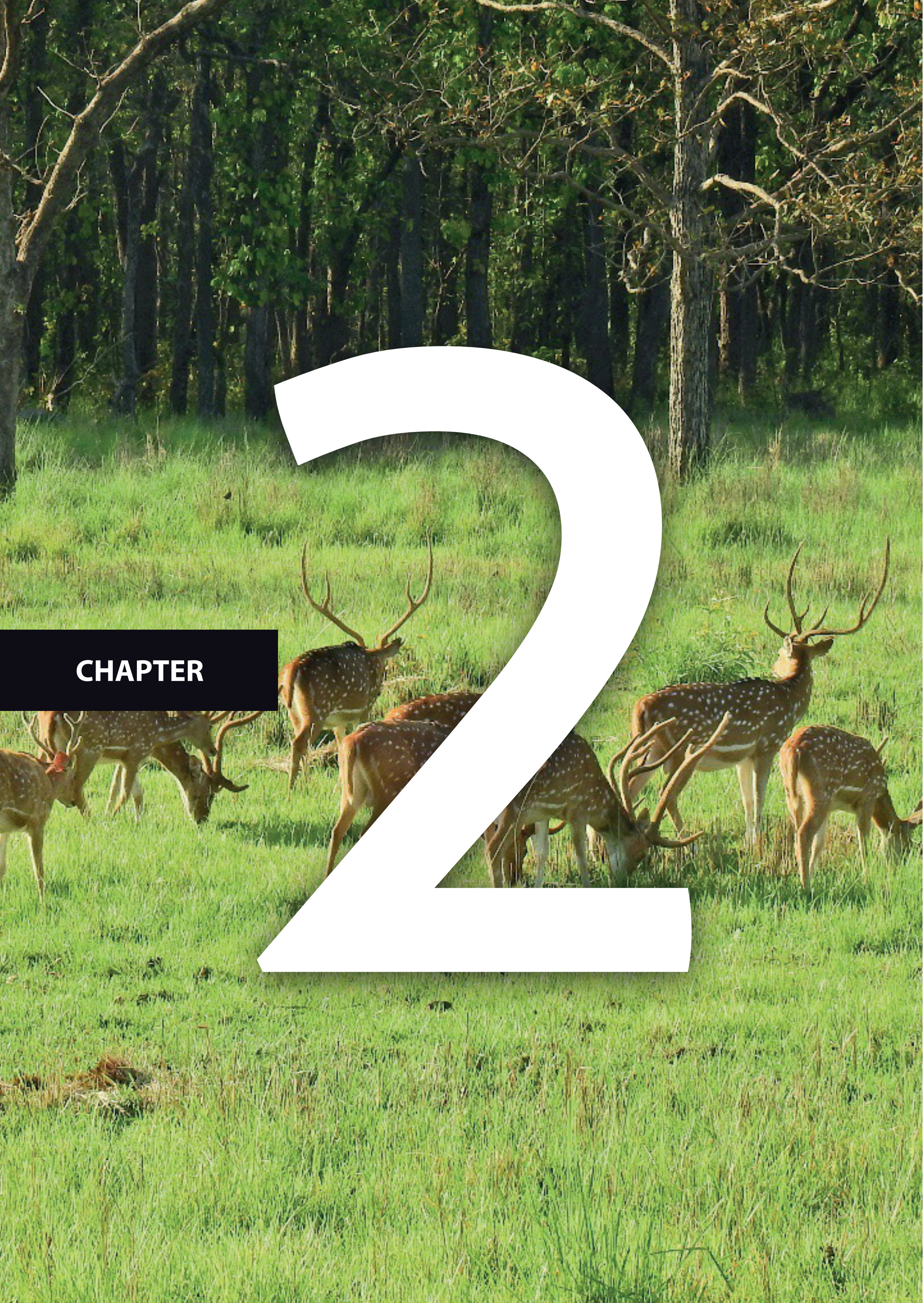
In Chapter 4, I investigated the applicability of the landscape of fear concept in grassland management by simultaneously examining the effect of altering resource quality (primarily through mowing and artificial fertilisation) and manipulating predation risk (primarily by creating open areas of different sizes - plot size) on the intensity of use of the managed grassland by mesoherbivores.

In Chapter 5, I assessed whether intensive grassland management interventions (e.g., mowing and addition of artificial fertilisation) could initiate grazing lawns in highly productive monsoon grasslands in Bardia National Park.

Finally, in Chapter 6, I summarised all the results obtained from my different chapters. I have attempted to discuss the possible mechanism for the formation and maintenance of grazing lawns in the subtropical monsoon grasslands of Asia and posit important conservation implications.

# CHAPTER

# 2



# Forage quality in grazing lawns and tall grasslands in the subtropical region of Nepal and implications for wild herbivores

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# Abstract

Subtropical grasslands interspersed in forests often present mosaics of tall grasslands and grazing lawns with a high variation in structure, biomass, and nutrient concentration. However, the impact of such variation on forage quality is still poorly known. We quantified physical and chemical properties of grasses of grazing lawns and tall grasslands, interspersed in the forested region of Bardia National Park, Nepal during the hot-dry season. This area falls within Cwa-climate (Köppen-Geigen climate classification). We found that grasses in grazing lawns had an average bulk density of ~5400 $g.m^{-3}$ whereas tall grasslands had an average bulk density of ~1000 $g.m^{-3}$ only. Forage in grazing lawns was comprised of a higher percentage of green leaf (up to 60%) compared to tall grassland (up to 40%). Phosphorus levels in green leaves were below maintenance requirements of wild herbivores (especially for grazers and mixed feeders) on both grazing lawns and tall grasslands. However, average crude protein levels in green leaves from both the grazing lawns and tall grasslands could meet the herbivores maintenance requirement (~7%). Only green leaves on grazing lawns had crude protein levels sufficient enough (9.7 %) to meet the requirements of herbivores for maintenance and gestation, though not for lactation. We conclude that, during the hot-dry season, grazing lawns provide forage with a higher quantity and quality than tall grasslands. Consequently, grazing lawns can make a significant contribution to the maintenance or even growth of the grassland dependent wild ungulate population, such as chital (*Axis axis*), a primary prey species of the endangered tiger (*Panthera tigris*) in Bardia National Park. The insight of this study will provide a basis for restoring grazing lawns for quality forage, and aid in the conservation and management of wild grazers and mixed feeders.

**Keywords:** grazing lawn, nutritional value, grazers and mixed feeders, ungulates, Bardia National Park

# Introduction

Grasslands in the subtropical region of Nepal (and in India) can broadly be categorised into (i) floodplain grasslands dominating in riverbanks and floodplains and (ii) grasslands established in abandoned agricultural fields originated from human interventions such as land conversion (forest into agriculture), livestock grazing, thatch harvesting and burning (Peet et al., 1999a). Grasslands established in abandoned agricultural fields frequently consist of mosaics of tall grasslands and grazing lawns (Ahrestani and Sankaran, 2016; Karki et al., 2000). This mosaic of tall grasslands and grazing lawns appears to be a key determinant for spatial and temporal heterogeneity of food resources that is necessary to meet the nutritional requirement of herbivore assemblages including grazers and mixed feeders (Bonnet et al., 2010; Cromsigt and Olff, 2006; Hempson et al., 2015; Prins and Van Langevelde, 2008; Raynor et al., 2016; Verweij et al., 2006; Wilmshurst et al., 1999). Furthermore, a large number of empirical and experimental studies have pointed out that vegetation nutritive value is related to vegetation physical properties such as height, biomass, proportion of leaves over stem, and proportion of green parts over dry (Drescher et al., 2006a; Durant et al., 2004; Mårell et al., 2006) which in turn govern rates of daily energy intake (Laca et al., 2010; Mezzalira et al., 2017; Searle and Shipley, 2008; Spalinger and Hobbs, 1992). For instance, amount of green leaves and bulk density are critical parameters that largely influence bite rate and bite size and hence the intake in herbivores (Drescher et al., 2006a; Stobbs, 1973). Therefore, knowledge on the physical and chemical characteristics of grassland vegetation is essential to understand the nutritional value of the vegetation that is on offer as food to wild herbivores.

The ultimate aim of a foraging herbivore is to satisfy its energy requirements for maintenance and reproduction. The amount of energy obtained by an individual is determined by various factors, such as the animal's body size and digestive system (Gordon and Illius, 1996), parts of the plant consumed (Drescher et al., 2006a; Prins and Beekman, 1989), the nutritional value of the consumed forage in terms of nutrient and digestible energy content (Van Soest, 1982), and the quantity of the forage consumed (van Langevelde et al., 2008). Plant parts and growth stages of plants present great differences in its physical properties, chemical composition, and nutritional value. For instance, grasses in an early growth stage have a higher proportion of leaf over stem and have a higher digestibility than older grasses (Prins, 1996). Digestibility is inversely related to fibre content (Van Soest, 1982); which means digestible energy content in a forage decreases with age and biomass. Due to these variations in the quality and quantity of the forage, herbivores are predicted to select those grassland patches from which they can maximise their daily energy intake (Fryxell, 1991). McNaughton (1984) showed that herbivores on the African savanna can maximise their energy and nutrient intake from grazing lawns. However, grazing lawns demand a certain degree of frequent grazing pressure for their persistence and if grazing pressure is relaxed, fast growing tall grasses may replace grazing tolerant, high-quality grasses (Archibald, 2008; van Langevelde et al., 2008).

Grasslands in the subtropical region of Asia are dominated by an assemblage of herbivores belonging to grazers and mixed feeders (Ahrestani and Sankaran, 2016). This herbivore assemblage, however, has suffered dramatic population declines and range reductions due to changes in the extent of grasslands as a result of strong naturally (succession, and flood) and anthropogenically (cutting, fire, and conversion into agricultural land) induced dynamics (Ahrestani and Sankaran, 2016; Biswas et al., 2014; Ratnam et al., 2019). Local extinction of large grazers has happened too, leading to 'undergrazing' (Jhala et al., 2021; Subedi et al., 2013). Notably, tall grasslands have increased at the expense of grazing lawns (Peet et al., 1999a), potentially, affecting forage quality and quantity for grazers and mixed feeders. Tall grasses with low nutrient and digestible energy content depress the intake rate of herbivores and thus hamper a positive energy balance for maintenance and production, especially in small and medium body-sized grazers and mixed feeders (Illius and Gordon, 1992; Wilmshurst et al., 2000). A handful of ecological investigations with chital (*Axis axis*) (Ahrestani et al., 2012; Moe and Wegge, 1994; Raman, 1997), gaur (*Bos gaurus*) (Ahrestani et al., 2012), and blackbuck (*Antilope cervicapra*) (Jhala, 1997) indicated that the amount of energy and nutrients consumed by these herbivores affects both their survival and reproduction. Hence, herbivores in the subtropical region are potentially limited in their numbers by the abundance of forage of high nutritional value.

Knowledge on the physical and chemical characteristics of grassland vegetation as food for herbivores is essential for understanding the nutritional value and availability of quality forage. However, studies on the nutritional quality of the different grassland states (grazing lawns and tall grasslands), are almost non-existent for the subtropical grasslands in Asia. Studies carried out in the subtropical Asian region have mostly focused either on vegetation classification (Dinerstein, 1979; Kumar et al., 2020; Lehmkuhl, 1994; Peet et al., 1999a; Ratnam et al., 2016, 2011; Sankaran, 2009), or on herbivore foraging behaviour (Ahrestani et al., 2011; Ahrestani and Sankaran, 2016; Moe, 1994; Moe and Wegge, 1997, 1994; Pokharel and Storch, 2016; Tuboi and Hussain, 2016; Wegge et al., 2006). Only a few studies have given strong attention to the chemical properties of grassland vegetation (Karki et al., 2000; Moe, 1994; Moe and Wegge, 2008). To our knowledge, the differences in chemical and physical properties between grazing lawns and tall grasslands in the sub-tropical region of South Asia have not yet been investigated.

Grasslands in the lowland Terai of Nepal are the last remaining examples of subtropical grasslands in the Indian subcontinent (Peet et al., 1999a) and represent a globally important ecoregion, the 'Terai-Duar Savanna and Grasslands' (Olson and Dinerstein, 2002). In the past centuries, these grasslands extended across north-eastern India, lowland Terai of Nepal to northern Bangladesh. At present, these grasslands are entirely restricted to ten protected areas in northern India and six protected areas within the Terai Arc Landscape in Nepal (Wikramanayake et al., 2010). A consequence of the loss of grasslands in the Terai Arc Landscape is a population decline and range reduction of a whole array of wild herbivores (Dinerstein, 1980; Karanth and Sunquist, 1992) and a near extinction of pigmy hog (*Porcula salvania*). Therefore, a prerequisite for the conservation of these herbivores, and their predators such as the endangered tiger (*Panthera tigris*), is to understand the nutritional dynamics of the vegetation on the mosaic of tall and short grassland of the subtropical region.

We investigated the physical and chemical properties of two important grassland states, namely *grazing lawns,* and *tall grasslands*, in Bardia National Park (Bardia NP) lying within the Terai Arc Landscape in the subtropical region of Nepal. As mentioned before, grasslands established in the abandoned agricultural field within forests can occur in two different states, namely, the 'lawn state' and the 'tall grassland state'. We assessed which of these two grassland states offers food of sufficient quality and in such a quantity that they can meet the nutritional requirements for maintenance and reproduction of the herbivore assemblage that is (still) present. Given that deer are typically observed in grazing lawns, we expected grazing lawns, but not tall grasslands, to meet the nutritional requirements of herbivores for maintenance and reproduction. Our overarching goal was to understand the characteristics of subtropical grasslands to provide a basis for the restoration of grazing lawns as a management tool in the conservation of wild herbivores and their predators in this type of landscape.

## Materials and Methods

### Study area

The study was conducted in Bardia NP which lies within the subtropical region in the western part of the Terai Arc Landscape of Nepal (centre of the park at $28^0 23'$ N, $81^0 30'$ E, elevation 100 to 200 m a.s.l., Figure 2.1). The park supports the second-largest tiger population of Nepal with about 90 adult tigers (DNPWC and DFSC, 2018). The dominant habitat types are Sal (*Shorea robusta*) forest and mixed riverine forests along with floodplain grasslands and grasslands interspersed within forests especially in the abandoned agricultural fields (Dinerstein, 1979; Peet et al., 1999a; Wegge et al., 2009). Grasslands established in abandoned agricultural field vary in size from 1 to 110 ha within the forest area and are dominated by an assemblage of *Imperata cylindrica* (L.), *Vetiveria zizanioides* (L.), Saccharum *spontaneum* (L.), *Saccharum bengalense* (Retz.), and *Narenga porphyrocoma* (Hance ex Trin.) Bor. (Peet et al., 1999a).

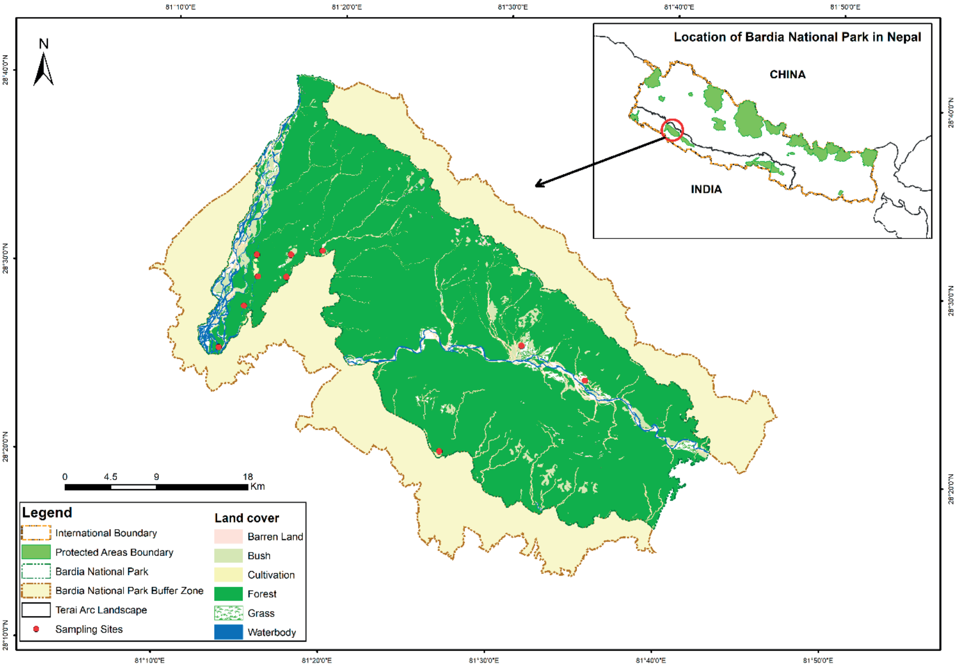


**Figure 2.1:** Location of Bardia National Park within Nepal. Bardia National Park lies within Terai Arc Landscape in a Köppen classification Cwa-Climate. The figure shows the locations of grazing lawns and tall grassland surveyed.

Most of the grasslands within forest are believed to originate from shifting cultivation and were subsequently maintained either by grazing, harvesting, or by fire (Bell and Oliver, 1992). Following the establishment of the park and relocation of people and livestock out of the area, the park has carried out grassland management, following recommendations from research carried out in the early 1990s. A grassland management involved annual cutting (including thatch harvesting) and burning both by local people and by park staff which might have retarded the successional change towards forest (Lehmkuhl, 1994) and have also facilitated in a development of small patches of grazing lawns in the tall bunch-grass matrix (Figure 2.2). These grazing lawns could have originated from grazing by deer immediately after patchy burning or cutting (Karki et al., 2000; Moe and Wegge, 1997). However, it is important to note here that during the 1990s, more than 30,000 people entered the park to harvest thatch grasses for 14 days but at present, people are allowed for three days only and the number of people entering the park for thatch collection has decreased drastically, possibly due to adoption of concrete houses with corrugated galvanised sheet roofs. A reduction of human activities (cutting and thatch harvesting) on the grasslands have facilitated the expansion and establishment of tall grasses and woody shrubs at the expense of grazing lawns.

**Figure 2.2:** A typical grazing lawn interspersed within a tall grassland in Bardia National Park, Nepal.

The grasslands of Bardia NP are important foraging areas for deer of different body-sizes, viz., from smaller to larger – hog deer (*Axis porcinus*), chital, swamp deer (*Rucervus duvaucelii*), and sambar (*Rusa unicolor*) (Pokharel and Storch, 2016; Wegge et al., 2009, 2006). Chital is the most abundant and at the moment the primary prey species of the tiger in Bardia NP (Upadhyaya et al., 2018) with a reported density of 56 km$^{-2}$ (DNPWC and DFSC, 2018). The area has three distinct seasons: the monsoon (June to September), dry winter (October to February) and the hot dry summer (March to May). The monthly mean temperature of the area ranges between 10 $^{0}$C in January and 45 $^{0}$C in June and the park receives a mean annual rainfall of ~1800 mm. According to the Köppen-Geigen climate classification, the area falls within a Cwa-climate: monsoon-influenced humid subtropical climate (Chen and Chen, 2013). Our investigations may thus be of relevance for a much wider area, as far as southern China, and North-east India, which have similar conservation issues (e.g., management of the endangered Eld's deer (*Rucervus eldii*) (Tuboi and Hussain, 2016; Zhang et al., 2019). The forage qualities may vary markedly between seasons, but the hot dry season represents a nutrient bottleneck during which ungulates are most likely to be nutritionally stressed. Therefore, we conducted this study during the hot dry season (April – May) of 2019.

## Vegetation and soil sampling

### Sampling protocol

We carried out our study in those grasslands of Bardia NP that are established in abandoned agricultural field within the forested landscape which are believed to originate and maintained either by grazing, harvesting, or by fire (Bell and Oliver, 1992; Mishra, 1982), hence, do not necessarily represent riverine floodplain grasslands developed in the riverbanks following river dynamics. Within the studied grasslands, we selected sampling sites in two conspicuous grassland states based on grassland characteristics, i.e., *grazing lawns* and *tall grasslands*; the latter were selected at minimally 50m from the grazing lawns to allow for paired statistical analyses. We categorised *grazing lawns* as small (<1 hectare) areas containing short grasses with low stature growth form, growing closer to the ground with prostate leaves and tillers established and maintained through intensive grazing by wild herbivores. Grazing lawns currently occur as small areas in the tall bunch-grass matrix (Karki et al., 2000). We categorised *tall grasslands* as the grasslands in their tall state with tall bunch grasses (Figure 2.2). The two grassland states have similar grass species composition (Table S2), but grazing lawns represent a short grassland state that have distinct growth forms due to frequent grazing (Hempson et al., 2015; Karki et al., 2000). The sampling locations for grazing lawns (n=10) and tall grasslands (n=10) were at the same topographic position in the landscape to minimise the confounding effect of topography and, for instance, depth of groundwater.

### Sward sampling

We randomly laid down 1m x 1m quadrats with equally spaced grids of 10cm x 10cm (Goodall, 1952; Zwerts et al., 2015) in different direction in both the grazing lawns and tall grasslands. While laying down quadrats in the tall grasslands, we avoided areas that were either cut or burnt in the previous days to have a good representative samples of tall grasses. We laid down a total of 160 quadrats (eight in each sampling site) based on species effort curve (Krebs, 1999) and recorded bare ground, litter, animal droppings and vegetation. Within each quadrat, we used the point intercept method at 100 sampling points to assess the percentage cover of the different plant species. We only used vegetation hits for calculating the Shannon-Wiener diversity index (H; Peet, 1974) and species richness (Chao index; Sarmah, 2017). We used grid corners as the point to record the hits.

We measured grass height at three random points within each 1m x 1m quadrat with a ruler to 0.5 cm precision. We chose three different points in different direction within a quadrat to measure the grass height. We assessed grazing intensity by visually estimating the bite marks (Sankaran, 2009) within a quadrat at a scale from 0 to 3 [i.e., 0 - not grazed, 1 - lightly grazed, up to 25% of quadrat area grazed; 2 - moderately grazed, (up to 50% grazed), and 3 - heavily grazed (more than 50 % grazed)].

We clipped the vegetation at ground level in a 20 x 20 cm frame in the centre of each quadrat and determined fresh weight using a digital weighing scale [with a capacity of 600 g and accuracy of 0.5 mg; Brand: Equal (class II)] immediately after clipping. We hand-sorted the samples into green leaf, green stem, dry leaf, and dry stem which were subsequently dried in the shade at ambient temperature (~$30^0$ C) for five days until air-dry before recording the air-dry weight. Air-dried samples of green leaf and green stem were stored in paper bags for separate chemical analyses.

We clipped samples of four graminoids (*viz.*, *I. cylindrica, V. zizanioides, Desmostachya bipinnata,* and *S. spontaneum*) from each grazing lawn and tall grassland sites for separate chemical analysis. These four grass species were the most abundant grass species in both the grasslands and occurred in all 20 sites (Table S2).

### Soil sampling

We collected soil subsamples from each quadrat. While collecting soil subsamples, surface litter was removed, and the top 15 cm of soil was sampled using a shovel. A subsample of 15 cm long and 5 cm thick was unloaded in a bucket. We repeated the procedure in each quadrat. We mixed the subsamples thoroughly for those of 'lawns' and of 'tall grass' yielding 20 composite soil samples. We sieved the subsamples to remove roots, stones, pebbles, and other non-soil materials. Quartering was done by dividing the thoroughly mixed soils into four equal parts. Two opposite quarters were discarded, the remaining two quarters were remixed, and the process was repeated until the sample reached 500 g. The soil samples (n=20) were placed in airtight zip-lock plastic bags for chemical analyses. While packing, precaution was taken not to lose the moisture.

### Chemical analysis

Air-dried green leaf and green stem were oven-dried for 48 hours at 60 °C, grinded and sieved over a 2mm sieve for chemical analysis. Crude protein (CP; defined as 6.25 x percentage nitrogen), phosphorus, acid detergent fibre (ADF), neutral detergent fibre (NDF) and silica were determined for green leaf and green stem. Nitrogen was determined by semi-micro Kjeldahl method in Dry-Block digester and phosphorus by tissue digestion in block digester (AOAC, 1990). NDF and ADF were measured by the methods described by (Van Soest, 1982). Silica concentration was determined by the gravimetric method (AOAC, 1990). All the measured nutrient concentrations were expressed as percentage dry matter (% DM). Soil pH was measured by the distilled water method (at a soil: water ratio of 1: 2.5) and soil moisture content in weight (w/w %) was calculated by the gravimetric method (Wilke, 2005). Soil organic matter was determined by the Walkely-Black wet combustion method (De Vos et al., 2007). Available phosphorus was determined by the modified Olsen's method and soil nitrogen (N) by spectrophotometric method (Schoenau and O'Halloran, 2008). Samples of vegetation and soils were chemically analysed by the Local Initiatives for Biodiversity, Research and Development (Li-Bird) in Pokhara, Nepal.

### Data analyses

To compare the forage qualities between grazing lawns and tall grasslands, we quantified structural [aboveground biomass ($g.m^{-2}$), height (cm), bulk density ($g.m^{-3}$), and proportion of green leaf and stem (dimensionless)] and chemical parameters (w/w %) of the vegetation. We transformed the response variables to meet the statistical assumptions of normality and homogeneity of variances using log-transformation in most of the cases and arcsine transformation for proportion and percentage data (Wilson et al., 2013). Aboveground biomass, bulk density, and proportion of green leaf were compared between grazing lawns and tall grasslands using paired t-tests. We compared height and proportion of green stem using a Wilcoxon signed-rank test.

We used beta regression (Ferrari and Cribari-Neto, 2004), which is more flexible than transformation-based analyses for percentage or proportion data (Douma and Weedon, 2019), to quantify the effect of grassland states (grazing lawn vs. tall grassland) and grass parts (leaf vs. stem) on nutrient concentration in the forage. The statistical significance of the observed deviation between the grazing lawns and tall grasslands and between grass parts was investigated by a posthoc Tukey-test. Nutrient concentration of four graminoids (viz., *I. cylindrica, V. zizanioides, D. bipinnata,* and *S. spontaneum*) that were most abundant on both the grazing lawns and tall grasslands (Table S2) were compared to determine the within-species variation that occurred due to grassland state (grazing lawn vs. tall grassland). We compared soil properties of both grasslands to investigate the characteristics of underlying soils. Soil moisture was compared using a Wilcoxon signed-rank test. Other soil parameters (soil pH, soil organic matter, soil nitrogen and available phosphorus) were compared using paired t-tests. Descriptive statistics of transformed data were back-transformed and presented for interpretation (for instance, for the 95% confidence intervals).

We used a multivariate technique PCA (principal component analysis) to determine the correlation between forage characteristics and grassland state. All statistical tests were performed using R software (R Core Team, 2021). R package *vegan* 2.5.6 (Oksanen et al., 2019) was used for species diversity analysis and multivariate analysis. All graphs were produced in R using *ggplot2* (Wickham, 2021).

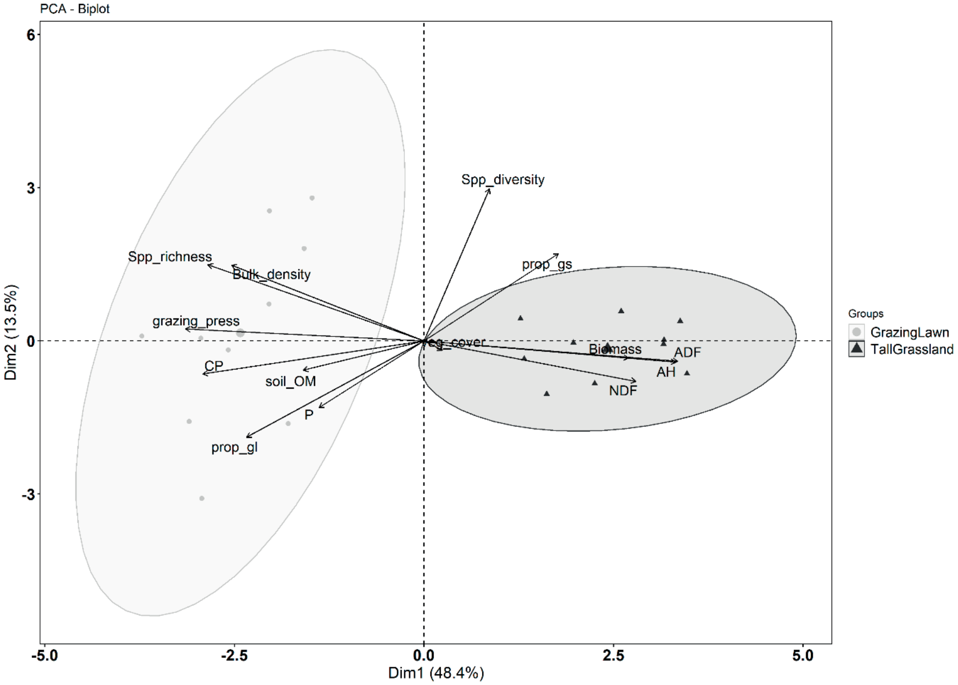


**Figure 2.3:** Principal component analysis (PCA) for variables related to forage physical and chemical properties between grazing lawns and tall grasslands from Bardia National Park. Grazing lawns are indicated by grey dots and tall grasslands by black triangles. The ellipses indicate the 95% confidence intervals. The length of the solid arrows is proportional to its importance and the angle between two arrows reflects the magnitude of the correlation between variables. Response variables are coded as: AH = average height, Biomass = aboveground biomass, Bulk_Density = bulk density, prop_gl = proportion of green leaf, prop_gs = proportion of green stem, veg_cover = percentage vegetation cover, grazing_press = grazing pressure, soil_OM = soil organic matter, CP = crude protein in vegetation, P = Phosphorus concentration in vegetation, NDF = neutral detergent fibre, ADF = Acid detergent fibre, Spp_diversity = Shannon diversity index, and Spp_richness = Chao1 index of species richness.

### Forage quality in grazing lawns and tall grasslands

Vegetation physical properties on grazing lawns were significantly different than on tall grasslands (Table 2.1). There was a difference in aboveground biomass between grazing lawns and tall grasslands. The ratio of aboveground biomass from grazing lawns to that from tall grasslands was 0.2 (95% CI: 0.15 – 0.28). Likewise, bulk density was significantly higher in grazing lawns than in their corresponding tall grasslands with a lawn-to-tall grass ratio of 5.4 (95% CI: 3.2 to 9.2). Vegetation height differed between grazing lawns and tall grasslands with a median difference of -95.82 cm (85% CI: -119.9 to -86.09). Grasses on the grazing lawns had a higher percentage of green leaf (up to 60%) compared to those on tall grasslands (up to 40%). There was no difference in the proportion of green stem between grazing lawns and tall grasslands (Table 2.1).

**Table 2.1:** Comparison of physical parameters of forage in Bardia National Park (Nepal) of grass in grazing lawns and of tall grasslands. Note that confidence limits (CI) are asymmetrical because of back-transformation.

| Physical parameters | Grazing lawns (GL) | | Tall grasslands (TG) | | Test statistics |
|---|---|---|---|---|---|
| | Mean | 95% CI | Mean | 95% CI | |
| Aboveground biomass (g.m$^{-2}$) | 200 | 134 - 270 | 922 | 602 - 1480 | Paired t-test (t = - 11.55, df = 9, *P<0.001*) *** |
| Bulk density (g.m$^{-3}$) | 5432 | 4024 - 8103 | 992 | 735 - 1480 | Paired t-test (t = 7.32, df = 9, *P<0.001*) *** |
| Average height (cm) | 4.0 | 3.0 - 5.0 | 100 | 87 - 120 | Wilcoxon signed-rank test (*Z = 0, N = 10, P = 0.002*) ** |
| Proportion of green leaf | 0.5 | 0.4 - 0.6 | 0.30 | 0.3 - 0.4 | Paired t-test (t = 3.7, df = 9, *P = 0.004*) ** |
| Proportion of green stem | 0.15 | 0.04 - 0.2 | 0.23 | 0.2 - 0.3 | Wilcoxon signed-rank test (*Z = 9, N = 10, P = 0.10*) ***ns*** |

*, **, *** indicate significant difference at *P*<0.05, <0.01, and <0.001, respectively. ***ns*** - indicates non-significant.

We found significant differences in vegetation nutrient concentration between grass parts (green leaf vs. green stem) and grassland states (grazing lawns vs. tall grasslands) (Table 2.2). Vegetation CP levels were higher in grazing lawns compared to tall grassland and in green leaves compared to green stem (Beta regression, z = -5.7, *P*<0.001, and Beta regression, z = -9.7, *P*<0.001, respectively; Table 2.2). The phosphorus level in lawn grass leaf and stem samples were significantly higher than in their corresponding tall grass samples (Beta regression, z = -3.6, *P<0.001*), whereas there was no difference in grass parts phosphorus levels within grasslands (Beta regression, z = -0.73, *P=0.46*). Likewise, NDF, and ADF concentration of grazing lawn green leaf and green stem were significantly lower than in their corresponding tall grass samples (Beta regression, z = 4.15, and 6.7, and *P<0.001*, respectively), however, the NDF and ADF concentration of grass parts were similar within grazing lawns and tall grasslands [Beta regression, z = 1.7 (*P=0.08*) and 1.9 (*P=0.058*), respectively]. Silica concentration in the vegetation was significantly higher in green leaf compared to stem in both the grasslands (Beta regression, z = -4.9, *P*<0.001), but remained proportionately the same between grassland states (Beta regression, z = 0.05, *P=0.95*).

**Table 2.2:** Chemical concentrations (dw/dw) (mean, 95% CI) of grass parts sampled from grazing lawns and tall grasslands. Note that confidence limits (CI) are asymmetrical because of back-transformation. Letters within the rows indicate significant differences at alpha =0.05 (beta regression followed by Tukey-test).

| Chemical parameters | Grazing lawns | | Tall grasslands | |
|---|---|---|---|---|
| | **Green leaf** | **Green stem** | **Green leaf** | **Green stem** |
| Crude Protein (%) | 9.7 (8.9 - 10) $^{d}$ | 6.5 (5.1 - 7.9) $^{b}$ | 7.7 (7.1 - 8.3) $^{c}$ | 4.2 (3.7 - 4.6) $^{a}$ |
| Phosphorus (%) | 0.2 (0.16 - 0.21) $^{c}$ | 0.2 (0.16 - 0.23) $^{bc}$ | 0.15 (0.12 - 0.18) $^{ab}$ | 0.13 (0.1 - 0.16) $^{a}$ |
| NDF (%) | 76 (74 - 77) $^{a}$ | 75 (71 - 79) $^{ab}$ | 78 (77 - 79) $^{bc}$ | 80 (79 - 81) $^{c}$ |
| ADF (%) | 36 (35 - 38) $^{a}$ | 36 (32 - 40) $^{a}$ | 41 (40 - 42) $^{b}$ | 44 (42 - 46) $^{b}$ |
| Silica (%) | 2.8 (2.4 - 3.1) $^{b}$ | 2.2 (1.7 - 2.7) $^{a}$ | 3 (2.6 - 3.4) $^{b}$ | 2 (1.6 - 2.2) $^{a}$ |

We found noticeable differences in chemical composition of the four graminoids that were most abundant in both grassland states viz., *I. cylindrica, V. zizanioides, D. bipinnata,* and *S. spontaneum* (Figure 2.4). These species represented on average 73 % and 78 % of all grass species on grazing lawns and tall grasslands, respectively. *I. cylindrica* was the most abundant species in both grassland states which represented 62 % and 30 % of all grass species, respectively (Table S2). We found a higher concentration of CP in *I. cylindrica*, *S. spontaneum*, and *V. zizanioides* on grazing lawns than on tall grasslands (Figure 2.4, a). *V. zizanioides* on grazing lawns had significantly higher phosphorus concentration than on tall grassland (Figure 2.4, b). Likewise, *I. cylindrica*, and *S. spontaneum* on grazing lawns had lower NDF and ADF than on tall grasslands (Figure 2.4, c & d). We further found that *S. spontaneum* had a significantly higher concentration of silica on grazing lawns than on tall grasslands (Figure 2.4, e).

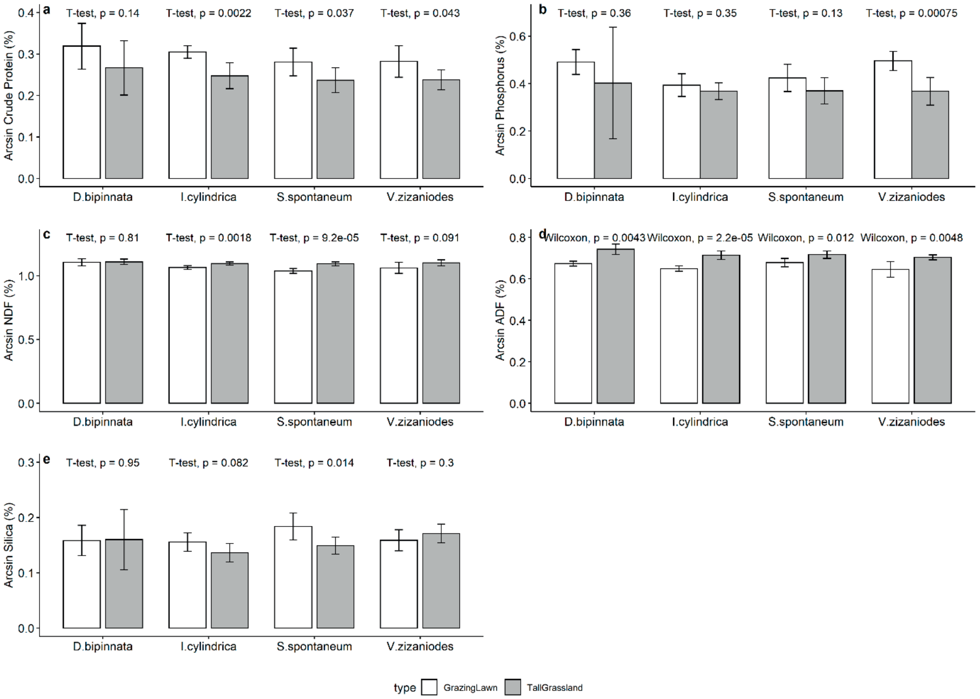


**Figure 2.4:** Comparison of nutrient concentration (a) Crude protein (b) phosphorus (c) NDF (d) ADF and (e) silica of grass species that are most abundant in grazing lawns and tall grasslands. Error bars indicate 95% confidence limits.

### Underlying soil properties

Soils of grazing lawns and tall grasslands did not differ significantly (Table 2.3) in terms of soil moisture, pH, soil, and available phosphorus. Soil organic matter differed significantly between grazing lawns and tall grasslands with lawns having higher loads than tall grasslands (Table 2.3).

**Table 2.3:** Underlying soil properties (mean, 95% CI) of grazing lawn and tall grassland. Note that confidence limits (CI) are asymmetrical because of back-transformation.

| Soil properties | Grazing lawns | Tall grasslands | Test statistics |
|---|---|---|---|
| Soil Moisture (%) | 8 (4.8 - 12) | 6 (3.0 - 10) | Wilcoxon signed-rank test (*Z=46, N=10, P=0.05*) **ns** |
| Soil pH | 7.4 (7.2 - 7.6) | 7.5 (7.3 - 7.6) | Paired t-test (t = - 0.91, df=9, *P = 0.38*) **ns** |
| Soil Organic Matter (%) | 1.4 (1.2 - 2.0) | 1.0 (0.7 - 1.4) | Paired t-test (t = 3.73, df = 9, *P = 0.004*) ** |
| Soil Nitrogen (%) | 0.15 (0.15 - 0.23) | 0.15 (0.09 - 0.23) | Paired t-test (t = 1.01, df = 9, *P = 0.33*) **ns** |
| Available phosphorus (ppm) | 15 (9.2 - 20) | 17 (9.8 - 24) | Paired t-test (t = - 1.3, df = 9, *P = 0.22*) **ns** |

** indicates significant difference at *P*<0.01. ***ns*** indicates non-significant.

# Discussion

### Forage quality in grasslands of Terai Arc Landscape

We analysed the physical and chemical composition of grassland vegetation from grazing lawns and tall grasslands in Bardia NP during the hot-dry season and found markedly different physical and chemical compositions. We found that grazing lawns were characterised by high bulk density, high proportion of green leaves, a high concentration of CP and phosphorus, and lower concentration of NDF and ADF. From the herbivore perspective, these are all desired characteristics. Hence, as expected, grazing pressure was higher in grazing lawns than in encroaching tall grasslands. The grazing lawns occurred in soils with a higher organic matter, and they had a higher species richness. Tall grasslands, on the other hand, had higher biomass, NDF and ADF. These findings corroborate the previous studies in grazing lawns from other parts of the world, viz., African savannas (Archibald, 2008; Arnold et al., 2014; Cromsigt et al., 2017; Cromsigt and Olff, 2008; Grant and Scholes, 2006; Hempson et al., 2015; McNaughton, 1984; Veldhuis et al., 2016, 2014; Verweij et al., 2006), and Asia (Ahrestani et al., 2011; Karki et al., 2000; Moe and Wegge, 2008) where grazing lawns are characterised by short, grazing-tolerant grasses with higher nutrient concentrations and digestible energy content, higher biomass per volume and higher proportions of leaves to stems. Our study expands the findings from much drier savannas into dry monsoon grasslands that reflect past human interventions (Kumar et al., 2020; Ratnam et al., 2019, 2016). Indeed, our study area with Cwa-climate (monsoon-influenced humid subtropical climate) has an average of 1800 mm annual precipitation. Very few studies (Karki et al., 2000; Moe and Wegge, 1997; Pradhan et al., 2008; Wegge et al., 2006) have been executed in the Terai-Duar Savanna and Grasslands with such a Cwa-climate, and thus, our study adds to insights gained in other areas far outside the climate envelope of savannas (Sankaran, 2005). Moreover, we draw attention to the fact that floristically the grassland states within forested landscape in the Terai-Duar Savanna and Grasslands are not different, but that lawns and tall grasslands represent two alternative states of a similar plant community. This is a marked difference from the iconic Serengeti ecosystem where the grazing lawns are floristically different from the tall grasslands (Cromsigt et al., 2017). And yet, despite the floristic similarity, we show a similar nutritional elevation in these man-made grazing lawns as found in African savanna grazing lawns.

### The implications of improved forage quality

Depending on herbivore mouth dimensions, the higher bulk density on grazing lawns will enable higher intake rates per bite compared to tall grass swards (Laca et al., 1992; Stobbs, 1973; van Langevelde et al., 2008). Moreover, the higher proportion of green leaf in grazing lawns will ensure that each bite will contain more green leaf, and hence will lead to higher rates of energy gain. Likewise, the improved leaf quality metrics (higher

CP and phosphorus and lower percentage of NDF and ADF) of grazing lawns should ensure higher digestibility and nutrient intake compared to that from tall grasslands. Hence, grazing lawns are likely important nutrient sources from where herbivores can maximise the concentration of protein and phosphorus in their diet.

Chital, the most abundant primary prey of the tiger in the Bardia NP, utilises open grassland heavily for grazing (Moe and Wegge, 1997, 1994; Pokharel and Storch, 2016). If we estimate the daily requirement of nitrogen for an adult female chital with an average body mass of 50 kg from the known allometric relationship (Ahrestani et al., 2012; Prins, 1996; Prins and Van Langevelde, 2008), then she requires 7.6% CP for maintenance, 9.2% CP for reproduction, and 11.8% CP for lactation, respectively. Chital can meet their nitrogen requirement from the grazing lawns for maintenance and reproduction, however, grass nitrogen is still below requirement for lactating females even from grazing lawns (Table 2.2). Likewise, phosphorus is a limiting factor for herbivores in the grasslands of the Bardia NP as the forage generally does not meet the minimum requirement reported for ruminants (0.2 – 0.4%; Moe, 1994). These requirements of nutrients are derived from livestock industry norms and may be too high for wild ruminants (e.g., Wallis De Vries et al., 1999). Notwithstanding these limitations, chital and other deer can obtain higher levels of nitrogen and phosphorus in the forage from the grazing lawns compared to the tall grasslands during the nutrient-bottleneck period i.e., during the hot-dry season. The hot-dry season is the peak lactating period of the deer when females require high nutrients compared to other seasons. Ahrestani et al., (2012) reported that chital in South Indian tiger reserves have parturition peak timing between February–April, the season when available plant quality was above the minimum required by lactating females. Likewise, Mishra (1982) documented a distinct seasonal pattern of breeding cycle in chital with December – March in Chitwan. The chital in Bardia NP also exhibited a peak parturition period between January – March (80% in the second week of February) where majority of Does were observed with fawns (pers. obs.), the season when grassland were preferentially used by chital in Bardia NP (Moe and Wegge, 1994). Hence, the availability of required nutrients during the nutrient-bottleneck season will influence both the survival and fitness of lactating females and fawns which have an implication on the species population dynamics. If nutrition falls below the minimum requirements, physiological functions like maintenance, growth, reproduction, and lactation are compromised (Kiffner and Lee, 2019; Van Soest, 1982) which may lead to poor health and reproduction of herbivores and might have a cascading negative effect on the tiger population due to food availability.

### Management implications

Tall grasslands in the study region with higher quantity but of lower quality vegetation are less beneficial for the small and medium body-sized herbivores. The forage requirement of these wild herbivores is different from large roughage feeders such as gaur, arna (*Bubalus arnee*), greater one-horned rhinoceros (*Rhinoceros unicornis*), and Asian elephant (*Elaphas maximus*) (Ahrestani et al., 2016, 2012; Pradhan et al., 2008; Wegge et al., 2006) because of body mass and digestive physiology (Illius and Gordon, 1992; Prins and Olff, 1998). The former requires higher quality forage for their maintenance and production. At present, there is a relatively low density of large roughage grazers in this subtropical region that at high density can possibly create, and certainly maintain grazing lawns (Ahrestani and Sankaran, 2016) but currently are unable to do so (often because they occur in such a low density that they are functionally extinct). In contrast to African white rhinoceroses (*Ceratotherium simum*), greater one-horned rhinoceroses do not closely crop the sward. Furthermore, greater one-horned rhinoceros graze predominantly on the riverine tall grassland dominated by *S. spontaneum* (Pradhan et al., 2008). Indeed, they appear to chomp off grasses to reach the sweet base of stems and are thus very atypical “grazers” (pers. obs.). With the existing rhinoceros density of 0.3 $km^{-2}$ in Bardia NP (Subedi et al., 2013) and with their grazing modus, it is therefore unlikely that they could create and maintain grazing lawns. Also, Asian elephants have never been reported to convert forests into grasslands (Pradhan et al., 2008). Medium body-sized herbivores do not seem to be able to create or maintain grazing lawns in the Terai grasslands. Thus, the Department of National Parks and Wildlife Conservation and National Trust for Nature Conservation of Nepal, may benefit from translocating large mammals like greater one-horned rhinoceros, arna and gaur in order to maintain and expand the necessary lawns.

Our study suggests that the mosaic of tall grassland and grazing lawns found in the study region is not caused by edaphic factors, such as soil nutrients, soil pH, or soil moisture (Table 3). This is in contrast to the conclusion by others that grazing lawns are often formed in areas where soil mineral concentrations are higher e.g., volcanic soils, sodic sites, near termite moulds, near elephant or rhinoceros dung piles, and abandoned kraals (Cromsigt et al., 2017; Fox et al., 2015; Grant and Scholes, 2006). We did find higher loads of soil organic matter in the soil under grazing lawns as compared to that of tall grasslands. This could however be due to the supplementation of dung and urine from herbivores to the lawns while grazing (Moe and Wegge, 2008). Moreover, high nutrient maintenance costs of continuously growing grasses in grazing lawns can only be achieved if there are sufficient nutrients to sustain it which could only be achieved with continual nutrient replenishment through dung and urine inputs. The improved nutritional properties of individual grass species when growing in grazing lawns, may be a result of plant phenology brought about by frequent grazing.

We, thus, posit that the grazing lawns in the Cwa-climate grasslands result from patch-selective grazing immediately after patchy burning or cutting and not by differences in underlying soil properties, but that some soil differentiation occurs after these lawns have formed and a positive feedback loop through a dung feedback cycle (or mineralization cycle) starts. We do not yet know how persistent these mosaics are, but from experience we know that the landscape patterns can be reset every year by a fire. Like African savannas, fire is an integral component of the subtropical grasslands (Ratnam et al., 2019; Sankaran et al., 2005). After burns, the entire burnt area consists of nutritious new re-sprout (Donaldson et al., 2018; Moe and Wegge, 1997) which interrupt the positive interaction between grazing and grazing lawns by diffusing the grazing pressure away from the lawns (Archibald et al., 2005; Van Langevelde et al., 2003).

The very high growth rate and fast production of combustible materials due to hot and humid growing season of this location as characterised by the Cwa-climate make these grasslands fundamentally different from savanna grasslands in arid and semi-arid ecosystems. This implies that African savanna studies on lawns cannot yield sufficient insight into how grazing lawns come into existence in the highly productive subtropical grasslands. Apart from major fires, we suspect that past agricultural practices in what are now the grasslands in the park and the ongoing grassland management by the park (cutting and burning) and thatch harvesting by local people are likely to be of utmost importance to understand the present-day functioning of grazing lawns for the prey-base of tigers in areas where the large roughage feeders are now absent or in low density.

## Conclusion

Grazing lawns constitute an important nutritional supplement to burning and grass cutting for maintaining abundant population of small to medium sized ungulates. Management actions such as large-scale burning may diffuse grazing pressure and lead to the disappearance of these lawns. Efforts to maintain these grazing lawns could prevent herbivores from needing to supplement their diet elsewhere in the park either with browse, forest grasses or agricultural crops. Hence, as long as the roughage grazers are absent, regular management of these highly productive subtropical grasslands is essential to maintain grazing lawns in the national parks of the Terai Arc Landscape

**Data availability:** The data that support the findings of this study are openly available in 4TU.ResearchData. dataset. https://doi.org/10.4121/17708117.v1

# Appendix

## Appendix 1

Table S1: Correlation coefficient (ordination scores) of the variables. Value ranges from -1 to 1. Positive value indicates strong positive correlation and negative value indicates negative correlation.

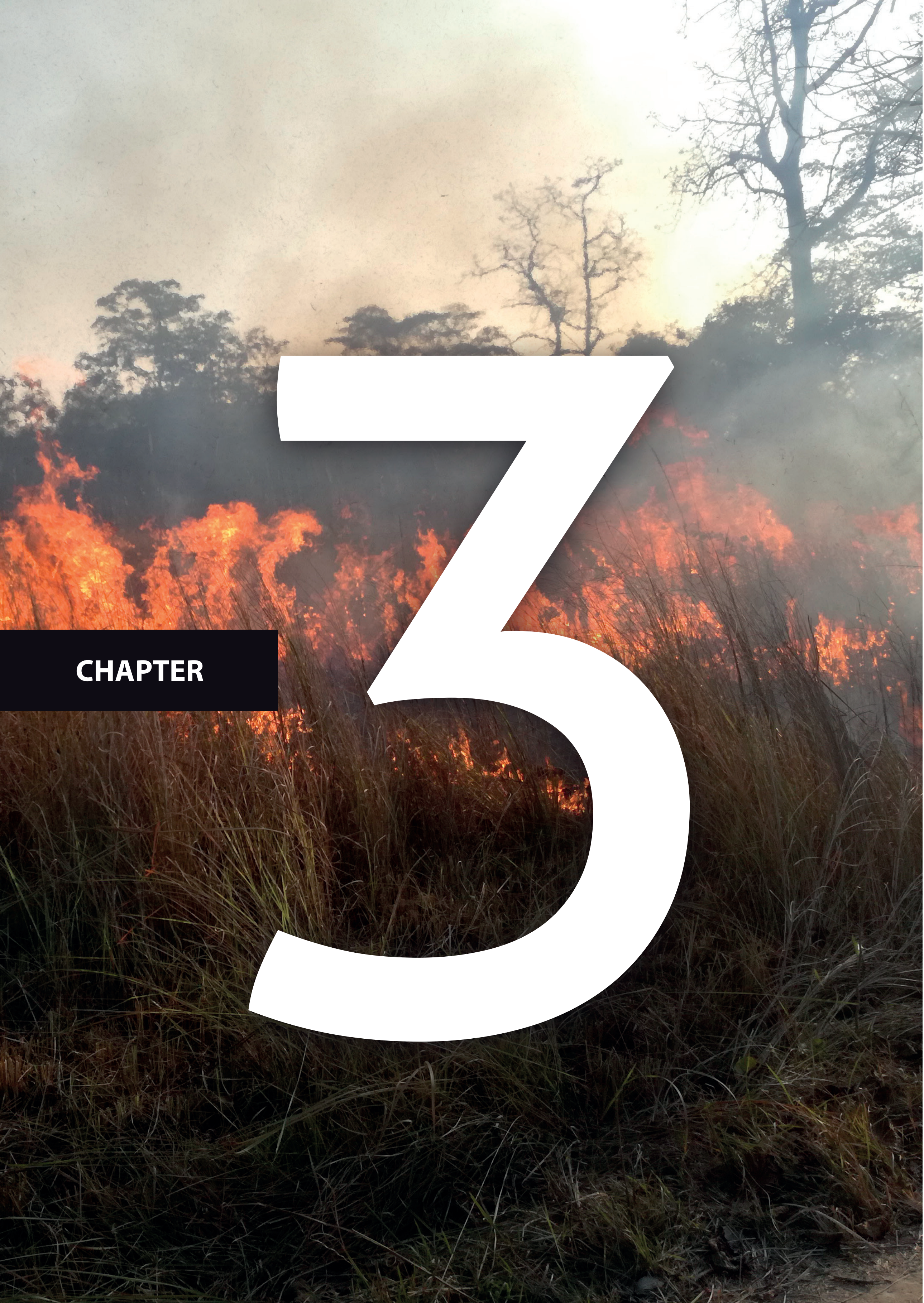
| Variables* | Dim.1 | Dim.2 | Dim.3 | Dim.4 | Dim.5 | Dim.6 | Dim.7 | Dim.8 | Dim.9 | Dim.10 |
|---|---|---|---|---|---|---|---|---|---|---|
| AH | 0.94 | -0.12 | 0.11 | -0.11 | 0.03 | -0.02 | 0.01 | -0.08 | -0.14 | -0.16 |
| Biomass | 0.77 | -0.09 | 0.1 | 0.24 | -0.39 | -0.17 | -0.17 | -0.31 | -0.15 | 0.06 |
| Bulk_density | -0.72 | 0.42 | 0.05 | 0.37 | -0.3 | 0.15 | -0.1 | 0.1 | 0.05 | -0.12 |
| prop_gl | -0.66 | -0.54 | 0.16 | -0.15 | 0.37 | -0.1 | -0.17 | -0.11 | -0.06 | -0.09 |
| prop_gs | 0.5 | 0.48 | 0.58 | -0.08 | 0.26 | -0.07 | -0.03 | -0.14 | 0.24 | -0.11 |
| veg_cover | 0.07 | -0.05 | 0.9 | -0.05 | -0.17 | -0.26 | 0.02 | 0.26 | -0.09 | 0.06 |
| grazing_press | -0.89 | 0.07 | 0.14 | 0.22 | -0.09 | -0.13 | -0.12 | -0.16 | 0.21 | 0.12 |
| soil_OM | -0.45 | -0.16 | 0.25 | -0.72 | -0.19 | 0.35 | -0.1 | -0.08 | 0.03 | 0.08 |
| CP | -0.83 | -0.18 | -0.02 | 0.18 | 0.4 | -0.2 | -0.06 | 0.02 | -0.09 | 0.07 |
| P | -0.39 | -0.37 | 0.49 | 0.47 | 0.06 | 0.42 | 0.21 | -0.1 | -0.09 | -0.01 |
| NDF | 0.79 | -0.23 | 0.05 | 0.27 | 0.2 | 0.25 | -0.33 | 0.11 | 0.09 | 0.03 |
| ADF | 0.95 | -0.11 | -0.02 | 0.07 | 0.06 | 0.09 | -0.15 | 0.14 | 0.02 | 0.08 |
| Spp_diversity | 0.24 | 0.85 | 0.08 | -0.02 | 0.36 | 0.13 | 0.04 | -0.08 | -0.18 | 0.14 |
| Spp_richness | -0.81 | 0.42 | 0.02 | -0.08 | -0.07 | 0.05 | -0.28 | 0.05 | -0.21 | -0.09 |

* AH = average height, Biomass = aboveground biomass, Bulk_Density = bulk density, prop_gl = proportion of green leaf, prop_gs = proportion of green stem, veg_cover = percentage vegetation cover, grazing_press = grazing pressure, soil_OM = soil organic matter, CP = crude protein in vegetation, P = Phosphorus concentration in vegetation, NDF = neutral detergent fibre, ADF = Acid detergent fibre, Spp_diversity = Shannon diversity index, and Spp_richness = Chao1 index of species richness.

## Appendix 2

Table S2: Relative abundance of grass species on grazing lawns and tall grasslands in Bardia National Park. We used local names for species which we were not able to identify. Nomenclature follows Bor (1960).

| Species | Family | Relative abundance in Grazing lawns (%) | Relative abundance in Tall grasslands (%) |
|---|---|---|---|
| *Imperata cylindrica* (L.) Raeusch. | Poaceae | 62 | 30 |
| *Vetiveria zizanioides* (L.) Nash | Poaceae | 6 | 17 |
| *Hemarthria compressa* (L. f.) R. Br. | Poaceae | 5 | 0 |
| *Desmostachya bipinnata* (L.) Stapf | Poaceae | 2 | 15 |
| *Cynodon dactylon* (L.) Pers. | Poaceae | 3 | 0 |
| *Saccharum spontaneum* (L.) | Poaceae | 3 | 16 |
| *Saccharum bengalense* (Retz.) | Poaceae | 0 | 4 |
| *Narenga porphyrocoma* (Hance ex Trin.) Bor. | Poaceae | 1 | 14 |
| *Digitaria spp* (Heister ex Fabr.) | Poaceae | 2 | 0 |
| *Chrysopogon aciculatus* (Retz.) Trin. | Poaceae | 5 | 0 |
| *Parthenium hysterophorus* (L.) | Asteraceae | 3 | 2 |
| *Ageratum houstonianum* (Mill.) | Asteraceae | 0 | 1 |
| *Oxalis spp* (L.) | Oxalidaceae | 2 | 0 |
| *Euphorbia spp* (L.) | Euphorbiaceae | 1 | 0 |
| *Cyperus spp* (L.) | Cyperaceae | 2 | 0 |
| Kharuki (unidentified B) | | 1 | 0 |



# CHAPTER

# 3

# Fire and forage quality: post-fire regrowth quality and pyric herbivory in subtropical grasslands of Nepal

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# Abstract

Fire is rampant throughout subtropical South and Southeast Asian grasslands. However, very little is known about the role of fire and pyric herbivory on the functioning of highly productive subtropical monsoon grasslands lying within the Cwa-climatic region. We assessed the temporal effect of fire on post-fire regrowth quality and associated pyric-herbivory in the subtropical monsoon grasslands of Bardia National Park, Nepal. Every year, grasslands are burned as a management intervention in the park, especially between March and May. Within a week after fire, at the end of March 2020, we established 60 m x 60 m plots within patches of burned grassland in the core area of the park. We collected grass samples from the plots and determined physical and chemical properties of the vegetation at regular 30-day intervals from April to July 2020, starting from 30 days after fire to assess post-fire regrowth forage quality. We counted pellet groups of cervids that are abundant in the area for the same four months from 2 m x 2 m quadrats that were permanently marked with pegs along the diagonal of each 60 m x 60 m plot to estimate intensity of use by deer to the progression of post-fire regrowth. We observed strong and significant reductions in crude protein (mean value 9.1 to 4.1 [55% decrease]) and phosphorus (mean value 0.2 to 0.11 [45% decrease]) in forage collected during different time intervals i.e., from 30 days to 120 days after fire. Deer utilised the burned areas extensively for a short period, *i.e.*, up to two months after fire when the burned areas contained short grasses with a higher level of crude protein and phosphorus. The level of use of post-fire regrowth by chital (*Axis axis*) differed significantly over time since fire, with higher intensity of use at 30 days after fire. The level of use of post-fire regrowth by swamp deer (*Rucervus duvaucelii*) did not differ significantly until 90 days after fire, however, decreased significantly after 90 days since fire. Large-scale single event fires, thus, may not fulfil nutritional requirements of all species in the deer assemblage in these subtropical monsoon grasslands. This is likely because the nutritional requirements of herbivores differ due to differences in body-size and physiological needs – maintenance, reproduction, and lactation. We recommend a spatio-temporal manipulation of fire to reinforce grazing feedback and to yield forage of high quality for the longest possible period for a sustainable high number of deer to maintain a viable tiger population within the park.

**Keywords:** burned grassland, Cwa climate, grazer and mixed feeders, grazing lawns, mesofaunal deer assemblage, nutrients.

# Introduction

Fire is an important component of grassland ecosystems and is considered a cost-effective management tool to prevent the successional change of grassland towards forests (Archibald, 2008; Ratnam et al., 2016, 2011; Sankaran et al., 2005; Van Langevelde et al., 2003). Numerous studies indicate that fire-grazing interactions, also termed 'pyric herbivory', are complex and can modify grassland systems by creating mosaics of vegetation that vary in structure, composition, quality, and quantity (Allred et al., 2011; Harrison et al., 2003; Klop et al., 2007; Sabiiti et al., 1992; Trollope, 2011). With these notable impacts, many wildlife managers consider pyric herbivory essential for the conservation and management of savannas and other grasslands, including the remaining subtropical grasslands of Asia. In Nepal and India, few subtropical monsoon grasslands remain at the foot of the Himalayas. These grasslands rank among the world's most productive (Lehmkuhl, 1994; Peet et al., 1999a) and represent the globally important ecoregion 'Terai-Duar Savanna and Grasslands' (Olson and Dinerstein, 2002). These grasslands are burned annually by park staff and local people to stimulate new grass growth, enhance grazing opportunities, increase the availability of good thatching grass, remove woody encroachment, increase visibility, and reduce fire hazards (Lehmkuhl, 1994; Peet et al., 1999a). In addition, much burning takes place due to accidents and lightning. Identifying the effects of fire on forage quality and associated pyric herbivory in the subtropical grasslands is paramount for wildlife conservation and management because the Asian subtropical monsoon grasslands host many threatened and endangered vertebrates, for example, Bengal florican (*Houbaropsis bengalensis*), hispid hare (*Caprolagus hispidus*), wild water buffalo (*Bubalus arnee*), Greater one-horned rhinoceros (*Rhinoceros unicornis*), Royal Bengal tiger (*Panthera tigris*), hog deer (*Axis porcinus*), and swamp deer (*Rucervus duvaucelii*).

The role of fire, herbivory, and their interaction effect on ecosystem functioning have been extensively studied through experiments and modelling on African savannas and North American prairies (Allred et al., 2011; Archibald and Bond, 2004; Archibald and Hempson, 2016; Donaldson et al., 2018; Fuhlendorf et al., 2009; Klop et al., 2007; Leverkus et al., 2018; Raynor et al., 2016; Van de Vijver et al., 1999; Veach et al., 2014). However, very little is known about the role of fire and pyric herbivory on functioning of the highly productive subtropical monsoon grasslands lying within the Cwa-climatic region (but see for example, (Ahrestani and Sankaran, 2016; Moe and Wegge, 1997; Ratnam et al., 2019, 2016; Sankaran, 2016), and experimental manipulative studies are largely lacking.

In subtropical monsoon grasslands, a large proportion of grasslands is burned every year, a practice that has long been an important element of grasslands in the region

(Dinerstein, 1979; Ratnam et al., 2016, 2011; Sankaran, 2016). Burning of subtropical monsoon grasslands has been promoted as a cost-effective method for grassland management in protected areas of the Cwa climate region (and also in Nepal). Therefore, we aimed at exploring the effect of fire on forage quality and associated pyric herbivory in an area that lies in the mesic region but receives a higher amount of mean annual precipitation than mesic savannas (*cf.* Ratnam et al., 2019, 2016; Sankaran et al., 2005).

Recent studies in pyric herbivory illustrate that burning can affect the movement of herbivores by attracting animals towards the burned areas due to regrowth after fire with higher concentrations of nutrients including nitrogen and phosphorus (Allred et al., 2011; Eby et al., 2014; Raynor et al., 2016). Recently burned grasslands contain forage in lower quantity but of higher quality (Allred et al., 2011) and are used more heavily by smaller body-sized ruminants than by larger body-sized herbivores (Donaldson et al., 2018; Eby et al., 2014). Unlike larger body-sized herbivores, small body-sized ruminants have high metabolic requirements, thus, need high forage quality to meet their metabolic demands (Gordon and Illius, 1996; Prins and Olff, 1998; van Langevelde et al., 2008). Thus, it can be argued that burning may not be an appropriate grassland management strategy used for herbivore conservation in areas with assemblages of different body-sized grazing herbivores. Fire can create a homogeneous landscape (Archibald et al., 2005) which may not be suitable for the existing assemblage of different body-sized grazing herbivores found in subtropical monsoon grassland in Nepal.

Burning interrupts the positive interaction between grazing and grazing lawns by diffusing grazing pressure away from grazing lawns. Grazing lawns are ‘nutrient hotspots’ from where herbivores can maximise their energy intake (Thapa et al., 2021) and require frequent grazing to persist (Hempson et al., 2015; McNaughton, 1984). However, frequent fire in a productive system (due to high rainfall) but a low density of grazing herbivores (Ratnam et al., 2019) may cause grazing lawns to disappear. Consequently, tall, and fast-growing vegetation may re-establish in the area, which is less beneficial to small and medium body-sized grazers. The resultant vegetation is highly flammable in the dry season when the tall graminoids have dried up (Ratnam et al., 2019), and if fire is anthropogenically induced, often indiscriminate (Van Langevelde et al., 2003).

Therefore, in order to use fire as a grassland management tool for the conservation and management of wild herbivores in subtropical grasslands, it is important to understand the dynamics of fire-grazing interactions and factors driving pyric herbivory. Here, we report on the effect of a single fire event on the post-fire regrowth quality, tested the quality of post-fire regrowth as forage, and the resultant response of grazing herbivores to post-fire regrowth in the subtropical grasslands of Bardia National Park (Bardia NP, West Nepal; Figure 1). First, we assessed the temporal pattern of post-fire regrowth quality. Second, to examine whether the intensity of use is a function of post-fire regrowth quality, we gauged the response of grazing herbivores to post-fire regrowth over time. The intensity of use of the burned area by different body-sized cervids may vary because of their body-size (Cromsigt et al., 2009; Prins and Beekman, 1989; Prins and Olff, 1998) and with respect to their feeding mode. Thus, we further assessed the intensity of use of post-fire regrowth by the two most abundant cervids, chital (*Axis axis*) and swamp deer.

## Materials and Methods

### Study area

We carried out our study in Bardia NP. The park lies in the Western Terai of Nepal (28$^0$23' N, 81$^0$30' E, elevation 100–1500 m a.s.l., Figure 3.1). The Terai denotes the lowlands between the Ganges and the Himalayan foothills. The park covers an area of ~ 970 km$^2$ and is surrounded by a buffer zone of ~ 500 km$^2$. The national park is a 'Level I – Tiger Conservation Unit' (Wikramanayake et al., 1998) and forms an essential component of the global tiger conservation strategy. The park and the surrounding buffer zone hold the second largest population of tiger in Nepal with an estimated density of ~ 5 individuals/100 km$^2$ and an estimated prey density of ~78 km$^{-2}$ (DNPWC and DFSC, 2018). The park is home to five cervids - from smaller to larger based on average adult body mass – northern red muntjac (*Muntiacus vaginalis*) with an average weight of ~ 30 kg, hog deer ~ 40 kg, chital ~ 50 kg, swamp deer ~ 150 kg, and sambar (*Rusa unicolor*) ~ 185 kg. Here, we classified the assemblage of these cervids as a mesofaunal deer community (Ahrestani et al., 2016). Chital is the most abundant and at the moment the primary prey species of the tiger in Bardia NP (Upadhyaya et al., 2018) with a reported density of ~ 50 deer.km$^{-2}$ (DNPWC and DFSC, 2018). Muntjac and sambar are forest dwellers; are classified as browsers (Ahrestani et al., 2016) and are seen very rarely in the grasslands. Hence, the animals of interest for our study were chital - mixed feeder, swamp deer and hog deer - categorised as grazers (Ahrestani et al., 2016).

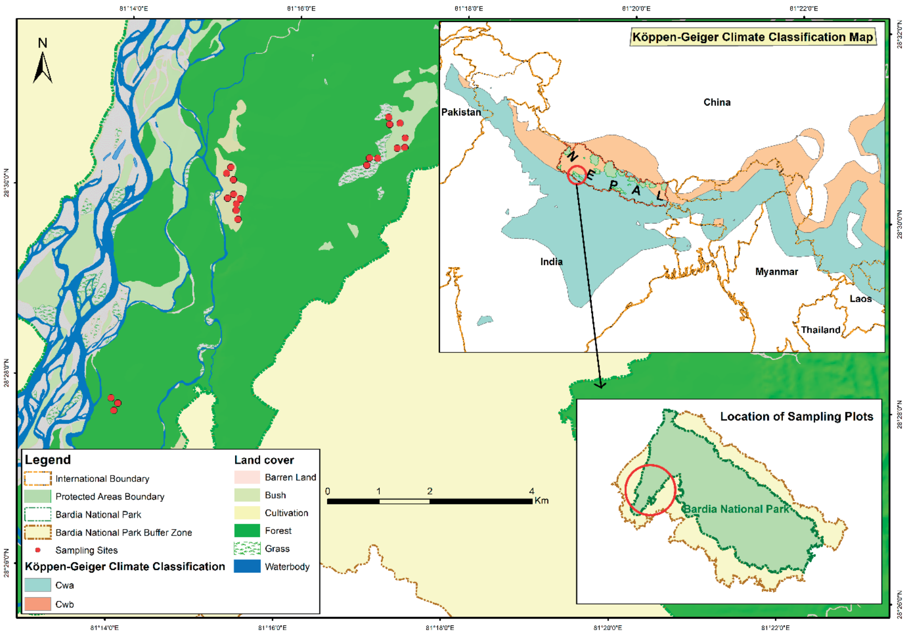


**Figure 3.1:** Locations of sampling plots within burned grasslands in Bardia National Park, Nepal. Bardia National Park lies within Terai Arc Landscape and has a Cwa-climate according the Köppen classification (areas with light blue in the inset, top-right).

The area has three distinct seasons: the very wet monsoon (June to September), the dry frost-free winter (October to January), and the hot dry summer (February to May). The monthly mean temperature of the area ranges between 10 $^0$C in January and 45 $^0$C in June and the park receives a mean annual rainfall of ~1,700 mm (Figure 3.2). According to the Köppen-Geigen climate classification, the area falls within a Cwa-climate: monsoon-influenced humid subtropical climate (Chen and Chen, 2013), which extends from the Indus River to the South China Sea (Figure 3.1).

Bardia NP consists of diverse landscape elements ranging from riverine floodplain grasslands in the floodplains of the Karnali River and the Babai River; riverine forest; sal (*Shorea robusta* Gaertn. f.) forest; and mosaics of grasslands interspersed within the forests. The grasslands interspersed within the forests originated from human activities (*i.e.*, land conversion) and are maintained either by grazing, grass harvesting or by fire (Brown, 1997; Lehmkuhl, 1994; Peet et al., 1999a; Wegge et al., 2000). *Imperata cylindrica* (L.), *Vetiveria zizanioides* (L.), *Narenga porphyrocoma* (Hance ex Trin.) Bor, and *Saccharum spontaneum* (Retz.) are the abundant graminoids in these grasslands (Peet et al., 1999a; Thapa et al., 2021). The riverine floodplain grasslands along with the grasslands that are interspersed within forests represent the globally important ecoregion 'Terai-Duar Savanna and Grasslands' (Olson and Dinerstein, 2002).

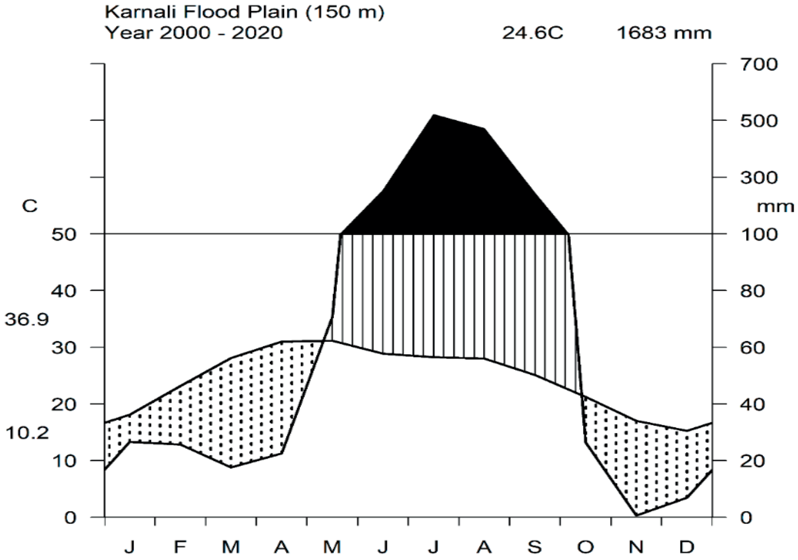


**Figure 3.2:** Walter -Lieth Climate diagram for Bardia NP. The diagram shows the mean rainfall and temperature for 2000 – 2020 (mean of the three weather stations Karnali-Chisapani, Rajapur and Guleriya). The values on the upper right corner indicate the annual average temperature (24.6 $^0$C) and annual total rainfall (1683 mm). Area marked with dots indicates the dry-period; area with vertical lines indicates the humid period; and area in solid black indicates the wet-period (data source: Department of Meteorology and Hydrology, Nepal). March, April, and May are the peak dry-period. This period is characterised by a high frequency of fires in the grasslands.

## Fire regime within Bardia NP

Based on freely available MODIS fire data, a total of 2,013 fires were recorded within Bardia NP and its buffer zone by MODIS satellites from January 2010 to December 2020, out of which, around 75% fires were detected with more than 50% confidence. The maximum number of fire incidents occurred in the year 2016, followed by 2012 and 2019, respectively. The majority of fire incidents is observed in April (~60%), followed by May (~30%), which is consistent with previous studies (Thapa et al., 2021). Except natural barriers (e.g., rivers), only few fire breaks (fire-line or forest roads) are constructed in the park to facilitate reducing the spread of surface fire. The forests in the Bardia NP (~70% of the area) are composed of subtropical species (e.g., sal) that shed large quantity of dry leaves during the winter, which results in a larger accumulation of fuel (Thapa et al., 2021). Likewise, grasslands are also composed of large quantities of litter (Thapa et al., 2021) that supports the spread of fire during the hot dry season.

Burning is common grassland management practice that is being carried out by the park authority since its establishment (Peet et al., 1999a). Local people also initiate fire to ensure good grass growth for next year thatch harvest, but it is not allowed by the park management. Thatch harvesting in grasslands of the protected areas is considered a means to pacify the park-people relationship (Brown, 1997). Fires take place in more than 80% of the total park area (including forests) and almost all the grasslands are burned annually either by park staff or by local people after thatch harvest especially during March – May.

### Experimental set-up

Since 2018, ~ 75 ha (out of ~ 250 ha) of grasslands in the Karnali floodplain are under a long-term experiment where grasses are being mowed frequently to establish the effect of cutting on nutrient concentrations in vegetation. These experimental areas were protected from fire and the remaining areas (~150 ha out of ~250 ha) were burned by park staff for grassland management. Within a week after such management fire at the end of March 2020, we established 60 m x 60 m plots (n=21) randomly in three locations within these 150 ha of burned grassland patches (Figure 3.1). This enabled us to quantify changes in vegetation properties and resultant use by herbivores over a period after the fire. Four quadrats of 2 m x 2 m were permanently marked with pegs along the diagonal of each 60 m x 60 m plot at an equal distance of 20 m from where intensity of use (through pellet groups count) were recorded at regular 30-day intervals for four months (end of April to end of July) from 30 days following the fire.

## Vegetation characteristics

We collected post-fire regrowth grass samples at regular 30-day intervals for four months (from end of April to end of July) from the centre of 60 m x 60 m plots. Post-fire regrowth grass samples were clipped at ground level in a 0.36 $m^2$ frame from each 60 m x 60 m plot and fresh weight was quantified using a digital weighing scale (with a capacity of 600 g and accuracy of 0.5 m; Brand: Equal [class II]) and estimated aboveground biomass. The clipped samples were hand-sorted into green leaf, green stem, dead leaf, and dead stem and left to air dry for 5-6 days at ambient room temperature. The air-dry weights of separated parts were recorded, and proportions of green leaf and dead parts were determined. The separated grass parts were mixed again and packed in a paper bag for chemical analyses. Mean grass height was calculated for each plot by measuring to the nearest centimetre at three points within each 2 m x 2 m quadrat while recording the pellet groups. The same observer collected grass samples, measured the height, and counted pellet groups.

Air-dried grass samples were oven-dried for 48 h at 60 $^{0}$C to prevent caramelisation, grinded, and sieved over a 2 mm sieve for chemical analyses. Nitrogen (N) was determined by a semi-micro Kjeldahl method in dry-block digester; phosphorus (P) by tissue digestion in block digester (AOAC, 1990); neutral detergent fiber (NDF) and acid detergent fiber (ADF) by the method described by Van Soest (1982); and silica by gravimetric method (AOAC, 1990). N:P ratios in plant tissues were calculated to test for nutrient limitation of vegetation growth (e.g., Koerselman and Meuleman, 1996; Ludwig et al., 2001). Nutrient concentrations were measured as percentage dry matter (% DM).

We estimated physical [biomass (g.m$^{-2}$), height (m), bulk density (biomass x height – g.m$^{-3}$), proportion of green leaf, and proportion of dead parts)] and chemical [crude protein (CP; calculated as 6.25 x percentage nitrogen), phosphorus, NDF, ADF and silica] parameters from post-fire regrowth grass samples to examine the effect of fire on post-fire regrowth quality.

## Herbivore use of post-fire regrowth

We used pellet groups as a proxy to measure the intensity of use for grazing (*cf*. Hegland et al., 2010; Kohn and Wayne, 1997; Putman, 1984; Sánchez-Rojas and Gallina, 2000; Skarin, 2007) by the mesofaunal deer assemblage (chital, swamp deer and hog deer) in relation to the post-fire regrowth. We observed deer very rarely lie down and rest in these grasslands, so we assumed that pellet density mainly reflects the intensity of use. Pellet groups were recorded by species based on individual pellet morphology which we were able to do after collecting droppings from deer sighted to defaecate. Pellets of hog deer are rounded more like pigeon-pea shape; pellets of swamp deer are big cylindrical and flat on both ends, whereas pellets of chital are narrow, long cylindrical, smaller than swamp deer and tapered at one end (Ahrestani et al., 2018). Yet, we are very aware of potential misidentification between ungulate dropping (see, for example, (Spitzer et al., 2019). We made our field team familiar with the different morphological features of pellets of the three species, and hence, reduced the possible error of misidentification.

Pellet groups were counted in the 2 m x 2 m quadrats (e.g., Supartono et al., 2021) at regular 30-day intervals for four months following the fire. Pellet groups of which the centre fell outside the boundary line of 2 m x 2 m quadrats were not included in the count and only pellet groups containing five or more pellets were recorded to prevent counting droppings of deer merely passing through. We removed all pellets from each quadrat to avoid recounting during the subsequent surveys. For each plot, we summed the pellets of individual species at the plot level and used them for statistical analysis.

## Data analysis

All statistical analyses were computed using the R-programme, version 4.1.0. (R Core Team, 2021). As there may be a spatial autocorrelation between the datapoints due to the spatial setup of the research design, we checked for spatial dependency of the response variable (especially pellet groups) with respect to places (plots in our case) by calculating Moran's I (Salima and Bellefon, 2018), and plotting the Moran's scatterplot using the 'spdep' package (Bivand and Wong, 2018). We found that there is no/hardly any autocorrelation present in the data (Moran's I = 0.18; Appendix 3.1). The Moran's I index ranges from − 1 (strong negative spatial autocorrelation) to 1 (strong positive spatial autocorrelation), and a value of zero indicates no spatial autocorrelation (Salima and Bellefon, 2018).

Changes in post-fire regrowth physical and chemical properties with respect to time after fire, namely, 30 days to 120 days after fire were estimated to depict the effects of fire on forage quality. A Kruskal-Wallis test using the 'kruskal.test' function followed by multiple comparisons using the 'kruskal' function ('agricola' package) was performed (due to non-normality nature of the data) to compare the differences in post-fire regrowth grass height measured at 30 days, 60 days, 90 days and 120 days after fire, respectively. Linear model analyses were performed for N:P ratios and log-transformed variables (biomass and bulk density) using the 'lm' function to estimate the changes in N:P ratio, biomass and bulk density in post-fire regrowth with respect to different sampling instances. Beta regression was performed for proportion and percentage data (*viz.,* CP, phosphorus, NDF, ADF, proportion of green leaf and dead parts) using the 'betareg' function ['betareg' package (Cribari-Neto and Zeileis, 2010)] to measure the changes in the parameters in the post-fire regrowth with respect to time since fire. The main effects of the beta regression models were evaluated by Type II Wald chi-square ($\chi^2$) tests using the 'Anova' function ['car' package (Fox and Weisberg, 2018)]. Post-hoc multiple comparisons tests were performed using the 'emmeans' function ('emmeans' package) and the 'cld' function ['multicomp' package (Hothorn et al., 2008)] after linear and beta regressions.

To assess the intensity of use (grazing) by the mesofaunal deer assemblage in relation to post-fire regrowth, we performed multiple tests using pellet group count data as a response variable. We tested two statistical models to assess the effects of the post-fire regrowth grass height on (i) intensity of use of burned areas for grazing by Generalised Linear Model (GLM) with Poisson distribution; and (ii) vegetation CP levels by GLM with gamma distribution. Likewise, we also tested the effect of CP levels on the intensity of use by GLM with a Poisson distribution. In addition, we also tested the effect of the post-fire regrowth biomass on the intensity of use by GLM with a Poisson distribution. The GLM analyses were performed using the 'glm' function. R-squared values for the GLM models were calculated using the 'rsq' function (type = KL, 'rsq' package). Wald test was performed to test for the significance of the coefficients of GLMs using the 'wald.test' function ('mdscore' package). We used GLM because of its flexibility and its ability to handle a larger class of distributions for the response variables (Guisan et al., 2002; Guisan and Harrell, 2000; O'Hara and Kotze, 2010; Okamura et al., 2012; Warton et al., 2016). For each GLM with a Poisson distribution model, the residuals were plotted against fitted values (Coelho et al., 2020) and checked for over/under dispersions (Appendix 3.5, 3.6 and 3.7). Likewise, we inspected the correlations between the variables using a correlation map (Appendix 3.2) using the 'ggcorplot' package (Kassambara, 2019). We have not used highly correlated variables (e.g., hight and biomass, Pearson correlation coefficient: r = 0.80) together in a single model, for that reason, we did not have to account for collinearity.

We binned the grass heights into six classes (*viz.*, 0 – 0.20 m; 0.21 – 0.40 m; 0.41 – 0.60 m; 0.61 – 0.80 m; 0-81 – 1.00 m; and > 1.00 m) to identify which grass height classes are favoured by the deer. For each height category, we reassigned '1' for presence of pellet group/s and '0' for absence of pellet group of either chital or swamp deer. We used a Chi-square ($\chi^2$) test to compare the observed pellet group frequency of chital and swamp deer within the different grass height classes. We further calculated the proportion of observed and expected pellet groups per height class for chital and swamp deer and presented it in a graph to assess which grass height classes were preferred by the two deer species. We did this to assess whether or not a differential use of the burned area by two abundant cervids (chital and swamp deer) took place because these two species have a distinct morphology and feeding behaviour. We expect their physiological needs to be different because of their differing body-sizes (Cromsigt et al., 2009; Prins and Olff, 1998). We did not include hog deer for analyses because of an insufficient amount of data due to their relative rarity.

Descriptive statistics (e.g., mean with 95% CI) for proportion data (proportion of green leaf and proportion of dead parts), and chemical parameters (CP, phosphorus, NDF, ADF, and silica) were calculated with arcsine transformed data and back-transformed for interpretation. All graphs were prepared using ggplot2 (Wickham, 2021).

## Results

### Post-fire regrowth chemical properties

Forage nutritive values were dependent upon time since fire. Significant differences were found for important chemical parameters (*viz*, CP, phosphorus, NDF, ADF and silica) in grass tissues while comparing for different times after fire, indicating a clear temporal sequence of differences (Figure 3.3). We found significantly higher concentration of crude protein, phosphorus and silica in grass tissues at 30 days after fire than at other sampling instances (Figure 3.3). We observed strong and significant reductions in crude protein (mean value 9.1 to 4.1 [55% decrease]; Type II Wald chi-square $\chi^2 = 116.64$, df = 3, $P < 0.001$), phosphorus (mean value 0.2 to 0.11 [45% decrease]; $\chi^2 = 22.59$, df = 3, $P < 0.001$) and silica (mean value 5.2 to 3.6 [31% decrease]; $\chi^2 = 14.84$, df = 3, $P < 0.001$) in forage samples collected during different time intervals i.e., from 30 days to 120 days after fire (Figure 3.3). Likewise, we found increased NDF and ADF levels (Figure 3.3) in grass samples from 30 days to 120 days after fire ($\chi^2 = 10.35$, df = 3, $P = 0.016$; and $\chi^2 = 34.96$, df = 3, $P < 0.001$). The N:P ratio did not differ significantly between the days after fire (linear model F = 0.48, df = 3, $P = 0.690$; Appendix 3.3A); but the N:P ratio was below 10 in the post-fire regrowth in each sampling instance after fire (Appendix 3.3B).

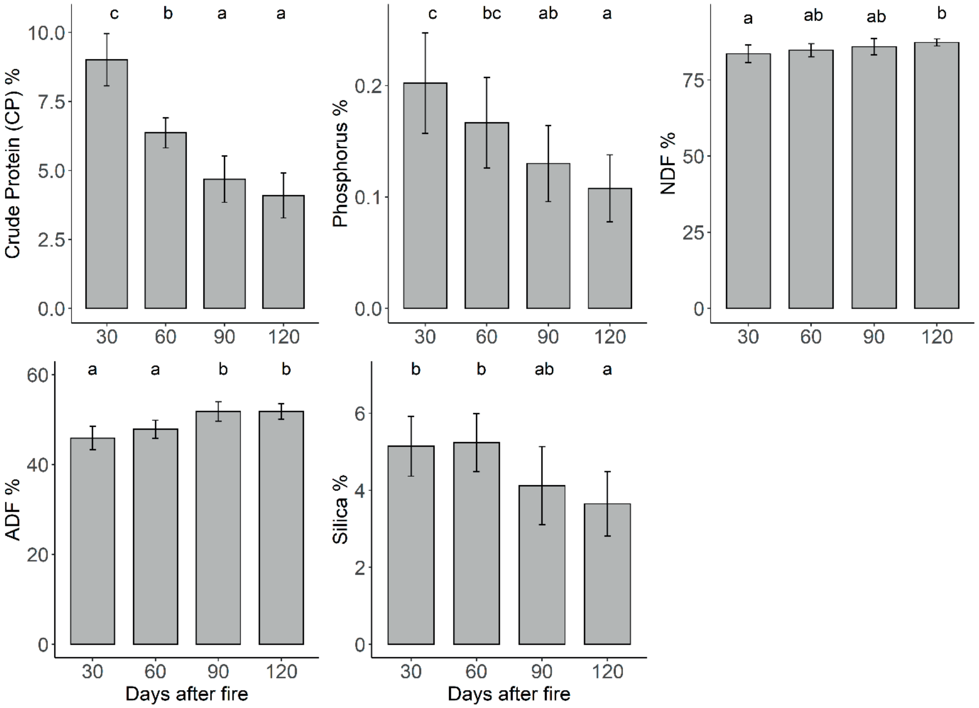


**Figure 3.3:** Chemical parameters (% DM) in post-fire regrowth grass tissues sampled from subtropical grasslands in Bardia NP, Nepal at different time intervals after fire. Bar graphs show mean (± 95% confidence interval – CI). Scale of y-axis varies with parameters indicated in the y-axis. Letters above each bar indicates a significant difference at alpha = 0.05, tested by estimated marginal means after beta regression. Group that shares same letter are not significantly different from each other.

### Post-fire regrowth physical properties

Post-fire regrowth height and biomass were significantly lower in the first sampling instance (*i.e.*, 30 days after fire) than at the other sampling instances (Kruskal-Wallis, $X^2 = 65.261$, df = 3, $P < 0.001$, and linear model, F = 101, df = 3, $P < 0.001$, respectively). In addition, plant height and biomass showed a significant increase with time since fire (Table 3.1). Bulk density was significantly higher in the first sampling instance (*i.e.*, 30 days after fire) when compared to other sampling instances (linear model, F = 14.46, df = 3, $P < 0.001$), while the proportion of green leaf was highest in the second sampling instance, *i.e.*, 60 days after fire (Type II Wald chi-square $\chi^2 = 31.33$, df = 3, $P < 0.001$, Table 3.1). Likewise, proportion of dead parts in the post-fire regrowth samples was significantly higher in 30 days after fire (Type II Wald chi-square $\chi^2 = 45.93$, df = 3, $P < 0.001$) and decreased with time since fire (Table 3.1).

**Table 3.1:** Mean with 95% CI for vegetation physical properties collected during four different time after fire from the grassland of Bardia NP. Letters in the cells indicate significant difference at alpha = 0.05. Group that shares the same letter are not significantly different from each other.

| Vegetation physical properties | Days after fire | | | | Method |
|---|---|---|---|---|---|
| | 30 days | 60 days | 90 days | 120 days | |
| Height (m) | 0.17<br>(0.14–0.19) $^a$ | 0.32<br>(0.26–0.38) $^b$ | 0.82<br>(0.71–0.92) $^c$ | 0.98<br>(0.85–1.11) $^d$ | Multiple comparison Fisher's least significant difference after Kruskal-Wallis test |
| Biomass ($g.m^{-2}$) | 171<br>(142–206) $^a$ | 194<br>(172–221) $^a$ | 388<br>(345–446) $^b$ | 713<br>(645–788) $^c$ | Multiple comparison with estimated marginal means after linear model |
| Bulk density ($g.m^{-3}$) | 1075<br>(863–1339) $^c$ | 658<br>(544–812) $^{ab}$ | 497<br>(445–601) $^a$ | 757<br>(665–897) $^b$ | Multiple comparison with estimated marginal means after linear model |
| Proportion of green leaf | 0.45<br>(0.39–0.50) $^a$ | 0.62<br>(0.57–0.67) $^b$ | 0.53<br>(0.49–0.58) $^a$ | 0.48<br>(0.43–0.52) $^b$ | Multiple comparison with estimated marginal means after beta regression |
| Proportion of dead parts | 0.48<br>(0.40–0.56) $^b$ | 0.31<br>(0.26–0.36) $^a$ | 0.25<br>(0.22–0.29) $^a$ | 0.24<br>(0.21–0.27) $^a$ | Multiple comparison with estimated marginal means after beta regression |

### Response of mesofaunal deer to post-fire regrowth

The effect of fire on grazing herbivores in the grasslands of Bardia NP was highest in the first sampling instance and decreased with time since fire. The intensity of use (based on pellet groups count) of post-fire regrowth by the mesofaunal deer assemblage (especially by chital, swamp deer and hog deer) showed a negative association with grass height (Wald test W = 140.49, *P* < 0.001; Figure 3.4) and biomass (Wald test W = 157.46, *P* < 0.001; Appendix 3.4).

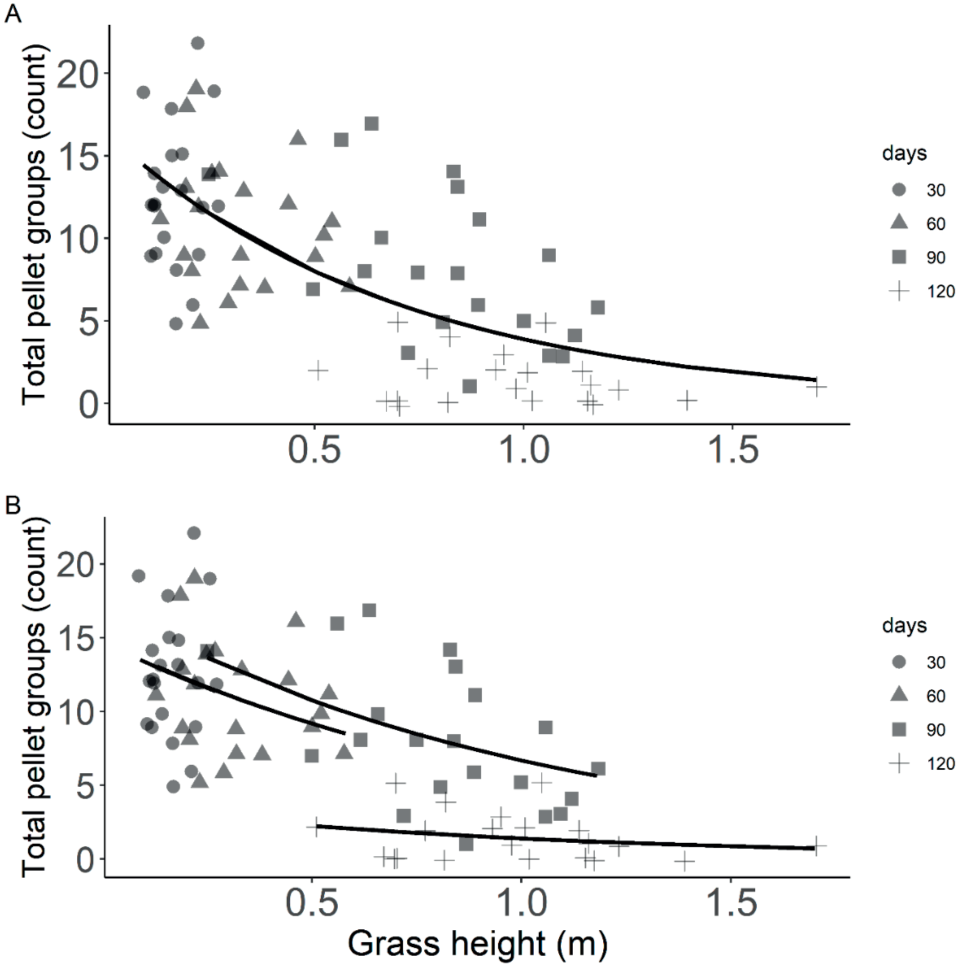


**Figure 3.4:** (A) Density of total pellet groups (proxy for the herbivore indicative of intensity of use of an area) in relation to grass height (cm) and time since fire (i.e., 30 days, 60 days, 90 days, and 120 days) in the burned grassland areas in Bardia NP. A: The equation of the line, generated by GLM with Poisson distribution, is **log(μ) = 2.8 -1.44 x grass height**; $R^2$ = 0.43. in which **μ** stands for pellet density. (B): Same data as in panel A but

with 'grass height' and 'days since fire' as covariates in the model. The equation for the lines are (i) for 30 days is: **$\log(\mu) = 2.688 - 0.95 \times$ grass height;** (ii) for 60 days: **$\log(\mu) = 2.69 - 0.95 \times$ grass height;** (iii) for 90 days: **$\log(\mu) = 2.85 - 0.95 \times$ grass height;** and (iv) for 120 days: **$\log(\mu) = 1.29 - 0.95 \times$ grass height**. **$\mu$** stands for pellet density.

Likewise, the level of crude protein in grass tissues decreased with increasing grass height (Wald test $W = 45.22$, $P < 0.001$; Figure 3.5A), and the intensity of use by meso-faunal deer was higher in the areas with higher levels of crude protein (Wald test $W = 42.91$, $P < 0.001$; Figure 3.5B).

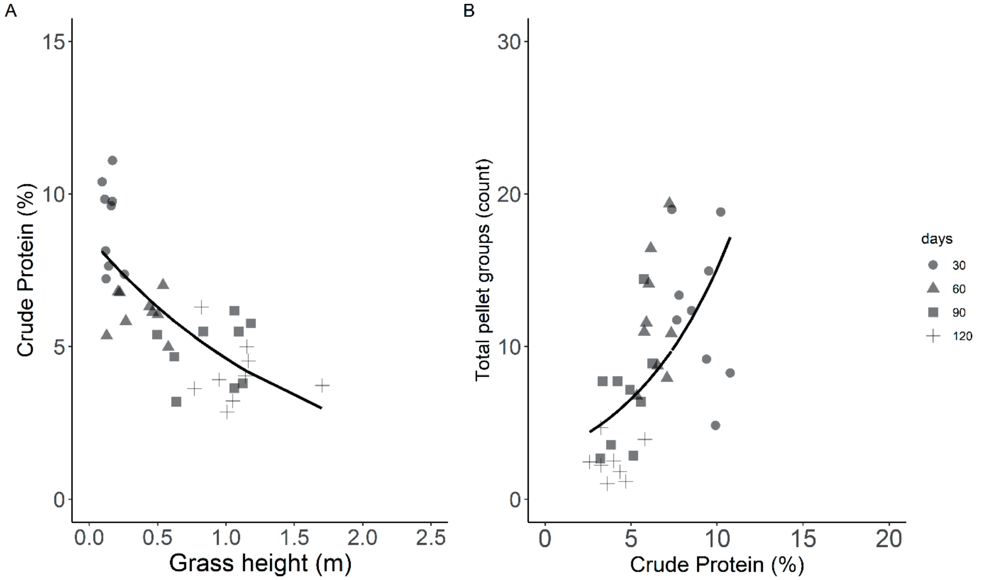


**Figure 3.5:** Panel **(A)** Relationship of post-fire regrowth grass crude protein (%) levels to grass height (m) and Panel **(B):** total pellet groups (as proxy for the herbivore foraging intensity) to grass crude protein (%) recorded along the time since fire (i.e., 30 days, 60 days, 90 days and 120 days) from the burned grassland areas in Bardia NP. The equation of the line for A is **$\log(\mu) = 2.15 - 0.62 \times$ grass height**; $R^2 = 0.56$ (generated by GLM with Gamma distribution), and that for B is **$\log(\mu) = 1.05 + 0.17 \times$ crude protein**; $R^2 = 0.31$ (generated by GLM with Poisson distribution). **$\mu$** stands for pellet density.

The intensity of use by chital to post-fire regrowth differed significantly over time since fire, with higher intensity of use at 30 days after fire (Figure 3.6A; Table 3.2). We did not find a significant difference in the intensity of use by swamp deer until 90 days after fire. However, level of use by swamp deer decreased significantly during the fourth sampling period (120 days after fire; Figure 3.6B; Table 3.2). The intensity of use by both chital and swamp deer was higher when post-fire regrowth grass heigh was below 40 cm and lower after 60 days post-fire (when the grass height exceeded 40 cm; Chi-square, $\chi^2$ = 12.737, P = 0.026; $\chi^2$ = 13.36, P = 0.030, respectively, Appendix 3.5).

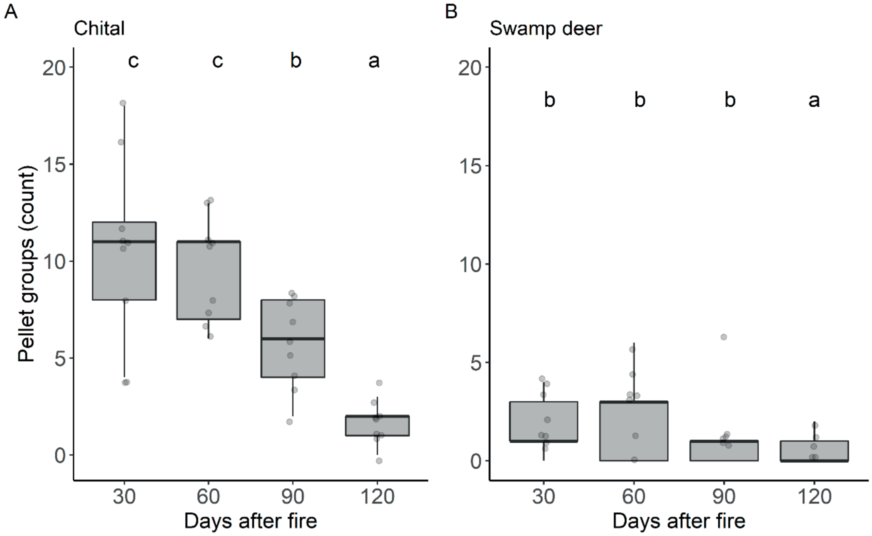


**Figure 3.6:** Pellet groups recorded from different periods after fire for (A) chital and (B) swamp deer. Letter above each boxplot show significant difference at alpha = 0.05, tested by estimated marginal means after GLM with Poisson distribution. Group that shares same letter are not significantly different from each other.

**Table 3.2:** Statistical parameters (estimated value for coefficient, SE-standard error for estimate of coefficient, z value and P value) from different time period after fire for chital and swamp deer.

| | | Estimate | SE | z value | P value |
|---|---|---|---|---|---|
| **Chital** | | | | | |
| | Intercept | 2.397 | 0.06 | 36.44 | < 0.001 |
| | 60 days after fire | -0.201 | 0.09 | -2.05 | 0.041 |
| | 90 days after fire | -0.552 | 0.11 | -5.07 | < 0.001 |
| | 120 days after fire | -2.184 | 0.21 | -10.56 | < 0.001 |
| **Swamp deer** | | | | | |
| | Intercept | 0.452 | 0.17 | 2.59 | 0.009 |
| | 60 days after fire | 0.217 | 0.23 | 0.93 | 0.353 |
| | 90 days after fire | 0.141 | 0.23 | 0.59 | 0.553 |
| | 120 days after fire | -1.887 | 0.48 | -3.93 | < 0.001 |

Note: Model parameters include pellet group count of either chital or swamp deer and days since fire (days) fitted with GLM Poisson distribution.

# Discussion

By quantifying physical and chemical parameters of post-fire regrowth on grasslands of Bardia NP over time for four months since fire, we were able to assess the primary factors explaining the aggregation of grazing herbivores in burned grasslands and better understand the temporal extent of pyric herbivory in the subtropical grasslands under control of the Cwa monsoon climate. Such temporal effect of fire on post-fire regrowth quality and associated pyric herbivory was already documented for African savannas (Archibald et al., 2005; Archibald and Bond, 2004; Archibald and Hempson, 2016; Donaldson et al., 2018; Eby et al., 2014; Klop et al., 2007; Van de Vijver et al., 1999) and North American prairies (Allred et al., 2011; Fuhlendorf et al., 2009; Leverkus et al., 2018; Raynor et al., 2016; Veach et al., 2014). Moreover, we showed that time since fire is indeed a critical determinant of the post-fire regrowth quality and associated pyric herbivory in subtropical monsoon grasslands that lies outside the average annual rainfall range of mesic savannas (*cf.* Ratnam et al., 2019, 2016; Sankaran et al., 2005). Only few studies on pyric herbivory (*e.g.,* Moe and Wegge, 1997; Sankaran, 2016) are available from this region. Furthermore, we showed that the pattern of usage of burned areas by two cervids *viz.,* chital and swamp deer differ significantly with respect to time since fire. Thus, our study adds important insights on pyric herbivory from this region which can be extended to a much larger area in Asia within the Cwa climate.

### Post-fire regrowth quality as a driver for pyric herbivory

We found a distinct temporal pattern of forage nutritive value of grasslands of Bardia NP induced by fire. Our results depicted that the post-fire regrowth grass quality was higher immediately after fire (*i.e.*, 30 days after fire) but decreased over time. Both physical and chemical properties of post-fire regrowth vegetation in the first weeks (*i.e.*, 30 days after fire) resulted in a higher food value for grazing herbivores when compared to later sampling instances (*i.e.*, 60 days, 90 days, and 120 days after fire; Table 3.1 and Figure 3.3). Fire increased forage crude protein (CP) and phosphorus (P) concentrations (refer to Figure 3.3) to the level that is required by mesofaunal deer (especially for chital) for maintenance and reproduction, but not for lactation (Thapa et al., 2021). But this increased forage CP and phosphorus is available only for a short period (not more than 60 days). Based on the known allometric relationship (Ahrestani et al., 2012; Prins and Van Langevelde, 2008), the nutritional requirements of deer differ due to differences in body-size and also with respect to physiological needs – maintenance, reproduction, and lactation. Peak parturition timing for chital is between February and April (Thapa et al., 2021), for swamp deer, it is late September (Dinerstein, 1980), and that for hog deer is March through April (Dhungel and O’Gara, 1991). Chital and hog deer may benefit briefly during the lactation period due to availability of higher levels of nitrogen and phosphorus in the post-fire regrowth vegetation. However, swamp deer may have to rely on nutrient-poor matured tall grasses even in the lactation period, a period when the animal has higher demand of nutrition to improve her lactation ability and milk quality (Ahrestani et al., 2012).

The CP concentration in the post-fire regrowth grass tissues collected after 30 days since fire was comparable to the levels reported from grazing lawns but higher than the levels reported from unburned tall grass samples. (Thapa et al., 2021) reported that the CP levels in green leaves from grasslands of Bardia NP ranged between 8.9 and 10.0 % for grazing lawns and for unburned tall grasses it ranged between 7.1 and 8.3 %. The level of CP in post-fire regrowth grasses after 60 days since fire, ranged between 5.8 and 6.9 %. This is lower than the CP level found in green leaves from unburned tall grasses (Thapa et al., 2021), indicating that the availability of a higher level of nitrogen from post-fire regrowth does not last long (not even for 60 days after fire). Similar findings of fire-induced nutritional increase for a short period have been reported for African savannas (Allred et al., 2011; Archibald and Bond, 2004; Eby et al., 2014; Van de Vijver et al., 1999). Following fire, forage quality declined when post-fire regrowth gained height and biomass (Table 3.1), affecting the intensity of use by mesofaunal deer (Figure 3.4, Figure 3.5, and Appendix 3.4). Both nutritive value and digestibility are inversely related to grass height and biomass; as grasses mature, height and biomass increase (Table 3.1), whereas quality (*e.g.*, CP; Figure 3.5A) and digestibility decreases (Anderson et al., 2007; Thapa et al., 2021; Van Soest, 1994).

Pyric herbivory is thus advantageous for mesofaunal deer, in particular during the hot dry season, as it stimulates fresh, high-quality new growth (albeit only up to two months). Yet, it appeared that the abundant mesofaunal deer in the grasslands of Bardia NP were not able to maintain the grasses in a short grazing lawn state [the desired state to realise high energy gain for grazing herbivores (Thapa et al., 2021)]. As a result, nutrients – especially nitrogen – diminished over time after fire and with grass height (see Table 3.1; Figure 3.3 and Figure 3.5A). It appears that the existing density of the grazing herbivores in these grasslands could not exert sufficient grazing pressure to culminate in herbivore-driven system (Smit and Coetsee, 2019) - a desired positive effect of pyric herbivory, or maybe because of the ‘magnet effect’ caused by the spatial extent of fire as explained by (Archibald et al., 2005). Besides, studies from African savannas indicated that a high fire frequency leads to decreased foliar nitrogen and phosphorus values (Anderson et al., 2007) and also, a loss of nitrogen from the system, leading to a decrease in productivity (Van de Vijver et al., 1999). The grasslands in Bardia NP, where our study was executed, are burned annually (Peet et al., 1999a) and our result also showed that the post-fire regrowth was N-limited for biomass production as the N: P ratio (such as estimated from foliar N and P) was < 10 (see Appendix 3.3).

## Post-fire regrowth and level of use by two cervids

Our findings showed that the mesofaunal deer utilised the burned areas extensively for a short period (up to 60 days after fire) until the area contained short grasses with lower levels of biomass (Figure 3.4 and Appendix 3.4) and a higher level of protein (Figure 3.5B). The findings support research related to the forage maturation hypothesis (see for detail (Fryxell, 1991; Olff et al., 2002; Prins and Olff, 1998; Raynor et al., 2016; Wilmshurst et al., 2000) which emphasise that grazing herbivores select the foraging ground containing low to intermediate biomass to maximise their daily rate of energy gain.

Chital and swamp deer showed different responses to the post-fire regrowth in Bardia NP (Figure 3.6 and Table 3.2). The intensity of use by chital, having a body-mass ~50 kg, to burned grasslands differed significantly with time since fire with a higher level of use up to 60 days after fire (Figure 3.6A, Table 3.2), while swamp deer, having a body mass ~150 kg, did not show a clear pattern of use up to 90 days since fire (Figure 3.6B and Table 3.2). These differences may be explained by the energy requirement with respect to body-mass (Illius and Gordon, 1992; Olff et al., 2002; Prins and Olff, 1998), as well as by the feeding mode of these two cervids. Chital is a mixed feeder and feeds primarily on grasses and switches to browse when grass quality declines and is considered more selective while cropping grass parts (Ahrestani et al., 2016). Swamp deer, on the other hand, is a grazer and feeds primarily on grasses and aquatic weeds (Ahrestani et al., 2016), and can digest taller and more coarse grasses than chital.

Our findings did not portray any evidence of differential use of burned areas to grass height (Appendix 3.5). Both species preferred to graze in grassland with a grass height lower than 40 cm. This is in contrast to studies that suggest resource-use partitioning through grass height (Cromsigt and Olff, 2006; Mandlate Jr et al., 2019). Along with short grasses with higher quality, one could argue that an increased aggregation of mesofauna deer in the burned areas could be attributed to the reduced predation risk as a result of increased visibility created by burning (as indicated by studies from other parts of the world, *e.g.*, Klop et al., 2007). In addition, environmental variables (*viz.,* distance to forest, water, and roads) associated with burned areas are important attributes that are likely to influence the foraging behaviour and space use by herbivores (Allred et al., 2011; Cherry et al., 2017; Marchand et al., 2017).

## Management implications

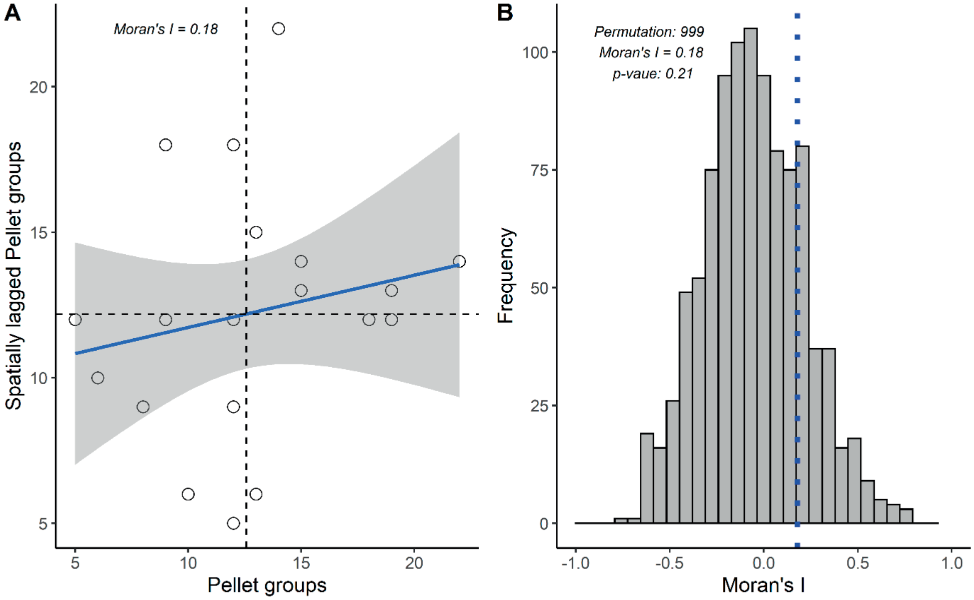
The most dominant graminoids viz., *Imperata cylindrica* (L.), *Vetiveria zizanioides* (L.), *Narenga porphyrocoma* (Hance ex Trin.) Bor, and *Saccharum spontaneum* (Retz.) in Bardia NP (Thapa et al., 2021) get moribund during the cool dry winter and are grazed less by the existing herbivores unless the dry aboveground biomass is removed either by burning or cutting (Moe and Wegge, 1997; Peet et al., 1999a; Wegge et al., 2006). The cool dry winter and hot dry summer seasons are a nutrient bottleneck period (Ahrestani et al., 2011) and during this time, a new flush of grasses becomes the valuable food source for herbivores. Given the widespread use of fire as a cost-effective grassland management tool in subtropical monsoon grasslands in the Cwa climate region, it is important to realise that the positive benefit of a single event fire for the conservation of large herbivores is time-specific, as the effect of fire on forage quality perhaps lasts for 60 days only. Chital is a mixed feeder whereas swamp deer is a grazer, and their level of energy requirements is different with respect to their body-size. Hence, large scale single event fires may not fulfil the nutritional requirements of all mesofaunal deer. Furthermore, larger-scale fires promote a uniform grazing environment where grazers are dispersed widely, resulting in a decreased grazing pressure in existing grazing lawns (Archibald et al., 2005; Archibald and Bond, 2004), and a fast increase in unpalatable grass biomass (Thapa et al., 2021).

Our results showed that biomass and height increased significantly with time resulting in the limited use of the burned areas after 60 days since fire. This indicated that the existing density of the mesofaunal deer assemblage in the Bardia NP was not able to maintain the grass height to the desired short state after fire occurrence. Furthermore, the grazing systems in the Cwa climate region is constrained by nitrogen for grass growth, as the N: P ratio estimated from foliar N and P was < 10 (Koerselman and Meuleman, 1996) and phosphorus for herbivore productivity (Thapa et al., 2021). Indeed, it is not a management goal to increase the enormous production of grasses in this monsoon grassland, rather, the stated management goal of Bardia NP is to be a safe habitat for the endangered tiger population for which sufficient prey must be available.

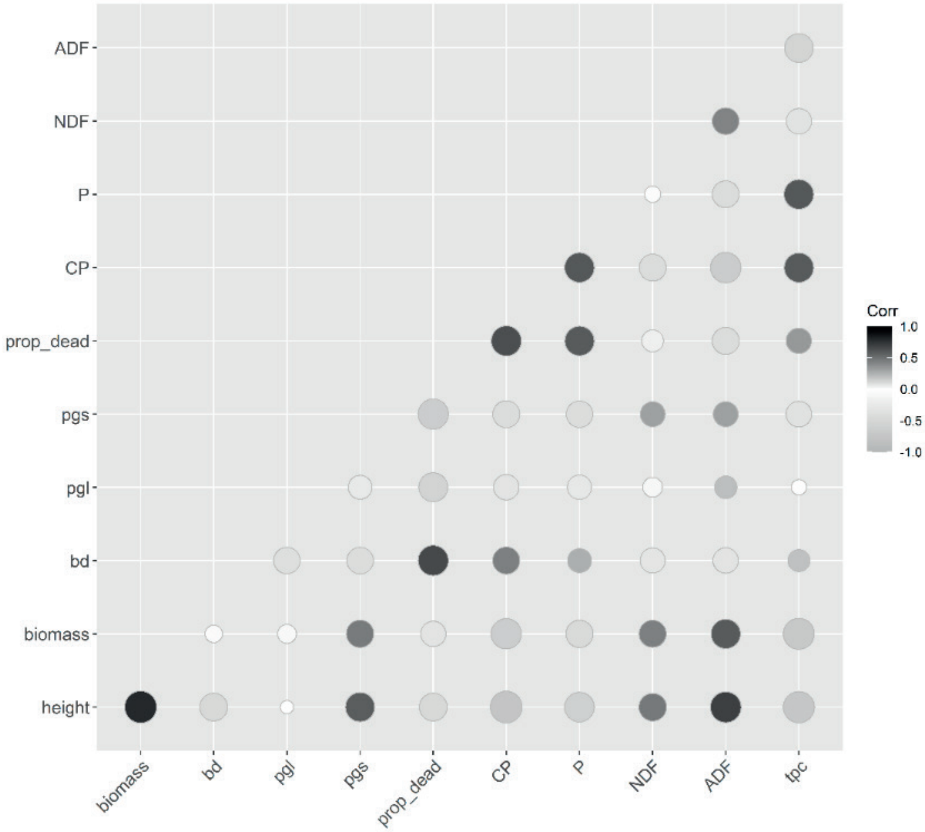
In this respect, we recommend considering a spatio-temporal manipulation of fire to reinforce the grazing feedback for culminating in from fire-dominated to herbivore-dominated state. It is likely that the burned mosaics of grassland patches are intensively grazed resulting in the establishment of grazing lawns (Hempson et al., 2015; Thapa et al., 2021). Hence, a series of fires, staggered over time, may thus yield for the longest possible period a good food supply during the nutrient bottleneck months (cool dry winter and hot dry summer seasons) till the next growing season (starting with monsoon June through September), thus facilitating maximum survival for the deer that are to be preyed upon by the tiger.

**Data availability:** The data that support the findings of this study are openly available in: Dryad, Dataset https://doi.org/10.5061/dryad.2jm63xsqz

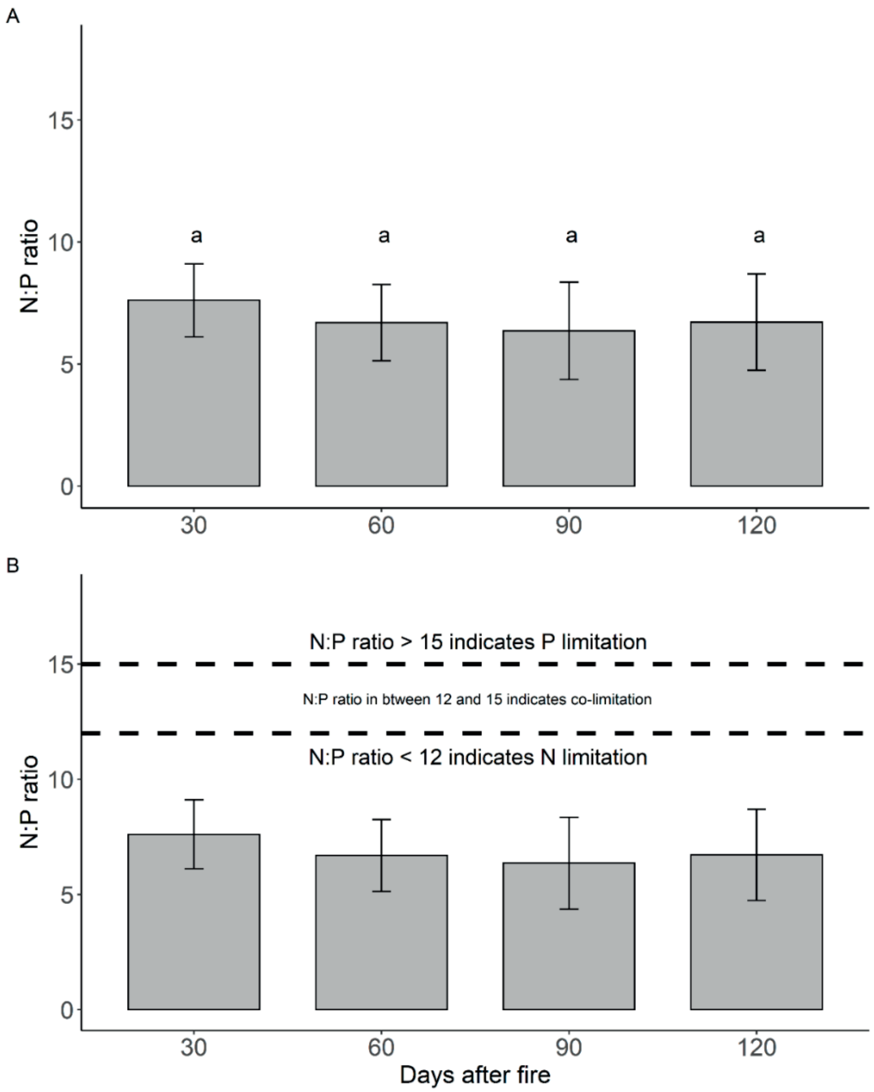
# Appendix



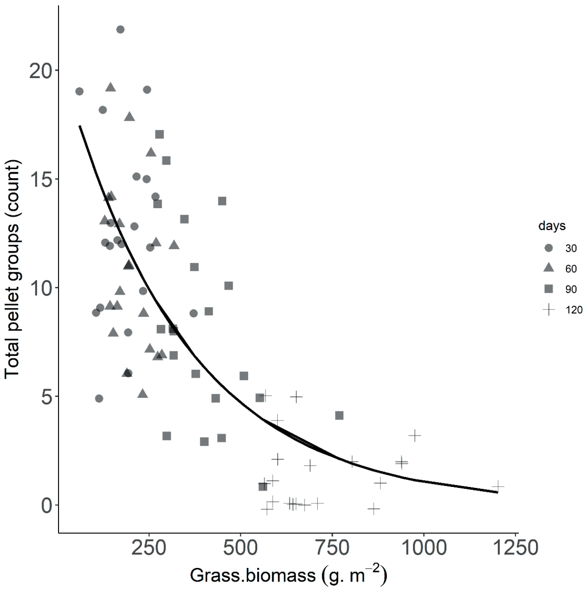
Appendix 3.1: Pane A: Moran's scatterplot with the spatially lagged (neighbour's weighted averaged value) variable (on y-axis) and the original variable (pellet groups – count data) on the x-axis. The slope of the blue line is an estimation of the Moran's I. Pane B: Distribution for Moran's I for all 999 permutation; blue dotted vertical line represent observed Moran's I value of 0.18 with the pseudo p-value of 0.21.



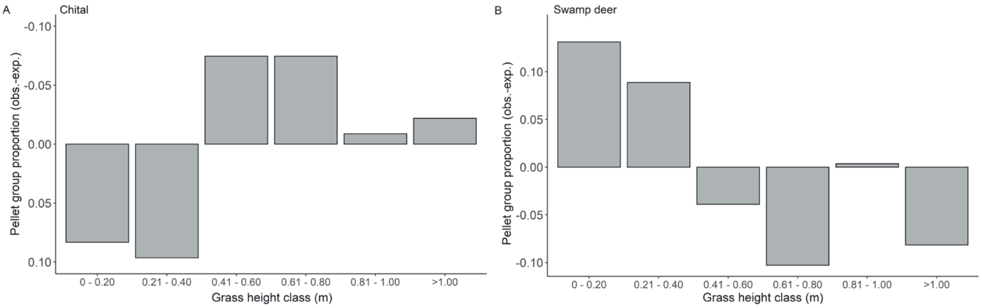
Appendix 3.2: Correlation map of the variables recorded/estimated along the time since fire (i.e., 30 days, 60 days, 90 days and 120 days) from the burned grassland areas in Bardia NP. Dark circles represent positive correlations, whereas light grey circles represent negative correlations. The size of the dots represents the degree of the correlation. Variables are coded as: biomass = aboveground biomass of grass, bd = bulk density, pgl = proportion of green leaf, pgs = proportion of green leaf, prop_dead = proportion of dead parts, CP = crude protein in grass, P = phosphorus concentration in grass vegetation, NDF = neutral detergent fibre in grass, ADF = acid detergent fibre in grass, tpc = total pellet groups.



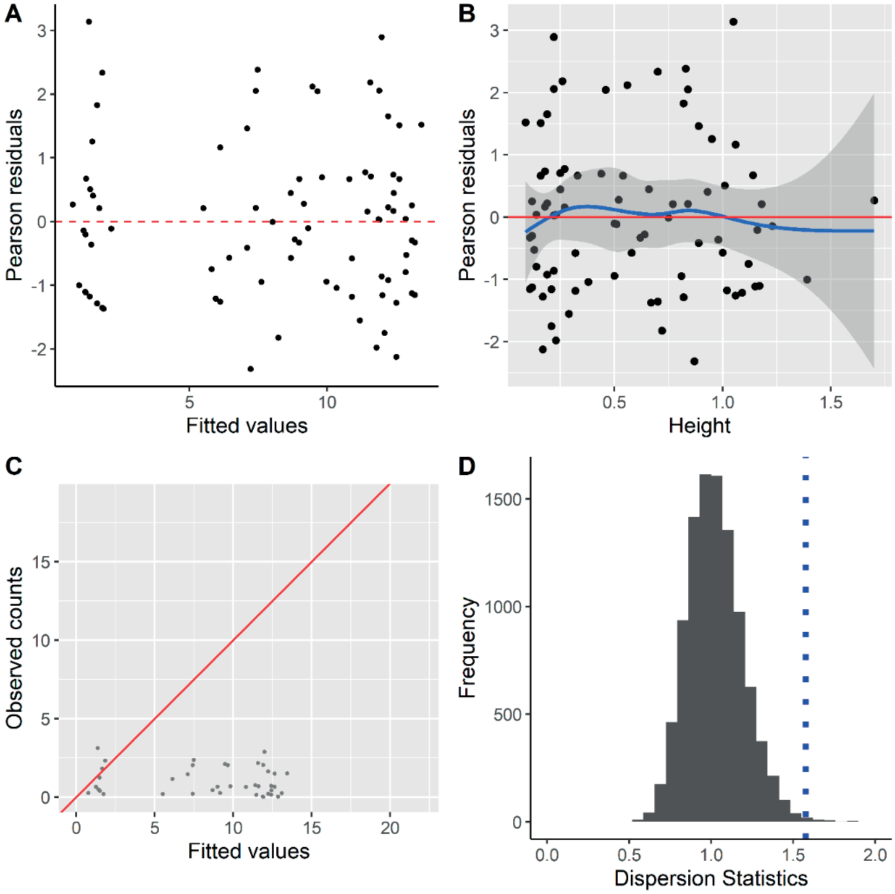
Appendix 3.3: N:P ratio in the post-fire regrowth grass in grasslands of Bardia NP. Bar graphs show mean (± 95% confidence interval – CI). **A.** Letters above each bar indicated significant difference at alpha = 0.05, tested using estimated marginal means after linear model. Group/s that shares same letter are not significantly different from each other. **B.** The same data as in panel A shows that grass vegetation in Bardia NP is nitrogen-limited (for grass growth) as the N:P ratio in the vegetation is below 10 in all sampling instances.



Appendix 3.4: Relationship of total pellet groups (proxy for the herbivore foraging intensity) to biomass (g.$m^{-2}$) recorded along the time since fire (i.e., 30 days, 60 days, 90 days, and 120 days) from the burned grassland areas in Bardia NP. The equation of the line, generated by GLM with Poisson distribution, is **log(μ) = 3.04 -0.003 x biomass**: $R^2$=0.56.



Appendix 3.5: Observed minus expected pellet groups proportion with respect to grass height class: A) for chital and B) for swamp deer in the subtropical grassland of Bardia NP.



Appendix 3.6: Model validation graphs for the GLM with Poisson distribution model: **log(μ) = 2.8 -1.44 x grass height** (Figure 4 A). A: Scatterplot for the Pearson residuals versus fitted values. B: Pearson residuals versus the covariate Grass Height. C: The total pellet group versus the fitted values of the model. D: Result of the simulated data for the model to investigate the range of the dispersion statistics – the vertical dotted line represents the dispersion statistics obtained by applying the model on the data.

# CHAPTER

# 4

# Integration of the landscape of fear concept in grassland management – an experimental study on subtropical monsoon grasslands in Bardia National Park, Nepal

Shyam Kumar Thapa, Joost F. de Jong, Anouschka R. Hof, Naresh Subedi, Yorick Liefting, Herbert H.T. Prins

# Abstract

Despite the popularity of the 'landscape of fear' concept, its integration into habitat management for wildlife conservation has remained largely unexplored. To address this, we conducted a multi-year experimental study in the subtropical monsoon grasslands within the core area of Bardia National Park, Nepal. This park has the highest density of tigers in Nepal, with an estimated density of ~ 7 individuals per 100 km$^2$. We used plots with varying mowing frequency (0-4 times), size (small: 49 m$^2$ to large: 3600 m$^2$), and artificial fertilisation type (none, phosphorus, nitrogen) to assess the trade-offs between probable predation risk and resources for three cervids: chital (*Axis axis*), swamp deer (*Rucervus duvaucelii*), and hog deer (*Axis porcinus*). Our results showed that these deer (primary prey species of tigers in Nepal) respond to the probable predation risk when using grasslands. Medium-sized deer such as chital and swamp deer strongly favoured large plots (mean = 0.1 pellet groups.m$^{-2}$ in 3600 m$^2$ plots, vs. 0.07 in 400 m$^2$, and 0.05 in 49 m$^2$ plots) and tended to use edge areas less (mean = 0.13 pellet groups.m$^{-2}$ at the edge vs. 0.21 at the centre). In contrast, smaller hog deer did not show any reaction to the treatments. We suggest that for medium-sized deer 'feeling safe' may be the main factor in using the managed habitat in subtropical monsoon grasslands. Our study provides novel insights into the applicability of the 'landscape of fear' concept in habitat management for the conservation of predator and prey in the ecosystem.

**Keywords:** predators, prey, predation risk, habitat, tigers, herbivores

## Introduction

The abundance and distribution of herbivores are often affected by predators in a system (Blumstein et al., 2006; Cherry et al., 2015; Kuijper et al., 2013; Wang et al., 2009). The 'landscape of fear' concept is a useful framework to understand how spatial variation in the mere risk of predation (not predation itself) influences prey behaviour and ecosystem processes (Fortin et al., 2005; Hernández and Laundré, 2005; Hof et al., 2012; Kohl et al., 2018; Laundre et al., 2010; Laundré et al., 2001; le Roux et al., 2018; Lima and Dill, 1990; Valeix et al., 2009; Wheeler and Hik, 2014). However, there has been little experimentation with manipulating (perceived) predation risk to investigate whether it can purposefully be used for wildlife management (but see Ford et al., 2014; Gaynor et al., 2021; le Roux et al., 2018).

The integration of the 'landscape of fear' concept into habitat management is crucial for balancing predator-prey dynamics (Gaynor et al., 2021; Laundré et al., 2014). Habitat management can alter predator-prey dynamics by either favouring predators or prey. For instance, creating open space may reduce risk perception for prey (le Roux et al., 2018), but such interventions may also influence the hunting success rate of ambush predators like tigers (Karanth and Sunquist, 2000; Sunquist, 2010). Furthermore, herbivores may avoid managed habitats if they perceive them as too risky (Hebblewhite and Merrill, 2009; Hernández and Laundré, 2005), and hence management interventions may turn out to be fruitless and may have (unforeseen) cascading effects (Gaynor et al., 2019). The landscape of fear concept can inform habitat management interventions that optimise the trade-off between risk and resources for herbivores, while still providing opportunities for predators to hunt effectively (e.g., Kuijper et al., 2013; Schmidt and Kuijper, 2015).

Herbivores are constrained by both top-down (predation) and bottom-up (food limitation) forces (Hopcraft et al., 2010; le Roux et al., 2018) and their survival and fitness depend largely on their ability to optimise foraging benefits (Hebblewhite and Merrill, 2009; Wirsing et al., 2007). The number of tigers (*Panthera tigris*) in Nepal has increased from an estimated 121 individuals in 2010 to 355 in 2022 (DNPWC and DFSC, 2022). Most tigers occur in national parks that are situated in the subtropical belt along the foothills of the Himalayas, which is the Terai in Nepal. With the increasing number of tigers within an otherwise unvarying area, the encounter frequency between predator and prey must increase, which makes it likely that individuals of the prey species become increasingly wary (e.g., Gaynor et al., 2019) and thus rely more and more on escape and avoidance tactics (Cromsigt et al., 2013; Lima and Dill, 1990). These antipredator responses often come at the cost of time spent on other essential activities such as foraging (Lima and

Bednekoff, 1999; Say-Sallaz et al., 2019). This can lead to a decrease in their performance (Clinchy et al., 2013) and ultimately affect their population dynamics.

The primary prey species of the tigers in Nepal consist of muntjac (*Muntiacus vaginalis*), hog deer (*Axis porcinus*), chital (*Axis axis*), swamp deer (*Rucervus duvaucelii*), and sambar (*Rusa unicolor*) besides wild boar (*Sus scrofa*) (Lamichhane et al., 2019; Upadhyaya et al., 2018) as large body-sized prey such as gaur (*Bos gaurus*) and nilgai (*Boselaphus tragocamelus*) occur in relatively low densities (DNPWC and DFSC, 2022). Because these small and medium-sized deer forages mostly on grasslands (Moe and Wegge, 1994; Wegge et al., 2006) and require high-quality forage to meet their nutritional requirements for survival (Ahrestani et al., 2012; Thapa et al., 2021), their foraging often translates into discernible vegetation patterning (Ford et al., 2014; Schmitz, 2008; Schmitz et al., 2004) as the predation risk has the potential to alter or modify herbivores' foraging pattern (Hebblewhite and Merrill, 2009; Hernández and Laundré, 2005).

The assemblage of predators and prey species in Bardia National Park (Bardia NP) in Nepal offers an ideal situation to experimentally test if herbivores can be successfully managed by manipulating predation risk. By simultaneously examining the effect of altering resource quality (primarily through mowing and artificial fertilisation) and manipulating predation risk (primarily by creating open areas of different sizes - plot size) on the level of use of the managed grassland by three cervids (small hog deer –with an average weight of ~40 kg, and medium-sized chital ~50 kg, and swamp ~ 150 kg), primary prey species of tigers, we explore the applicability of the 'landscape of fear' concept in habitat management. To our knowledge, this is the first landscape level empirical study from this region where we incorporate the concept of landscape of fear into habitat management (Figure 4.1). Here, we report on a series of experiments that were executed to incorporate the 'landscape of fear' concept into grassland management in the subtropical monsoon grasslands in Nepal. Our study provides novel insights into the applicability of the 'landscape of fear' concept in grassland management and contributes to the conservation of predator and prey in the ecosystem.

**Figure 4.1:** Aerial view of experimental plots in one of the open grasslands locally known as Baghaura phanta in Bardia National Park. A landscape with clearly distinguishable plots of different sizes with short grasses and surrounding tall grasses create gradients of predation risk. The grassland is frequently visited by tigers and small and medium-sized deer.

## Material and Methods

### Study site

We conducted our study in the subtropical monsoon grasslands in Bardia NP of Nepal within the Cwa-climate: monsoon-influenced humid subtropical climate (Chen and Chen, 2013) region (Figure 4.2). Bardia NP is one of the largest national parks within the Terai Arc Landscape covering an area of 968 km$^2$ (centre of the park at 28$^0$23′ N, 81$^0$30′ E).

Bardia NP has monsoon (June – September), winter (October – February) and summer (March-May) seasons. The mean monthly temperature ranges from a minimum of 10 $^{\circ}$C to a maximum of 45 $^{\circ}$C. The park receives a mean annual rainfall of ~ 1700 mm (Thapa et al., 2022). Bardia NP consists of subtropical vegetation with riverine forest, riverine floodplain grasslands along the two major rivers (Karnali and Babai rivers), *sal* (*Shorea robusta*) forest with interspersed grasslands, and mixed hardwood forests (Dinerstein, 1979).

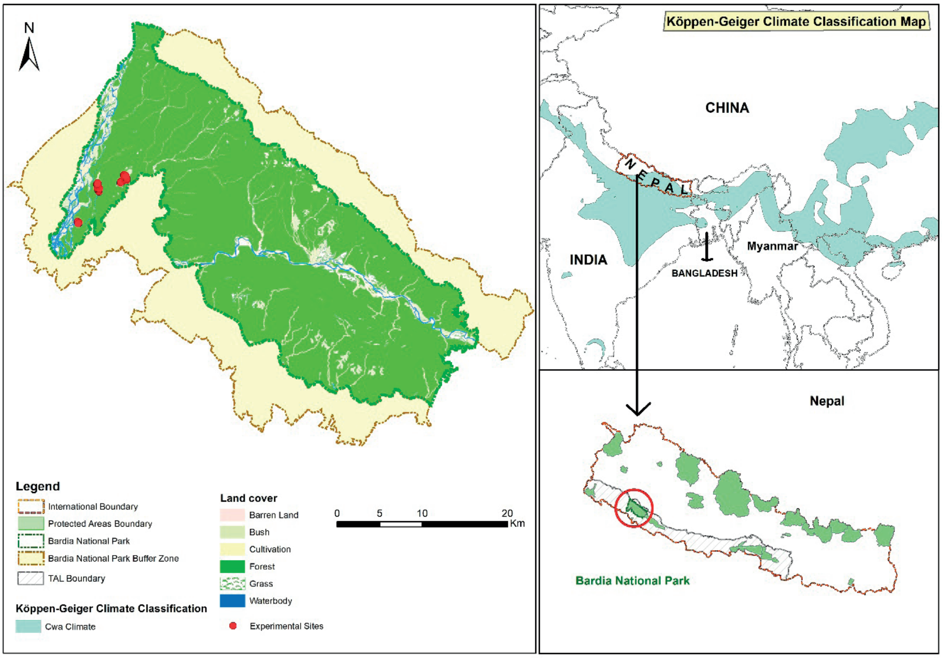


**Figure 4.2:** Experimental plots were established within the subtropical monsoon grasslands of Bardia National Park, an important tiger bearing protected area within the Terai Arc Landscape of Nepal. The park lies in a region with a Cwa climate, indicating a monsoon-influenced humid subtropical climate under the Köppen classification (light blue area on the top-right inset map).

The park holds the highest density of tigers in Nepal with an estimated density of ~7 individuals.100 $km^{-2}$ and an estimated prey density of ~90 individuals.$km^{-2}$ (DNPWC and DFSC, 2022). The primary prey of the tiger in Bardia NP includes five cervids of different body sizes, viz., from smaller to larger - muntjac (an average mass of ~ 20 kg), hog deer (40 kg), chital (50 kg), swamp deer (150 kg), and sambar (185 kg). Chital, at present, is the most abundant primary prey in the system (Upadhyaya et al., 2018) with a reported density of ~ 45 deer.$km^{-2}$ (DNPWC and DFSC, 2022) after larger prey species (arna [*Bubalis arnee*], and gaur) went extinct (Jhala et al., 2021) or got reduced to fewer than a handful e.g., nilgai (Wegge et al., 2009). Tigers exclusively reside within the core area of the park and the studied grassland sites are within the area with the highest density of tigers in the park (Figure S3, DNPWC and DFSC, 2022). Thus, deer in Bardia NP live under high predation risk and most of the direct and indirect predator-prey interactions occur within the core area of the park as a dispersal of the animals is limited by surrounding farmland and settlements within the buffer zone (Figure 4.2).

The tiger is of main concern because of its threatened status on the IUCN red-list and the wish of the Government of Nepal to maintain its population at the recently achieved high numbers without aggravating the precarious status quo with villagers living in surrounding settlements by keeping the number of human killing incidents as close as possible to zero.

## Experimental design

The experimental sites were situated in the western section of the park in the three disjointed patches of open grassland that are interspersed within *sal* forests (Figure 4.2). We set up multi-year large-scale experimental plots (n=189, Table 4.1) in the core area of Bardia NP, thus, giving us unique opportunities to test empirically the applicability of the 'landscape of fear' concept in grassland management for ungulates. We outlined 189 plots in three disjoined patches of open grassland (e.g., Figure 4.3) where we manipulated resources and the risk of predation. The distance between the patches was between 1 to 2 km. These patches were at the same topographic positions in the landscape and comprised similar vegetation (Thapa et al., 2021) and are frequently used by medium-sized swamp deer and chital, and the smaller hog deer (Thapa et al., 2022). We merely considered these three deer species for this study as the other species are only present in small numbers.

**Table 4.1:** Total number of experimental plots with different levels of treatments.

| | **No mowing** | | | **2 times mowing** | | | **4 times mowing** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Plot size** | **No fertilisation** | **Nitrogen** | **Phosphorus** | **No fertilisation** | **Nitrogen** | **Phosphorus** | **No fertilisation** | **Nitrogen** | **Phosphorus** | **Total** |
| 49 $m^2$ | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 63 |
| 400 $m^2$ | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 63 |
| 3600 $m^2$ | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 63 |
| **Total** | 21 | 21 | 21 | 21 | 21 | 21 | 21 | 21 | 21 | **189** |

We reckoned the size of the experimental plots and grass height as important attributes that creates gradients of predation risk due to visibility, detection probability and fleeing ability (Laundre et al., 2010; le Roux et al., 2018). We mowed grasses and spread chemical fertilisers in the experimental plots to attract herbivores to the plots. Because we are interested in trade-offs between risks and resources, we used chemical fertilisers together with mowing to make attractive environment for grazing.

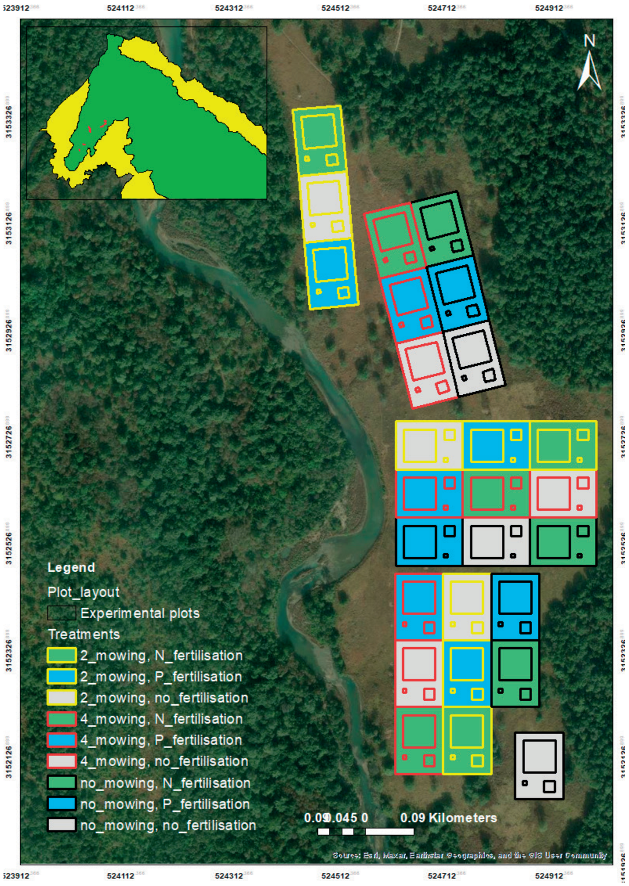


**Figure 4.3:** Complete set of experimental design in one of the locations (Baghaura phanta, n = 81) within Bardia NP. One replication unit consisted of 27 plots. There are a total of 7 replications within three sites. The colour of the borderline of the square plots indicated the types of mowing treatment received by respective plots - black borderline for no mowing, yellow for two times mowing, and red for four times mowing per year. Likewise, filled colours within square plots represent types of fertilisation treatment received by respective plots - green for nitrogen fertilisation, blue for phosphorous, and grey for no fertilisation. The size of the square represents either 3600 m$^2$ or 400 m$^2$ or 49 m$^2$ plots.

### Experimental plot set-up

The experimental design incorporated three treatment factors: mowing; artificial fertilisation, and plot size. There were a total of seven replications spread over three sites, forming a complete design with 189 experimental plots (Table 4.1). The scale of the landscape did not allow for more plots. We laid out square plots of different sizes (3600 $m^2$; 400 $m^2$, and 49 $m^2$) in each replication. One complete replication contained plots with different levels of mowing and fertilisation treatments (Figure 4.3), creating a gradient of fear and food availability. Plots received different levels of mowing (no mowing, two times mowing, and four times mowing per year) and fertilisation treatments (nitrogen fertilisation, phosphorus fertilisation, or no fertilisation) at random. We determined the level of mowing and fertilisation treatments for each plot using computer-generated random numbers.

The mowing treatments were applied in 2019 and 2020. Tall dense grasses (~1.5 m to ~3 m tall) were mowed at a height of around 5 cm from the ground. Grasses were mown in January/February and August/September in plots that received two times mowing treatments. Grass vegetation were mown in January/February, April/May, August/September, and November/December in plots that received the four times mowing treatment. We did not cut grasses from the plots that received no mowing treatment. We removed aboveground biomass after mowing from the mown plots. We applied either urea (46% N) or single superphosphate (SSP with $P_2O_5$ 16%) in those plots that were labelled to receive respective fertilisers (Table 1, Figure 3). We spread fertilisers three times (2018, 2019 and 2020) to stimulate nutrient-rich regrowth. The first two applications equated to 15 $g.m^{-2}$ of urea, and 15 $g.m^{-2}$ of SSP (in March 2018 and April 2019). We increased the load in the third application and spread 40 $g.m^{-2}$ of urea and 60 $g.m^{-2}$ of SSP in January 2020, because the low application of fertilisers in previous years resulted in a weak contrast between treated and non-treated plots. We used plots that received no mowing and no fertilisation (n = 21, Table 4.1) as controls.

### Data collection

### Pellet density to estimate level of use by deer

To assess the level of use of the experimental plots by small and medium-sized deer (*viz.*, hog deer, chital, and swamp deer), we estimated pellet group density expressed as pellet groups.$m^{-2}$. Pellet group count may not be the best method to quantify habitat selection for foraging, but it provides a reliable estimate for the level of use of the habitat (Cromsigt et al., 2009; Härkönen and Heikkilä, 1999; Månsson et al., 2011; Thapa et al., 2022). We distinguished pellet groups at the species level based on the pellet morphology (see, for example, (Thapa et al., 2022) and recorded them separately. We used a 2 x 2 m frame to record pellet groups from sampling points in each experiment plot. Only pellet groups with five or more pellets were recorded and pellet groups with more than 75% of the pellets outside of the frame were not recorded. We surveyed approximately 2% of each plot area, except for 49 $m^2$ plots where we recorded pellet groups from one sampling point at the centre. In 400 $m^2$ plots, we recorded pellet groups from two sampling points (one at the edge and one at the centre) and in 3600 $m^2$ plots, we systematically laid out 21 evenly spaced sampling points (see Figure S4 for the spatial layout of sampling points). We recorded pellet groups in each plot (n = 189) monthly and used an average value per plot for seasonal comparisons. We also measured grass height for each plot within 2m x 2m sampling frame and averaged it at plot level.

The spatial layout of sampling points in 3600 $m^2$ plots allowed us to measure and compare the pellet density at the edge and central areas of the plots. Because of the predation risk, we considered it likely that the edge and central (core) area of the treatment plots are differentially used by the deer with the possibility of aggregation of deer at the core area where they apparently feel safe and the likelihood of early detection of predators is also high.

## Data analyses

We used a linear mixed-effect model to compare pellet density with different levels of treatments on a plot. We used $\log_e$ transformed plot size as a fixed component and replication within location as random intercepts in the model. Since the level of use of the habitat by deer differs with seasons (Moe and Wegge, 1994) and species of deer, we included these two terms in the model. Pellet density was modelled with treatments (mowing, fertilisation, and plot size), seasons, species, and their interactions as fixed terms. We included vegetation height as a covariate in the model (Table S1). As random effects, we had intercept for replications within locations in the model. The vegetation height is an important factor that affects the visibility and detection probability of predators, and hence the level of risk perception.

We also examined the differences in pellet density between the edge and centre (or core area) of the experimental plots on a subset of the 3600 $m^2$ plots that received two and four times mowing (n = 42, Table 4.1). Pellet density was modelled with treatments (mowing, fertilisation, and plot size), season, species, point (edge or centre of the plot), and their interactions as fixed components (Table S2). We included replications within locations as a random factor in the model. Visual inspection of residual plots (histogram, normal probability plot, residuals vs. fitted values) from all the mixed models did not reveal any violation of the linear mixed-effects model assumptions *viz.*, residuals were normally distributed, error terms were normally distributed, and no obvious deviations from normality were detected.

All statistical analyses were performed in R, version 4.1.0 (R Core Team, 2021). We used the "lme4" package (Bates et al., 2015) for linear mixed-effects models. Post hoc multiple comparisons tests were performed using the "emmeans" package (Lenth et al., 2021) after the linear mixed-effects model. All graphs were prepared using the "ggplot2" package (Wickham, 2021).

## Results

### Pellet density with respect to the spatial scale of the interventions

We recorded twice the density of pellet groups in 3600 $m^2$ plots [mean = 0.1 pellet groups.$m^{-2}$ (95% CI: 0.10 – 0.13)] as in 49 $m^2$ plots [mean = 0.05 pellet groups.$m^{-2}$ (95% CI: 0.04 – 0.06)] and 1.5 times higher than in 400 $m^2$ plots [mean = 0.07 pellet groups.$m^{-2}$ (95% CI: 0.06 – 0.08)]. The pellet density increased significantly (F = 64.99, $P < 0.001$) with $\log_e$ transformed plot sizes (Figure 4.4). Pellet density increased with a unit of 0.015 for every one unit increase in $\log_e$ transformed plot size.

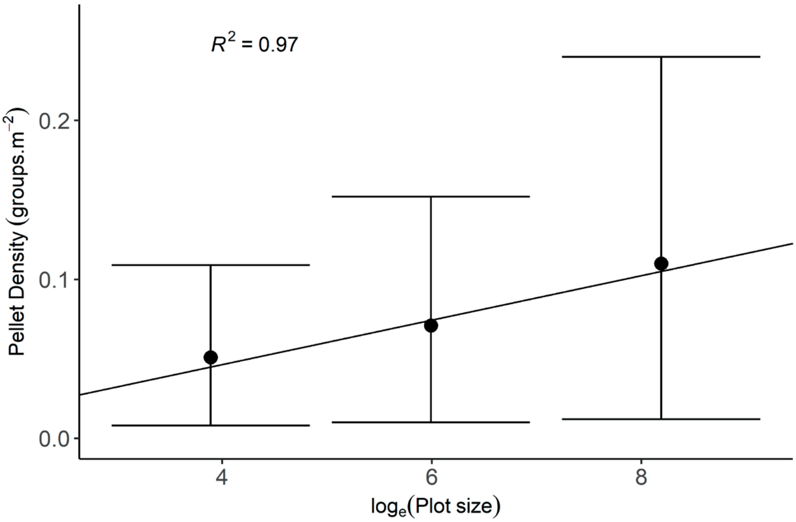


**Figure 4.4:** Pellet density (groups.$m^{-2}$) in different-sized experiment plots expressed as $\log_e$ (plot size). Error bars represent 95% CI. The equation for the line is **$y = -0.0096 + 0.015x$** and is obtained from a linear mixed effect model with $\log_e$ (plot size) as a fixed factor. Here, y stands for pellet density and x is the $\log_e$ transformed plot size.

## Management interventions and pellet density

Pellet density varied in plots with respect to treatments: mowing, fertilisation, plot size, and the interaction effects with species, and season (Table S1). Vegetation height had a significant effect on the level of use of the managed areas (F = 18.06, *P* < 0.001, Table S1). Vegetation height decreased significantly with mowing (F = 154.95, *P* < 0.001, Figure S5) and had a significant effect on the level of use by the deer (F = 610.09, *P* < 0.001, Figure S6). At the species level, pellet groups of chital and swamp deer were higher in 3600 $m^2$ plots than in 400 $m^2$ or 49 $m^2$ plots. In contrast, pellet density of small hog deer did not differ significantly with plot size (Figure 4.5).

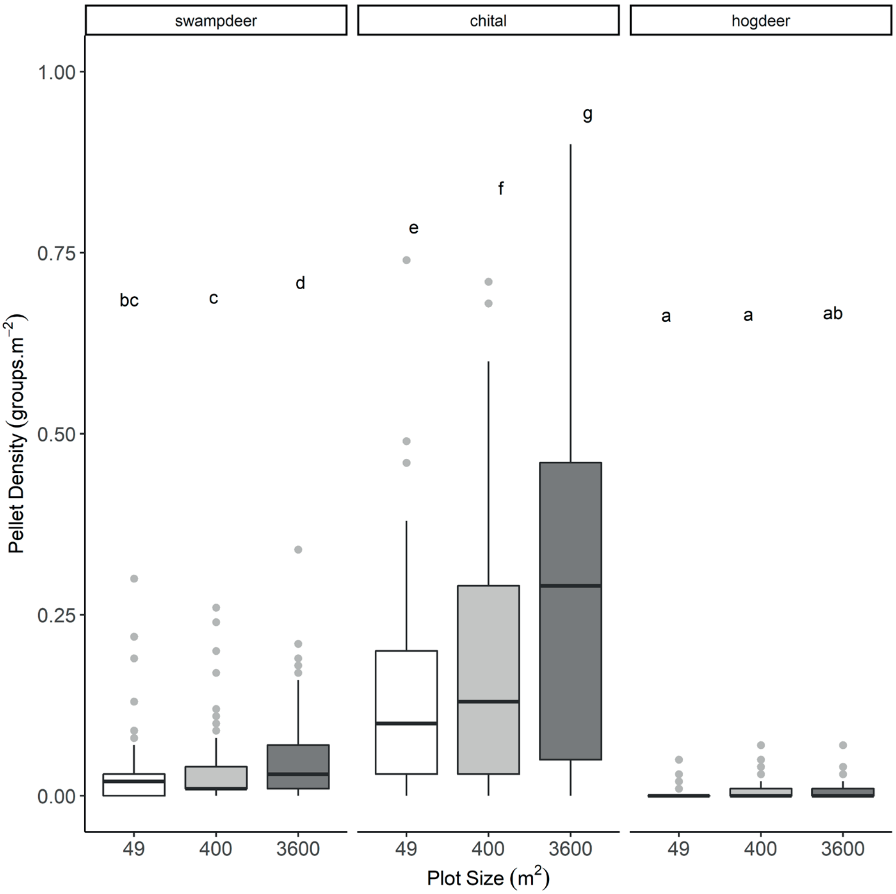


**Figure 4.5:** Level of use (measured through pellet groups.m$^{-2}$) of the three deer species in different-sized plots. Letters above each boxplot indicate a significant difference at alpha = 0.05, tested by estimated marginal means after the linear mixed effect model (Table S1). Groups that share the same letter are not significantly different from each other.

Pellet density of chital and swamp deer was higher in the 3600 m$^2$ plots that were mown four times (F = 50.12, $P < 0.001$; Figure 4.6a). The interaction effect of season and mowing was significant for chital, while the effect for swamp deer was significant only in winter (F = 9.83, $P < 0.001$; Figure 4.6b). On the contrary, pellet density of hog deer did not differ significantly with mowing, plot size, and season (Figure 4.6).

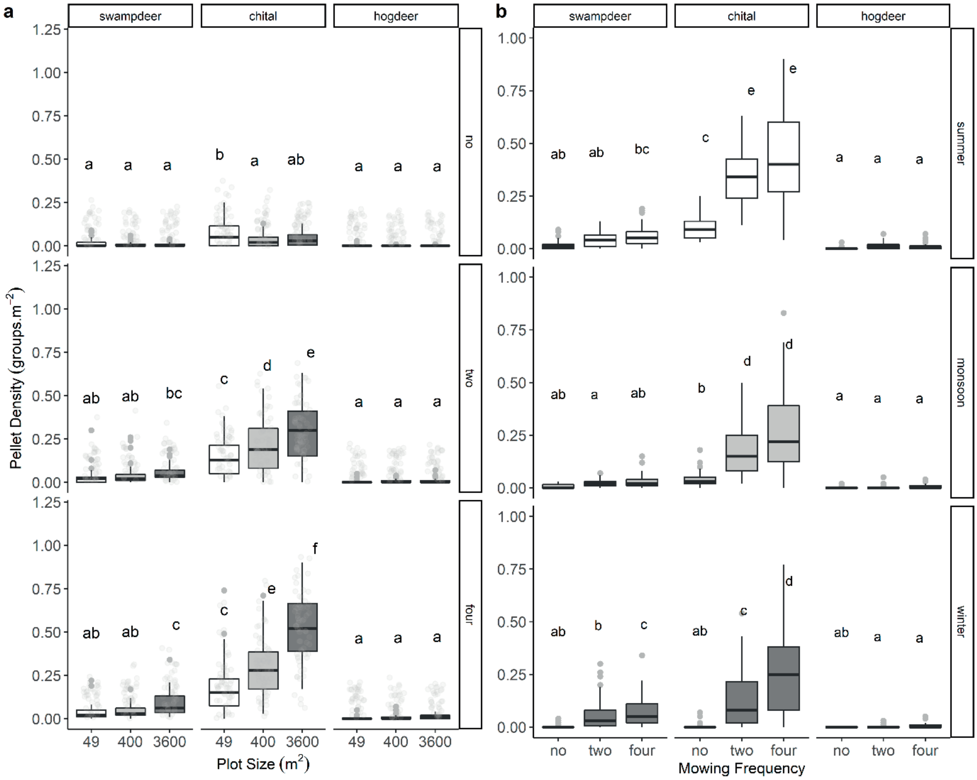


**Figure 4.6**: Level of use of the managed grasslands by the three deer species with respect to **a:** plot size, mowing, and species; and **b:** plot sizes, fertilisation, and species. The level of use was measured through pellet density (groups.m$^{-2}$) recorded in each experimental plot. Letters above each boxplot indicate a significant difference at alpha = 0.05, tested by estimated marginal means grouped by mowing after the linear mixed effect model (Table S1). Groups that share the same letter are not significantly different from each other.

## Pellet density at a fine scale

At a finer scale, pellet density was higher in the central (core) area of the 3600 m$^2$ plot than in the edge area of the plot (F=171.55, $P < 0.001$, Figure 4.7). The interaction effect of mowing, species, and area within the plot (point in the model, F = 9.73, *P* <0.001, Table S2), and the interaction effect of species, season, and area within the plot (F = 3.13, *P* < 0.015, Table S2) showed significant effect on pellet density in plots.

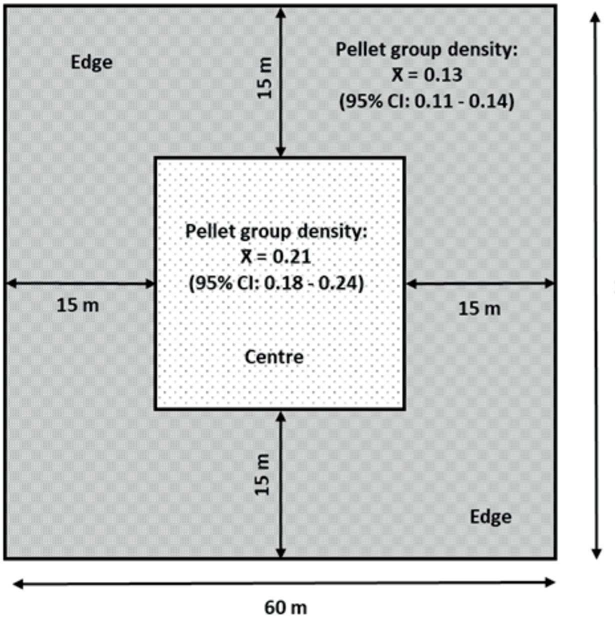


**Figure 4.7:** Pellet density (groups.m$^{-2}$) at the edge and central area of the 3600 m$^2$ plot. The Grey shaded area represents the edge and the white with dots represents a central area of the plot.

Pellet density of chital and swamp deer was significantly higher in the central area of the plots than in the edge of the plots (Figure 4.8a). Chital's pellet groups in the core area of both two and four-times mown plots were significantly more than in the edge area of these plots (Figure 4.8 b, c). Pellet groups of swamp deer were higher in the central area of four times mown plots only during winter (Figure 4.8 b, c). In contrast, the pellet groups of small hog deer did not differ significantly between the edge and the centre irrespective of mowing and seasons (Figure 4.8).

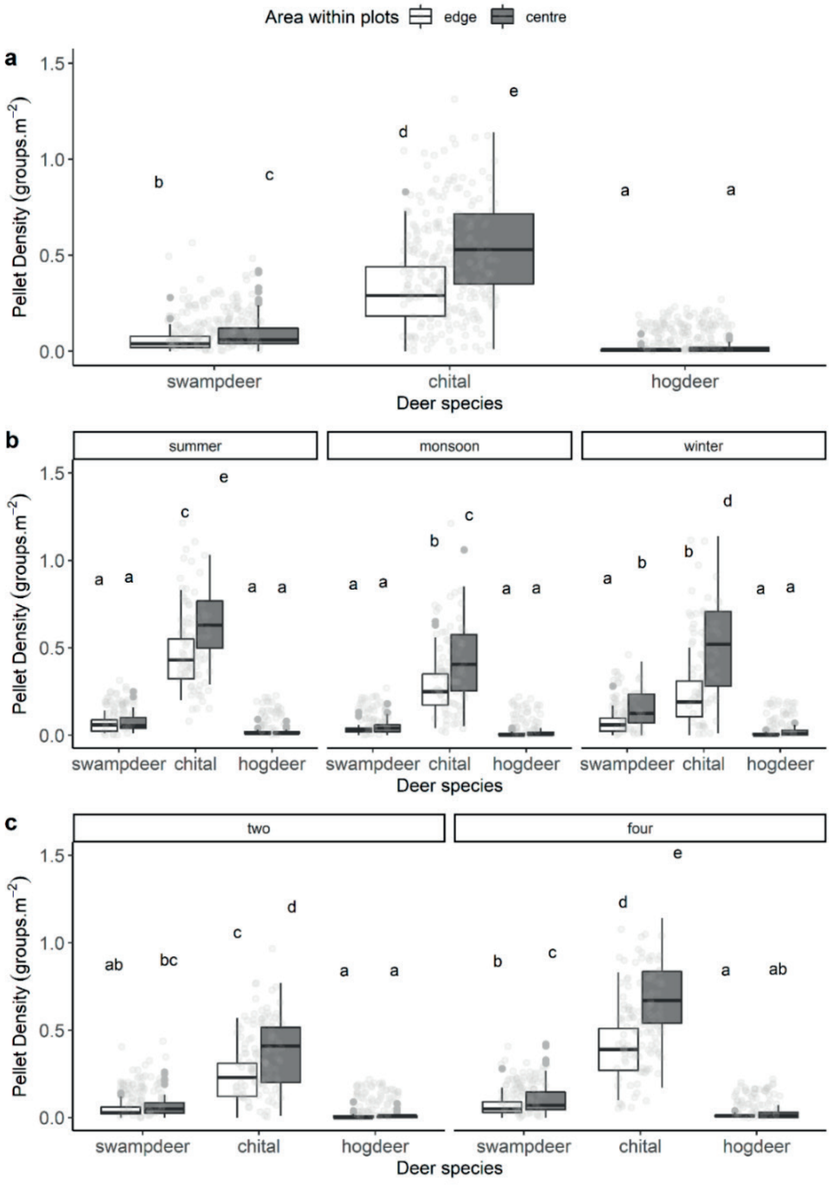


**Figure 4.8**: Level of use of the edge and centre areas of the plots in Bardia NP differs with respect to (a) species, (b) season, and (c) mowing. The white boxplot denotes the edge area, and the grey-shaded boxplot represents a central (or core) area of the plots. Letters above each boxplot indicate a significant difference at alpha = 0.05, tested by estimated marginal means grouped by point (area with plots) after the linear mixed effect model (Table S2). Groups that share the same letter are not significantly different from each other.

# Discussion

Through a landscape-scale experiment in the core area of Bardia NP, Nepal, we manipulated quality of the forage (by mowing and fertilisation) and modified the risk perception of deer (by creating open areas of different sizes which we called plots) and quantified the response of small and medium-sized deer in terms of level of use through pellet density. Our results showed that chital and swamp deer indeed select managed larger grasslands patches with short grasses over unmanaged patches and surrounding edges with tall grasses. We hypothesise that these deer feel safer in large plots with short grasses because there is a higher likelihood of early detection of approaching tigers, and a better chance of escaping from predation than in small plots. Our study on prey-predator system shows how habitat management affects fear levels across trophic levels, with insights relevant beyond our study area. Since tigers stalk their prey, fear of predation is strong (Schmitz, 2008); even stronger perhaps than previous studies on the 'landscape of fear'.

By removing tall grasses to create open patches, deer use increased when compared to unmanaged (un-mown) plots, as previously demonstrated (le Roux et al., 2018; Moe and Wegge, 1997). Our study further establishes that the level of use is directly related to the extent of openness and grass height (visibility), while forage quality plays a lesser role. This finding aligns with previous studies that identified visibility (Wheeler and Hik, 2014), detection probability (Valeix et al., 2009), fleeing or escaping ability (Iribarren and Kotler, 2012), and distance to refuge habitat (Cresswell et al., 2010) as critical determinants of predation risk perception and response in prey species (Gaynor et al., 2019). Importantly, our study extends this understanding to habitat management for prey species conservation and management, an aspect not addressed in previous studies.

Quantifying predation risk and associated behavioural responses of prey is a challenging task. We used pellet density as a proxy to quantify the level of use of the given area by deer assuming that presence of pellet groups means animals have visited and utilised the area. Presence of pellet groups does not necessarily provide information on the extent of use of the area, activities that they are performing in the area, and also does not give information on the number of animals using the area. GPS-collar and camera traps are being used widely to quantify predation risk and prey response in carnivore-ungulate systems (Moll et al., 2017; Prugh et al., 2019). Emerging and advance technologies such as drones and GPS video collars have the potential to provide comprehensive information about the impact of manipulating predation risks and resource on the corresponding response of prey and predators (Prugh et al., 2019).

We found that large (3600 $m^2$) plots and within those large plots, core areas of the plots had relatively high density of pellets of swamp deer and chital, and relatively low pellet density of hog deer. 'Landscape of fear' is species specific (e.g., (Hopcraft et al., 2010; Le Roux et al., 2019), and so is integration of 'landscape of fear' in habitat management. A study on hunting success of female lions found that when the distance between a female lion and its prey was 20 m, most of prey animals were able to escape predation (Elliott et al., 1977). The core areas of larger plots with short grasses should provide these deer with a higher probability of detecting approaching predators early and a greater likelihood of escape with the necessary flight distance (Cresswell et al., 2010; Stankowich and Coss, 2006) compared to smaller plots. This could be a reason for low pellet density in smaller plots (49 $m^2$ and 200 $m^2$) even though the smaller plots are, from a resource perspective, attractive to deer. Therefore, making small plots in sub-tropical monsoon grasslands where grass can grow over 2 m high (Lehmkuhl, 1994; Peet et al., 1999a; Thapa et al., 2021) and easily conceal tigers is a waste of time and effort. Moreover, we suggest that creating and maintaining mosaics of large patches of short grasses within grasslands would benefit chital and swamp deer by allowing them to optimise the trade-off between risk and resources.

Creating open habitats and providing space for deer to escape from predators could be an effective habitat management strategy from deer's perspective, as these features have been shown to reduce their vulnerability to predation. Our results also showed that pellet density is directly related to the spatial extent of openness and grass height, and to a lesser extent quality of the forage, but these factors are also modulated by the level of predation risk (Gaynor et al., 2019). Stalking predators like tigers may not benefit from such features, as the same features (e.g., openness and visibility) may reduce their hunting success rate (Karanth and Sunquist, 2000; Sunquist, 2010). This pose a conundrum for park managers: how to manage the habitat in the park so that both predators and deer may benefit?

Applying lessons from the 'landscape of fear' concept and experimental results to grassland management would be a novel approach with many opportunities to further enhance ecologically well-reasoned interactions between predators and their prey, as well as for the conservation of the predator and prey populations (Gaynor et al., 2021). For instance, park manager can reduce predation risk in high-risk areas creating open areas or creating refuges for prey species, while in low predation risk areas, interventions such as increasing vegetation cover or creating water sources can be implemented to attract predators and hence predation risk.

# Conclusion

The overwhelming success of tiger conservation in Nepal and a subsequent increasing number of incidents of human-tiger conflicts (Fitzmaurice et al., 2021) stresses the urgency to manage the habitat that is within the park for both the predators and the prey if the authorities in charge are to maintain the sizeable tiger population for the future generation. The challenge the Government of Nepal has is to entice the estimated 355 adult tigers (DNPWC and DFSC, 2022) and their offspring to stay in the unfenced national parks at the numbers that have been achieved through dedicated protection, and to maintain the cervid prey base at its level to feed those tigers. What we thus seek is science-based management interventions that exclude killing of tigers, but where habitat management (i.e., mowing, burning, fertilising of the grass resource; perhaps logging and uprooting of woody perennials to create open patches) is now becoming permissible for the management authority. The scientific underpinning of the 'landscape of fear' concept fundamentally addresses this interaction between predators, prey, and vegetation in a spatial context. With the increasing trend of degradation of grassland habitats in the subtropical region of the Indian subcontinent (Ratnam et al., 2016; Sankaran, 2005) and a consequent threat of local extinction of globally threatened faunal species, we posit important conservation implications of our findings.

**Data availability**

The data that support the findings of this study are openly available in Mendeley Data repository:

https://data.mendeley.com/datasets/wrm8838htz/draft?a=47441546-bdf6-4449-b8f4-7d751dc7a4b6

## Appendix: Supplemental information

**Table S1:** Results of the linear mixed effects model on the effect of mowing, fertilisation, plot size, species, season, and vegetation height on the level of use of the experimental plots by the three deer species.

| Treatments | Sum of Squares | Mean Squares | DF | F value | P value |
|---|---|---|---|---|---|
| **Mowing** | **0.20** | **0.10** | **2** | **29.65** | **< 0.001 ***** |
| **Fertilisation** | **0.04** | **0.02** | **2** | **6.26** | **0.002 **** |
| **Plot size** | **1.13** | **0.57** | **2** | **169.71** | **< 0.001 ***** |
| **Species** | **12.00** | **6.00** | **2** | **1799.23** | **< 0.001 ***** |
| **Season** | **0.60** | **0.30** | **2** | **89.42** | **< 0.001 ***** |
| **Mowing * Fertilisation** | **0.06** | **0.02** | **4** | **4.54** | **0.001 **** |
| **Mowing * Plot size** | **1.06** | **0.27** | **4** | **79.64** | **< 0.001 ***** |
| **Fertilisation * Plot size** | **0.05** | **0.01** | **4** | **3.53** | **0.007 **** |
| **Mowing * Species** | **4.19** | **1.05** | **4** | **313.98** | **< 0.001 ***** |
| **Fertilisation * Species** | **0.04** | **0.01** | **4** | **3.09** | **0.015 *** |
| **Plot size * Species** | **1.38** | **0.35** | **4** | **103.60** | **< 0.001 ***** |
| **Mowing * Season** | **0.15** | **0.04** | **4** | **10.96** | **< 0.001 ***** |
| Fertilisation * Season | 0.01 | 0.00 | 4 | 0.47 | 0.76 |
| Plot size * Season | 0.02 | 0.00 | 4 | 1.23 | 0.29 |
| **Species * Season** | **1.68** | **0.42** | **4** | **125.88** | **< 0.001** |
| Mowing * Fertilisation * Plot size | 0.04 | 0.01 | 8 | 1.54 | 0.14 |
| Mowing * Fertilisation * Species | 0.04 | 0.01 | 8 | 1.59 | 0.12 |
| **Mowing * Plot size * Species** | **1.34** | **0.17** | **8** | **50.12** | **< 0.001** |
| **Fertilisation * Plot size * Species** | **0.06** | **0.01** | **8** | **2.34** | **0.02 *** |
| Mowing * Fertilisation * Season | 0.04 | 0.00 | 8 | 1.38 | 0.2 |
| Mowing * Plot size * Season | 0.04 | 0.00 | 8 | 1.32 | 0.23 |
| Fertilisation * Plot size * Season | 0.01 | 0.00 | 8 | 0.41 | 0.92 |
| **Mowing * Species * Season** | **0.26** | **0.03** | **8** | **9.83** | **< 0.001 ***** |
| Fertilisation * Species * Season | 0.02 | 0.00 | 8 | 0.76 | 0.63 |
| Plot size * Species * Season | 0.01 | 0.00 | 8 | 0.47 | 0.88 |
| Mowing * Fertilisation * Plot size * Species | 0.07 | 0.00 | 16 | 1.36 | 0.15 |
| Mowing * Fertilisation * Plot size * Season | 0.03 | 0.00 | 16 | 0.51 | 0.94 |
| Mowing * Fertilisation * Species * Season | 0.07 | 0.00 | 16 | 1.40 | 0.13 |
| Mowing * Plot size * Species * Season | 0.07 | 0.00 | 16 | 1.23 | 0.24 |
| Fertilisation * Plot size * Species * Season | 0.02 | 0.00 | 16 | 0.43 | 0.97 |
| Mowing * Fertilisation * Plot size * Species * Season | 0.04 | 0.00 | 32 | 0.41 | 0.99 |
| **Grass average height (co-variate)** | **0.06** | **0.06** | **1** | **18.06** | **< 0.001 ***** |

Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; $p > 0.05$ = ns.

**Table S2:** Results of the linear mixed effects model on the effects of mowing, fertilisation, species, and season on the level of use by the three deer species between the edge and the centre of the 3600 $m^2$ plots (point).

| Treatments | Sum of Squares | Mean Squares | DF | F value | P value |
|---|---|---|---|---|---|
| **Mowing** | 0.904 | 0.904 | 1 | 112.3 | < **0.001** *** |
| **Fertilisation** | 0.249 | 0.125 | 2 | 15.48 | < **0.001** *** |
| **Species** | 24.571 | 12.285 | 2 | 1526.26 | < **0.001** *** |
| **Season** | 0.742 | 0.371 | 2 | 46.12 | < **0.001** *** |
| **Point** | 1.381 | 1.381 | 1 | 171.55 | < **0.001** *** |
| Mowing * Fertilisation | 0.002 | 0.001 | 2 | 0.15 | 0.857 |
| **Mowing * Species** | 2.095 | 1.048 | 2 | 130.14 | < **0.001** *** |
| **Fertilisation * Species** | 0.262 | 0.066 | 4 | 8.14 | < **0.001** *** |
| Mowing * Species | 0.047 | 0.023 | 2 | 2.91 | 0.055 |
| Fertilisation * Season | 0.026 | 0.007 | 4 | 0.82 | 0.513 |
| **Species * Season** | 1.446 | 0.362 | 4 | 44.92 | < **0.001** *** |
| **Mowing * Point** | 0.142 | 0.142 | 1 | 17.67 | < **0.001** *** |
| Fertilisation * Point | 0.034 | 0.017 | 2 | 2.13 | 0.12 |
| **Species * Point** | 1.59 | 0.795 | 2 | 98.79 | < **0.001** *** |
| **Season * Point** | 0.195 | 0.097 | 2 | 12.11 | < **0.001** *** |
| Mowing * Fertilisation * Species | 0.018 | 0.004 | 4 | 0.56 | 0.695 |
| Mowing * Fertilisation * Season | 0.018 | 0.005 | 4 | 0.56 | 0.689 |
| Mowing * Species * Season | 0.044 | 0.011 | 4 | 1.37 | 0.242 |
| Fertilisation * Species * Season | 0.068 | 0.009 | 8 | 1.06 | 0.391 |
| Mowing * Fertilisation * Point | 0.005 | 0.002 | 2 | 0.29 | 0.748 |
| **Mowing * Species * Point** | 0.157 | 0.078 | 2 | 9.73 | < **0.001** *** |
| Fertilisation * Species * Point | 0.03 | 0.008 | 4 | 0.94 | 0.438 |
| **Mowing * Season * Point** | 0.059 | 0.029 | 2 | 3.65 | **0.027** * |
| Fertilisation * Season * Point | 0.001 | 0 | 4 | 0.04 | 0.997 |
| **Species * Season * Point** | 0.101 | 0.025 | 4 | 3.13 | **0.0146** * |
| Mowing * Fertilisation * Species * Season | 0.062 | 0.008 | 8 | 0.96 | 0.4672 |
| Mowing * Fertilisation * Species * Point | 0.003 | 0.001 | 4 | 0.08 | 0.9877 |
| Mowing * Fertilisation * Season * Point | 0.004 | 0.001 | 4 | 0.14 | 0.9678 |
| Mowing * Species * Season * Point | 0.061 | 0.015 | 4 | 1.9 | 0.1095 |
| Fertilisation * Species * Season * Point | 0.012 | 0.002 | 8 | 0.19 | 0.9922 |
| Mowing * Fertilisation * Species * Season * Point | 0.023 | 0.003 | 8 | 0.35 | 0.9444 |

Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

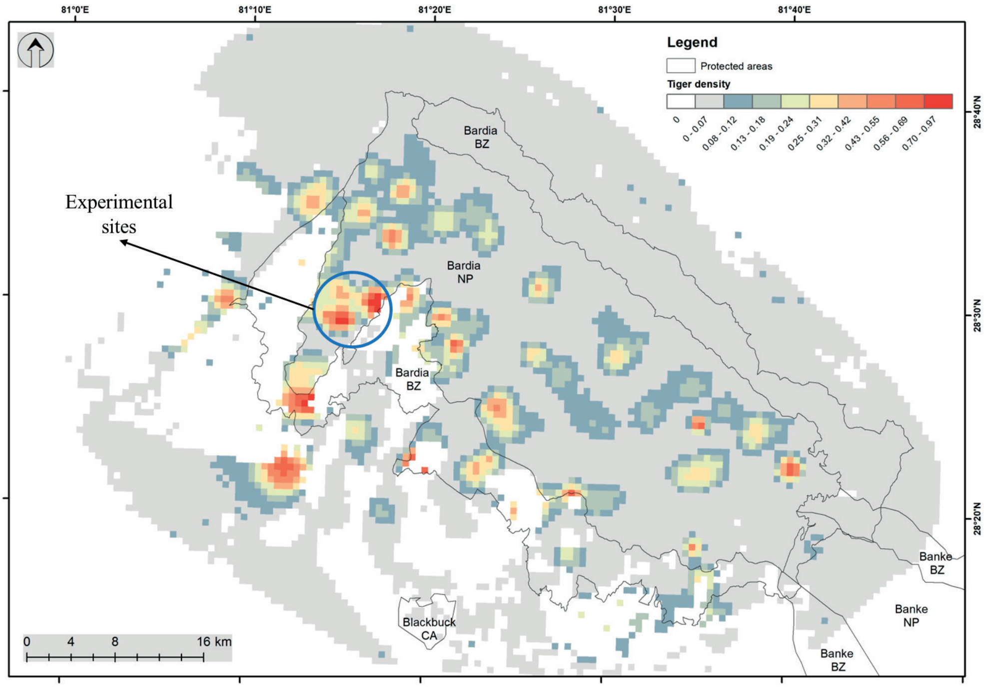


**Figure S3**: Tiger density map of Bardia NP (DNPWC and DFSC, 2022). Density of tiger in Bardia National Park has increased from 4.74 individuals. 100 km$^{-2}$ in 2018 to ~7.15 individuals. 100 km$^{-2}$ in 2022 (DNPWC and DFSC, 2022). The experimental sites have the highest density of tigers.

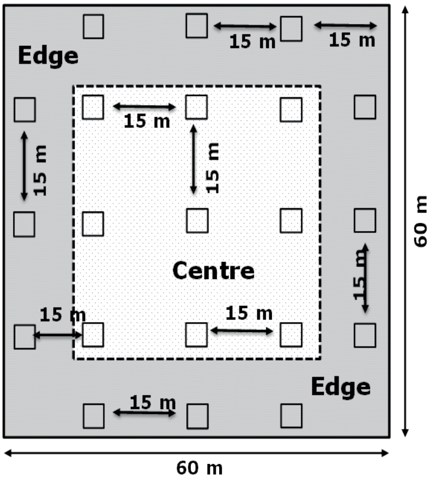


**Figure S4:** Spatial layout of sampling points in 3600 $m^2$ plots. Each sampling point (indicated by small squares – measuring 2 m x 2m) is 15 m in distance from each other and also from the corner of the plot. The edge area of the plot is denoted by a grey shed and the central area is by white with grey dots.

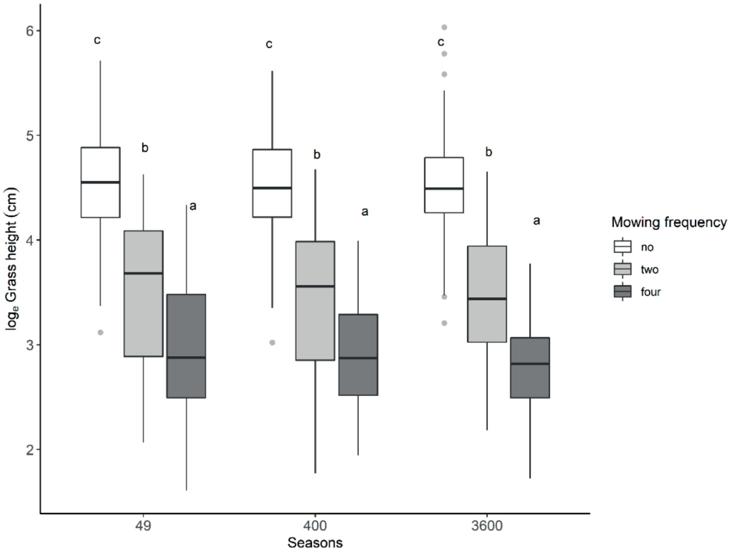


**Figure S5:** Vegetation height with respect to treatment. Vegetation height was significantly lower in four times mown plots (F = 154.95, P < 0.001) with is evident but, alteration in vegetation height may change risk perception in herbivores through modification in visibility and detection probability. Letters above each boxplot indicate a significant difference at alpha = 0.05, tested by estimated marginal means after the linear mixed effect model. Groups that share the same letter are not significantly different from each other. We used mowing, and plot size as fixed factors and replications within locations as random factor.

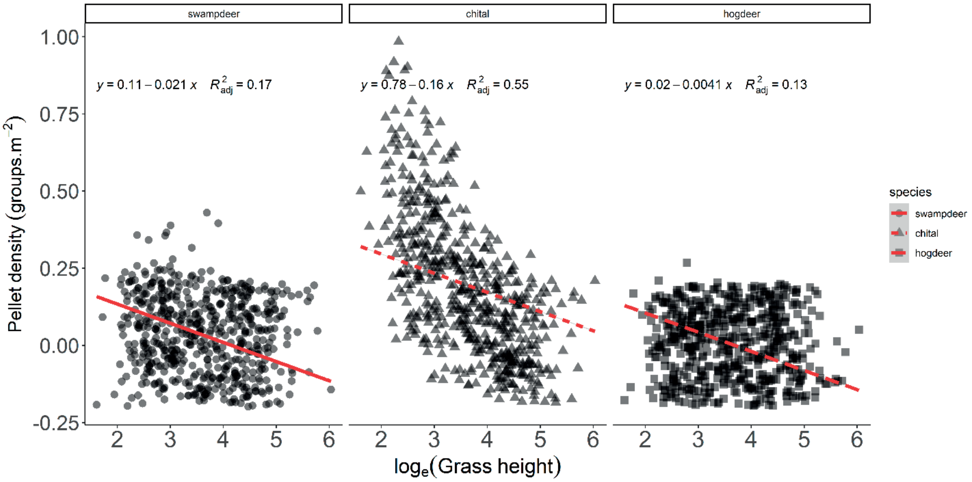
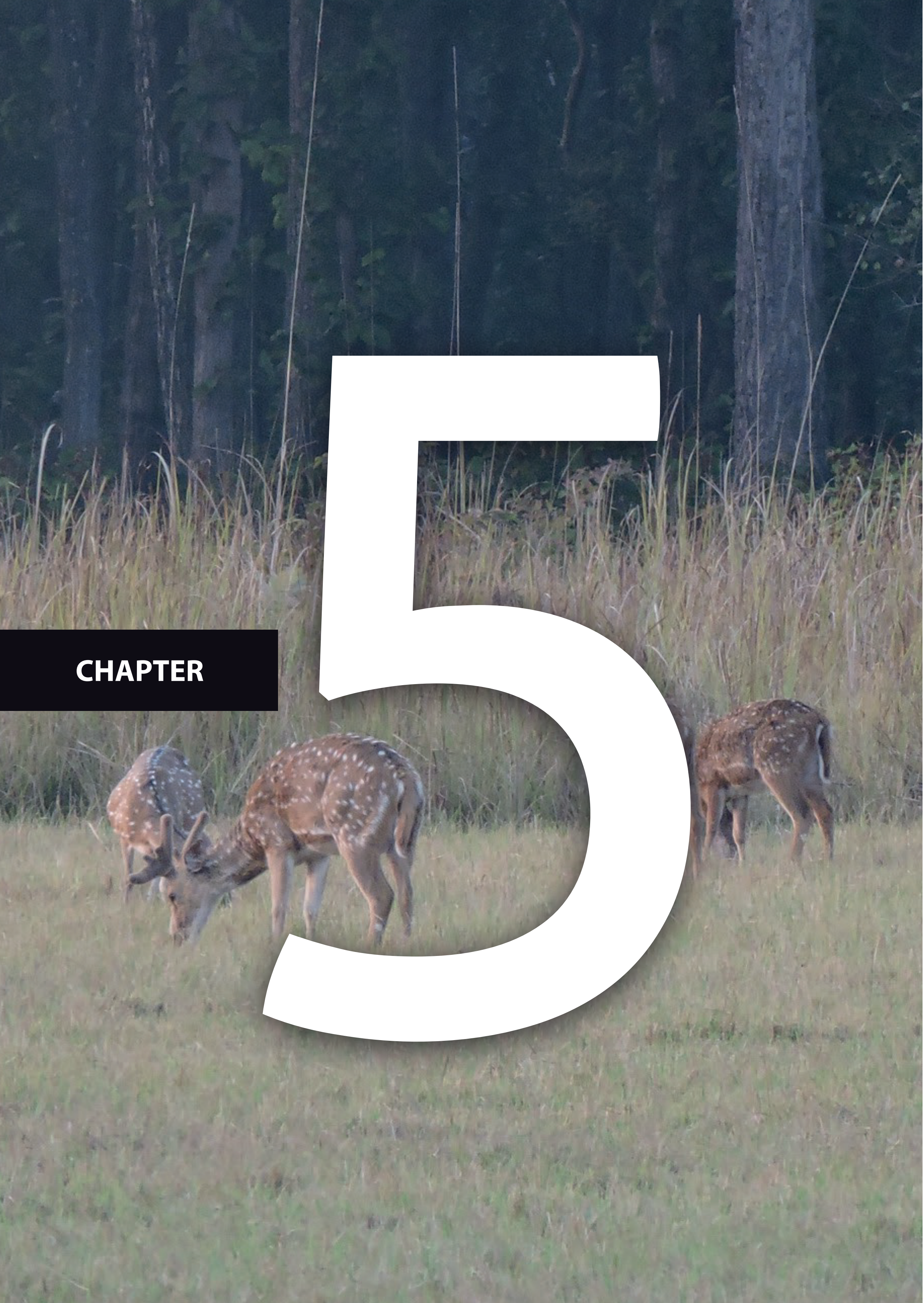


**Figure S6:** Relationship between grass height and level of use (in terms of pellet group density) by deer species. Deer species respond to grass height differently (F = 610.09, P < 0.001) indicating, differential risk perception between deer species. Level of use decreases with grass height. Grass height expressed as log$^e$ grass height. Regression lines were obtained from liner mixed effect model with heigh and species as predictor variables and replications within locations as random effect.



# CHAPTER 5

# Enhancing subtropical monsoon grassland management: Investigating mowing and nutrient input effects on initiation of grazing lawns

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# Abstract

Subtropical monsoon grasslands in Asia are commonly in a fire-dominated state with tall grasses (> 2m) that provide poor-quality forage for mammalian herbivores. In contrast, small patches of grazing lawns with short, nutritious grasses are sparsely distributed within these subtropical monsoon grasslands. Despite the importance of grazing lawns in providing high-quality forage for mammalian herbivores, the process of formation and maintenance of grazing lawns has not been studied in the monsoon grasslands of subtropical Asian region. We conducted a large-scale multi-year experiment in subtropical monsoon grasslands within a protected area in Nepal to examine whether mowing tall grasses at different frequencies and spatial scales, along with the application of chemical fertilisers (urea or single superphosphate), could change tall grasslands into grazing lawns. We found that nitrogen and phosphorus concentrations in grasses increased to levels exceeding the minimum maintenance requirements for ruminants in 3600 $m^2$ plots that were mown four times and fertilised. The concentrations of nitrogen and phosphorus remained below the minimum maintenance level for ruminants in unfertilised and unmown plots and in small plots that were four-time mown and fertilised. The frequently mown plots exhibited a significant increase in the proportion of ground cover of lawn grass, from 1% to 3%, and a corresponding decrease in the proportion of ground cover of tall grasses, from 24% to 1%. These results supported our hypothesis that frequent mowing at a larger spatial scale with the addition of chemical fertilisers and grazing leads to the inception of grazing lawns that are favourable for wild herbivores. However, the persistence of the grazing lawns presents challenges due to the highly productive monsoon season and the functional extinction of large bulk grazers. To our knowledge, this is the first empirical study conducted in the subtropical monsoon grasslands of Asia to experimentally demonstrate the importance of active management for the initiation of grazing lawns. Our findings have important implications for the management of subtropical monsoon grasslands.

**Keywords:** forage quality, management, mesoherbivores, ruminants, tall grasses, short grasses

## Introduction

Grazing lawns are an important component of savanna and grassland systems and have been extensively researched, especially in Africa (Archibald, 2008; Bonnet et al., 2010; Coetsee et al., 2011; Cromsigt et al., 2017; Cromsigt and Olff, 2008; Donaldson et al., 2018; Hempson et al., 2015; McNaughton, 1984; Person et al., 2003; Veldhuis et al., 2014). Grazing lawns are important nutrient hotspots from where grazing herbivores can maximise their energy and nutrient intake (Bergman et al., 2001; Thapa et al., 2021; van Langevelde et al., 2008; Verweij et al., 2006; Wilmshurst et al., 1995). Despite the significance of grazing lawns for grazing herbivores, grazing lawns and the factors underlying their formation, maintenance, and disappearance have received little attention in the Asian subtropical monsoon grasslands. Yet, a whole suite of mammalian herbivores depends on these monsoon grasslands, as in many African savannas, ranging from megaherbivores (wild Asian elephant - *Elaphus maximus*) to small herbivores such as hispid hare (*Caprolagus hispidus*) (Ahrestani and Sankaran, 2016).

Within the tall-bunch-grass matrix in subtropical monsoon grasslands of the Indian subcontinent, small areas of grazing lawns are sparsely distributed (Karki et al., 2000; Thapa et al., 2021). While the establishment of grassy vegetation in South Asia can be dated back to the Late Miocene (Armstrong-Altrin et al., 2009; Dengler et al., 2020; Morley, 2012), the origin of grazing lawns within these grasslands remains uncertain. It is believed that patch-selective grazing in combination with patch burning and cutting, contributes to the formation of grazing lawns in the subtropical monsoon grasslands of Asia. However, current knowledge about grazing lawns and their formation in the Asian subtropical region is largely based on anecdotal information and assumptions (Karki et al., 2000; Peet et al., 1999a; Thapa et al., 2021). Understanding the factors associated with the formation and maintenance of grazing lawns in the Asian subtropical monsoon grasslands is of particular interest to park managers, especially in protected areas that contain tigers (*Panthera tigris*) where the grassland management objectives are intended to maintain an abundant population of mesoherbivores (small and medium body sized cervids) as they are the primary prey species of tigers, besides wild boar (*Sus scrofa*) (Thapa and Kelly, 2017; Upadhyaya et al., 2018).

The existing subtropical monsoon grasslands of Asia are characterised by tall grasses (> 2 m) with high biomass (Lehmkuhl, 1994; Peet et al., 1999a; Ratnam et al., 2019) and the nutritional quality of these tall grasses falls below the maintenance requirements of mesoherbivores (Ahrestani et al., 2011; Thapa et al., 2021). While the current extent and structural composition of the tall grasslands may support megaherbivores such as wild Asian elephants and Greater one-horned rhinoceros (*Rhinoceros unicornis*), it remains challenging to meet the nutritional requirements of the existing assemblage of mesoherbivores (Thapa et al., 2021). This applies, in particular, to the assemblage of chital (*Axis axis*), swamp deer (*Rucervus duvaucelii*), and hog deer (*Axis porcinus*) which are frequent users of the monsoon grasslands in the Indian subcontinent (Moe and Wegge, 1994; Wegge et al., 2006). The digestive physiology and higher body-mass energy requirements of the mesoherbivores make them particularly dependent on high-quality forage (Prins and Olff, 1998; Prins and Van Langevelde, 2008; van Langevelde et al., 2008), and are thus affected by the dearth of nutrient availability.

A large body of literature from Africa and other regions highlight that grazing lawns are animal driven and the persistence of grazing lawns depends on the intensity of grazing pressure (e.g., Cromsigt et al., 2017b; Donaldson et al., 2018; Hempson et al., 2015; McNaughton, 1984). Together with grazing, other factors like soil nutrient status, soil moisture, and previous land-use practices (abandoned agricultural land or cattle kraals; van der Waal et al., 2011), fire and rainfall (Archibald, 2008), megaherbivores (De Knegt et al., 2008), and predation risk (Anderson et al., 2010) play an important role in the formation and persistence of grazing lawns. Experimental studies in South African savannas demonstrated that grazing lawns can be established when the management interventions promote frequent grazing and thereby induce positive feedback between grazing and grazing lawn formation (Cromsigt and Olff, 2008). Similarly, Schroder (2021) showed that the addition of chemical fertilisers can increase nutrient concentrations in forage which attract herbivores, the elevated grazing pressure of which initiates the establishment of grazing lawns.

Studies on grazing lawns in African savannas do not yield comprehensive insight to fully understand the grazing lawn formation processes in Asian subtropical monsoon grasslands. Subtropical monsoon grasslands in Asia are highly productive and receive over 1200 mm of rainfall annually (Ratnam et al., 2019, 2016). The very high growth rate and fast production of combustible materials (Ahrestani et al., 2011) due to the hot and humid growing season characterised by monsoon-influenced humid subtropical climate (referred to as Cwa-climate in the Köppen-classification; Chen and Chen 2013) make these grasslands fundamentally different from savanna grasslands in arid and semi-arid ecosystems (Ratnam et al., 2019, 2016; Sankaran et al., 2005). Subtropical monsoon grasslands tend to shift to forests as high precipitation (where mean annual precipitation exceeds 1200 mm) favours trees establishment in grasslands (Sankaran et al., 2005; Staver et al., 2011; Van Langevelde et al., 2003). The coexistence of grasses and trees in the high-rainfall region of subtropical Asia is maintained by frequent fire, herbivory, and human activities (Banerjee et al., 2023; Ratnam et al., 2016, 2011; Sankaran, 2016; Sankaran et al., 2005; Van Langevelde et al., 2003). A change in the fire regime, herbivory or human activities might increase the risk of the establishment of forests in grasslands (Banerjee et al., 2023; Gross et al., 2013; Kumar et al., 2021, 2020), as observed in high-rainfall regions of Australia, Africa and South America (Sankaran et al., 2005; Staver et al., 2011). This may have negative consequences for the availability of quality forage for grazing herbivores.

While fire plays an important role in maintaining the coexistence of grasses and trees (Ratnam et al., 2016, 2011; Sankaran, 2016; Staver et al., 2011; Van Langevelde et al., 2003), it can disrupt the positive interaction between grazing and grazing lawns (Archibald et al., 2005). Fire generally occurs at the landscape scale during the dry season, and after a burn, the entire burned area consists of nutritious new re-sprouts (Donaldson et al., 2018; Moe and Wegge, 1997; Van de Vijver et al., 1999). Herbivores are dispersed over the post-burn landscape due to the availability of post-burn nutritious regrowth (Archibald et al., 2005; Donaldson et al., 2018) which results in a reduction in localised grazing pressure and promote tall grasses in grazing lawns. In contrast, small-scale disturbances such as mowing tall grasses and nutrient addition promote concentrated grazing and initiate the process of grazing lawn formation (Cromsigt and Olff, 2008; Schroder, 2021). Therefore, we predict that the removal of tall grasses through mowing and the addition of artificial fertilisers creates patches of short grasses with higher nutrient concentrations. We further expect that the availability of high-quality forage will attract herbivores to graze in the area, resulting in increased grazing pressure that initiates the process of grazing lawn formation (Cromsigt and Olff, 2008; Hempson et al., 2015; McNaughton, 1984). Specifically, we predict that mowing in combination with nutrient input will (i) enhance forage quality; (ii) increase herbivore consumption rate (i.e., increases grazing pressure, and (iii) decrease and increase the proportion of tall grasses and lawn grasses, respectively.

To test these predictions, we conducted a multi-year large-scale experimental study in the subtropical monsoon grasslands within the core area of Bardia National Park (Bardia NP), Nepal. We mowed tall grasslands at different frequencies at different spatial scales and added artificial fertilisers (nitrogen and phosphorus) to stimulate nutrient-rich regrowth. We monitored forage quality, grazing pressure, and vegetation development on experimental plots to assess which intervention regimes favoured the formation of grazing lawns. Our study contributes to the understanding of grazing lawn formation processes in the Asian subtropical monsoon grasslands, an ecosystem that is distinct from savannas in arid and semi-arid regions.

# Methods

## Study area

We conducted our study in the subtropical monsoon grasslands in Bardia NP of Nepal which has a subtropical monsoonal climate (Cwa-climate; Chen and Chen 2013). Bardia NP has a distinct monsoon (June – September), winter (October – January) and hot dry summer (February-May) seasons with mean annual rainfall of approximately 1700 mm (see for example Thapa et al., 2022) and a temperature range from 10 °C to a maximum of 45 °C. Covering an area of 968 km$^2$ and located in the lowland Terai within the Terai Arc Landscape, Bardia NP is one of the largest national parks in the lowland Terai (centre of the park at 28$^0$23′ N, 81$^0$30′ E, Figure 5.1). The park is home to both megaherbivores (e.g., rhinoceros and wild Asian elephant) and mesoherbivores (e.g., chital, swamp deer, sambar - *Rusa unicolor,* hog deer, and muntjac - *Muntiacus vaginalis*). These mesoherbivores are important prey of the tigers in the park (Upadhyaya et al., 2018). The park holds the highest density of tigers in Nepal with an estimated density of ~7 individuals.100 km$^{-2}$ (DNPWC and DFSC, 2022).

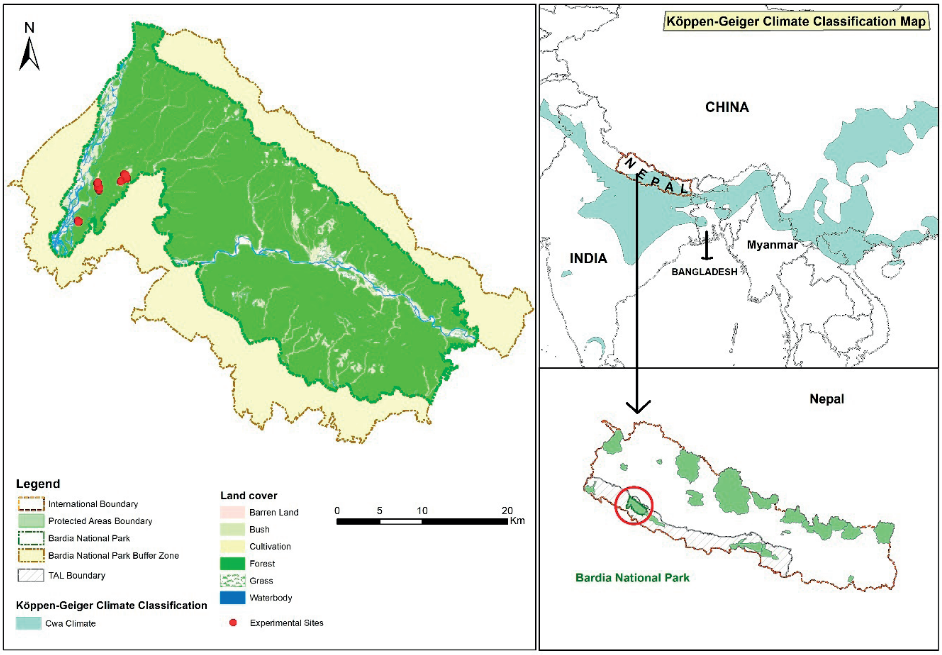


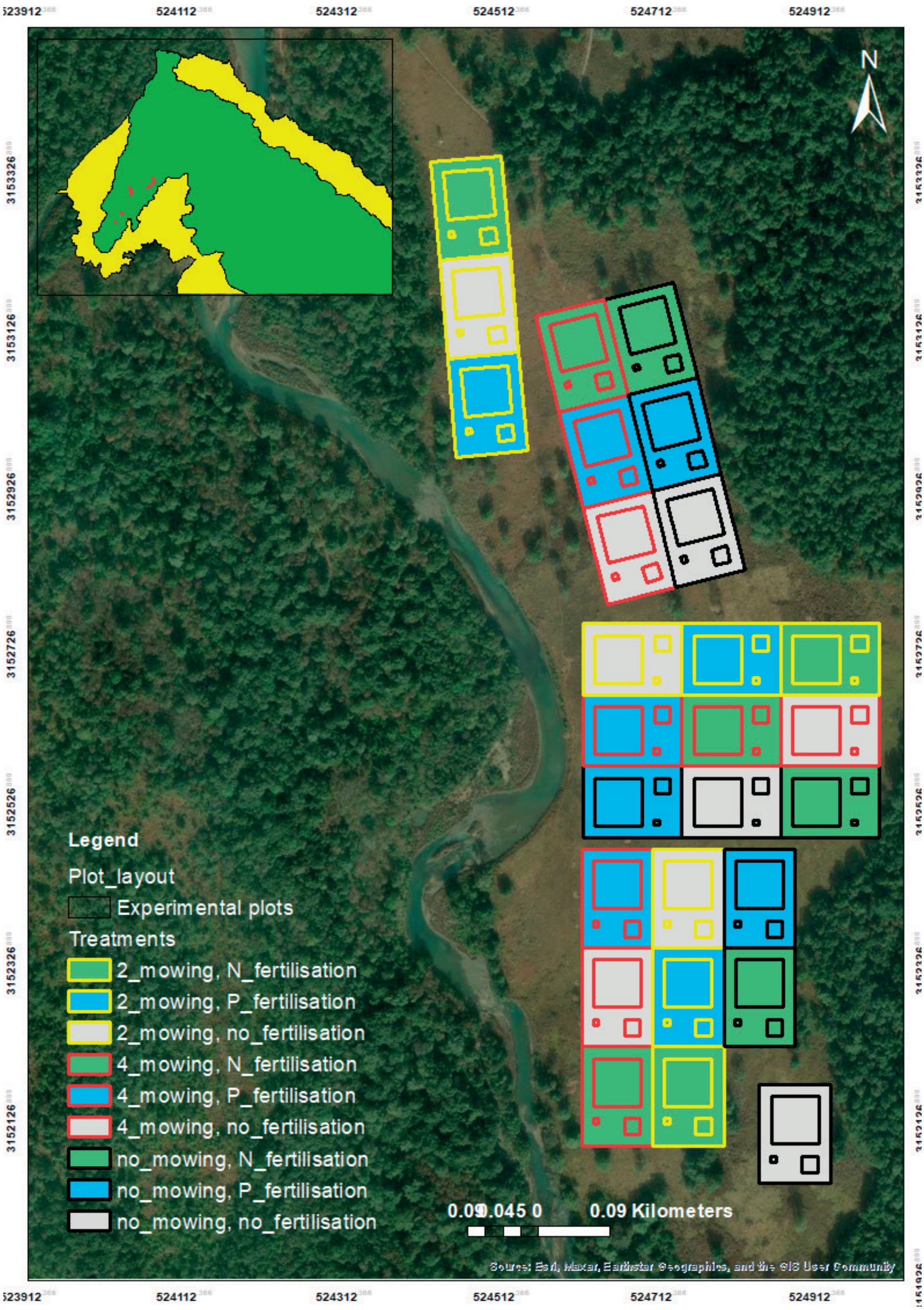
**Figure 5.1:** Experimental sites within Bardia National Park. The park harbours one of the most significant tiger populations within the Terai Arc Landscape of Nepal. The park lies within Cwa climate, indicating a monsoon-influenced humid subtropical climate under the Köppen classification (light blue area on the top-right inset map).

The park consists of subtropical vegetation with riverine forest, riverine floodplain grasslands along the two major rivers (Karnali and Babai Rivers), and *sal* (*Shorea robusta*) forest with interspersed grasslands. Assemblages of *Imperata cylindrica* (L.), *Saccharum spontaneum* (L.), *Vetiveria zizanioides* (L.), *Saccharum bengalense* (Retz.) and *Narenga porphyrocoma* (Hance ex Trin.) Bor. are reported from the grasslands that are interspersed within *sal* forest (Peet et al., 1999a; Thapa et al., 2021).

After the park was established in the late 1970s, settlements within the park's core area were relocated and human activities such as agriculture and livestock grazing were completely stopped. Thatch harvesting and grass cutting, which are allowed to continue, have decreased over time. In the 1990s more than 30,000 people entered the park to harvest thatch for 14 days but at present, only about 10,000 people enter the park and harvest thatch for three days. This is mainly due to the adoption of concrete houses with corrugated galvanised sheet roofs and the number of livestock holdings per household is also in decreasing trend. The sudden exclusion of grazing by bulk grazers such as cattle and domestic buffaloes, and the reduction in thatch harvesting have led to the regeneration and colonisation by woody plants and invasive weeds in grasslands (Murphy et al., 2013; van Lunenburg et al., 2017; Wegge et al., 2009), resulting in a decrease in the extent and abundance of short grassland patches (Bijlmakers et al., 2023). The ban on human activities and domestic large herbivores followed by the reduction in thatch harvesting and subsequent increased occurrence of fire (Thapa et al., 2022) has caused tall grasses to recolonise in grazing lawns, thus forming a continuum of nutrient-poor tall grasses.

## Experimental design

The experiment was conducted in three separate grassland patches (locally known as Lamkauli Phanta, Baghaura Phanta, and Khauraha Phanta) located in the western section of the park, interspersed within *sal* forest (Figure 5.1). The sites were 1 – 2 km apart, had similar topography and have a similar assemblage of grass species (Thapa et al., 2021). In 2018, we created a total of 189 experimental plots (Table S1) of three different sizes *viz*. 3600 $m^2$ (n = 63), 400 $m^2$ (n = 63), and 49 $m^2$ (n = 63). Each plot was randomly assigned different mowing frequencies (four times, two times or no mowing) and fertilisation levels (nitrogen, phosphorus, or no fertilisation) using computer-generated random numbers (Figure 5.2).



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Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community

**Figure 5.2:** Complete set of experimental design in one of the locations (Baghaura phanta, n = 81) within Bardia NP. One replicate consisted of 27 plots. There are a total of 7 replications within three sites. The colour of the borderline of the square plots indicated the types of mowing treatment received by respective plots - black borderline for no mowing, yellow for two times mowing, and red for four times mowing. Likewise, filled colours within square plots represent types of fertilisation treatment received by respective plots - green for nitrogen fertilisation, blue for phosphorous, and grey for no fertilisation. The size of the square represents either 3600 $m^2$ or 400 $m^2$ or 49 $m^2$ plots.

We mowed tall grasses (~1.5 m to ~3 m tall) at a height of around 5 cm from the ground using handheld grass mowers (Honda Brush Cutter UMR 435T) and removed the cut biomass from the plots. Labourers were used for this purpose, and we estimated that approximately 10 to 15 tonne/ha of biomass was removed from the plots annually. Grasses were mown in January/February and August/September on the plots that received the two times mowing treatment. Likewise, grasses were mown in January/February, April/May, August/September, and November/December on the plots that were subjected to the four times mowing treatment. We applied the mowing regimes continuously for two years in 2019 and 2020. We applied chemical fertilisers viz., urea (46 % N), and single superphosphate (SSP with $P_2O_5$ 16 %) three times (2018, 2019 and 2020) to stimulate nutrient-rich regrowth. The first two applications equated to 15 $g.m^{-2}$ of urea, and 15 $g.m^{-2}$ of SSP (in March 2018 and April 2019). We increased the load in the third application and spread 40 $g.m^{-2}$ of urea and 60 $g.m^{-2}$ of SSP in January 2020. Both nitrogen (for growth) and phosphorus (for reproduction and lactation) are important for the survival of free-roaming herbivores (Prins and Van Langevelde, 2008), thus, we chose to use nitrogen and phosphorus in our experiment. Plots that received neither mowing nor fertilisation treatments (n = 21) were used as controls.

## Data collection

### Vegetation composition

We determined the percentage cover of grass species in plots in January 2021 by laying down quadrats at five different locations (one in the middle and four on each side of the plots). We used 1 m x 1 m quadrat with equally spaced 100 sampling points and recorded bare ground, litter, animal droppings and vegetation following the point intercept method. We used grid corners as the point to record the hits (see for example Thapa et al. 2021). We measured grass height randomly at three spots within each 1 m × 1 m quadrat with a ruler to 0.5 cm precision and used average height per plot for analysis. In addition, we categorised the plots as grazed or not-grazed by visually observing grazing marks (see Sankaran 2009; Thapa et al. 2021) in the grasses within 1 m x 1m quadrats.

### Vegetation samples

We clipped and weighed grass vegetation from the centre of each plot (n = 189) using a digital weighing scale (600 g capacity, with a precision of 1 g; Brand: Equal [class II]). After drying the samples for five days at ambient temperature (~30°C), we recorded the air-dry weight and stored the samples in paper bags for chemical analyses. We collected grass samples monthly in 2021 from 3600 $m^2$ plots (n=63, Table S1) to examine the effect of treatments on forage quality across seasons (summer, monsoon, and winter). Grass samples were clipped from a 0.36 $m^2$ frame and air-dried before being stored in paper bags for chemical analyses.

### Herbivore consumption

We measured the proportion of vegetation consumed by mesoherbivores under different treatments using a moveable cage experiment (e.g., Veldhuis et al. 2016). We used 3600 $m^2$ plots that received two and four times mowing (n =42, Table S1), installed two iron cages of 1 m x 1 m x1 m in each plot, and fixed the cages to the ground. The cages were wrapped in chicken wire netting to prevent grazing. We determined the initial biomass of vegetation from clipped grasses from 0.36 $m^2$ frame near the cage and measured fresh weight. We placed the cages for 30 days and subsequently clipped grasses from 0.36 $m^2$ frame from outside and inside the cage. We measured fresh weight using a digital weighing scale (with a capacity of 600 g and accuracy of 0.5 mg; Brand: Equal [class II]). The cages were left for 30 days, and we measured the fresh weight of grass from inside and outside the cage to calculate herbivore percentage consumption [i.e., consumption % = (inside cage biomass – outside cage biomass)/inside cage biomass * 100%]. We calculated primary production as inside cage biomass after 30 days minus initial biomass. We also measured grass height from outside and inside the cage while installing and removing the cages.

### Chemical analysis of vegetation samples

Crude protein (CP; expressed as 6.25 x percentage nitrogen), and phosphorous concentration were determined for grass samples. Nitrogen was determined by semi-micro Kjeldahl method in a dry-block digester, and phosphorus by tissue digestion in a block digester (AOAC, 1990). All the measurements were expressed as percentage dry matter (% DM) of a forage. Samples were chemically analysed at the Anmol Agri-tech Pvt. Ltd in Chitwan, Nepal.

## Data analysis

### Daily requirements of crude protein

We derived the daily requirement of crude protein (CP) for maintenance, pregnancy and lactation in adult female chital (with a body mass of ~50 kg; Mishra 1982), swamp deer (~150 kg; Dinerstein 1980), and hog deer (~30 kg; Dhungel and O'Gara 1991) using known allometric relationship (Table 5.1) and compared with the values obtained from grass sample chemical analysis.

**Table 5.1:** Daily crude protein requirement for adult female chital, swamp deer, and hog deer. W stands for body mass (kg), BW for body mass of adult female, and DM for dry matter of the forage.

| Activity | Allometric function* | Crude Protein requirement (% DM. $d^{-1}$) | | |
|---|---|---|---|---|
| | | Chital (50 Kg BW) | Swamp deer (150 kg BW) | Hog deer (30 kg BW) |
| Maintenance | $0.65 \times W^{0.75}$ | 7.6 | 5.8 | 8.8 |
| Pregnancy | $0.78 \times W^{0.75}$ | 9.2 | 7.1 | 10.4 |
| Lactation | $1.01 \times W^{0.75}$ | 11.8 | 9.0 | 13.5 |

* (Ahrestani et al., 2012). It is estimated that ruminants consume approximately 2% of their body weight in dry matter on a daily basis (Ahrestani et al., 2012). Crude protein requirement is expressed in % Dry Matter (DM).

### Effect of treatment on nutrient concentration of grasses

To test our prediction "mowing in combination with nutrient input will enhance forage quality," we used linear mixed-effects models (LMMs) with mowing, fertilisation, plot size, and their interactions (both two ways and three ways) as fixed factors; and replications within locations as random factors. We compared mean differences in crude protein (CP) and phosphorus concentration in grass samples with respect to treatments using multiple comparison tests after LMMs. Likewise, we included season and biomass along with treatments (mowing, fertilisation, and plot) in LMMs to compare the variation in CP with regard to treatments and season for the data obtained from 3600 $m^2$ plots.

### Herbivore consumption with respect to treatment

To test whether there was an increase in herbivore consumption in areas with high mowing frequencies, we used LMMs with mowing, fertilisation and their interactions as fixed factors and location as a random factor. We used primary production as a covariate in the model. We measured differences in percentage consumption of vegetation by herbivores through multiple comparison tests after LMMs.

### Change in vegetation development

We analysed three grass species – *Imperata cylindrica*, *Narenga porphyrocoma*, and *Hemarthria compressa* (L. f.) R. Br. using LMMs to test our prediction of a decrease in percentage cover of tall grasses and an increase in the percentage cover of lawn grasses in frequently mown areas. *I. cylindrica* and *N. porphyrocoma* are common tall grasses and *H. compressa* is commonly found in grazing lawns in the grassland of Bardia NP (Thapa et al., 2021). First, we started with a full model with mowing, fertilisation, plot size, and their interactions as fixed factors and used backward stepwise removal of non-significant terms to obtain the final model. The final model included mowing as a fixed factor. We then used multiple comparison tests to measure the change in percentage cover of the grass species as a result of mowing treatment. Further to quantify vegetation development with respect to treatments, we compared average vegetation height using LMMs with treatments as fixed factors and replication within locations as a random factor. We included grazing as a covariate in the model. As the residuals from the LMMs were not normally distributed, we used $\log_e$ height for analysis.

### Statistical packages

All statistical analyses were performed in R, version 4.1.0 (R Core Team, 2021). We used the "lme4" package (Bates et al., 2015) for Linear mixed effects models (LMMs). Post hoc multiple comparisons tests were performed using the "emmeans" package (Lenth et al., 2021) after LMMs. All graphs were prepared using the "ggplot2" package (Wickham, 2021). We checked the validity of LMMs through residual plots (histogram, normal probability plot, and residuals vs fitted values – Figure S2).

## Results

### Effect of treatment on nutrient concentration of grasses

The treatments (mowing, fertilisation, and scale of treatment i.e., the plot size) affected both nitrogen and phosphorus concentration in grasses (Table 5.2).

**Table 5.2:** Results of linear mixed-effect model for predicting the effect of treatments. Conditional $R^2$ (Con. $R^2$) and Marginal $R^2$ (Mar. $R^2$) represent the explained variation, *df* for corresponding degrees of freedom, *F* for *F* value and *P* for *P* value obtained from respective linear mixed-effects model (LMMs). Significant predictors ($P < 0.05$) are shown in bold.

| Response variable | Model parameter | Con. $R^2$ | Mar. $R^2$ | *df* | *F* | *P* |
|---|---|---|---|---|---|---|
| Crude Protein (CP) | | 0.54 | 0.51 | | | |
| | **Mowing** | | | 2 | 47.89 | < **0.001** |
| | Fertilisation | | | 2 | 1.85 | 0.16 |
| | **Plot size** | | | 2 | 39.75 | < **0.001** |
| | Mowing*Fertilisation | | | 4 | 1.17 | 0.33 |
| | **Mowing*Plot size** | | | 4 | 4.36 | **0.002** |
| | Fertilisation*Plot size | | | 4 | 0.84 | 0.5 |
| | Mowing*Fertilisation*Plot size | | | 8 | 0.37 | 0.93 |
| Phosphorus | | 0.61 | 0.42 | | | |
| | **Mowing** | | | 2 | 43.65 | < **0.001** |
| | **Fertilisation** | | | 2 | 5.59 | **0.005** |
| | **Plot size** | | | 2 | 30.84 | < **0.001** |
| | **Mowing*Fertilisation** | | | 4 | 3.64 | **0.007** |
| | Mowing*Plot size | | | 4 | 1.21 | 0.31 |
| | **Fertilisation*Plot size** | | | 4 | 2.72 | **0.03** |
| | Mowing*Fertilisation*Plot size | | | 8 | 1.15 | 0.33 |
| Seasonal variation in CP | | 0.62 | 0.54 | | | |
| | **Mowing** | | | 2 | 9.17 | < **0.001** |
| | **Fertilisation** | | | 2 | 4.31 | **0.02** |
| | **Season** | | | 2 | 12.51 | < **0.001** |
| | **Biomass** | | | 1 | 4.17 | **0.04** |
| | **Mowing*Fertilisation** | | | 4 | 2.48 | 0.05 |
| | **Mowing*Season** | | | 4 | 6.03 | < **0.001** |
| | Fertilisation*Season | | | 4 | 0.89 | 0.47 |
| | Mowing*Fertilisation*Season | | | 8 | 0.98 | 0.45 |
| Seasonal variation in Phosphorus | | 0.58 | 0.45 | | | |
| | **Mowing** | | | 2 | 10.11 | < **0.001** |
| | **Fertilisation** | | | 2 | 11.53 | < **0.001** |
| | **Season** | | | 2 | 12.19 | < **0.001** |
| | Biomass | | | 1 | 0.15 | 0.69 |
| | Mowing*Fertilisation | | | 4 | 1.83 | 0.13 |
| | **Mowing*Season** | | | 4 | 3.46 | **0.01** |

| Response variable | Model parameter | Con. $R^2$ | Mar. $R^2$ | *df* | *F* | *P* |
|---|---|---|---|---|---|---|
| | Fertilisation*Season | | | 4 | 1.79 | 0.14 |
| | Mowing*Fertilisation*Season | | | 8 | 0.71 | 0.69 |
| Herbivore percentage consumption | | 0.73 | 0.71 | | | |
| | **Mowing** | | | 1 | 164.19 | < **0.001** |
| | **Fertilisation** | | | 2 | 16.32 | < **0.001** |
| | **Primary Production** | | | 1 | 4.64 | **0.03** |
| | **Mowing*Fertilisation** | | | 2 | 5.68 | **0.01** |
| Vegetation height (log$_e$) | | 0.94 | 0.82 | | | |
| | **Mowing** | | | 2 | 36.65 | < **0.001** |
| | **Fertilisation** | | | 2 | 3.02 | 0.06 |
| | **Plot size** | | | 2 | 28.66 | < **0.001** |
| | **Grazing** | | | 1 | 20.03 | < **0.001** |
| | Mowing*Fertilisation | | | 4 | 1.87 | 0.14 |
| | **Mowing*Plot size** | | | 4 | 16.29 | < **0.001** |
| | Fertilisation*Plot size | | | 4 | 0.97 | 0.43 |
| | Mowing*Fertilisation*Plot size | | | 8 | 1.19 | 0.31 |
| *Imperata cylindrica* | | 0.26 | 0.13 | | | |
| | **Mowing** | | | 2 | 15.98 | < **0.001** |
| *Narenga Porphyrocoma* | | 0.49 | 0.29 | | | |
| | **Mowing** | | | 2 | 53.97 | < **0.001** |
| *Hemarthria compressa* | | | 0.12 | | | |
| | **Mowing** | | | 2 | 12.71 | < **0.001** |

Grasses collected from the four-time mown 3600 m$^2$ plots that were fertilised with nitrogen exhibited a higher level of crude protein, exceeding the minimum requirement level of ~7.6% for chital (Figure 5.3). However, the increase in crude protein was not observed in plots that were smaller or mown less frequently and also in 3600 m$^2$ that were not fertilised or mown less frequently. Phosphorus concentration in grass samples exceeded the minimum requirement threshold of 0.2 % for ruminants in 3600 m$^2$ plots that were mown four times a year and fertilised with phosphorus. This pattern was not observed in other 3600 m$^2$ plots that were not fertilized or mown less frequently, as well as in other smaller plots with different levels of treatments (Figure 5.3).

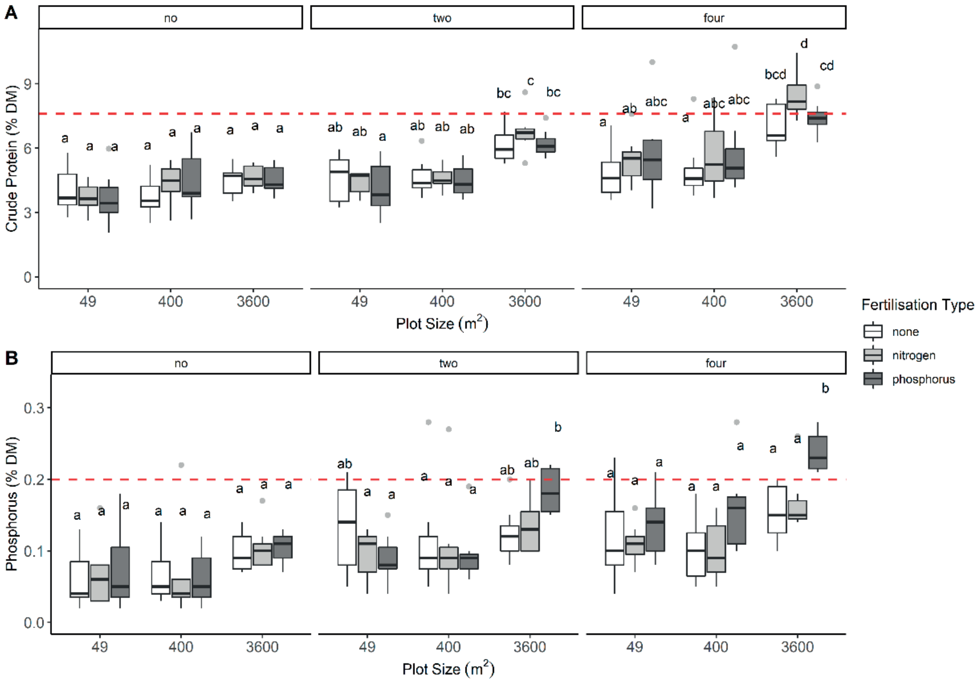

**Figure 5.3:** Crude Protein (A) and phosphorus (B) concentration in grass samples from plots with different levels of treatments. Letters above each boxplot indicate a significant difference at alpha = 0.05, tested by estimated marginal means after the linear mixed effects model (grouped by mowing treatment). Groups that share the same letter are not significantly different from each other. The horizontal red dotted line in panel A indicates the minimum level of crude protein (~7.6 %) required by adult female chital of 50 kg body weight for maintenance, and in panel B denotes the minimum level of phosphorus (~0.2 %) required by ruminants for maintenance, respectively.

Crude protein (CP) and phosphorus concentrations in the grass samples varied with the level of treatments and seasons in 3600 m$^2$ plots (Table 5.2, Figure 5.4). Mowing the grasses four times a year and fertilising the plots with nitrogen resulted in a significantly higher CP level, reaching the level that meets the maintenance requirement of CP (~7.6 %) for chital across all seasons in 3600 m$^2$ plots (Figure 5.4). Mowing the grass four times and fertilising the plots with either nitrogen or phosphorus resulted in CP concentration in grasses that meet the level (~ 9.2 %) required for chital during pregnancy, but only during the winter season in 3600 m$^2$ plots (Figure 5.4). However, none of the treatments was able to raise the CP levels in grasses to meet the requirement of CP (~11.8 %) of lactating chital (Figure 5.4; Table 5.1). Phosphorus concentration in grasses was higher during monsoon and winter, while remaining below critical levels (~ 0.2 %) for the deer during the summer, even when the grasses were mown four times in 3600 m$^2$ plots

(Figure 5.4). None of the treatments raised the CP concentration in grasses to meet the minimum maintenance requirement for hog deer throughout the year even in 3600 m$^2$ plots (Figure 5.4, Table 5.1).

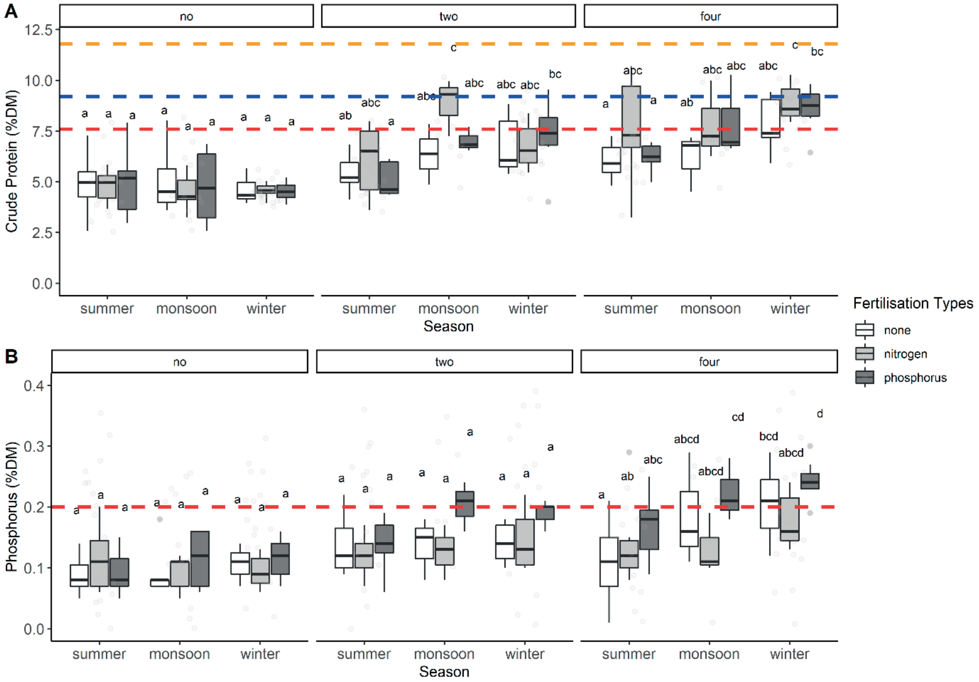

**Figure 5.4:** Effect of mowing, fertilisation, and season on nitrogen (expressed as crude protein, i.e., 6.25 x nitrogen) and phosphorus concentrations in grasses in 3600 m$^2$ plots. Letters above each boxplot indicate a significant difference at alpha = 0.05, tested by estimated marginal means after the linear mixed effects model (grouped by mowing treatment). Groups that share the same letter are not significantly different from each other. The upper panel A is for crude protein concentration in grasses across seasons; the horizontal red dotted line indicates the minimum maintenance requirement level (~7.6 %) of crude protein; blue dotted line for the requirement level (~ 9.2 %) of crude protein for reproduction, and orange dotted line for the requirement level (~11.8 %) of crude protein for lactation. All the requirement levels are expressed for the adult female chital of 50 kg body weight. The lower panel B is for phosphorus concentration across seasons; the horizontal red dotted line represents the minimum requirement (~0.2%) of phosphorus for ruminants.

## Vegetation development

Mesoherbivores consumed more grasses from the plots that were mown four times and fertilised with either nitrogen or phosphorus (Table 5.2, Figure 5.5). We found a substantial increase in grass height inside the cage in four times mown plots, with a mean height of 25 cm (95%CI: 20 – 29), compared to a mean height of 10 cm (95% CI: 8 – 13) outside the cage.

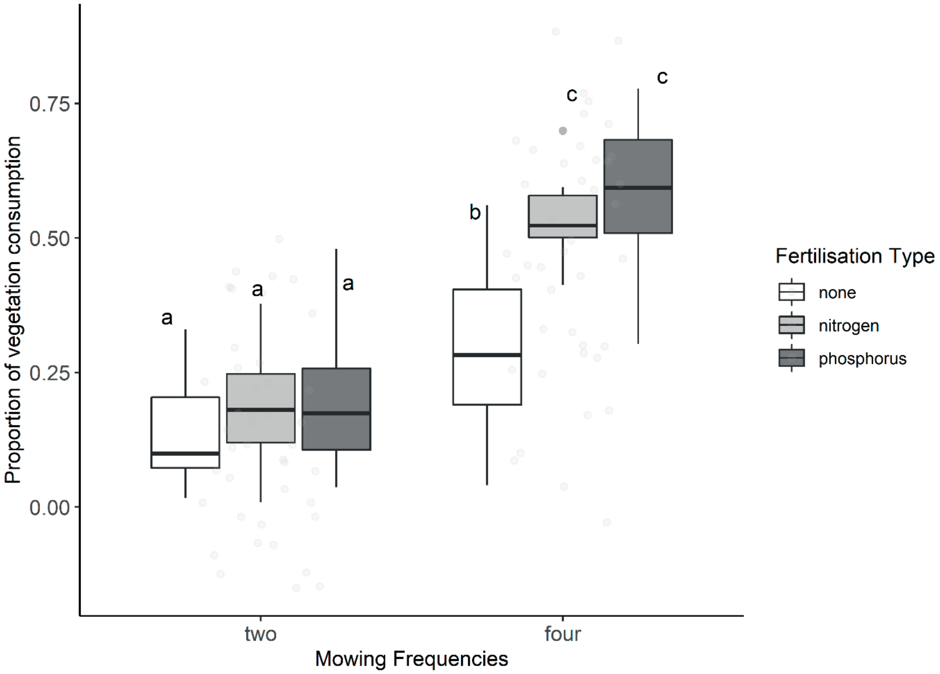

**Figure 5.5:** Proportion of vegetation consumed by herbivores in relation to mowing and fertilisation treatments. Proportion of vegetation consumption was measured using movable cages in 3600 m$^2$ plots that received mowing and fertilisation treatments (n = 42). Letters above each boxplot indicate a significant difference at alpha = 0.05, tested by estimated marginal means after the linear mixed effects model (grouped by mowing treatment). Groups that share the same letter are not significantly different from each other.

Vegetation height decreased with plot size in the four-time mown plots, while the grass height remained constant for unmown and two-time mown plots (Figure 5.6). Mowing, plot size, grazing, and interaction effect of mowing and plot size had a significant impact on grass height (Table 5.2). Grasses in 3600 m$^2$ plots that were mown four times and fertilised with nitrogen remained at an average height of 12.7 cm (95% CI: 10 – 15). In contrast, the average grass height was 41 cm (95% CI: 27 – 56) for plots that were mown two times and fertilized with nitrogen, and 104 cm (95% CI: 66 – 141) for plots that were not mown but fertilised with nitrogen (Figure 5.6).

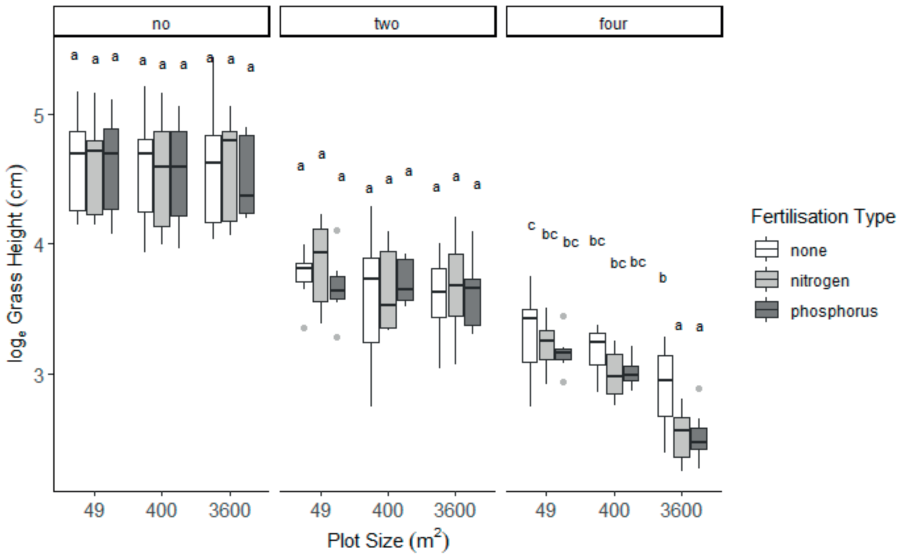

**Figure 5.6:** Effect of treatments on grass height. Grass height is expressed as $\log_e$ (grass height [cm]). Letters above each boxplot indicate a significant difference at alpha = 0.05, tested by estimated marginal means after the linear mixed effects model (grouped by mowing treatment). Groups that share the same letter are not significantly different from each other.

Mowing also affected the proportion of *I. cylindrica*, *N. porphyrocoma*, and *H. compressa* in the plots (Table 5.2), with *H. compressa* (a grazing lawn grass) showing a significant increase and *N. porphyrocoma* significant decrease in percentage cover the four times mown plots (Table 5.3).

**Table 5.3:** Mean percentage cover of the three dominant grass species as a result of mowing treatment. Letters in a row indicate a significant difference at alpha = 0.05, tested by estimated marginal means after the linear mixed-effects model. Cells that have the same letter in a row are not significantly different from each other.

| Grass species | Mean percentage cover (95% CI) | | |
|---|---|---|---|
| | No mowing | Two times mowing | Four times mowing |
| *Imperata cylindrica* | 0.33 (0.28 - 0.39) $^{a}$ | 0.49 (0.44 - 0.54) $^{b}$ | 0.51 (0.46 - 0.55) $^{b}$ |
| *Narenga porphyrocoma* | 0.24 (0.17 - 0.31) $^{b}$ | 0.03 (0.01 - 0.05) $^{a}$ | 0.01 (0.001 - 0.01) $^{a}$ |
| *Hemarthria compressa* | 0.01 (0.00 - 0.01) $^{a}$ | 0.02 (0.01 - 0.02) $^{b}$ | 0.03 (0.02 - 0.04) $^{c}$ |

## Discussion

The objective of this study was to investigate the factors that initiate the grazing lawns in the subtropical monsoon grasslands of Asia. We found that frequent mowing and artificial fertilisation increase the nutrient concentration in grasses to a level that meets the minimum maintenance requirements for ruminants. We conclude that frequent mowing together with grazing maintains grasses at a short height, enhances nutrient concentration within the grasses, and increases the proportion of lawn grasses in productive monsoon-influenced grasslands. This characteristic unequivocally signifies the initiation of grazing lawns. To our knowledge, this is the first empirical study conducted in the subtropical monsoon grasslands of Asia where the possible mechanism for the formation of grazing lawns is experimentally proven. The study demonstrated that the process of grazing lawn formation can be induced in subtropical monsoon grasslands through intensive management interventions such as mowing and fertilisation. These findings contribute to our understanding of the potential mechanisms for the inception of grazing lawns in the subtropical monsoon grasslands in Asia. By implementing such intensive management practices, it is possible to manipulate grassland vegetation structure and composition to support the development and persistence of grazing lawns in the subtropical monsoon grasslands of Asia.

Our results showed that frequent mowing and the addition of artificial fertilisers enhance the nutritious quality of the grassland to a level that it provides sufficient nutrients to meet the maintenance requirement of mesoherbivores. The subtropical monsoon grasslands in Asia are vulnerable to encroachment by tree species due to high mean annual rainfall and changes in factors like fire, herbivory, and human activities that otherwise limit the expansion of trees into grasslands (Banerjee et al., 2023). The establishment of Bardia National Park in the 1970s led to the imposition of restrictions on human activities and livestock grazing inside the park, which had a significant impact on the grassland dynamics. In 1975, the biomass of livestock was 15 – 17 times higher than that of wild ungulates in the park (Dinerstein, 1980). Grazing pressure plays a positive role in maintaining grazing lawns by removing tall grasses and preventing woody encroachment (Allred et al., 2012; van Langevelde et al., 2008; Veldhuis et al., 2014; Voysey et al., 2021). When livestock and human activities were removed from the park after its establishment, wild herbivores alone were unable to maintain the grazing lawns. As a result, tall grasses recolonised in grazing lawns and also forest areas increased at the expense of grasslands (Bijlmakers et al., 2023; Wegge et al., 2009). The three grassland areas where our study was conducted (*viz.*, Lamkauli Phanta, Baghaura Phanta, and Khauraha Phanta) have received constant management focus for maintenance. These grasslands are managed through annual fire and the removal of woody species, which we believe are major factors that are maintaining these grasslands and preventing tree encroachment (see for example Ding and Eldridge 2023). In the context of a national park like Bardia NP that contain endangered tigers, the goal of maintaining grasslands must be reconciled with ensuring nutrient availability for the existing assemblage of mesoherbivores, which serve as primary prey species for tigers (Lamichhane et al., 2019; Upadhyaya et al., 2018). Our results suggest that intensive management interventions can change nutrient-poor tall grasslands into grazing lawns, providing nutritious forage for the existing assemblage of mesoherbivores to support their fitness and survival.

The results of our spatial size treatment showed that the effect of mowing and fertilisation was significant in 3600 $m^2$ plots, indicating that a larger managed area provides greater benefits for mesoherbivores in terms of availability of quality forage. In addition, open areas with short grasses are favoured by herbivores for grazing which could be related to their behavioural response to predation risk (le Roux et al., 2018). However, the creation of homogeneous large areas probably will disperse grazers and diminish grazing pressure, similar to the effects observed following a large-scale fire (Archibald et al., 2005; Thapa et al., 2022). Subsequently, as grazing pressure is reduced, grasses start to grow fast and attain height and biomass, resulting in reduced grazing pressure (Karki et al., 2000; Veldhuis et al., 2016). As a result, the management goal of establishing grazing lawns cannot be realised.

The difference in grass height between the inside and outside of the cage is mainly due to the effect of mowing and grazing. We hypothesise that frequent mowing of grasses plays a role in maintaining grassland patches of short nutritious grasses, which is a characteristic of grazing lawns (Thapa et al., 2021). However, we propose that the persistence of the grazing lawns will be compromised if there is insufficient grazing pressure, as the grasses have the potential to regrow taller when mowing frequency or grazing pressure decreases. It is because grazing lawns and tall grasslands in the studied area are floristically similar and represent two alternative states of a similar plant community (Thapa et al., 2021). Factors that reduce localised grazing pressure could, therefore, hinder the establishment of grazing lawns in the highly productive monsoon grassland. For instance, large-scale burning, a common grassland management practice in the subtropical region of Nepal and India often carried out to provide quality forage for herbivores during the dry season, is not an appropriate management strategy when the objective is to establish and maintain grazing lawns for mesoherbivores (see Archibald et al., 2005; Thapa et al., 2022). Large-scale fires distribute grazing pressure homogeneously throughout the burned area, due to the availability of new growth after the burn, which in turn reduces localised grazing pressure and limits the inception of grazing lawn (Archibald et al., 2005; Donaldson et al., 2018). The process of grazing lawn formation is influenced by the grazing intensity experienced by the area (Cromsigt and Olff, 2008; Veldhuis et al., 2014). Moreover, we showed an increased proportion of ground cover of lawn grass and a decreased proportion of ground cover of tall grasses in the four-time mown plots. This result supports the idea that lawn grasses can establish under a high defoliation regime (Hempson et al., 2015; McNaughton, 1984). Our findings imply that ensuring a balance between frequent mowing, adequate grazing pressure, and avoiding large-scale burning will promote the establishment and persistence of grazing lawns in monsoon grassland systems.

Frequent mowing of tall grasses plays an important role in creating a suitable grazing environment for mesoherbivores, which in turn initiate the grazing lawns, particularly in a highly productive systems that lack large bulk grazers. Our field observation showed that even after two years of intensive management involving mowing and artificial fertilisation, the existing density of mesoherbivores was not able to maintain the positive feedback between grazing and grazing lawn formation. A potential explanation for this observation is the absence of bulk grazers in the study area. Rhinoceros and nilgai (*Boselaphus tragocamelus*) occur at relatively low densities (Adhikari and Khadka, 2009; Kral et al., 2017; Subedi et al., 2013) and are considered functionally extinct. Until the 1980s nilgai used to be the second most abundant prey biomass in Bardia NP after chital (Dinerstein, 1980). Gaur (*Bos gaurus*) and arna (*Bubalus arnee*) are locally extinct (Jhala et al., 2021) from the study area. Since the establishment of the Bardia National Park in the 1970s, domestic livestock grazing has been prohibited inside the park (Dinerstein, 1980). In contrast to these absent bulk grazers, mesoherbivores such as chital, swamp deer, and hog deer are morphologically and physiologically limited in their capacity to remove nutrient-poor matured tall grasses through grazing (Ahrestani et al., 2016; Fryxell, 1991; Prins and Olff, 1998; Wilmshurst et al., 1995). This limitation may explain the challenge of maintaining grazing lawns solely through the grazing activities of these mesoherbivores in the productive monsoon grasslands. This applies to most of the reserves that are home to endangered tigers in the Asian subtropical region within the Cwa climate, especially within the Terai Arc Landscape. It is because, large wild bulk grazers *viz.,* gaur and wild water buffalo are now extirpated from most of the reserves lying within the Cwa climate (including Nepal and Inda); only a few remnant populations are sparsely distributed in a few isolated protected areas (Jhala et al., 2018; Sarkar et al., 2021). Therefore, the absence of bulk grazers and the limited grazing capacity of mesoherbivores emphasise the need for intensive management of tall grasslands to promote grazing by mesoherbivores for the development and persistence of grazing lawns in the productive monsoon grasslands that are within most of the reserves in Terai Arc Landscape in the Asian subtropical region.

## Conclusion and management implications

In conclusion, our study implies that increasing forage quality is an initial step in establishing grazing lawns in subtropical monsoon grasslands that contain nutrient-poor tall grasses. Frequent mowing and fertilisation resulted in increased nutrient concentration in grasses. The increase in nutrient availability will yield a positive effect on nutrient intake, thereby enhancing the growth, reproduction, and survival of herbivores (Bayliss and Choquenot, 2002; Sinclair and Krebs, 2002). These benefits to herbivores will be beneficial for the conservation of the tiger population (Karanth et al., 2004; Karanth and Sunquist, 1995). The use of chemical fertilisers in national parks that are intended to preserve their ecosystems and habitats in a natural state raises management implications and potential environmental costs. We posit that for small, protected areas like Bardia NP, which are surrounded by human settlements, intensive management is necessary to conserve endangered fauna and their habitats effectively, despite the challenges associated with maintaining the natural state of ecosystems.

Our study demonstrated the necessity of frequent mowing to create an attractive grazing environment for mesoherbivores and initiate grazing lawns. However, the manual grass-mowing method employed in our study was time-consuming and potentially impractical for managing large grassland areas. In our study, it took approximately 25 days to mow a 15-ha tall grassland patch using three hand-held grass mowers and eight labours. This could possibly explain the reason behind fire being used as a grassland management strategy. Therefore, mechanising grass-mowing methods should be explored as a possible immediate solution to manage grasslands intensively and frequently over extended periods, thus promoting positive feedback between grazing and grazing lawns. In the long run, increasing the density of rhinoceros and reintroducing large bulk grazers such as arna, gaur, and nilgai should be considered for extensive grassland management. We suggest conducting a similar experiment in areas where bulk grazers are present, such as Chitwan National Park, where gaur are present (DNPWC and DFSC, 2022) and rhinoceros density is higher than that of Bardia NP (Subedi et al., 2013). This would give an opportunity to empirically test whether bulk grazers together with intensive management will facilitate the initiation of much-needed grazing lawns in the subtropical monsoon grassland in Asia.

If grazing lawns are assumed to be important grazing areas for mesoherbivores from where these animals obtain quality forage for their energy requirement for maintenance and physiological needs, what then is an appropriate grassland management regime for the highly productive subtropical monsoon grasslands?  Our recommendation is to create mosaics of one to two hectares of permanent plots scattered within the existing grassland areas. These plots should be large enough to accommodate existing local densities of mesoherbivores and also make them feel safe from predation while grazing. We propose that these plots should be mowed three to four times a year to keep the grass height below 10 cm, as nutrient concentration and grazing in grassland patches decrease with grass height ((Thapa et al., 2022). Regular mowing will stimulate new growth and increase the nutritional value of grasses throughout the year. To ensure aggregated grazing by mesoherbivores in the initial years, artificial fertilisation should be applied in these plots. Additionally, we recommend suppressing fires in the plots and surrounding areas to prevent a reduction in localised grazing pressure in the plots. We recommend carrying out intensive mowing on these plots for three to four years and closely monitoring the effects of mowing on the vegetation structure and composition, and the density of mesoherbivores using the plots. We believe that grazing lawn formation can be induced in subtropical grasslands with intensive management interventions, yet the productive monsoon season remains a challenge.

In summary, our findings suggest that the scale-dependent consumer-resource feedback developed by Cromsigt and Olff (2008) can be practically implemented to initiate grazing lawns in the subtropical monsoon grasslands of Asia. The establishment and maintenance of grazing lawns can play a vital role in providing high-quality forage for herbivores and contribute to the conservation of endangered species. It calls for intensive management approaches for the development and persistence of grazing lawns in subtropical monsoon grasslands, considering the dynamic nature of the subtropical monsoon grasslands and the challenges posed by climate change and human activities.

**Data Availability**

The data that support the findings of this study are openly available in Mendeley Data Repository: https://data.mendeley.com/datasets/2stvd55h44/draft?a=02982a7c-8a0e-44ed-a724-190417460a6e

# Supplementary materials

**Table S1:** Total number of plots with different levels of treatment received

| **Plot size** | **No mowing** | | | **2 times mowing** | | | **4 times mowing** | | | **Total** |
|---|---|---|---|---|---|---|---|---|---|---|
| | **No fertilisation** | **Nitrogen** | **Phosphorus** | **No fertilisation** | **Nitrogen** | **Phosphorus** | **No fertilisation** | **Nitrogen** | **Phosphorus** | |
| 49 $m^2$ | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 63 |
| 400 $m^2$ | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 63 |
| 3600 $m^2$ | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 63 |
| **Total** | 21 | 21 | 21 | 21 | 21 | 21 | 21 | 21 | 21 | **189** |

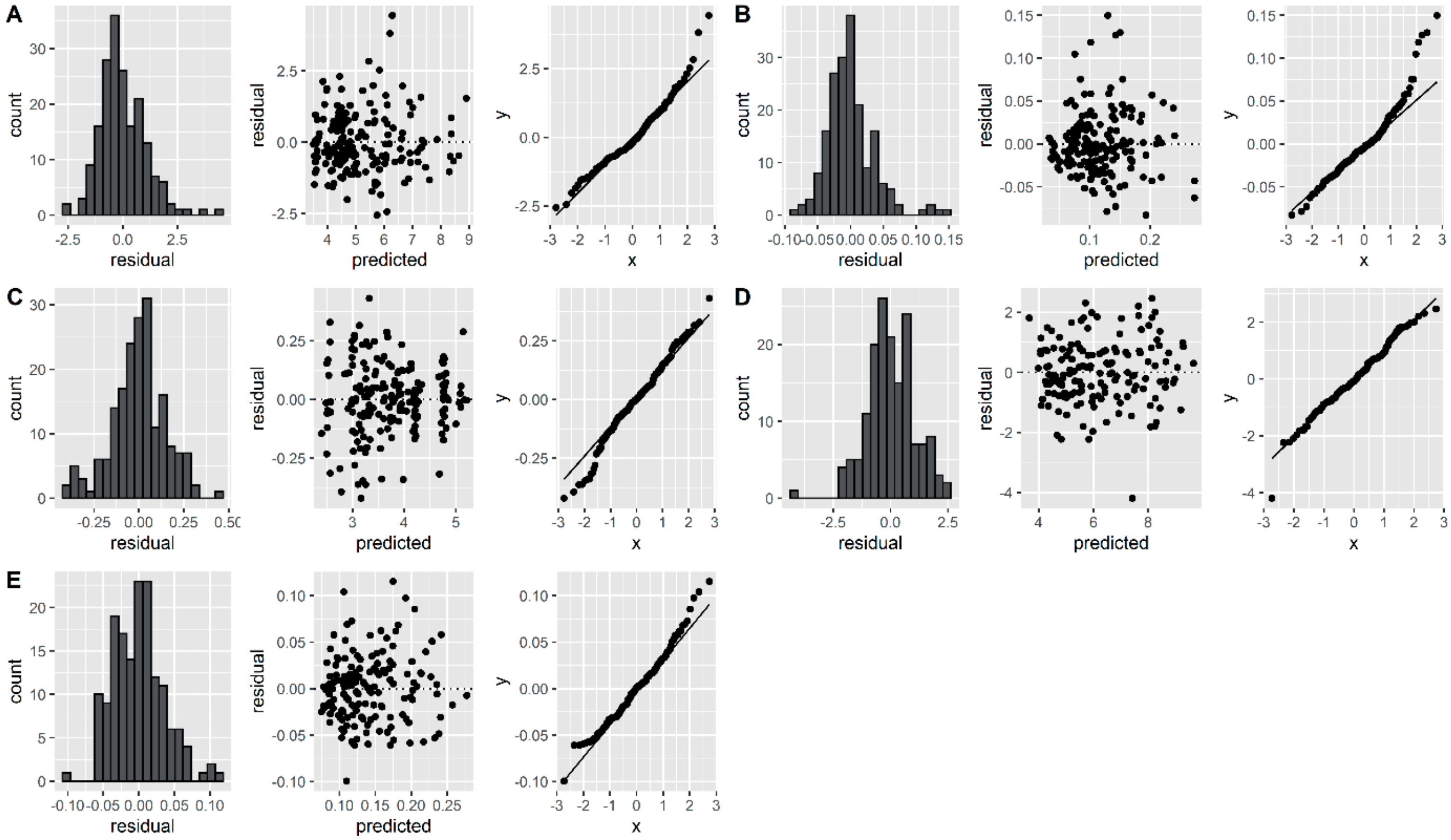

**Figure S2:** Model validation graphs for A: crude protein; B: phosphorus; C grass height; D: seasonal variation in crude protein; and E: seasonal variation in phosphorus.

# CHAPTER 6

# Synthesis

## Enhancing subtropical monsoon grassland management: Investigating mowing and nutrient input effects on initiation of grazing lawns

Shyam Kumar Thapa

## Introduction

The existing subtropical monsoon grasslands in Nepal are characterised by tall (> 2 m) grasses with high biomass (Lehmkuhl, 1994; Peet et al., 1999a; Ratnam et al., 2019) but low nutrient concentrations (Ahrestani et al., 2011; Thapa et al., 2021). While the current extent and structural composition of the subtropical monsoon grasslands of the area may support mega and large herbivores such as wild Asian elephants (*Elaphus maximus*), Greater one-horned rhinoceros (*Rhinoceros unicornis*), gaur (*Bos gaurus*), nilgai (*Boselaphus tragocamelus*), and arna (*Bubalus arne*), it remains challenging to meet the nutritional requirements of the existing assemblage of small and medium body sized herbivores (Thapa et al., 2021). Forest areas increased at the expense of grassland which reduces the extent and abundance of grassland patches (Bijlmakers et al., 2023). This negatively influences the nutritional requirements of the existing assemblage of small and medium body sized herbivores as they require high-quality forage to meet their body-mass energy requirement (Prins and Olff, 1998; Prins and Van Langevelde, 2008; van Langevelde et al., 2008). Consequently, their population is thus affected by the dearth of grass nutrients. This applies, in particular, to chital (*Axis axis*), swamp deer (*Rucervus duvaucelii*), and hog deer (*Axis porcinus*) (*viz.,* mesoherbivores) which are frequent users of the monsoon grasslands in Nepal (Moe and Wegge, 1994; Wegge et al., 2006). This impacts tiger (*Panthera tigris*) conservation in Nepal because these mesoherbivores are currently the primary prey species of tigers (Lamichhane et al., 2019; Upadhyaya et al., 2018).

Within the tall-bunch-grass matrix in subtropical monsoon grasslands, small areas of grazing lawns are sparsely distributed (Karki et al., 2000; Thapa et al., 2021). Grazing lawns are important foraging grounds for grazing herbivores where herbivores maximise their energy and nutrient intake (Bergman et al., 2001; Drescher et al., 2006b; Thapa et al., 2021; van Langevelde et al., 2008; Verweij et al., 2006; Wilmshurst et al., 1995). Grazing lawns contain short grasses with a greater proportion of high-quality forage parts (i.e., leaves), have higher bulk density, and digestibility, and have a higher concentration of nutrients (Chapter 2), and hence are important for supplying nutrients to the existing assemblage of mesoherbivores. Despite the importance of grazing lawns for mesoherbivores, little is known about grazing lawns and the factors underlying their formation in the subtropical monsoon grasslands of Asia.

Central to this, the overarching aim of my research was to investigate whether it is possible to change nutrient-poor tall grasslands into a more favourable grazing lawn state that supports higher densities of mesoherbivores and sustains the tiger population. To achieve this aim, I carried out an experiment in the monsoon grasslands of Bardia National Park. First, I explored the characteristics and features that differentiate grazing lawns from tall grasses and the implications for mammalian herbivores. I investigated the effect of fire on grassland quality, considering the dominance of fire in the grasslands. Finally, I explored whether human intervention such as mowing and nutrient input can facilitate the formation of grazing lawns in highly productive grassland systems.

In Chapter 2, I showed that grazing lawns are highly beneficial for mesoherbivores in order to optimise their nutrient uptake. In Chapter 3, I reported that the effect of large-scale burning (a common grassland management practice in the subtropical region of Nepal and India often carried out to provide quality forage for herbivores during the dry season) is not beneficial for mesoherbivores in terms of availability of quality forage. In Chapter 4, I found that the spatial scale of grassland management interventions is an important factor to consider while managing the grasslands. This is because these mesoherbivores prefer to forage on open larger areas with short grasses to minimise predation risk. The availability of quality forage during different seasons of the year is crucial for the survival and fitness of mesoherbivores. As the subtropical monsoon grasslands of the Indian subcontinent exhibit high seasonal variation in forage quality and availability (Ahrestani et al., 2012), affecting the availability of nutrients for different physiological functions like growth, reproduction, and lactation. I showed in Chapter 5 that areas that were frequently mown (four times a year) and fertilised with either nitrogen or phosphorus have higher nitrogen concentration in grasses than unmown plots throughout the season so that the seasonal nutrient requirements of mesoherbivores are fulfilled.

This thesis yields additional insights into grazing lawns of subtropical monsoon grasslands of Asia, as much of our current knowledge on the grasslands, grazing lawns, and associated ecosystem functioning are from studies carried out in Africa and other arid and semi-arid regions (Archibald, 2008; Cromsigt et al., 2017; Donaldson et al., 2018; Hempson et al., 2015; Verweij et al., 2006). My research found that grazing lawns, like in African savannas, are important components of the subtropical monsoon grasslands of Asia and play a crucial role in meeting the nutritional requirement of the existing assemblage of mesoherbivores. Furthermore, I found that intensive management is required to initiate grazing lawns in the highly productive subtropical monsoon grasslands. I synthesised here what I learnt and observed during my intensive fieldwork in the core area of Bardia National Park, Nepal.

### Initiation of grazing lawns in subtropical monsoon grasslands through management interventions

While the establishment of grassy vegetation in South Asia can be dated back to the Late Miocene (Armstrong-Altrin et al., 2009; Dengler et al., 2020; Morley, 2012), the historical distribution and extent of grasslands in the subtropical region of Asia are unknown

(Peet et al., 1999a; Ratnam et al., 2016). However, it is believed that grassland patches in the subtropical region of the Indian subcontinent were derived from forests resulting from human use (Ratnam et al., 2016, 2011) and maintained either by grazing by large herbivores, fire or floods or a combination of these three factors (Lehmkuhl, 1994; Peet et al., 1999a; Ratnam et al., 2011).

The grassland areas where I did my experimental research carry a legacy of intensive human use. Until the 1970s, there used to be agricultural fields in what are now the grasslands in the park. Settlements were removed from the core area of the park, and livestock grazing inside the park was prohibited after the establishment of national parks in the 1970s. This sudden removal of settlements and domestic livestock from the park likely reduced the scale of interventions required to maintain the grasslands. As a result, it caused a change in the structure, composition and spatial extent of short grassland patches (Bijlmakers et al., 2023; Murphy et al., 2013; van Lunenburg et al., 2017; Wegge et al., 2009), which resulted in negative consequences on mesoherbivores' forage availability and consequently the population dynamics of herbivores (Wegge et al., 2009).

It is not possible nor desirable to revive all the historical components (e.g., agricultural practices and cattle grazing) again inside the protected areas. But it is possible to create similar effects in grassland systems through management interventions like mowing tall grasses and creating openings for megaherbivores to graze. Formation and persistence of grazing lawns largely depend on the frequency and intensity of grazing (Cromsigt and Olff, 2008; Hempson et al., 2015; McNaughton, 1984; Veldhuis et al., 2014; Voysey et al., 2021). Therefore, grassland management interventions should create an environment to initiate a positive cycle of grazing where grazing shapes the structure and composition of grasslands (De Knegt et al., 2008; Hempson et al., 2015).

According to the results of my study, two key factors significantly determine the degree of localised grazing pressure exerted by the present mesoherbivores assemblage in subtropical monsoon grasslands. These two key factors are the availability of high-quality forage and the spatial scale of management interventions. Grassland management interventions that improve forage quality directly affect the feeding preferences of mesoherbivores, thereby influencing the intensity of grazing within the managed area and subsequently affecting the maintenance of the area through grazing activities. Likewise, the spatial scale of management interventions plays a significant role in optimising the trade-off between the risk of predation and resources, thereby shaping the distribution and grazing patterns of mesoherbivores and impacting the persistence of grazing lawns. The interplay between these two factors emphasises their importance in regulating grazing dynamics and maintaining the ecological function of grazing lawns in subtropical monsoon grasslands.

**i. Improving forage quality to make the area attractive to mesoherbivores for grazing**
Mesoherbivores are in search of quality forage to meet their nutritional requirements for their fitness. Forage quality for herbivores is determined by both physical and chemical properties such as the proportion of quality forage parts (e.g., leaves), nutrient concentration, and digestibility (Prins, 1996; Prins and Van Langevelde, 2008; Weterings et al., 2018). My results from Chapter 2 found that grazing lawns in subtropical monsoon grasslands have high forage quality in terms of nutrient concentrations, digestibility, the proportion of quality parts (i.e., leaves), and quantity of quality forage parts consumed (bulk density). Therefore, to make an area attractive for grazing by mesoherbivores, the management interventions should create a foraging ground that contains forage with quality that is comparable to grazing lawns. My results from Chapter 5 showed that frequent mowing, in combination with nutrient supplementation, increases the nutrient concentration of grasses to a level that meets the minimum maintenance requirements for ruminants throughout the year. Furthermore, in Chapter 5, I found that frequent mowing together with grazing by mesoherbivores maintain the grass at short height and also increase the percentage cover of lawn grasses and subsequently decrease in percentage cover of tall grasses. I found in Chapter 5 that herbivores consume more grasses from the plots that were frequently mown and fertilised. This helped to conclude that a process for the formation of grazing lawns can be initiated only when the interventions are large enough to maintain the attractiveness of the area for grazing by herbivores.

In highly productive monsoon grasslands, frequent mowing and fertilisation are necessary to maintain the grass at short height and to attract herbivores for grazing, which facilitate the formation of grazing lawns. The grassland where I carried out my experimental study received a high mean annual rainfall of more than 1500 mm. Because of high rainfall, these monsoon grasslands are vulnerable to transition to forests (Ratnam et al., 2019; Sankaran, 2005; Staver et al., 2011). In addition, seasonal variation in forage quality and quantity is high in the Asian subtropical grasslands (Ahrestani et al., 2011). Due to fast growth, nutrient concentration in grasses decreases rapidly with respect to biomass and height (Ahrestani et al., 2011; Drescher et al., 2006b). Because bulk grazers are functionally extinct from most of the subtropical monsoon grasslands of Asia (Jhala et al., 2018), it necessitates park managers to strategically apply mowing treatment multiple times a year and for multiple years to maintain the grasses at short height with high nutrient concentration. The process results in forage of sufficiently high quality, which mesoherbivores aggregate to graze on in order to obtain nutrients (especially nitrogen and phosphorus) to meet their requirements for maintenance, reproduction, and lactation. More importantly, localised grazing pressure exerted by mesoherbivores in patches with high-quality forage likely influenced the nutrient mineralisation process (Augustine and Frank, 2011; van der Waal et al., 2011) through the addition of manures via dung and urination (Moe and Wegge, 2008), and soil moisture content through trampling (van der Waal et al., 2011) and facilitate the formation of grazing lawns. Ultimately, frequent, and repeated grazing by mesoherbivores maintains the grazing lawns in the productive monsoon grasslands.

### ii. Spatial scale of intervention

Along with food availability, predation is also an important factor that influences the foraging behaviour of herbivores (Altendorf et al., 2001; Kie, 1995; Pierce et al., 2004; White et al., 2003). Mammalian herbivores balance their forage intake with risk factors (for example predation risk) to increase their fitness (Cherry et al., 2015; Hopcraft et al., 2012; Pierce et al., 2004; Tolon et al., 2009; Veldhuis et al., 2020; Weterings et al., 2018). In Chapter 4, I examined the effect of patch size on the level of use by mesoherbivores and found that the level of use was higher in larger plots compared to smaller plots that received the same set of treatments (mowing and fertilisation). More importantly, I found that mesoherbivores prefer to use the centre of larger plots compared to the edge, a clear indication of balancing food intake and risk avoidance. Likewise, I argued in Chapter 4 that small patches serve as ‘death traps’ for deer because smaller open plots with surrounding tall grasses increase the contrast between the open and covered habitat features which are favoured by tigers to ambush their prey (Karanth and Sunquist, 2000). Furthermore, my results in Chapter 4 indicated that the requirement of both predator and prey should be considered while managing grasslands. For instance, the openness of the habitat, fleeing ability, and proximity to a refuge habitat could be advantageous for deer and they may thus positively respond to habitat management that creates openness and provides space to escape by elevating their level of use. But, for stalking predators like tigers, the same features (e.g., openness and visibility) may not be beneficial as such features may reduce their hunting success rate (Karanth and Sunquist, 2000).

In Chapter 5, I showed that frequent mowing and the addition of artificial fertilisers improve the nutritious quality of the grassland to a level that provides sufficient nutrients to meet the maintenance requirement of mesoherbivores. I found that the effect of mowing and fertilisation was significant in larger plots, indicating that a larger managed area provides greater benefits for mesoherbivores in terms of the availability of quality forage. The creation of homogeneous large areas will disperse grazers and diminish grazing pressure, similar to the effects observed following a large-scale fire (Archibald et al., 2005; Thapa et al., 2022). Subsequently, as grazing pressure is reduced, grasses start to grow fast and attain height and biomass, resulting in reduced grazing pressure (Karki et al., 2000; Veldhuis et al., 2016). My results in Chapter 3 showed that grasses quickly attain height and biomass with a reduction in nutrient concentration over time after fire as a result of decreased grazing pressure. Therefore, I argued that the spatial scale of management interventions (e.g., mowing) should be large enough to optimise the trade-off between risk and resources and to continuously supply quality forage to the local densities of mesoherbivores. It is likely that the sizable patches with high-quality forage are intensively grazed by mesoherbivores resulting in the establishment and maintenance of grazing lawns.

### Grazing lawns and forage quality: implication on prey-predator dynamics

Numerous studies showed direct relationships between herbivores' functional and numerical responses and forage availability. For instance, Bayliss & Choquenot, (2002) showed that population growth in western grey kangaroos (*Macropus fulginosus*) was negative during low food availability and increased and remained constant when food availability is high. Likewise, Caughley and Gunn (1993) reported that herbivore populations are primarily influenced by food availability rather than by competition for food. A similar positive growth rate in response to the availability of food was observed in feral donkeys (*Equus asinus*) in northern Australia (Choquenot, 1991) and further reported that the survival of young depends on the nutritional status of lactating females. A study by Rowland et al., (2018) reported that the availability of nutrition to female elk (*Cervus canadensis*) in North America has a direct implication on calf and yearling growth rates, age-at-first breeding, the timing of breeding, and pregnancy rate, important factors determining numerical response in herbivores. Thus, mesoherbivores likely show positive numerical response through the survival and recruitment of young when grazing lawns offer high-quality forage throughout the seasons in Asian subtropical monsoon grasslands. This ultimately helps to feed and maintain the population dynamics of tigers that depend on these mesoherbivores, as the density of predators is directly related to the density of their prey (Karanth et al., 2004).

### Management implications

Nepal and India are the two countries that have been able to increase their wild tiger populations as per the global commitment they made in 2010. With the increasing tiger population, human-tiger conflicts have also increased in the buffer zone of national parks that housed tigers (Fitzmaurice et al., 2021). Protected areas with tigers in Nepal and also in India are surrounded by buffer zones with high human density. A study by Lamichhane et al., (2017), reported that residential tigers are less likely to be involved in conflict with a human when there is sufficient wild prey available within their habitat. Therefore, to maintain the tiger population and to reduce human-tiger conflict, the focus should be given to increasing the density of prey, especially mesoherbivores density, as they are the primary prey of tigers in protected areas that contain tigers in Nepal and India.

When short nutritious grasses are not available in the grasslands within a core area of the park, especially during monsoon and winter, the mesoherbivores aggregate in the fringe area close to agricultural fields and venture out to forage nutritious crops (Gross et al., 2018). When tiger prey is in close proximity to settlements near the park boundaries, there is likely to be an increase in human-tiger conflict cases (Lamichhane et al., 2017). To confine tiger's primary prey species within a core area and also increase their density, there should be sufficient quality food available throughout the season, and intensive grassland management is indicated.

This study provides practical directions for park managers to manage grasslands while considering the requirement of mesoherbivores and their predators. Some important practical implications of this research include:

1. Grazing lawns, compared to tall grasslands are important foraging grounds where mesoherbivores can obtain a nutritious diet to meet their basic requirements.
2. The establishment of grazing lawns in a highly productive subtropical monsoon grassland is possible only when intensive and continuous management interventions such as mowing, and fertilisation are carried out for a longer period.
3. A spatial scale of interventions is an important aspect to consider while managing grasslands.

a. Small managed patches (for example less than 0.5 ha) do not create suitable foraging ground for the mesoherbivores. Such small patches serve as 'death traps' for deer, as the surrounding tall grasses can easily conceal tigers to launch a surprise attack. In such a scenario, either deer will be subject to unsustainable losses from predation by an increasing number of tigers or move to the forest or close to the settlement with likely increasing possibility of human-tiger conflict.

b. Large-scale management (for example > 10 ha) provides sufficient opportunities for deer to obtain quality food in large areas which reduces concentrated grazing pressure. As a result, grasses attain their height and biomass and are not useful for the mesoherbivores to obtain required nutrients which will have long-term implications on the population dynamics of mesoherbivores. Furthermore, park management needs to carry out management interventions continuously which will increase the cost of management. When larger areas of grasslands are managed by mowing tall grasses it will increase the visibility. As a result, tigers hunting success rate may decline due to high visibility and tigers may venture to the fringe area in search of easy prey (e.g., domestic cattle) and the possibility of frequent encounters with humans. Therefore, creating mosaics of one to two hectares of intensively managed patches scattered over the grassland will help to induce grazing feedback and hence the formation of grazing lawns.

c. Large-scale fire has a similar effect to large-scale mowing. Instead of producing high-quality forage, large-scale fire increases the enormous production of grasses in this monsoon grassland, and it is not a management goal of the park to produce biomass. The burned mosaics of small-sized grassland patches may likely reinforce grazing feedback that may result in the establishment of grazing lawns.

4. Mesoherbivores especially chital and swamp deer are mix-feeders (Ahrestani et al., 2016) and can also obtain nutritious food from browse and also from understory grass vegetation in the forest adjacent to the grasslands when in demand of high nutrition. I found that understory grasses have a higher concentration of phosphorus than grass samples from unmanaged tall grasslands (Table 6.1). Sambar is also a mixed feeder and forage mostly in forests (Pokharel and Storch, 2016). Opening up understory vegetation in the forest areas may create foraging ground for sambar, and also for chital and swamp deer. Therefore, I argue that clearing bushes and tall grasses and increasing growing space for palatable understory grasses in a forest may improve the availability of quality forage for mesoherbivores during the nutrient bottleneck period.

**Table 6.1:** Nutrient concentration (% DM) in grass samples*

| Month | Understory grasses from forest | | From four-time mown 3600 $m^2$ plots | | Unmanaged tall grassland | |
|---|---|---|---|---|---|---|
| | CP | Phosphorus | CP | Phosphorus | CP | Phosphorus |
| April | 4.25 | 0.17 | 8.52 | 0.18 | 4.88 | 0.12 |
| July | 6.37 | 0.12 | 7.31 | 0.18 | 5.14 | 0.09 |
| October | 5.98 | 0.13 | 9.67 | 0.23 | 6.65 | 0.11 |
| November | 7.38 | 0.19 | 9.54 | 0.18 | 4.61 | 0.11 |
| December | 5.82 | 0.15 | 7.83 | 0.21 | 4.2 | 0.11 |

*Grass samples were purposefully collected from understory grasses within 100 m to 500 m distance from the study sites.

5. Intensive and continuous mowing of tall grasses is necessary to maintain the forage quality in the highly productive grassland system that lacks large bulk grazers. This applies to most of the protected areas that are home to endangered tigers in the Asian subtropical region within the Cwa climate, especially within the Terai Arc Landscape. The absence of bulk grazers and the limited grazing capacity of mesoherbivores emphasise the need for intensive management of tall grasslands to promote grazing for the development and persistence of grazing lawns. In the long run, consideration should be given to increasing the density of large bulk

grazers such as arna, gaur, and nilgai (either through rewilding or reintroduction) for extensive management of subtropical monsoon grasslands. Large herbivores or bulk grazers are able to consume and digest nutrient-poor tall grasses (Illius and Gordon, 1992; Prins and Olff, 1998). The indiscriminate consumption of tall grasses by large herbivores creates openings that stimulate the regrowth of short nutritious grasses. This process results in the availability of high-quality forage for mesoherbivores (e.g., van Langevelde et al., 2008). In the past, grazing by mega and large herbivores together with human disturbances (such as thatch grass harvesting, livestock grazing, and controlled burning) could have played a crucial role in maintaining the quality and quantity of herbaceous biomass by creating mosaics of tall and short grassland patches within the grasslands of the region that are favoured by mesoherbivores.

In addition to the important findings with empirical applications, my thesis raised some important questions which require further investigation. It is important to understand the effects of past disturbances such as agricultural practices, thatch harvesting, cattle grazing, and fire on the composition and structure of the existing grasslands to make informed management decisions in grassland systems. Another important question that requires further investigation is identifying the desired spatial scale of management. My research showed that small patches (49 m$^2$ and 200 m$^2$) were not significantly attractive to mesoherbivores for grazing. The effect of mowing and fertilisation was significantly higher in the larger 3600 m$^2$ plots, consequently a higher level of use by mesoherbivores. However, from a management perspective, a 3600 m$^2$ plot may also be considered small when the park managers have to manage grasslands larger than 100 ha at a time. Cutting nutrient-poor tall grasses is labour-intensive and time-consuming. Thus, it may become increasingly necessary for park managers to explore the possibility of mechanising grass-cutting methods to cut grasses frequently and efficiently. Further exploration is needed into the effect of using machines on forage quality. A long-term study is needed to examine the effect of forage availability on the functional and numerical response of mesoherbivores. Opening up understory vegetation may create an environment conducive to growing palatable grasses which would benefit mixed feeders like chital and sambar. However, a long-term study is needed to quantify how such openings in forests affect both forging behaviour among existing herbivore populations and tiger predation ecology. Bulk grazers are important engineers of grasslands and play an important role in grazing lawn formation. Exploring the possibility of creating a historical assemblage of herbivores in tiger-bearing protected areas may not only help to form and maintain grazing lawns, but importantly, it also benefits tigers with the availability of larger body-sized prey. A similar experiment should be conducted in areas where bulk grazers are present, for instance, Chitwan National Park, where gaur are present (DNPWC and DFSC, 2022) and rhinoceros density is higher (Subedi et al., 2013), to test whether bulk grazers, together with intensive management, can facilitate the initiation of grazing lawns in the subtropical monsoon grassland in Asia.

As shown in my research, intensive habitat management has positive implications on the availability of quality forage for mesoherbivores and hence their population dynamics. With an increased prey density, it is likely that the population of tigers will further increase in small isolated unfenced national parks surrounded by human settlements, as tiger density largely depends on habitat quality and prey availability (Dahal et al., 2023; Karanth et al., 2004). On one hand, free-ranging tiger populations present important conservation resources and potentially increase park revenue from wildlife tourism. On the other hand, there may be management implications such as human-tiger conflicts, as well as prey and habitat management. As a good starting point, the Government of Nepal has assessed tiger ecological carrying capacity with respect to prey abundance (Dahal et al., 2023), and indicated that the tigers in the Chitwan National Park are nearing the ecological carrying capacity of the park. However, when parks exceed their carrying capacity, the Government of Nepal does not have a strategy or policy in place to manage the tiger population. Based on such studies, park managers should be asking how many tigers their parks need and how many they can manage.

In many protected areas, removal of animals through translocation, euthanasia or hunting is considered an important management strategy (Croft et al., 2020; Miguel et al., 2020; Miller et al., 2013). The Government of Nepal has been removing the problem and injured tigers from the wild (without killing them) and placing them in enclosures. Additionally, there are cases of local people killing problem tigers in retribution (Lamichhane et al., 2017). A sizeable number of problem tigers have been removed from protected areas in Nepal (Lamichhane et al., 2017). However, simply removing (without killing) problem tigers is not a viable long-term solution, as enclosures and rescue centres will eventually run out of capacity. The option of 'euthanasia' can be implemented cautiously, and park managers may decide to euthanise a tiger based on factors such as the severity of the injury, age, or multiple fatalities caused by that tiger. Due to limited space, translocation may not be feasible in Nepal. Trophy hunting of endangered tigers is not legally allowed because of national acts/regulations and international commitments such as CITES. However, park management should develop pragmatic policies for wildlife conservation in the near future, otherwise, density-dependent factors like food, and competition (Karanth et al., 2004) will continue to pose a management challenge for the conservation of threatened fauna like tigers and their prey. Resulting wildlife management policies should provide a framework for formulating future grassland management in the national parks with tigers.

## Conclusion

While much of the knowledge on grazing lawns and their ecological functions is from the African savanna, my findings showed that grazing lawns in Asian subtropical monsoon grasslands are also important foraging grounds for mesoherbivores from where they can increase their energy uptake. My findings show that nutrient concentration in post-fire regrowth decreases quickly over time, which means that post-fire regrowth may not meet the nutrient requirements of the mesoherbivores community. Therefore, annual large-scale fire as a grassland management tool is not beneficial for herbivores from a forage quality perspective. I found that intensive management interventions such as mowing and fertilising if carried out for a longer period can convert tall nutrient-poor grasslands to more favourable nutrient-rich grazing lawns. More importantly, I found that a spatial scale of intervention is necessary to initiate a positive feedback loop between grazing lawns and herbivores. The findings of this thesis add to a growing body of work that provides a better understanding of grazing lawns from the Asian subtropical monsoon grasslands and their functioning.

Large wild bulk grazers *viz.,* gaur and arna are now extirpated from most of the protected areas lying within the Cwa climate (including Nepal and India); only a few remnant populations are sparsely distributed in a few isolated protected areas (Jhala et al., 2018; Sarkar et al., 2021). Therefore, the absence of bulk grazers and the limited grazing capacity of mesoherbivores emphasise the need for intensive management of tall grasslands to promote grazing by mesoherbivores for the development and persistence of grazing lawns in the productive monsoon grasslands that are within most of the protected areas in Terai Arc Landscape in Nepal and India. Grazing lawns play a vital role in providing high-quality forage for herbivores. Therefore, my study provides practical guidance for park managers on how to manage highly productive subtropical monsoon grasslands in a way that meets the needs of mesoherbivores and their predators.

# Reference

Adhikari, S., Khadka, A., 2009. Study on relative abundance and distribution of tiger prey base (ungulates) in Khata Corridor, Bardia National Park. Kathmandu University Journal of Science, Engineering and Technology 5, 121–135.

Ahrestani, F.S., Heitkönig, I.M.A., Matsubayashi, H., Prins, H.H.T., 2016. Grazing and browsing by large herbivores in South and Southeast Asia, in: The Ecology of Large Herbivores in South and Southeast Asia. Springer, pp. 99–120.

Ahrestani, F.S., Heitkönig, I.M.A., Prins, H.H.T., 2011. Herbaceous production in South India-limiting factors and implications for large herbivores. Plant Soil 349, 319–330. https://doi.org/10.1007/s11104-011-0876-x

Ahrestani, F.S., Kumar, N.S., Vaidyanathan, S., Hiby, L., Jathanna, D., Karanth, K.U., 2018. Estimating densities of large herbivores in tropical forests: Rigorous evaluation of a dung-based method. Ecol Evol 8, 7312–7322.

Ahrestani, F.S., Sankaran, M., 2016. The ecology of large herbivores in south and southeast Asia. Springer.

Ahrestani, F.S., Van Langevelde, F., Heitkönig, I.M.A., Prins, H.H.T., 2012. Contrasting timing of parturition of chital Axis axis and gaur Bos gaurus in tropical South India - the role of body mass and seasonal forage quality. Oikos 121, 1300–1310. https://doi.org/10.1111/j.1600-0706.2011.20244.x

Allred, B.W., Fuhlendorf, S.D., Engle, D.M., Elmore, R.D., 2011. Ungulate preference for burned patches reveals strength of fire–grazing interaction. Ecol Evol 1, 132–144.

Allred, B.W., Fuhlendorf, S.D., Smeins, F.E., Taylor, C.A., 2012. Herbivore species and grazing intensity regulate community composition and an encroaching woody plant in semi-arid rangeland. Basic Appl Ecol 13, 149–158. https://doi.org/https://doi.org/10.1016/j.baae.2012.02.007

Altendorf, K.B., Laundre, J.W., Lopez-Gonzalez, C.A., 2001. Assessing effects of predation risk on foraging behavior of mule deer. J Mammal 82, 430–439.

Anderson, T.M., Hopcraft, J.G.C., Stephanie, E., Ritchie, M., Grace, J.B., Olff, H., 2010. Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. Ecology 91, 1519–1529. https://doi.org/10.1890/09-0739.1

Anderson, T.M., Ritchie, M.E., Mayemba, E., Eby, S., Grace, J.B., McNaughton, S.J., 2007. Forage nutritive quality in the Serengeti ecosystem: the roles of fire and herbivory. Am Nat 170, 343–357.

AOAC, 1990. Official methods of analysis. Assoc Anal Chem.

Archibald, S., 2008. African Grazing Lawns—How Fire, Rainfall, and Grazer Numbers Interact to Affect Grass Community States. Journal of Wildlife Management 72, 492–501. https://doi.org/10.2193/2007-045

Archibald, S., Bond, W.J., 2004. Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. Int J Wildland Fire 13, 377–385.

Archibald, S., Bond, W.J., Stock, W.D., Fairbanks, D.H.K., 2005. Shaping the Landscape : Fire – Grazer Interactions in an African Savanna. Ecological Applications 15, 96–109. https://doi.org/10.1890/03-5210

Archibald, S., Hempson, G.P., 2016. Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. Philosophical Transactions of the Royal Society B: Biological Sciences 371, 20150309.

Armstrong-Altrin, J.S., Lee, Y. Il, Verma, S.P., Worden, R.H., 2009. Carbon, oxygen, and strontium isotope geochemistry of carbonate rocks of the upper Miocene Kudankulam Formation, southern India: Implications for paleoenvironment and diagenesis. Geochemistry 69, 45–60.

Arnold, S.G., Anderson, T.M., Holdo, R.M., 2014. Edaphic, nutritive, and species assemblage differences between hotspots and matrix vegetation: Two african case studies. Biotropica 46, 387–394. https://doi.org/10.1111/btp.12116

Augustine, D.J., Frank, D. a, 2011. Effects of Migratory Grazers on Spatial Heterogeneity of Soil Nitrogen Properties in a Grassland Ecosystem. Ecology 82, 3149–3162.

Banerjee, S., Das, D., Zhang, H., John, R., 2023. Grassland-woodland transitions over decadal timescales in the Terai-Duar savanna and grasslands of the Indian subcontinent. For Ecol Manage 530, 120764. https://doi.org/https://doi.org/10.1016/j.foreco.2022.120764

Bardgett, R.D., Bullock, J.M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M., Durigan, G., L Fry, E., Johnson, D., 2021. Combatting global grassland degradation. Nat Rev Earth Environ 2, 720–735.

Bates, D., Maechler, M., Bolker, B.M., Walker, S., 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48.

Baudena, M., Dekker, S.C., van Bodegom, P.M., Cuesta, B., Higgins, S.I., Lehsten, V., Reick, C.H., Rietkerk, M., Scheiter, S., Yin, Z., 2015. Forests, savannas, and grasslands: bridging the knowledge gap between ecology and Dynamic Global Vegetation Models. Biogeosciences 12, 1833–1848.

Bayliss, P., Choquenot, D., 2002. The numerical response: rate of increase and food limitation in herbivores and predators. Philos Trans R Soc Lond B Biol Sci 357, 1233–1248.

Bell, D., Oliver, W.L.R., 1992. Northern Indian tall grasslands: management and species conservation with special reference to fire.

Bengtsson, J., Bullock, J.M., Egoh, B., Everson, C., Everson, T., O'connor, T., O'farrell, P., Smith, H.G., Lindborg, R., 2019. Grasslands—more important for ecosystem services than you might think. Ecosphere 10, e02582.

Bergman, C.M., Fryxell, J.M., Gates, C.C., Fortin, D., 2001. Ungulate foraging strategies: energy maximizating or time minimizing? Journal of Animal Ecology 70, 289–300–289–300. https://doi.org/10.1111/j.1365-2656.2001.00496.x

Bijlmakers, J., Griffioen, J., Karssenberg, D., 2023. Environmental drivers of spatio-temporal dynamics in floodplain vegetation: grasslands as habitat for megafauna in Bardia National Park (Nepal). Biogeosciences 20, 1113–1144. https://doi.org/10.5194/bg-20-1113-2023

Biswas, T., 2010. A spatio-temporal analysis of landscape change within the Eastern Terai, India: Linking grassland and forest loss to changes in river course and land use. Utah State University.

Biswas, T., Ramsey, R.D., Bissonette, J.A., Symanzik, J., 2014. Integration of two spectral indices to monitor loss of moist grasslands within the Jaldapara Wildlife Sanctuary, India. Int J Remote Sens 35, 1038–1063.

Bivand, R.S., Wong, D.W.S., 2018. Comparing implementations of global and local indicators of spatial association. Test 27, 716–748.

Blumstein, D.T., Ozgul, A., Yovovich, V., Van Vuren, D.H., Armitage, K.B., 2006. Effect of predation risk on the presence and persistence of yellow-bellied marmot (Marmota flaviventris) colonies. J Zool 270, 132–138.

Bonnet, O., Fritz, H., Gignoux, J., Meuret, M., 2010. Challenges of foraging on a high-quality but unpredictable food source: the dynamics of grass production and consumption in savanna grazing lawns. Journal of Ecology 98, 908–916. https://doi.org/10.1111/j.1365-2745.2010.01663.x

Brown, K., 1997. Plain tales from the grasslands: extraction, value and utilization of biomass in Royal BardiaNational Park, Nepal. Biodivers Conserv 6, 59–74.

Buitenwerf, R., Bond, W.J., Stevens, N., Trollope, Wsw., 2012. Increased tree densities in S outh A frican savannas:> 50 years of data suggests CO 2 as a driver. Glob Chang Biol 18, 675–684.

Caughley, G., Gunn, A., 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. Oikos 47–55.

Chen, D., Chen, H.W., 2013. Using the Köppen classification to quantify climate variation and change: An example for 1901–2010. Environ Dev 6, 69–79.

Cherry, M.J., Conner, L.M., Warren, R.J., 2015. Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. Behavioral Ecology 26, 1091–1099.

Cherry, M.J., Warren, R.J., Conner, L.M., 2017. Fire-mediated foraging tradeoffs in white-tailed deer. Ecosphere 8, e01784–e01784.

Choquenot, D., 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. Ecology 72, 805–813.

Clinchy, M., Sheriff, M.J., Zanette, L.Y., 2013. Predator-induced stress and the ecology of fear. Funct Ecol 27, 56–65.

Coelho, R., Infante, P., Santos, M.N., 2020. Comparing GLM, GLMM, and GEE modeling approaches for catch rates of bycatch species: A case study of blue shark fisheries in the South Atlantic. Fish Oceanogr 29, 169–184. https://doi.org/https://doi.org/10.1111/fog.12462

Coetsee, C., Stock, W.D., Craine, J.M., 2011. Do grazers alter nitrogen dynamics on grazing lawns in a South African savannah? Afr J Ecol 49, 62–69.

Cresswell, W., Lind, J., Quinn, J.L., 2010. Predator-hunting success and prey vulnerability: quantifying the spatial scale over which lethal and non-lethal effects of predation occur. Journal of Animal Ecology 79, 556–562. https://doi.org/https://doi.org/10.1111/j.1365-2656.2010.01671.x

Cribari-Neto, F., Zeileis, A., 2010. Beta regression in R. J Stat Softw 34, 1–24.

Croft, S., Franzetti, B., Gill, R., Massei, G., 2020. Too many wild boar? Modelling fertility control and culling to reduce wild boar numbers in isolated populations. PLoS One 15, e0238429.

Cromsigt, J.P.G.M., Kuijper, D.P.J., Adam, M., Beschta, R.L., Churski, M., Eycott, A., Kerley, G.I.H., Mysterud, A., Schmidt, K., West, K., 2013. Hunting for fear: innovating management of human–wildlife conflicts. Journal of Applied Ecology 50, 544–549. https://doi.org/https://doi.org/10.1111/1365-2664.12076

Cromsigt, J.P.G.M., Olff, H., 2008. Dynamics of grazing lawn formation: An experimental test of the role of scale-dependent processes. Oikos 117, 1444–1452. https://doi.org/10.1111/j.0030-1299.2008.16651.x

Cromsigt, J.P.G.M., Olff, H., 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: An experimental approach. Ecology 87, 1532–1541. https://doi.org/10.1890/0012-9658(2006)87[1532:RPASGM]2.0.CO;2

Cromsigt, J.P.G.M., Prins, H.H.T., Olff, H., 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. Divers Distrib 15, 513–522.

Cromsigt, J.P.G.M., Veldhuis, M., Stock, W., Roux, E. le, Gosling, C., Archibald, SALLY, Cromsigt, J., Archibald, S, Owen-Smith, N., 2017. The functional ecology of grazing lawns—how grazers, termites, people, and fire shape HiP's savanna grassland mosaic. Conserving Africa's megadiversity in the Anthropocene: the Hluhluwe-iMfolozi Park story. Cambridge University Press, Cambridge, UK 135–160.

Dahal, B.R., Amin, R., Lamichhane, B.R., Giri, S.R., Acharya, H., Acharya, H.R., Harihar, A., 2023. Setting recovery targets for a charismatic species in an iconic protected area complex: The case of tigers (Panthera tigris) in Chitwan–Parsa National Parks, Nepal. Conserv Sci Pract e12930.

De Knegt, H.J., Groen, T.A., Van De Vijver, C.A.D.M., Prins, H.H.T., Van Langevelde, F., 2008. Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning. Oikos 117, 543–554.

De Vos, B., Lettens, S., Muys, B., Deckers, J.A., 2007. Walkley–Black analysis of forest soil organic carbon: recovery, limitations and uncertainty. Soil Use Manag 23, 221–229.

Dengler, J., Biurrun, I., Boch, S., Dembicz, I., Török, P., 2020. Grasslands of the Palaearctic biogeographic realm: introduction and synthesis. Encyclopedia of the world's biomes 3, 617–637.

Dhungel, S.K., O'Gara, B.W., 1991. Ecology of the hog deer in Royal Chitwan National Park, Nepal. Wildlife monographs 3–40.

Dinerstein, E., 1980. An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal: part III: ungulate populations. Biol Conserv 18, 5–37.

Dinerstein, E., 1979. An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Part I: vegetation, modifying factors, and successional relationships. Biol Conserv 15, 127–150.

Ding, J., Eldridge, D., 2023. The success of woody plant removal depends on encroachment stage and plant traits. Nat Plants 9, 58–67. https://doi.org/10.1038/s41477-022-01307-7

DNPWC, DFSC, 2022. Status of Tigers and Prey in Nepal 2022. Department of National Parks and Wildlife Conservation & Department of Forests and Soil Conservation. Ministry of Forests and Environment, Kathmandu, Nepal.

DNPWC, DFSC, 2018. Status of Tigers and Prey in Nepal 2018. Department of National Parks and Wildlife Conservation & Department of Forests and Soil Conservation. Ministry of Forests and Environment, Kathmandu, Nepal.

Donaldson, J.E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z., Parr, C.L., 2018. Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. Journal of Applied Ecology 55, 225–235.

Douma, J.C., Weedon, J.T., 2019. Analysing continuous proportions in ecology and evolution: A practical introduction to beta and Dirichlet regression. Methods Ecol Evol 10, 1412–1430.

Drescher, M., Heitkönig, I.M.A., Raats, J.G., Prins, H.H.T., 2006a. The role of grass stems as structural foraging deterrents and their effects on the foraging behaviour of cattle. Appl Anim Behav Sci 101, 10–26.

Drescher, M., Heitkönig, I.M.A., Van Den Brink, P.J., Prins, H.H.T., 2006b. Effects of sward structure on herbivore foraging behaviour in a South African savanna: An investigation of the forage maturation hypothesis. Austral Ecol 31, 76–87. https://doi.org/10.1111/j.1442-9993.2006.01552.x

Durant, D., Fritz, H., Duncan, P., 2004. Feeding patch selection by herbivorous Anatidae: the influence of body size, and of plant quantity and quality. J Avian Biol 35, 144–152.

Eby, S.L., Anderson, T.M., Mayemba, E.P., Ritchie, M.E., 2014. The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics. Journal of Animal Ecology 83, 1196–1205.

Elliott, J.P., Cowan, I.M., Holling, C.S., 1977. Prey capture by the African lion. Can J Zool 55, 1811–1828.

Epperly, H.K., Clinchy, M., Zanette, L.Y., McCleery, R.A., 2021. Fear of large carnivores is tied to ungulate habitat use: evidence from a bifactorial experiment. Sci Rep 11, 1–11.

Ferrari, S., Cribari-Neto, F., 2004. Beta regression for modelling rates and proportions. J Appl Stat 31, 799–815.

Fitzmaurice, A., Poudel, P., Offord-Woolley, S., Macdonald, D., Thapa, S., Lamichhane, B.R., Baral, A., Yadav, B.P., 2021. Complex consequences of conservation success: Emerging human-tiger conflicts in Nepal. CatNews.

Ford, A.T., Goheen, J.R., Otieno, T.O., Bidner, L., Isbell, L.A., Palmer, T.M., Ward, D., Woodroffe, R., Pringle, R.M., 2014. Large carnivores make savanna tree communities less thorny. Science (1979) 346, 346–349.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., Mao, J.S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86, 1320–1330.

Fox, H.V., Bonnet, O., Cromsigt, J.P.G.M., Fritz, H., Shrader, A.M., 2015. Legacy effects of different land-use histories interact with current grazing patterns to determine grazing lawn soil properties. Ecosystems 18, 720–733.

Fox, J., Weisberg, S., 2018. An R companion to applied regression. Sage publications.

Fryxell, J.M., 1991. Forage Quality and Aggregation by Large Herbivores. Am Nat 138, 478–498. https://doi.org/10.1086/285227

Fuhlendorf, S.D., ENGLE, D.M., KERBY, J.A.Y., HAMILTON, R., 2009. Pyric Herbivory: Rewilding Landscapes through the Recoupling of Fire and Grazing. Conservation Biology 23, 588–598. https://doi.org/https://doi.org/10.1111/j.1523-1739.2008.01139.x

Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E., Brashares, J.S., 2019. Landscapes of fear: spatial patterns of risk perception and response. Trends Ecol Evol 34, 355–368.

Gaynor, K.M., Cherry, M.J., Gilbert, S.L., Kohl, M.T., Larson, C.L., Newsome, T.M., Prugh, L.R., Suraci, J.P., Young, J.K., Smith, J.A., 2021. An applied ecology of fear framework: linking theory to conservation practice. Anim Conserv 24, 308–321.

Goodall, D.W., 1952. Some considerations in the use of point quadrats for the analysis of vegetation. Aust J Biol Sci 5, 1–41. https://doi.org/10.1071/BI9520001

Gordon, I.J., Illius, A.W., 1996. The nutritional ecology of African ruminants: a reinterpretation. Journal of Animal Ecology 18–28.

Grant, C.C., Scholes, M.C., 2006. The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. Biol Conserv 130, 426–437.

Gross, D., Dubois, G., Pekel, J.-F., Mayaux, P., Holmgren, M., Prins, H.H.T., Rondinini, C., Boitani, L., 2013. Monitoring land cover changes in African protected areas in the 21st century. Ecol Inform 14, 31–37. https://doi.org/https://doi.org/10.1016/j.ecoinf.2012.12.002

Gross, E.M., Lahkar, B.P., Subedi, N., Nyirenda, V.R., Lichtenfeld, L.L., Jakoby, O., 2018. Seasonality, crop type and crop phenology influence crop damage by wildlife herbivores in Africa and Asia. Biodivers Conserv 27, 2029–2050.

Guisan, A., Edwards Jr, T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol Modell 157, 89–100.

Guisan, A., Harrell, F.E., 2000. Ordinal response regression models in ecology. Journal of Vegetation Science 11, 617–626.

Härkönen, S., Heikkilä, R., 1999. Use of pellet group counts in determining density and habitat use of moose Alces alces in Finland. Wildlife Biol 5, 233–239.

Harrison, S., Inouye, B.D., Safford, H.D., 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. Conservation Biology 17, 837–845.

Hebblewhite, M., Merrill, E.H., 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90, 3445–3454.

Hegland, S.J., Jongejans, E., Rydgren, K., 2010. Investigating the interaction between ungulate grazing and resource effects on Vaccinium myrtillus populations with integral projection models. Oecologia 163, 695–706.

Hempson, G.P., Archibald, S., Bond, W.J., Ellis, R.P., Grant, C.C., Kruger, F.J., Kruger, L.M., Moxley, C., Owen-Smith, N., Peel, M.J.S., Smit, I.P.J., Vickers, K.J., 2015. Ecology of grazing lawns in Africa. Biological Reviews 90, 979–994. https://doi.org/10.1111/brv.12145

Hernández, L., Laundré, J.W., 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk Cervus elaphus and bison Bison bison. Wildlife Biol 11, 215–220. https://doi.org/10.2981/0909-6396(2005)11[215:FITLOF]2.0.CO;2

Hof, A.R., Snellenberg, J., Bright, P.W., 2012. Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. Anim Behav 83, 1099–1106.

Hopcraft, J.G.C., Anderson, T.M., Pérez-Vila, S., Mayemba, E., Olff, H., 2012. Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. Journal of Animal Ecology 81, 201–213.

Hopcraft, J.G.C., Olff, H., Sinclair, A.R.E., 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends Ecol Evol 25, 119–128. https://doi.org/10.1016/j.tree.2009.08.001

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical Journal: Journal of Mathematical Methods in Biosciences 50, 346–363.

Illius, A.W., Gordon, I.J., 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia 89, 428–434.

Iribarren, C., Kotler, B.P., 2012. Foraging patterns of habitat use reveal landscape of fear of Nubian ibex Capra nubiana. Wildlife Biol 18, 194–201.

Jhala, H.Y., Qureshi, Q., Jhala, Y. V, Black, S.A., 2021. Feasibility of reintroducing grassland megaherbivores, the greater one-horned rhinoceros, and swamp buffalo within their historic global range. Sci Rep 11, 1–15.

Jhala, Y. V, 1997. Seasonal effects on the nutritional ecology of blackbuck Antelope cervicapra. Journal of Applied Ecology 34, 1348–1358. https://doi.org/10.2307/2405252

Jhala, Y.V., Qureshi, Q., Nayak, A.K., 2018. Status of tigers, copredators and prey in India. National Tiger Conservation Authority, Government of India, New Delhi, and Wildlife Institute of India, Dehradun.

Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., Hines, J.E., 2004. Tigers and their prey: Predicting carnivore densities from prey abundance. Proceedings of the National Academy of Sciences 101, 4854–4858. https://doi.org/10.1073/pnas.0306210101

Karanth, K.U., Sunquist, M.E., 2000. Behavioural correlates of predation by tiger (Panthera tigris), leopard (Panthera pardus) and dhole (Cuon alpinus) in Nagarahole, India. J Zool 250, 255–265.

Karanth, K.U., Sunquist, M.E., 1995. Prey selection by tiger, leopard and dhole in tropical forests. Journal of Animal Ecology 439–450.

Karanth, K.U., Sunquist, M.E., 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarahole, India. J Trop Ecol 8, 21–35.

Karki, J.B., Jhala, Y. V, Khanna, P.P., 2000. Grazing Lawns in Terai Grasslands, Royal Bardia National Park, Nepal1. Biotropica 32, 423–429. https://doi.org/10.1111/j.1744-7429.2000.tb00489.x

Kassambara, A., 2019. ggcorrplot: Visualization of a Correlation Matrix using'ggplot2'. R package version 0.1 3.

Kie, J.G., 1995. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. J Mammal 80, 1114–1129.

Kiffner, C., Lee, D.E., 2019. Population Dynamics of Browsing and Grazing Ungulates in the Anthropocene, in: The Ecology of Browsing and Grazing II. Springer, pp. 155–179.

Klop, E., Van Goethem, J., De Iongh, H.H., 2007. Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. Wildlife Research 34, 77–83. https://doi.org/10.1071/WR06052

Koerselman, W., Meuleman, A.F.M., 1996. The vegetation N: P ratio: a new tool to detect the nature of nutrient limitation. Journal of applied Ecology 1441–1450.

Kohl, M.T., Stahler, D.R., Metz, M.C., Forester, J.D., Kauffman, M.J., Varley, N., White, P.J., Smith, D.W., MacNulty, D.R., 2018. Diel predator activity drives a dynamic landscape of fear. Ecol Monogr 88, 638–652.

Kohn, M.H., Wayne, R.K., 1997. Facts from feces revisited. Trends Ecol Evol 12, 223–227.

Kral, M.J.C., van Lunenburg, M., van Alphen, J.J.M., 2017. The spatial distribution of ungulates and primates across the vegetation gradient in Bardiya National Park, West Nepal. Asian J Conserv Biol 6, 38–44.

Krebs, J.C., 1999. Ecological methodology, Ecological methodology. Menlo Park, California. Addison Wesley. 1999. xii, 620 p.

Kuijper, D.P.J., De Kleine, C., Churski, M., Van Hooft, P., Bubnicki, J., Jędrzejewska, B., 2013. Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. Ecography 36, 1263–1275.

Kumar, D., Pfeiffer, M., Gaillard, C., Langan, L., Martens, C., Scheiter, S., 2020. Misinterpretation of Asian savannas as degraded forest can mislead management and conservation policy under climate change. Biol Conserv 241, 108293.

Kumar, D., Pfeiffer, M., Gaillard, C., Langan, L., Scheiter, S., 2021. Climate change and elevated CO 2 favor forest over savanna under different future scenarios in South Asia. Biogeosciences 18, 2957–2979.

Laca, E.A., Sokolow, S., Galli, J.R., Cangiano, C.A., 2010. Allometry and spatial scales of foraging in mammalian herbivores. Ecol Lett 13, 311–320. https://doi.org/10.1111/j.1461-0248.2009.01423.x

Laca, E.A., Ungar, E.D., Seligman, N., Demment, M.W., 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass and Forage Science 47, 91–102. https://doi.org/10.1111/j.1365-2494.1992.tb02251.x

Lamichhane, B.R., Leirs, H., Persoon, G.A., Subedi, N., Dhakal, M., Oli, B.N., Reynaert, S., Sluydts, V., Pokheral, C.P., Poudyal, L.P., Malla, S., de Iongh, H.H., 2019. Factors associated with co-occurrence of large carnivores in a human-dominated landscape. Biodivers Conserv 28, 1473–1491. https://doi.org/10.1007/s10531-019-01737-4

Lamichhane, B.R., Persoon, G.A., Leirs, H., Musters, C.J.M., Subedi, N., Gairhe, K.P., Pokheral, C.P., Poudel, S., Mishra, R., Dhakal, M., 2017. Are conflict-causing tigers different? Another perspective for understanding human-tiger conflict in Chitwan National Park, Nepal. Glob Ecol Conserv 11, 177–187.

Laundré, J.W., Hernández, L., Altendorf, K.B., 2001. Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. Can J Zool 79, 1401–1409.

Laundré, J.W., Hernández, L., Medina, P.L., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K.M., Burke, A.M., Gronemeyer, P., Browning, D.M., 2014. The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? Ecology 95, 1141–1152.

Laundre, J.W., Hernandez, L., Ripple, W.J., 2010. The Landscape of Fear: Ecological Implications of Being Afraid~!2009-09-09~!2009-11-16~!2010-02-02~! The Open Ecology Journal 3, 1–7. https://doi.org/10.2174/1874213001003030001

le Roux, E., Kerley, G.I.H., Cromsigt, J.P.G.M., 2018. Megaherbivores Modify Trophic Cascades Triggered by Fear of Predation in an African Savanna Ecosystem. Current Biology 28, 2493-2499. e3. https://doi.org/10.1016/j.cub.2018.05.088

Le Roux, E., Marneweck, D.G., Clinning, G., Druce, D.J., Kerley, G.I.H., Cromsigt, J.P.G.M., 2019. Top–down limits on prey populations may be more severe in larger prey species, despite having fewer predators. Ecography 42, 1115–1123.

Lehmkuhl, J.F., 1994. A classification of subtropical riverine grassland and forest in Chitwan National Park, Nepal. Vegetatio 111, 29–43. https://doi.org/10.1007/BF00045575

Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M., 2021. Emmeans: Estimated marginal means, aka least-squares means. R Package Version 1 (2018).

Leverkus, S.E.R., Fuhlendorf, S.D., Geertsema, M., Allred, B.W., Gregory, M., Bevington, A.R., Engle, D.M., Scasta, J.D., 2018. Resource selection of free-ranging horses influenced by fire in northern Canada. Human–Wildlife Interactions 12, 10.

Lima, S.L., Bednekoff, P.A., 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. Am Nat 153, 649–659.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68, 619–640.

Ludwig, F., de Kroon, H., Prins, H.H.T., Berendse, F., 2001. Effects of nutrients and shade on tree-grass interactions in an East African savanna. Journal of Vegetation Science 12, 579–588.

Mandlate Jr, L.C., Arsenault, R., Rodrigues, F.H.G., 2019. Grass greenness and grass height promote the resource partitioning among reintroduced Burchell's zebra and blue wildebeest in southern Mozambique. Austral Ecol 44, 648–657. https://doi.org/https://doi.org/10.1111/aec.12708

Månsson, J., Andrén, H., Sand, H., 2011. Can pellet counts be used to accurately describe winter habitat selection by moose Alces alces? Eur J Wildl Res 57, 1017–1023.

Marchand, P., Garel, M., Bourgoin, G., Duparc, A., Dubray, D., Maillard, D., Loison, A., 2017. Combining familiarity and landscape features helps break down the barriers between movements and home ranges in a non-territorial large herbivore. Journal of Animal Ecology 86, 371–383. https://doi.org/https://doi.org/10.1111/1365-2656.12616

Mårell, A., Hofgaard, A., Danell, K., 2006. Nutrient dynamics of reindeer forage species along snowmelt gradients at different ecological scales. Basic Appl Ecol 7, 13–30. https://doi.org/https://doi.org/10.1016/j.baae.2005.04.005

Mayengo, G., Piel, A.K., Treydte, A.C., 2020. The importance of nutrient hotspots for grazing ungulates in a Miombo ecosystem, Tanzania. PLoS One 15, e0230192.

McNaughton, S.J., 1984. Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist 124, 863–886.

Mezzalira, J.C., Bonnet, O.J.F., Carvalho, P.C. de F., Fonseca, L., Bremm, C., Mezzalira, C.C., Laca, E.A., 2017. Mechanisms and implications of a type IV functional response for short-term intake rate of dry matter in large mammalian herbivores. Journal of Animal Ecology 86, 1159–1168. https://doi.org/10.1111/1365-2656.12698

Miguel, E., Grosbois, V., Caron, A., Pople, D., Roche, B., Donnelly, C.A., 2020. A systemic approach to assess the potential and risks of wildlife culling for infectious disease control. Commun Biol 3, 353.

Miller, S.M., Bissett, C., Parker, D.M., Burger, A., Courtenay, B., Dickerson, T., Naylor, S., Druce, D.J., Ferreira, S., Slotow, R., 2013. Management of reintroduced lions in small, fenced reserves in South Africa: an assessment and guidelines. South African Journal of Wildlife Research-24-month delayed open access 43, 138–154.

Mishra, H.R., 1982. The ecology and behaviour of chital (Axis axis) in the Royal Chitwan National Park, Nepal: with comparative studies of hog deer (Axis porcinus), sambar (Cervus unicolor) and barking deer (Muntiacus muntjak).

Moe, S.R., 1994. The Importance of Aquatic Vegetation for the Management of the Barasingha Cervus-Duvauceli in Nepal. Biol Conserv 70, 33.

Moe, S.R., Wegge, P., 2008. Effects of deposition of deer dung on nutrient redistribution and on soil and plant nutrients on intensively grazed grasslands in lowland Nepal. Ecol Res 23, 227–234. https://doi.org/10.1007/s11284-007-0367-y

Moe, S.R., Wegge, P., 1997. The effects of cutting and burning on grass quality and axis deer (Axis axis) use of grassland in lowland Nepal. J Trop Ecol 13, 279–292. https://doi.org/10.1017/S0266467400010452

Moe, S.R., Wegge, P., 1994. Spacing behaviour and habitat use of axis deer (Axis axis) in lowland Nepal. Can J Zool 72, 1735–1744.

Moll, R.J., Redilla, K.M., Mudumba, T., Muneza, A.B., Gray, S.M., Abade, L., Hayward, M.W., Millspaugh, J.J., Montgomery, R.A., 2017. The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. Journal of Animal Ecology 86, 749–765.

Morley, R.J., 2012. A review of the Cenozoic palaeoclimate history of Southeast Asia. Biotic evolution and environmental change in Southeast Asia 82, 79.

Murphy, B.P., Andersen, A.N., Parr, C.L., 2016. The underestimated biodiversity of tropical grassy biomes. Philosophical Transactions of the Royal Society B: Biological Sciences 371, 20150319.

Murphy, S.T., Subedi, N., Jnawali, S.R., Lamichhane, B.R., Upadhyay, G.P., Kock, R., Amin, R., 2013. Invasive mikania in Chitwan National Park, Nepal: The threat to the greater one-horned rhinoceros Rhinoceros unicornis and factors driving the invasion. Oryx 47, 361–368. https://doi.org/10.1017/S003060531200124X

O'Hara, R., Kotze, J., 2010. Do not log-transform count data. Nature Precedings 1.

Okamura, H., Punt, A.E., Amano, T., 2012. A generalized model for overdispersed count data. Popul Ecol 54, 467–474.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Jari Oksanen Michael Friendly Roeland Kindt Pierre, F.G.B., Legendre Peter R. Minchin R. B. O'Hara Gavin L. Simpson Peter, D.M., Solymos Eduard Szoecs and Helene Wagner, M.H.H.S., 2019. vegan: Community Ecology Package. R package version 2.5-6.

Olff, H., Ritchie, M.E., Prins, H.H.T., 2002. Global environmental controls of diversity in large herbivores. Nature 415, 901–904.

Olson, D.M., Dinerstein, E., 2002. The Global 200: Priority ecoregions for global conservation. Annals of the Missouri Botanical garden 199–224.

O'Mara, F.P., 2012. The role of grasslands in food security and climate change. Ann Bot 110, 1263–1270.

Peet, N.B., Watkinson, A.R., Bell, D.J., Kattel, B.J., 1999a. Plant diversity in the threatened sub-tropical grasslands of Nepal. Biol Conserv 88, 193–206. https://doi.org/https://doi.org/10.1016/S0006-3207(98)00104-9

Peet, N.B., Watkinson, A.R., Bell, D.J., Sharma, Uday.R., 1999b. The conservation management of Imperata cylindrica grassland in Nepal with fire and cutting: an experimental approach.

Journal of Applied Ecology 36, 374–387. https://doi.org/https://doi.org/10.1046/j.1365-2664.1999.00405.x

Peet, R.K., 1974. The measurement of species diversity. Annu Rev Ecol Syst 285–307.

Person, B.T., Herzog, M.P., Ruess, R.W., Sedinger, J.S., Anthony, R.M., Babcock, C.A., 2003. Feedback dynamics of grazing lawns: Coupling vegetation change with animal growth. Oecologia 135, 583–592. https://doi.org/10.1007/s00442-003-1197-4

Pierce, B.M., Bowyer, R.T., Bleich, V.C., 2004. Habitat selection by mule deer: forage benefits or risk of predation? J Wildl Manage 68, 533–541.

Pokharel, K.P., Storch, I., 2016. Habitat niche relationships within an assemblage of ungulates in Bardia National Park, Nepal. Acta oecologica 70, 29–36.

Pradhan, N.M.B., Wegge, P., Moe, S.R., Shrestha, A.K., 2008. Feeding ecology of two endangered sympatric megaherbivores: Asianelephant Elephas maximus and greater one-horned rhinoceros Rhinoceros unicornis in lowland Nepal. Wildlife Biol 14, 147–154.

Prins, H.H.T., 1996. Ecology and behaviour of the African buffalo: social inequality and decision making. Springer Science & Business Media.

Prins, H.H.T., Beekman, J.H., 1989. A balanced diet as goal of grazing: The food ofthe Manyara buffalo. Journal of African Ecology27 129–147.

Prins, H.H.T., Olff, H., 1998. Species richness of African grazer assemblages: towards a functional explanation, in: Dynamics of Tropical Communities. Cambridge University Press, pp. 449–490. https://doi.org/10.1017/CBO9781107415324.004

Prins, H.H.T., Van Langevelde, F., 2008. Assembling a diet from different places, in: Resource Ecology. Springer, pp. 129–155.

Prugh, L.R., Sivy, K.J., Mahoney, P.J., Ganz, T.R., Ditmer, M.A., van de Kerk, M., Gilbert, S.L., Montgomery, R.A., 2019. Designing studies of predation risk for improved inference in carnivore-ungulate systems. Biol Conserv 232, 194–207.

Putman, R.J., 1984. Facts from faeces. Mamm Rev 14, 79–97.

R Core Team, 2021. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Ram, A.K., Yadav, N.K., Kandel, P.N., Mondol, S., Pandav, B., Natarajan, L., Subedi, N., Naha, D., Reddy, C.S., Lamichhane, B.R., 2021. Tracking forest loss and fragmentation between 1930 and 2020 in Asian elephant (Elephas maximus) range in Nepal. Sci Rep 11, 19514.

Raman, T.R.S., 1997. Factors influencing seasonal and monthly changes in the group size of chital or axis deer in southern India. J Biosci 22, 203–218.

Ramesh, T., Snehalatha, V., Sankar, K., Qureshi, Q., 2009. Food habits and prey selection of tiger and leopard in Mudumalai Tiger Reserve, Tamil Nadu, India. Journal of Scientific Transactions in Environment and Technovation 2, 170–181.

Ratnam, J., Bond, W.J., Fensham, R.J., Hoffmann, W.A., Archibald, S., Lehmann, C.E.R., Anderson, M.T., Higgins, S.I., Sankaran, M., 2011. When is a 'forest'a savanna, and why does it matter? Global Ecology and Biogeography 20, 653–660.

Ratnam, J., Sheth, C., Sankaran, M., 2019. African and Asian Savannas: Comparisons of Vegetation Composition and Drivers of Vegetation Structure and Function. Savanna Woody Plants and Large Herbivores 25–49.

Ratnam, J., Tomlinson, K.W., Rasquinha, D.N., Sankaran, M., 2016. Savannahs of Asia: antiquity, biogeography, and an uncertain future. Philosophical Transactions of the Royal Society B: Biological Sciences 371, 20150305.

Raynor, E.J., Joern, A., Nippert, J.B., Briggs, J.M., 2016. Foraging decisions underlying restricted space use: effects of fire and forage maturation on large herbivore nutrient uptake. Ecol Evol 6, 5843–5853. https://doi.org/10.1002/ece3.2304

Reich, P.B., Hobbie, S.E., Lee, T.D., Pastore, M.A., 2018. Unexpected reversal of C3 versus C4 grass response to elevated CO2 during a 20-year field experiment. Science (1979) 360, 317–320.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H., Levi, T., Lindsey, P.A., 2015. Collapse of the world's largest herbivores. Sci Adv 1, e1400103.

Rowland, M.M., Wisdom, M.J., Nielson, R.M., Cook, J.G., Cook, R.C., Johnson, B.K., Coe, P.K., Hafer, J.M., Naylor, B.J., Vales, D.J., 2018. Modeling elk nutrition and habitat use in western Oregon and Washington. Wildlife Monographs 199, 1–69.

Sabiiti, E.N., Wamara, J.B., Ogen-Odoi, A.A., Wein, R.W., 1992. The Role of Fire in Pasture and Rangeland Management. Nomad People 107–110.

Salima, B.A., Bellefon, M.D., 2018. Spatial autocorrelation indices. Handbook of Spatial Analysis: Theory Aplication with R 51–68.

Sánchez-Rojas, G., Gallina, S., 2000. Factors affecting habitat use by mule deer (Odocoileus hemionus) in the central part of the Chihuahuan Desert, Mexico: an assessment with univariate and multivariate methods. Ethol Ecol Evol 12, 405–417.

Sankaran, M., 2016. Grazing and Fire Effects on Community and Ecosystem Processes in a Tall-Grass Mesic Savanna Ecosystem in Southern India, in: Ahrestani, F.S., Sankaran, M. (Eds.), The Ecology of Large Herbivores in South and Southeast Asia. Springer Netherlands, Dordrecht, pp. 187–205. https://doi.org/10.1007/978-94-017-7570-0_8

Sankaran, M., 2009. Diversity patterns in savanna grassland communities: implications for conservation strategies in a biodiversity hotspot. Biodivers Conserv 18, 1099–1115.

Sankaran, M., 2005. Fire, grazing and the dynamics of tall-grass savannas in the Kalakad-Mundanthurai Tiger Reserve, South India. Conservation and Society 4–25.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., 2005. Determinants of woody cover in African savannas. Nature 438, 846–849.

Sarkar, M.S., Amonge, D.E., Pradhan, N., Naing, H., Huang, Z., Lodhi, M.S., 2021. A Review of Two Decades of Conservation Efforts on Tigers, Co-Predators and Prey at the Junction of Three Global Biodiversity Hotspots in the Transboundary Far-Eastern Himalayan Landscape. Animals 11, 2365.

Sarmah, C.K., 2017. Chao, jackknife and bootstrap estimators of species richness. IJAMAA 12 (1) 7–15.

Say-Sallaz, E., Chamaillé-Jammes, S., Fritz, H., Valeix, M., 2019. Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg. Biol Conserv 235, 36–52.

Schmidt, K., Kuijper, D.P.J., 2015. A "death trap" in the landscape of fear. Mamm Res 60, 275–284.

Schmitz, O.J., 2008. Effects of predator hunting mode on grassland ecosystem function. Science (1979) 319, 952–954.

Schmitz, O.J., Krivan, V., Ovadia, O., 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecol Lett 7, 153–163.

Schoenau, J.J., O'Halloran, I.P., 2008. Sodium bicarbonate-extractable phosphorus. Soil sampling and methods of analysis 2.

Schroder, B., 2021. Methods to improve forage quality for mammalian herbivores in nutrient poor savannas.

Searle, K.R., Shipley, L.A., 2008. The comparative feeding bahaviour of large browsing and grazing herbivores, in: The Ecology of Browsing and Grazing. Springer, pp. 117–148.

Shipley, L.A., Gross, J.E., Spalinger, D.E., Hobbs, N.T., Wunder, B.A., 1994. The scaling of intake rate in mammalian herbivores. Am Nat 143, 1055–1082.

Sinclair, A.R.E., Krebs, C.J., 2002. Complex numerical responses to top–down and bottom–up processes in vertebrate populations. Philos Trans R Soc Lond B Biol Sci 357, 1221–1231.

Skarin, A., 2007. Habitat use by semi-domesticated reindeer, estimated with pellet-group counts. Rangifer 27, 121–132.

Smit, I.P.J., Coetsee, C., 2019. Interactions between fire and herbivory: current understanding and management implications, in: The Ecology of Browsing and Grazing II. Springer, pp. 301–319.

Spalinger, D.E., Hobbs, N.T., 1992. Mechanisms of Foraging in Mammalian Herbivores: New Models of Functional Response. Am Nat 140, 325–348. https://doi.org/10.1086/285415

Spitzer, R., Churski, M., Felton, A., Heurich, M., Kuijper, D.P.J., Landman, M., Rodriguez, E., Singh, N.J., Taberlet, P., van Beeck Calkoen, S.T.S., Widemo, F., Cromsigt, J.P.G.M., 2019. Doubting dung: eDNA reveals high rates of misidentification in diverse European ungulate communities. Eur J Wildl Res 65, 28. https://doi.org/10.1007/s10344-019-1264-8

Stankowich, T., Coss, R.G., 2006. Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. Behavioral Ecology 17, 246–254. https://doi.org/10.1093/beheco/arj020

Staver, A.C., Archibald, S., Levin, S.A., 2011. The Global Extent and Determinants of Savanna and Forest as Alternative Biome States. Science (1979) 334, 230–232. https://doi.org/10.1126/science.1210465

Stevens, N., Lehmann, C.E.R., Murphy, B.P., Durigan, G., 2017. Savanna woody encroachment is widespread across three continents. Glob Chang Biol 23, 235–244.

Stobbs, T.H., 1973. The effect of plant structure on the intake of tropical pastures. II.* Differences in sward structure, nutritive value, and bite size of animals grazing Setaria anceps and Chloris gayana at various stages of growth. Aust J Agric Res 24, 821–829.

Subedi, N., Jnawali, S.R., Dhakal, M., Pradhan, N.M.B., Lamichhane, B.R., Malla, S., Amin, R., Jhala, Y. V, 2013. Population status, structure and distribution of the greater one-horned rhinoceros *Rhinoceros unicornis* in Nepal. Oryx 47, 352–360. https://doi.org/10.1017/S0030605313000562

Sunquist, M., 2010. Chapter 2 - What Is a Tiger? Ecology and Behavior, in: Tilson, R., Nyhus, P.J.B.T.-T. of the W. (Second E. (Eds.), Noyes Series in Animal Behavior, Ecology, Conservation, and Management. William Andrew Publishing, Boston, pp. 19–33. https://doi.org/https://doi.org/10.1016/B978-0-8155-1570-8.00002-5

Supartono, T., Adhya, I., Hendrayana, Y., Kosasih, D., Yudayana, B., 2021. Use of faecal pellet count method in estimating population density of mammals in Gunung Ciremai National Park, in: IOP Conference Series: Earth and Environmental Science. IOP Publishing, p. 12079.

Thapa, K., Kelly, M.J., 2017. Density and carrying capacity in the forgotten tigerland: Tigers in the understudied Nepalese Churia. Integr Zool 12, 211–227.

Thapa, S.K., de Jong, J.F., Hof, A.R., Subedi, N., Joshi, L.R., Prins, H.H.T., 2022. Fire and forage quality: Postfire regrowth quality and pyric herbivory in subtropical grasslands of Nepal. Ecol Evol 12, e8794–e8794.

Thapa, S.K., de Jong, J.F., Subedi, N., Hof, A.R., Corradini, G., Basnet, S., Prins, H.H.T., 2021. Forage quality in grazing lawns and tall grasslands in the subtropical region of Nepal and implications for wild herbivores. Glob Ecol Conserv 30, e01747. https://doi.org/10.1016/J.GECCO.2021.E01747

Tolon, V., Dray, S., Loison, A., Zeileis, A., Fischer, C., Baubet, E., 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. Can J Zool 87, 1129–1137.

Trollope, W.S.W., 2011. Personal Perspectives on Commercial versus Communal African Fire Paradigms when Using Fire to Manage Rangelands for Domestic Livestock and Wildlife in Southern and East African Ecosystems. Fire Ecology 7, 57–73. https://doi.org/10.4996/fireecology.0701057

Tuboi, C., Hussain, S.A., 2016. Factors affecting forage selection by the endangered Eld's deer and hog deer in the floating meadows of Barak-Chindwin basin of North-east India. Mammalian Biology 81, 53–60.

Upadhyaya, S.K., Musters, C.J.M., Lamichhane, B.R., de Snoo, G.R., Thapa, P., Dhakal, M., Karmacharya, D., Shrestha, P.M., de Iongh, H.H., 2018. An insight into the diet and prey preference of tigers in Bardia National Park, Nepal. Trop Conserv Sci 11, 1940082918799476–1940082918799476.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., Macdonald, D.W., 2009. Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. Ecology 90, 23–30. https://doi.org/10.1890/08-0606.1

Van de Vijver, C., Poot, P., Prins, H.H.T., 1999. Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. Plant Soil 214, 173–185.

van der Waal, C., Kool, A., Meijer, S.S., Kohi, E., Heitkönig, I.M.A., de Boer, W.F., van Langevelde, F., Grant, R.C., Peel, M.J.S., Slotow, R., de Knegt, H.J., Prins, H.H.T., de Kroon, H., 2011. Large herbivores may alter vegetation structure of semi-arid savannas through soil nutrient mediation. Oecologia 165, 1095–1107. https://doi.org/10.1007/s00442-010-1899-3

van Langevelde, F., Drescher, M., Heitkönig, I.M.A., Prins, H.H.T., 2008. Instantaneous intake rate of herbivores as function of forage quality and mass: Effects on facilitative and competitive interactions. Ecol Modell. https://doi.org/10.1016/j.ecolmodel.2007.12.009

Van Langevelde, F., Van De Vijver, C.A.D.M., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84, 337–350.

van Lunenburg, M., Kral, M.J.C., van Alphen, J.J.M., 2017. Decreased ungulate density in Bardiya National Park, West Nepal, and the implications for increasing tiger populations. A comment on Thapa et al. (2015). Ethol Ecol Evol 29, 304–309. https://doi.org/10.1080/03949370.2016.1145147

Van Soest, P.J., 1994. Nutritional ecology of the ruminant, Second edition. Cornell University Press. https://doi.org/10.1016/0301-6226(95)90011-X

Van Soest, P.J., 1982. Nutritional ecology of the ruminant. O & B Books. Inc., Corvallis, OR 374.

Veach, A.M., Dodds, W.K., Skibbe, A., 2014. Fire and grazing influences on rates of riparian woody plant expansion along grassland streams. PLoS One 9, e106922–e106922.

Veldhuis, M.P., Fakkert, H.F., Berg, M.P., Olff, H., 2016. Grassland structural heterogeneity in a savanna is driven more by productivity differences than by consumption differences between lawn and bunch grasses. Oecologia 182, 841–853. https://doi.org/10.1007/s00442-016-3698-y

Veldhuis, M.P., Hofmeester, T.R., Balme, G., Druce, D.J., Pitman, R.T., Cromsigt, J.P.G.M., 2020. Predation risk constrains herbivores' adaptive capacity to warming. Nat Ecol Evol 4, 1069–1074.

Veldhuis, M.P., Howison, R.A., Fokkema, R.W., Tielens, E., Olff, H., 2014. A novel mechanism for grazing lawn formation: Large herbivore-induced modification of the plant-soil water balance. Journal of Ecology 102, 1506–1517. https://doi.org/10.1111/1365-2745.12322

Verweij, R.J.T., Verrelst, J., Loth, P.E., Heitkönig, I.M.A., Brunsting, A.M.H., 2006. Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. Oikos 114, 108–116. https://doi.org/10.1111/j.2006.0030-1299.14209.x

Voysey, M.D., Archibald, S., Bond, W.J., Donaldson, J.E., Carla Staver, A., Greve, M., 2021. The role of browsers in maintaining the openness of savanna grazing lawns. Journal of Ecology 109, 913–926. https://doi.org/https://doi.org/10.1111/1365-2745.13518

Wallis De Vries, M.F., Laca, E.A., Demment, M.W., 1999. The importance of scale of patchiness for selectivity in grazing herbivores. Oecologia 121, 355–363. https://doi.org/10.1007/s004420050939

Wang, G., Hobbs, N.T., Twombly, S., Boone, R.B., Illius, A.W., Gordon, I.J., Gross, J.E., 2009. Density dependence in northern ungulates: interactions with predation and resources. Popul Ecol 51, 123–132.

Warton, D.I., Lyons, M., Stoklosa, J., Ives, A.R., 2016. Three points to consider when choosing a LM or GLM test for count data. Methods Ecol Evol 7, 882–890.

Wegge, P., Jnawali, S.R., Storaas, T., Odden, M., 2000. Grasslands and large mammal conservation in the lowland Terai: a preliminary synthesis based on field research conducted in Royal Bardia National Park, Nepal., in: Grassland Ecology and Management in Protected Areas of Nepal. Proceedings of a Workshop, Royal Bardia National Park, Thakurdwara, Bardia, Nepal, 15-19 March, 1999. Volume 2: Terai Protected Areas. International Centre for Integrated Mountain Development, pp. 50–57.

Wegge, P., Odden, M., Pokharel, C.P., Storaas, T., 2009. Predator-prey relationships and responses of ungulates and their predators to the establishment of protected areas: A case study of tigers, leopards and their prey in Bardia National Park, Nepal. Biol Conserv 142, 189–202. https://doi.org/10.1016/j.biocon.2008.10.020

Wegge, P., Shrestha, A.K., Moe, S.R., 2006. Dry season diets of sympatric ungulates in lowland Nepal: competition and facilitation in alluvial tall grasslands. Ecol Res 21, 698–706.

Weterings, M.J.A., Moonen, S., Prins, H.H.T., Van Wieren, S.E., Van Langevelde, F., 2018. Food quality and quantity are more important in explaining foraging of an intermediate-sized mammalian herbivore than predation risk or competition. International Journal of Business Innovation and Research 17, 8419–8432. https://doi.org/10.1002/ece3.4372

Wheeler, H.C., Hik, D.S., 2014. Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on arctic ground squirrels. Anim Behav 95, 1–8.

White, C.A., Feller, M.C., Bayley, S., 2003. Predation risk and the functional response of elk–aspen herbivory. For Ecol Manage 181, 77–97.

Wickham, H., 2021. ggplot2: elegant graphics for data analysis 2016. https://ggplot2. tidyverse. org. doi 10, 973–978.

Wikramanayake, E., Manandhar, A., Bajimaya, S., Nepal, S., Thapa, G., Thapa, K., 2010. The Terai Arc Landscape: A tiger conservation success story in a human-dominated landscape, in: Tigers of the World. Elsevier, pp. 163–173.

Wikramanayake, E.D., Dinerstein, E., Robinson, J.G., Karanth, U., Rabinowitz, A., Olson, D., Mathew, T., Hedao, P., Conner, M., Hemley, G., Bolze, D., 1998. An ecology-based method for defining priorities for large mammal conservation: The tiger as case study. Conservation Biology 12, 865–878.

Wilke, B.-M., 2005. Determination of chemical and physical soil properties, in: Monitoring and Assessing Soil Bioremediation. Springer, pp. 47–95.

Wilmshurst, J.F., Fryxell, J.M., Bergman, C.M., 2000. The allometry of patch selection in ruminants. Proc R Soc Lond B Biol Sci 267, 345–349.

Wilmshurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E., Henschel, C.P., 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Can J Zool 77, 1223–1232. https://doi.org/10.1139/cjz-77-8-1223

Wilmshurst, J.F., Fryxell, J.M., Hudson, R.J., 1995. Forage quality and patch choice by wapiti (Cervus elaphus). Behavioral Ecology 6, 209–217. https://doi.org/10.1093/beheco/6.2.209

Wilson, E., Underwood, M., Puckrin, O., Letto, K., Doyle, R., Caravan, H., Camus, S., Bassett, K., 2013. The arcsine transformation: has the time come for retirement. Unpublished manuscript, Memorial University of Newfoundland, Newfoundland and Labrador, Canada.

Wirsing, A.J., Heithaus, M.R., Dill, L.M., 2007. Fear factor: do dugongs (Dugong dugon) trade food for safety from tiger sharks (Galeocerdo cuvier)? Oecologia 153, 1031–1040.

Zhang, H., Zhang, S., Fu, M., Chang, H., He, G., Hou, R., Pan, R., Li, B., Guo, S., 2019. Habitat manipulation preferred by Eld's Deer in Hainan Island, China. J Nat Conserv 48, 21–26. https://doi.org/https://doi.org/10.1016/j.jnc.2019.01.004

Zwerts, J.A., Prins, H.H.T., Bomhoff, D., Verhagen, I., Swart, J.M., De Boer, W.F., 2015. Competition between a lawn-forming cynodon dactylon and a tufted grass species hyparrhenia hirta on a south-african dystrophic savanna. PLoS One 10. https://doi.org/10.1371/journal.pone.0140789

# Summary

***“Deer for the Tiger: managing subtropical monsoon grasslands for preserving a flagship species”***

The subtropical monsoon grasslands of Asia also known as ‘Terai-Duar Savanna and Grasslands’, once extending from beyond Myanmar in the East into Pakistan in the West, are now largely confined to some isolated protected areas in Nepal and India. The reduction in the spatial extent of these Terai-Duar grasslands has led to a severe decline in the sizes of populations and ranges of many species that are now becoming vulnerable to extinction. This went hand in hand with changes in critical characteristics of these grasslands, such as community structure and composition, and quality and quantity of herbaceous vegetation, with cascading negative effects on grassland ecosystems.

Forage quality in a grazing system is determined by the physical and chemical properties of forage including vegetation height, biomass, proportion of leaves over stem, and nutrient and digestible energy content in grasses. Management interventions can increase nutrient concentrations in forage which attract herbivores and the resulting grazing pressure induces grazing lawns. The aim then is to generate a positive feedback loop of grazing for the persistence of grazing lawns. In my thesis, I report on the status of forage quality in Nepal’s existing subtropical monsoon grassland, and I explore mechanisms for improving subtropical monsoon grassland management. Nepal offers a unique managerial setting in which through close cooperation between the protected area management and its main conservation partners—the National Trust for Nature Conservation, scientific experiments aiming at better conservation can be executed in the core areas of national parks. It thus can serve as a natural laboratory for other Asian countries. I did this research in Bardia National Park, situated in the Terai Arc Landscape of Nepal.

First, I compared the forage quality of two different grassland states – grazing lawns and tall grasslands. Grazing lawns in the subtropical monsoon grasslands in Asia contain high-quality forage, both in terms of physical and chemical properties, allowing herbivores to maximise their energy intake. I then examined the effect of fire on forage quality, emphasising that large-scale single-event fires are not fruitful for fulfilling the nutritional requirements of existing free-ranging deer populations *viz.*, chital, swamp deer, and hog deer (named as mesoherbivores). The availability of new regrowth after a fire disperses grazing pressure across the burnt area. As a consequence, grasses attain height and biomass, leading to a reduction in nutrient concentrations and the disappearance of grazing lawns. I continued to examine the effectiveness of management interventions in providing quality forage to the existing assemblage of deer species. I experimentally examined the applicability of the landscape of fear concept in grassland management. I showed that grassland management interventions become productive when the management interventions optimise the trade-off between predation risk and resources for herbivores, while still providing opportunities for predators to hunt effectively. Furthermore, I examined the possibility of establishing grazing lawns in the highly productive subtropical monsoon grasslands, where large bulk grazers are functionally extinct. For Bardia, we are not too certain which large bulk grazers lived here before they were exterminated by humans. In the Terai Arc Landscape, these bulk grazers were ancestral forms of the indigenous zebu, or bantengs or even gaurs and possibly arna (wild water buffalo). Historically, their roles were similar to that of domestic cattle and domestic water buffalo, which were removed when the area became a national park. Mimicking their effect, I demonstrated that frequent mowing of tall grasses and the addition of chemical fertilisers can elevate nitrogen and phosphorus concentrations beyond the minimum maintenance requirement level for mesoherbivores. Increased forage quality due to management interventions attracts abundantly present mesoherbivores and the resulting grazing intensity initiates the grazing lawns. I showed that intensive management interventions together with grazing favour grazing lawn grasses to establish by replacing tall grasses. These results emphasised that intensive management is required to initiate grazing lawns in the highly productive subtropical monsoon grasslands which in turn fulfil the nutritional requirement of mesoherbivores that are present here.

In the concluding chapter, I synthesised the results and discussed the management implications of my findings. From a practical conservation perspective, I emphasised the significance of two elements – (i) spatial scale of intervention (size of the intervention area) and (ii) frequency of interventions (multiple times a year and over multiple years) – in achieving the desired outcome of enhancing forage quality for herbivores in subtropical monsoon grasslands. The spatial scale of interventions plays an important role in balancing a trade-off between predation risk and resources for mesoherbivores. The frequency of interventions is essential for maintaining grass height and quality in grassland systems with insufficient grazing intensity. Furthermore, I discussed that with the availability of quality forage as a result of management interventions, mesoherbivores will likely show positive numerical responses through the survival and recruitment of young individuals. This, in turn, supports the population dynamics of tigers, which currently depend on these mesoherbivores for survival because of the absence of bulk grazers such as gaur, and arna. Historical sources are inadequate to know for certain which wild bulk grazers could have been maintaining the grazing lawns to the benefit of the deer. These could have been the wild ancestors of the zebu, perhaps the banteng, and probably the gaur. Yet, when the area (Bardia National Park) became a protected area, their functional role had been taken over by domestic

cattle and water buffalo. My thesis provides scientific insights into the mechanisms for improving subtropical monsoon grassland management for the conservation of priority wildlife such as tigers and their prey species. In conclusion, my study highlights the necessity of adopting intensive management approaches to initiate grazing lawns to meet the nutritional requirement of mesoherbivores in grassland systems dominated by nutrient-poor tall grasses. The more practical and cheaper means is the reintroduction of the wild bulk grazers (gaur and arna). The practical applications of these findings extend to the management of highly productive subtropical monsoon grasslands within the protected areas of the Terai Arc Landscape and other Asian countries which serve as critical habitats for tigers and their prey.

# Samenvatting

## Deer for de Tiger: beheer van subtropische moessongraslanden voor het behoud van een vlaggenschipsoort

De subtropische moessongraslanden van Azië, ook bekend als 'Terai-Duar-graslanden', strekten zich ooit uit van Myanmar in het oosten tot Pakistan in het westen. Tegenwoordig bestaan deze graslanden uitsluitend nog als geïsoleerde beschermde gebieden in Nepal en India. De grote afname in oppervlakte van deze Terai-Duar-graslanden heeft geleid tot een ernstige reductie van geschikt leefgebied voor de vele diersoorten die er leven, waardoor veel populaties nu kwetsbaar zijn en worden bedreigd met uitsterven. Daarnaast hebben veranderingen in eigenschappen van deze graslanden, zoals vegetatiestructuur, soortensamenstelling en de kwaliteit en kwantiteit van kruidachtige vegetatie, negatieve effecten gehad op de grasland ecosystemen.

De voedselkwaliteit in een begrazingssysteem wordt met name bepaald door de fysieke en chemische eigenschappen van de vegetatie, waaronder vegetatiehoogte, biomassa, de verhouding van blad tot stengel en het voedings- en verteerbare energiegehalte in grassen. Beheersmaatregelen kunnen de kwaliteit van de vegetatie verhogen, waardoor deze aantrekkelijker wordt voor herbivoren en de dieren worden aangetrokken tot bepaalde gebieden. Vervolgens neemt in deze aantrekkelijke gebieden de begrazingsdruk toe, waardoor zogenaamde graasweiden kunnen ontstaan. In een graasweide is de graasdruk op de vegetatie zo hoog, dat continue teruggroei van voedselrijke vegetatie wordt gestimuleerd. Idealiter ontstaat er een positieve feedback tussen begrazing en vegetatie, waardoor begrazingsweiden in stand kunnen worden gehouden door herbivoren alleen, zonder beheersmaatregelen. In mijn proefschrift onderzoek ik de voedselkwaliteit en interactie tussen herbivoren en vegetatie in de subtropische moessongraslanden van Nepal. Daarnaast onderzoek ik hoe beheer van subtropische moessongraslanden de vegetatiekwaliteit voor herbivoren kan verbeteren. Nepal biedt een unieke omgeving waarin wetenschappelijke experimenten gericht op betere natuurbescherming kunnen worden uitgevoerd in de kerngebieden van nationale parken door een nauwe samenwerking tussen beheerders van beschermde gebieden en hun belangrijkste partner voor natuurbescherming, de National Trust for Nature Conservation. Deze samenwerking staat toe dat Nationale Parken in Nepal kunnen dienen als een natuurlijk laboratorium, en als voorbeeld voor andere Aziatische landen. Mijn onderzoek is uitgevoerd in Bardia National Park, gelegen in het Terai Arc Landschape Nepal.

Allereerst heb ik de voedselkwaliteit van twee verschillende toestanden in grasland vergeleken - graasweiden en hoge graslanden. Graasweiden in de subtropische moessongraslanden van Azië worden gekenmerkt door korte, voedselrijke vegetatie en bevatten hoogwaardig voer voor herbivoren, zowel qua fysieke als qua chemische eigenschappen. Hierdoor kunnen herbivoren hun energieopname maximaliseren ten opzichte van hoge graslanden, die worden gekenmerkt door een hoge biomassa, maar kwalitatief slechte vegetatie voor herbivoren. Vervolgens heb ik het effect van vuur op voedselkwaliteit onderzocht, waarbij ik vaststel dat grootschalige en eenmalige branden geen grote bijdrage leveren in het vervullen van de voedselbehoeften van lokale hertenpopulaties, zoals axishert, moerashert en varkenshert. De gelijktijdige en grootschalige teruggroei van de vegetatie na een brand levert weliswaar kortstondig voedselrijke vegetatie op, maar verspreidt daardoor de begrazingsdruk over het hele verbrande gebied. Hierdoor is de totale graasdruk op een gegeven locatie erg laag, waardoor grassen snel doorgroeien tot een hoog grasland, wat leidt tot een afname van voedingsstoffenconcentraties en het verdwijnen van begrazingsweiden. Een dergelijke brand wist als het ware de graasweiden uit, door op een groot oppervlakte de hele vegetatie op hetzelfde moment te laten teruggroeien.

Ik onderzocht tevens de effectiviteit van bepaalde beheersmaatregelen (maaien, bemesten) bij het verbeteren van de kwaliteit van de vegetatie vanuit het oogpunt van de lokaal voorkomende hertensoorten. In een experiment onderzocht ik of het concept van het ‘landschap van angst’ in graslandbeheer van toepassing is op de situatie in Bardia. Ik toon aan dat beheersmaatregelen pas effectief worden wanneer het predatierisico en de voedselkwaliteit van de vegetatie voor herbivoren worden geoptimaliseerd. Verder onderzocht ik of graasweiden überhaupt kunnen ontstaan in de hoogproductieve subtropische moessongraslanden, waar grote grazers functioneel uitgestorven zijn. Het is niet bekend precies welke grote grazers in Bardia leefden voordat deze werden uitgeroeid door mensen. In het Terai Arc Landschap als geheel komen grote grazersoorten voor, zoals de inheemse zebu, banteng, gaur en wilde waterbuffel. Historisch gezien zijn deze soorten eerst vervangen door vee, dat werd verwijderd ui Bardia toen het gebied een nationaal park werd. Door het effect van deze grote grazers na te bootsen door middel van maaien, toonde ik aan dat het frequent maaien van hoog gras en het toevoegen van chemische meststoffen de stikstof- en fosforconcentraties in de vegetatie kan verhogen boven het minimum niveau dat nodig is voor mesoherbivoren om zich in stand te houden. Ik toon aan dat verhoogde vegetatiekwaliteit als gevolg van beheersmaatregelen mesoherbivoren aantrekt, die op hun beurt de lokale graasdruk verhogen en op die manier het ontstaan van graasweiden faciliteren. Mijn resultaten laten zien dat intensief beheer vereist is om graasweiden die voldoende kwalitatieve voeding bieden aan de aanwezige mesoherbivoren te laten ontstaan in de hoogproductieve subtropische moessongraslanden.

In het afsluitende hoofdstuk bespreek ik de implicaties van mijn resultaten voor natuurbescherming. Vanuit het perspectief van natuurbescherming benadruk ik twee elementen - (i) de ruimtelijke schaal van beheer (grootte van het interventiegebied) en (ii) de frequentie van beheer (meerdere keren per jaar en over meerdere jaren) – zijn van belang om het gewenste resultaat van het verbeteren van de vegetatiekwaliteit voor herbivoren in subtropische moessongraslanden te bereiken. De ruimtelijke schaal van beheer speelt een belangrijke rol bij de afweging die mesoherbivoren maken tussen predatierisico en vegetatiekwaliteit. De frequentie van beheer is essentieel voor het behouden van de optimale vegetatiehoogte en -kwaliteit in graslandsystemen met onvoldoende graasdruk. Verder bespreek ik dat, met de beschikbaarheid van vegetatie met hoge voedselkwaliteit als gevolg van beheersmaatregelen, er bij mesoherbivoren waarschijnlijk sprake zal zijn van hogere reproductie en overleving van nakomelingen. Dit ondersteunt de populatiedynamiek van tijgers, die gezien de afwezigheid van grote grazers grotendeels afhankelijk zijn van deze mesoherbivoren voor hun voortbestaan. Mijn proefschrift biedt wetenschappelijke inzichten voor het verbeteren van het beheer van subtropische moessongraslanden omwille vande instandhouding en bescherming van diersoorten zoals tijgers en hun prooidieren. Tot slot benadrukt mijn onderzoek de noodzaak tot intensief beheer om graasweiden te initiëren om zo te voldoen aan de voedingsvereisten van mesoherbivoren in graslandsystemen die worden gedomineerd door voedingsarme hoge grassen. Gezien de hoge kosten van beheersmaatregelen, is de meest praktische en goedkope methode de herintroductie van wilde grote grazers (gaurs, wilde waterbuffels). De praktische toepassingen van mijn bevindingen strekken zich uit tot het beheer van zeer productieve subtropische moessongraslanden binnen de beschermde gebieden van het Terai Arc Landschape andere Aziatische landen die dienen als kritieke habitats voor tijgers en hun prooidieren.

# Summary in Chinese

## 概括

## 为老虎提供鹿：管理亚热带季风草原以保护旗舰物种

亚洲的亚热带季风草原，也被称为“特拉伊-杜尔稀树草原”，曾从东部延伸至缅甸，直至西部的巴基斯坦，但现在大部分仅限于尼泊尔和印度的一些与外界隔离的保护区。这种特拉伊-杜尔草地空间范围的减小导致了许多物种的种群和分布范围严重下降，甚至濒临灭绝。与此同时，这些草原的关键特性，例如群落结构和组成，以及草本植被的质量和数量等，也发生了变化， 从而对草地生态系统产生了连锁负面影响。

在放牧系统中，牧草的质量由牧草的物理和化学特性决定，包括植被高度，生物量，叶片与茎的比例，以及草本植物中的营养物质和可消化能量含量。管理干预可以增加牧草中的营养物质浓度，从而吸引食草动物，且由此产生的放牧压力也形成了牧草。因此，形成一个积极的放牧反馈循环以维持放牧草坪的存在至关重要。本次研究报告了尼泊尔现有亚热带季风草原的饲料质量状况，并探讨了应对亚热带季风草原管理的改善机制。尼泊尔提供了一个独特的管理背景，在此背景下，通过保护区管理与主要保护合作伙伴，即国家自然保护信托基金会的紧密合作，使得保护性的科学实验能在国家公园的核心区更好地进行。因此，尼泊尔可以作为其他亚洲国家的自然实验室。本研究的研究地点位于尼泊尔特拉伊弧景观的巴尔迪亚国家公园 。

首先，本次研究比较了两种不同草地状态，即放牧草坪和高草地的饲料质量。亚洲亚热带季风草原中的放牧草坪含有高质量的饲料，无论是从物理特性还是化学特性上看，都能使食草动物最大限度地摄取能量。本次研究首先检验了火灾对饲料质量的影响，强调了大规模单次火灾对满足现有自由放牧鹿类（如斑鹿、沼泽鹿和猪鹿，即中型食草动物）营养需求的效果不明显。火灾后的再生植被分散了火烧区的放牧压力，从而增加了草地高度和生物量，导致营养物质浓度降低，放牧草地消失。本次研究检查了管理干预在为现有鹿类提供优质饲料方面的有效性以及景观恐惧理论在草地管理中的适用性，证明了当管理干预在捕食风险和食草动物资源之间取得平衡时，草地管理干预才能够发挥作用，且继续为捕食者提供有效捕猎的机会。此外，本次研究还探讨了在大型群体性食草动物已经功能性灭绝的高生产力的亚热带季风草原中建立放牧草地的可能性。在巴尔迪亚地区，无法确定具体有哪些大型群体性食草动物曾在被人类灭绝之前生活在这里。在特拉伊弧景观中，这些大型群体性食草动物是当地宗教的斑牛，或野牛，甚至是印度野牛或水牛。从历史上看，它们的作用类似于家牛和家水牛，而这些动物在该地区成为国家公园后被移除。通过模仿它们的作用，本次研究证明了经常修剪高草以及添加化学肥料可以将氮和磷的浓度提高到中型食草动物的最低维护要求水平以上。管理干预提高的饲料

质量吸引了大量存在的中型食草动物，而由此产生的放牧强度形成了放牧草地。本次研究证明了密集的管理干预和放牧有利于放牧草坪草取代高草。这些结果强调了在高生产力的亚热带季风草地中启动放牧草地所需采用的强化管理方法，进而满足这里的中型食草动物的营养需求。

结论章节综合了研究结果，并讨论了本次研究结果对管理的意义。从实际的保护角度来看，本次研究强调了两个因素的重要性，即（一）干预的空间尺度（干预区域的大小）和（二）干预的频率（每年多次和长年）。这有助于在亚热带季风草地中平衡中型食草动物的捕食风险和资源。干预的频率对于在放牧压力不足的草原系统中维持草地高度和质量至关重要。此外，本次研究还讨论了通过管理干预产生优质饲料后，中型食草动物可能通过幼年个体的存活而呈增长趋势，从而有利于虎的种群动态。目前因为牛或野水牛等大型群体性食草动物的缺失，虎的生存依赖于这些中型食草动物。由于历史资料不足，无法确定哪些野生大型群体性食草动物可能维持了放牧草地从而使鹿类受益。这些可能是斑牛或牛的野生祖先，也可能是野牛。然而，当该地区（巴尔迪亚国家公园）成为保护区时，这些动物的功能角色已被家牛和家水牛所取代。本次研究为改善亚热带季风草原管理以保护虎及其猎物等重点野生动物提供了科学洞察力。综上所述，本次研究强调了在营养贫乏的高草地主导的草原系统中启动放牧草坪所需采用的强化管理方法的必要性。更实用和经济的方法是重新引入野生的大型群体性食草动物（野牛和野水牛）。这些发现的实际应用适用于特拉伊弧景观以及其他亚洲国家的保护区内高生产力的亚热带季风草原管理，同时这些地区也是虎及其猎物的重要的栖息地。

# Summary in Nepali language

## सारांश

### बाघ तथा मृग प्रजातिहरुको संरक्षणको लागि घाँसेमैदान व्यवस्थापन

एसियाको ‘तराई-दुआर सवाना र घाँसेमैदान’ जैकिक विविधताको हिसावले संसारको महत्वपूर्ण घाँसेमैदानको रूपमा चिनिन्छ । कुनै समयमा यी घाँसेमैदानहरू पूर्वमा म्यान्मारदेखि पश्चिममा पाकिस्तानसम्म फैलिएका थिए । तर मानवीय चापका कारण यी घाँसेमैदानहरू हाल नेपाल र भारतका केही संरक्षित क्षेत्रहरूमा मात्र सीमित रहेका छन् । यी घाँसेमैदानहरूको क्षयीकरण सँगै घाँसेमैदानमा आश्रित धेरै प्रजातिका वन्यजन्तुहरूको संख्या र विचरणगर्ने क्षेत्रमा गम्भीर गिरावट आएको छ; जसका कारण त्यस्ता प्रजातिहरू लोप हुने खतरामा छन् । यसका साथै यी घाँसेमैदानहरूको संरचनामा भएको परिवर्तनका कारण पारीस्थितिकीय प्रणाली र घाँसेमैदानको विशेषता र भूमिकामा नकारात्मक प्रभाव परेको छ ।

घाँसेमैदानको गुणस्तर त्यस घाँसेमैदानमा भएका घाँसहरूको उचाइ, बायोमास, डाँठ र पातहरूको अनुपात र घाँसमा पाउने पोषण तत्त्व (जस्तै नाइट्रोजन र फोस्फरस) को मात्राले निर्धारण गर्दछ । घाँस काट्ने, आगो लगाउने जस्ता घाँसेमैदान व्यवस्थापन सम्बन्धी क्रियाकलापद्वारा घाँसेमैदानको गुणस्तरमा वृद्धि ल्याउन सकिन्छ । घाँसेमैदानको गुणस्तरमा वृद्धि भएसगै त्यस्ता घाँसेमैदानमा आश्रित मृगलगायतका अन्य वन्यजन्तुहरू आकर्षित हुन्छन् र निरन्तररूपमा चर्न रुचाउँछन् । यसरी हुने जनावरहरूको चरीचरणको चापले गर्दा घाँसको गुणस्तरमा थप वृद्धि हुन जान्छ र चरिचरण र घाँसेमैदानबीच सकारात्मक चक्रिय प्रणाली स्थापना हुन गई घाँसेमैदानहरूको प्राकृतिक रूपमा नै व्यवस्थापन हुन्छन् तर मृगलगायत ठूला जनावरहरुको संख्यामा ह्रास आएका कारणले त्यस्ता जनावरहरूको प्रयोगमा पनि कमी हुन जाने हुँदा घाँसेमैदानहरू प्राकृतिकरूपमा व्यवस्थापन हुन सकेका छैनन् र घाँसेमैदानको गुणस्तर तथा पारिस्थितिकीय प्रणालीमा नकारात्मक प्रभाव परिरहेको छ ।

यो अध्ययन नेपालको तराई क्षेत्रमा अवस्थित घाँसेमैदानहरूको गुणस्तरको अवस्था र घाँसेमैदान व्यवस्थापन गर्दा के-कस्ता कुरामा ध्यान दिनुपर्छ भनेर गरिएको हो । यो अध्ययन बर्दिया राष्ट्रिय

निकुञ्जमा अवस्थित घाँसेमैदानहरूलाई आधार बनाई गरिएको छ । पहिला, दुई फरक प्रकृतिका घाँसेमैदानहरू - ग्रेजिङ लन (राम्रो चरीचरण भएको क्षेत्र) र अग्ला घाँस भएको घाँसेमैदानहरूको भौतिक तथा रासायनिक विशेषताहरूको तुलना गरियो । ग्रेजिङ लनमा घाँसको भौतिक (जस्तै घाँसको उचाइ, हरिया पातहरूको मात्रा र घनत्व) तथा रासायनिक (जस्तै नाइट्रोजन र फोस्फरसको मात्रा) विशेषताहरूको दृष्टिकोणले उच्च गुणस्तरको रहेको पाइएको छ । घाँस अग्लिँदै र छिप्पिदै जाँदा त्यस्ता घाँसमा पाउने पोषण तत्त्वमा ह्रास आउँछ र मृग प्रजातिका जनावरहरूले त्यस्ता छिप्पिएको घाँस खान रुचाउँदैनन् । साथै छिप्पिएका घाँसहरूबाट मृग प्रजातिका जनावरहरूले आफुलाई चाहिने पोषण तत्त्वको मात्रा प्राप्त गर्न सक्दैनन् । ग्रेजिङ लनमा घाँसहरू मुख्यतया छोटा तथा कलिला अवस्थाका हुन्छन् तथा नाइट्रोजन र फोस्फरसको मात्रा अग्ला घाँसहरूमा भन्दा तुलनात्मक हिसाबले धेरै हुन्छ । फलस्वरूप ग्रेजिङ लनबाट मृग प्रजातिका जनावरहरू मुख्यतय चित्तल, लगुना तथा बाह्रसिंगाहरूले आफूलाई चाहिने पोषण तत्त्व सजिलै प्राप्त गर्न सक्छन् ।

नेपालको तराई क्षेत्रमा अवस्थित घाँसेमैदानको व्यवस्थापन गर्दा आगोको ब्यापकरूपमा प्रयोग हुन्छ । आगो प्रयोग गरी व्यवस्थापन गरिएको घाँसेमैदानहरूको गुणस्तरको अवस्था तथा आगो लगाइएका घाँसेमैदानहरूबाट मृग प्रजातिका जनावरहरूलाई चाहिने पोषण तत्त्वहरुको उपलब्धता सम्बन्धी पनि अध्ययन गरियो । यस अध्ययनले के देखाएको छ भने सुख्खायाममा आगो लगाई व्यवस्थापन गरिएका घाँसेमैदानहरूमा मृग प्रजातिका जनावरहरूलाई चाहिने पोषण तत्त्वहरुको उपलब्धतामा छोटो समयमानै ह्रास आउन जान्छ । गई मृगहरूले त्यसरी आगो लगाई व्यवस्थापन गरिएका घाँसेमैदानहरूको प्रयोगमा कमी आएको पाईयो । यसका अलावा ठूलो क्षेत्रमा आगो लगाउने र आगो लागेको सबै क्षेत्रमा केही समयमा नै एकैपटक घाँसका कलिला पालुवाहरू पलाउने हुनाले मृगहरु छरिएर चर्ने गर्दछन् जसले गर्दा चरीचरनको चापमा कमी हुनगई घाँसहरू अग्ला र छिप्पिंदै जान्छन् र ग्रेजिङ लनहरू क्रमशः अग्ला घाँस भएको घाँसेमैदानमा परिणत हुन्छन् ।

नेपालमा बाघ पाउने संरक्षित क्षेत्रहरूमध्ये बर्दिया राष्ट्रिय निकुञ्जमा बाघको घनत्व सबैभन्दा बढी छ । हाल बाघको मुख्य आहारा प्रजातिमा मृग (चित्तल लगायतका) जनावरहरू पर्दछन् । बाघको संख्यामा वृद्धि भएसँगै चित्तल जस्ता आहारा प्रजातिमा बाघबाट हुने सिकारको जोखिम पनि स्वाभाविकरूपमा नै वृद्धि भएको छ । ‘ल्यान्डस्केप अफ फिएर’ को अवधारणाअनुसार उच्च सिकारको जोखिम भएको क्षेत्रमा गुणस्तरीय खानेकुरा (गुणस्तरीय घाँस) भएतापनि सिकारको

जोखिमका कारण आहारा प्रजातिहरू त्यस्ता क्षेत्रमा विचरण गर्दैनन् । तसर्थ प्रयोगात्मक विधिबाट घाँसेमैदान व्यवस्थापन गर्दा ‘ल्यान्डस्केप अफ फिएर’ को अवधारणालाई कसरी अनुसरण गर्न सकिन्छ भनेर अध्ययन गरिएको छ । यस अध्ययनअनुसार घाँसेमैदान व्यवस्थापनको उपयोगिता व्यवस्थापन गरिएको क्षेत्रफलले निर्धारण गर्ने रहेछ । नेपालका तराई क्षेत्रको घाँसेमैदानहरू बाघको महत्त्वपूर्ण बासस्थानको रूपमा समेत चिनिन्छन् । अग्ला घाँसहरूमा बाघ सजिलै लुक्न सक्ने भएकाले अग्ला घाँसेमैदानहरूले बाघलाई सिकार गर्न उपयुक्त वातावरण प्रदान गर्दछ । तसर्थ यदि स-साना क्षेत्रफलमा घाँसेमैदान व्यवस्थापन गरियो भने वरपर भएका अग्ला घाँसहरूले गर्दा चित्तलजस्ता आहारा प्रजातिहरुले असुरक्षित महसुस गरी त्यस्ता क्षेत्रमा कम विचरण गर्दछन् र व्यवस्थापनका कार्यले सोचेअनुरूप उपलब्धि हासिल गर्न सक्दैन । त्यस्तै यदि ठूलो क्षेत्रफलमा व्यवस्थापनका कार्य गरियो भने चित्तलजस्ता आहारा प्रजातिहरुले बाघबाट त सुरक्षित महसुस गर्दछन् तर घाँसेमैदानलाई चाहिने मात्रामा चरीचरणको चापमा कमि हुन गई छोटा घाँसहरू छिटै अग्ला घाँसहरूमा परिणत हुन्छन् र चित्तल लगायत अन्य मृग प्रजातिहरूलाई चाहिने पोषण तत्त्वको उपलब्धतामा कमी हुन जान्छ । यसका अलावा ठूलो क्षेत्रफलमा अग्ला घाँसहरू हटाउँदा त्यस्ता क्षेत्र खुला हुने र सिकार गर्न प्रयासरत बाघलाई चित्तलजस्ता आहारा प्रजातिहरूले टाढैबाट ठम्याउने र सुरक्षित स्थानतर्फ भाग्न सफल हुने भएकाले बाघ संरक्षणको दृष्टिकोणबाट धेरै ठूलो क्षेत्रफलमा गरिएको व्यवस्थापन कार्य सोचेअनुरूप फलदायि नहुने देखिन्छ । त्यसैले घाँसेमैदान व्यवस्थापनगर्दा दुबै बाघ र चित्तल जस्ता आहारा प्रजातिलाई उपयुक्त हुने र चरिचरण र घाँसेमैदानबीच सकारात्मक चक्रीय प्रणाली स्थापना हुने गरी व्यवस्थापन गरिएको खण्डमा त्यस्ता कार्यले सोचेअनुरूप उपलब्धि हासिल गर्न सक्दछ ।

यसबाहेक, घाँसेमैदानहरूमा ग्रेजिङ लनहरू स्थापना गर्न सकिन्छ कि सकिँदैन भनेर पनि अध्ययन गरिएको छ । बर्दिया राष्ट्रिय निकुञ्ज स्थापना हुनुपूर्व सन् १९७० को दशकतिर हजारौँको संख्यामा गाईवस्तुहरु चरीचरण गर्थे र स्थानीय जनताले पनि ठूलै परिमाणमा खरघाँस काटेर लग्दथे, जसका कारण घाँसेमैदानहरू नियमित रूपमा परम्परागत तरिकाले नै व्यवस्थापन भइरहेका हुन्थे । तर निकुञ्जको स्थापनापछि गाईवस्तुहरु चरिचरणमा रोक लगाइयो र खरघाँस काटेर लग्ने चलनमा क्रमशः कमी आयो र बिस्तारै ग्रेजिङ लनहरू अग्ला घाँसेमैदानहरूमा परिणत भए । अग्ला घाँसहरू वर्षमा कम्तीमा तीनपटकसम्म काट्ने र रासायनिक मल थप्ने जस्ता व्यवस्थापनका क्रियाकलापले घाँसमा नाइट्रोजन र फस्फोरसको मात्रा चित्तलजस्ता मृग प्रजातिहरूलाई आवश्यक पर्ने न्यूनतम

मात्राभन्दा माथि बढाउन सकिन्छ भनेर यस अध्ययनले देखाएको छ। घाँसको गुणस्तरमा वृद्धि भएसँगै चित्तललगायत अन्य मृग प्रजातिहरु - लगुना तथा बाह्रसिंगाहरू त्यस्ता क्षेत्रतर्फ आकर्षित हुन्छन् र परिणामस्वरूप चरीचरणको चापले ग्रेजिङ लनहरू बन्न सुरु हुन्छ तर त्यसरी बनेका ग्रेजिङ लनहरूमा यदि चरिचरणको चाप कम भएमा पुनः अग्ला घाँसेमैदानमा परिणत हुन्छन्। तसर्थ नियमित तथा इन्टेन्सिभरूपमा घाँसेमैदानहरू व्यवस्थापन गरिएको खण्डमा ग्रेजिङ लनहरू निर्माण गर्न सकिन्छ भनेर यस अध्ययनको निष्कर्ष रहेको छ।

अन्तमा, यस अध्ययनबाट प्राप्त नतिजाहरूको संश्लेषण गरी प्राप्त निष्कर्षहरूको व्यावहारिक पक्षबाट विश्लेषण गरिएको छ। संसारभर महत्त्व राख्ने तराई-दुआर सवाना र घाँसेमैदानहरूको संरक्षण तथा व्यवस्थापनको परिप्रेक्ष्यबाट यस अध्ययनमा दुई महत्त्वपूर्ण तत्त्वहरुलाई जोड दिईएको छ (१) व्यवस्थापनका लागि छुट्ट्याइएको क्षेत्रफल - कति ठूलो वा कति सानो र (२) कुन वा कति हदसम्म - वर्षमा कति पटक सम्म अग्ला घाँसहरू काट्ने। माथि उल्लेख गरे अनुरूप उचित क्षेत्रफल निर्धारण गरी त्यस क्षेत्रमा वर्षमा कम्तीमा तीन पटक सम्म नियमितरूपमा अग्ला घाँसहरू काटेको खण्डमा चरिचरण र घाँसेमैदान बीचमा सकारात्मक चक्रीय प्रणाली स्थापना हुन गई ग्रेजिङ लनहरू  निर्माण हुन्छन्। यसबाहेक, यस शोधपत्रमा गुणस्तरीय घाँसको उपलब्धताले गर्दा चित्तललगायत अन्य मृग प्रजातिहरूको संख्यामा वृद्धि भई बाघ संरक्षणमा महत्त्वपूर्ण भूमिका खेल्दछ भनेर तर्क गरिएको छ। यसरी वैज्ञानिक तरिकाबाट घाँसेमैदानहरूको व्यवस्थापन गरिएको खण्डमा बाघ तथा आहारा प्रजातिहरूको को संरक्षणका साथसाथै बढ्दो मानव-वन्यजन्तु द्वन्द्वलाई पनि न्यूनीकरण गर्न सकिन्छ भनेर पनि तर्क गरिएको छ। अन्तमा, बाघ पाइने एसियाका संरक्षित क्षेत्रहरूका घाँसेमैदानहरूको व्यवस्थापनमा यस अध्ययनबाट प्राप्त निष्कर्षहरू व्यावहारिक रूपमा प्रयोगमा ल्याएको खण्डमा घाँसेमैदानहरूको संरक्षणका साथसाथै घाँसेमैदानमा आश्रित बाघ तथा आहारा प्रजातिहरुको समेत दीर्घकालीन संरक्षण गर्न सकिन्छ।

धन्यवाद।

श्याम कुमार थापा
अनुसन्धानकर्ता

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# About the Author

Shyam Kumar Thapa was born on 5 May 1978 in Nepal. In 1990 he obtained his school leaving certificate (SLC) from Arniko Secondary Boarding School, Nepal. After SLC, he completed an intermediate in science degree (I.Sc.) with biology as a major subject. Subsequently, he earned a B.Sc. (Hons.) in environment science from Kathmandu University and completed his M.Sc. in environment science from the same university in 2004.

Shyam got his first opportunity to work as a conservationist in the position of field officer at Bardia National Park, Nepal in 2007. During his tenure as a field officer, he worked closely with park management and the local community living adjacent to the park. In 2012, he joined the National Trust for Nature Conservation (NTNC), a national not-for-profit autonomous organisation dedicated to working in the field of nature conservation in Nepal. During his tenure, he gained valuable experience and knowledge in ecological research and was actively involved in wildlife research and monitoring.

In 2016, to pursue a PhD with the Wildlife Ecology and Conservation (WEC) group (then Resource Ecology Group), he enrolled in a pre-PhD course, where he took various courses to further enhance his knowledge on wildlife ecology and ecological methods. After being formally admitted as a PhD candidate of WEC in 2017 he spent four years in the field and undertook both his PhD and his full-time job as a conservation officer at NTNC. In December 2020, he was transferred to NTNC head office in Kathmandu, and in May 2023, he was promoted to Senior Conservation Officer and given responsibility of focal person of ecological research unit within NTNC.

# List of publications:

## Peer-reviewed Journals

**Shyam Kumar Thapa**, Joost F. de Jong, Anouschka R. Hof, Naresh Subedi and Herbert H.T. Prins, Enhancing subtropical monsoon grassland management: Investigating mowing and nutrient input effects on initiation of grazing lawns, *Global Ecology and Conservation*, (2023). doi:https://doi.org/10.1016/j.gecco.2023.e02686

**Thapa, S. K.,** de Jong, J. F., Hof, A. R., Subedi, N., Joshi, L. R., & Prins, H. H. T. (2022). Fire and forage quality: Postfire regrowth quality and pyric herbivory in subtropical grasslands of Nepal. *Ecology and Evolution*, 12, e8794. https://doi.org/10.1002/ece3.8794.

**Thapa, S. K.,** de Jong, J.F., Subedi, N., Hof, A.R., Corradini, G., Basnet, S., Prins, H.H.T., (2021). Forage quality in grazing lawns and tall grasslands in the subtropical region of Nepal and implications for wild herbivores. *Glob. Ecol. Conserv.* 30, e01747. https://doi.org/10.1016/j.gecco.2021.e01747

Lamichhane, B. R., Lamichhane, S., Regmi, R., Dhungana, M., **Thapa, S. K.**, Prasai, A., Gurung, A., Bhattarai, S., Paudel, R. P., & Subedi, N. (2021). Leopard (Panthera pardus) occupancy in the Chure range of Nepal. *Ecology and Evolution*, 11, 13641–13660. https://doi.org/10.1002/ece3.8105

Fitzmaurice, A., P. Poudel, S. Offord-Woolley, D. Macdonald, **S. Thapa**, B. R. Lamichhane, A. Baral, and B. P. Yadav. Complex consequences of conservation success: Emerging human-tiger conflicts in Nepal. *CatNews*.

# PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

**Review/project proposal (4.5 ECTS)**

- Grazing lawns and herbivore foraging behaviour

**Post-graduate courses (10 ECTS)**

- Multivariate analysis; PE&RC (2020)
- Introduction to zero inflated GLMs and GLMMs with R; PE&RC (2021)
- Tidy data transformation and visualisation with R; PE&RC (2021)
- Linear models; PE&RC (2021)
- Essentials of modelling; PE&RC (2023)
- Insects and ecosystem services what's bugging you; PE&RC (2023)
- National tiger workshop; Bardia National Park, Nepal (2023)

**Deficiency, refresh, brush-up courses (6 ECTS)**

- Animal nutrition & physiology; WUR (2023)

**Laboratory training and working visits (2 ECTS)**

- Grass nutrient analysis; Kathmandu University, Nepal; Nepal Agriculture and Research Centre, Nepal (2018, 2020)

**Invited review of journal manuscripts (1 ECTS)**

- PeerJ Life & Environment: factors affecting crop field use by Blackbuck in Krishnasaar conservation area, Nepal (2023)

**Competence strengthening/skills courses (2.3 ECTS)**

- Research data management; PE&RC (2018)
- Writing grant proposal; WUR Library (2020)
- Writing propositions for your PhD; WUR Library  (2021)

**Scientific integrity/ethics in science activities (0.6 ECTS)**

- Scientific integrity; PE&RC (2018)

**PE&RC Annual meetings, seminars and the PE&RC weekend (0.6 ECTS)**

- PE&RC Last year's retreat (2023)

**Discussion groups/local seminars or scientific meetings (5.2 ECTS)**

- Landscape dynamics; WUR, the Netherlands (2018)
- Warden seminar; oral presentation; Kathmandu, Nepal (2018)
- Conference: prey base of tigers in Bardia National Park; oral presentation; Kathmandu, Nepal (2021)
- R Users group; WUR, the Netherlands (2022)
- Third Asian elephant range states meeting; Kathmandu, Nepal (2022)

**International symposia, workshops and conferences (3.1 ECTS)**

- Save the tiger; oral presentation; NWO funded project (2022)
- 59th Annual meeting of the association for tropical biology and conservation; Coimbatore, India (2023)

**Societally relevant exposure (1.3 ECTS)**

- Training to rangers and officers of national parks on grassland management for herbivores; Himalayas, Nepal (2022)
- Guest lecture habitat management for conservation of tigers; Himalayas, Nepal (2022)

**BSc/MSc thesis supervision (2 ECTS)**

- Quality of forage for deer in Bardia National Park, Nepal