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Ecology of Chital Deer in North Queensland

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Statement of the Contribution of Others

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Chapter Details

Chapter Number	Details of chapter	Nature and extent of the contribution of each author to the chapter
2	Kelly, C.L., Schwarzkopf, L., Gordon, I.J. & Hirsch, B. (2021) Population growth lags in introduced ungulates. *Ecology and Evolution* 11(9): 4577-4587	The authors co-developed the topic of this paper. CK reviewed the literature, conducted analyses, and lead the writing of the paper. All authors contributed critically to drafts and gave final approval for publication.

3	Kelly, C.L., Schwarzkopf, L., Gordon, I.J., Pople, A. & Hirsch, B. (2021) Proximity to water and soil mineral content determine habitat selection of invasive chital deer. *Under consideration Austral Ecology*	CK, TP, and BH co-developed the research question. CK collected and analysed the data and lead the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.
4	Kelly, C.L., Schwarzkopf, L., Gordon, I.J., Pople, A., Kelly, D.L. & Hirsch, B.T. (2021) Reproductive asynchrony of the sexes in introduced Australian chital deer. *Under consideration Oecologia*	CK, LS, IG, TP, and BH developed the research question. TP and CK collected the data. DK generated equations to model foetal growth parameters. CK analysed the data and lead the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.
5	Kelly C.L., Gordon, I.J., Schwarzkopf, L., Pintor, A., West, P., & Hirsch, B.T. Wild deer exhibit environmental niche shifts in Australia: where to from here? – *manuscript in preparation*	CK, LS, BH, and IG developed the research question. AP conducted modelling of habitat suitability. PW provided dataset of deer records in Australia. CK modelled niche shifts and analysed the data and lead the writing of the manuscript. All authors contributed critically to drafts.

Ethics Declaration

I have been supported by the Australian Postgraduate Award, courtesy of the Australian Government throughout my candidature. My research funds were provided by the Department of Agriculture and Fisheries, and the Sport Shooters Association of Australia Bursary Grant. In Chapter Four (Reproductive asynchrony in Australian chital deer: implications for adaptation to climate change), the **c**ulls were funded by an Australian Government grant to the North Queensland Dry Tropics Natural Resource Management group (NQ Dry Tropics) as part of a drought assistance program. Because chital deer are legally declared a pest animal (Queensland's Biosecurity Act 2014), no permits were required for culls on private lands.

All data were collected within the guidelines for the ethical treatment of animals and approved by the Department of Agriculture and Fisheries and James Cook University (Ethics permit number: SA 2014/07/475; animal ethics permit #A2448, respectively).

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. The template and methodology for this survey was approved by the Human Ethics Committee of James Cook University (approval number: H7666).

Abstract

Invasive species are a leading cause of biodiversity loss worldwide. Deer have been introduced to environments around the world, and many species have gone on to become invasive. Feral deer potentially compete with native species and livestock, pose risks to vehicles or by acting as vectors of disease, as well as contributing to economic and social losses. Presently there are six free-living deer species in Australia: chital (*Axis axis*), fallow (*Dama dama*), hog (*Axis porcinus*), red (*Cervus elaphus*), rusa (*Rusa timorensis*), and sambar (*Rusa unicolor*). Four chital deer were liberated on Maryvale Station in Northern Queensland in 1886 and since then, the number and range of chital deer has slowly increased. It is unknown whether factors, such as how they select and use habitat as well as the cues that drive their reproduction, have contributed to their delayed growth and sudden range and population increase. Considering the broad economic and environmental impact chital could have on this region, understanding their ecology is critical to developing more effective management and control strategies, as well as predicting where these feral species are likely to spread next.

I investigated aspects relating to the past, present, and future of chital deer in Australia. First, I aimed to determine if introduced ungulate populations can exhibit prolonged lags in population growth, and then sought to identify the factors that contributed to their delayed population growth and spread. Data were collected from the literature on 36 different introduced ungulate populations of 25 species from around the world. I found that chital (along with 16/36 other introduced ungulate populations from across the world that were examined) exhibited a prolonged lag phase. I also found that no variables that were examined contributed to either the occurrence or the length of prolonged lags. While ungulates may exhibit prolonged lags in population growth, the factors that may cause lags are idiosyncratic. Simply because an introduced population is present in low numbers now does not mean that it will remain that way in the future and managers should be cautious of the potential of these sleeper species.

Secondly, I aimed to identify the environmental features that influence habitat selection on a fine and a broad scale to determine how chital deer distribute themselves in the landscape. For fine scale selection I used camera traps on a property in Charters Towers, and to investigate broad scale landscape use, I used a regional survey. I found that chital habitat selection and landscape use was positively correlated with proximity to water and soil phosphorus content, as well as negatively correlated with soil sodium content on both scales that were examined. This implied that these features were fundamentally important to how chital select and use habitat. It should be areas that possess these features that should be the focus for management and control as it is this favourable habitat that is the most vulnerable to invasion of chital deer.

Thirdly, as reproductive patterns may contribute to population growth rates, I aimed to determine the cues that drive reproductive activity in male and female chital deer. To investigate patterns of seasonality in male and female chital deer, I used data collected on male and female reproductive state to generate observed measures of reproductive activity. I found that while male and female chital deer exhibit seasonal patterns of reproduction, the cues that drive male and female reproduction are not only different, but they are out of sync. Male chital reproduction in this system is driven by day length, while female reproduction is driven by rainfall, the timing of which varies from year to year. This has two significant potential implications. First, differing cues that drive male and female reproduction may alter selection pressure on males to follow cues that trigger female reproduction. Secondly, increasing mismatch between males and females increases the reproductive skew of that population by reducing the overlap between mate availability. While this may not be detrimental to an invasive species, uncoupling reproductive systems and the associated increase in reproductive skew could have serious consequences in native populations that may be unable to adapt.

Finally, I used these data to examine niche shifts in the six established deer in Australia, and then map areas vulnerable to future spread. To investigate niche shifts, I collected international

occurrence records for the six feral deer species in Australia and identified 16 environmental variables as potentially important predictors of abundance. Five of the six deer species (hog, fallow, red, rusa, and sambar deer) exhibited niche shifts between international and Australian ranges. When examining habitat suitability, chital deer had the largest area of potential spread outside of presently occupied habitat. Of the six species, three (fallow, red, and sambar deer) have already expanded beyond ranges that would be predicted to be suitable. Here, I demonstrated that deer, like other invasive species, are highly adaptable and can shift niches following invasion, thus highlighting the ability of invasive species to spread beyond areas that would be predicted to be suitable.

My research demonstrates the importance of understanding invasive species ecology, particularly when that species remains in low abundance for an extended period of time. The factors that influence how an invasive species grows and spreads are idiosyncratic and are, therefore, very difficult to predict. This research highlights how adaptable invasive species can be, and, therefore, emphasizes the importance of understanding these species for more effective pre-emptive control and management.

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(drawing by author)

Chapter One: Introduction

Invasive species are a major factor causing environmental change, damaging habitats and ecosystems, contributing to the extinction of native flora and fauna, and facilitating subsequent invasions (Holdaway 1989; Walker & Steffen 1997; Didham et al. 2005; Arim et al. 2006; Woinarski et al. 2015). Invasive species are recognised as a major threat to global biodiversity, second in severity only to habitat loss and fragmentation (Walker & Steffen 1997; Crooks & Soule 1999; Sakai et al. 2001).

Human-assisted movement has facilitated the spread of non-native species to ecosystems around the world (King 2005; Hulme et al 2008). As such, many species have been moved to, and subsequently established in, areas that previously were inaccessible (Tingley et al. 2014; Hernandez et al. 2018; Da Re et al. 2020). Many invasive species, in particular invasive mammals, were introduced for the purposes of food and game resources (Forsyth & Hickling 1998; Ikagawa 2013), although pest control and aesthetic introductions were also common (McNeely 2001; Shine et al. 2010; Kannan et al. 2014).

Aspects of a species' ecology, including habitat selection, reproductive behaviour, or habitat suitability, may be influenced by different factors in a species' novel range compared to their native range (Hejda et al. 2015). A species' biotic and abiotic interactions may be different in a new environment, and therefore different aspects of that species' ecology may change in its invaded range (Fitzpatrick et al. 2007; Morehouse & Tobler 2013; Parravincini et al. 2015). Management of invasive species often relies on an understanding of the species' ecology; i.e., invasive species management is typically focused in areas where density is the highest, or designed to remove a species' access to critical resources such as water, or both (Underhill et al. 2007; Florance et al. 2011; Letnic et al. 2015. Similarly, managers can use information on the ecology of these species to help determine areas vulnerable to invasion in the future. Thus, understanding the ecology of different pest species, and how they react in novel environments, is integral to present and future management.

Deer have been introduced around the world and many have gone on to become invasive (Bentley 1967; Fraser 1996; Hudson & Jeon 2003; King 2005; Fautley et al. 2012). Like many invasive species, deer have the capacity to have severe negative impacts on ecosystems through habitat degradation and competition with native species (Doran & Laffan 2005; Dolman & Waber 2008; Ens et al. 2016; Hess 2016) as well as negative economic impacts, e.g., spreading of livestock disease and parasites, competing with livestock for feed, and posing risks to motor vehicles (Jesser 2005; McLeod 2009; Kusta et al. 2017).

Deer (family Cervidae) have been widely introduced outside of their native ranges, including in Australia (Davis et al. 2016). Prior to European settlement in 1788, Australia possessed an assemblage of native mammals, namely monotremes, marsupials, and eutherians (Woinarski et al. 2015). European arrival brought with it 25 species of introduced mammals including rodents, rabbits, feral dogs, cats, foxes, and ungulates (Wilson et al. 1992). Ungulates made up 14 of the introduced species that successfully established in Australia (Forsyth et al. 2004). Of the 29 species and subspecies of deer that were brought to Australia, six species successfully established: chital deer, fallow deer, red deer, sambar deer, rusa deer, and hog deer (Bentley 1967; Moriarty 2004). These species pose not only environmental risks, but also risks to agriculture and infrastructure.

A deer species of particular concern in Australia, is the Chital deer (otherwise known as axis or spotted deer; *Axis axis*), which is a medium-sized cervid native to India, Sri Lanka, Bangladesh, and Nepal (Chapple 1989). Males weigh between 68 and 82 kg and stand approximately 940 mm at the shoulder. Females are smaller and weigh approximately 50kg and are approximately 760mm at the shoulder (Graf & Nichols 1966; Bentley 1967; King 2005). Stags, like most tropical deer, have three-tined antlers on a long upright beam (55-70cm).

Chital were initially introduced to Australia for farming in Bathurst, New South Wales in 1803 (Moriarty 2004). In 1886, four chital deer were liberated on Maryvale Station, Queensland (Figure 2). Their spread was initially slow, but has increased in recent years, and they have since been declared a restricted invasive animal under the Biosecurity Act 2014 (Brennan & Pople 2016). Considering the broad economic and environmental impact chital deer could have on this region, understanding their ecology is critical to developing effective management and control strategies, and to predicting where these feral species are likely to spread next.

Thesis structure and overview

This thesis aims to investigate the ecology of invasive chital deer in North Queensland. It is split into a series of questions structured as publications that each investigate an aspect of chital deer ecology. In Chapter Two, I reviewed population growth rates of introduced ungulates around the world using records from the literature of ungulate introductions and subsequent population size, to compare them with chital population growth rates, to determine if chital deer population growth lagged compared to other introduced deer.

In Chapter Three, I examined habitat selection and landscape use of chital deer in North Queensland, Australia. I examined the relationship between chital abundance and environmental variables at two scales, local and regional, using a camera trap study and a regional survey, respectively. These data allowed me to determine the environmental factors related to chital population success at two different scales.

In Chapter Four, I examined reproduction in chital from North Queensland. Chital reproduction is not strongly seasonal in their native range, so I used chital deer in North Queensland as a study system to compare the relative seasonality of male and female reproduction using physiological data collected from culls, camera traps, and incidental observations.

In Chapter Five, I investigated niche shifts, and predicted the potential future spread of the six deer species in Australia using both international and Australian occurrence records.

The sixth and final chapter summarises the results from previous chapters including conclusions and suggestions for future research.

Chital deer stag

(drawing by author)

Chapter Two: Population growth lags in introduced species

Adapted from: Kelly C.L., Schwarzkopf, L., Gordon, I. J. & Hirsch, B. (2021) Population growth lags in introduced species. *Ecology and Evolution* 11(9): 4577-4587

Introduction

Non-native species have been introduced worldwide and often demonstrate rapid population growth post-release (Chollet et al. 2015; Froese et al. 2017; Ikagawa 2013). Many introduced species threaten their introduced environments by competing directly and indirectly with native species for food and water (Dolman & Waber 2008; Witte et al. 2010), consuming native species (Angel et al. 2009; Cole & Litton 2014; Innes et al. 2010; Kardol et al. 2014), and spreading disease (Crowl et al. 2008; Strickland et al. 2015).

After a species is introduced to a non-native environment, its population may increase rapidly. Even in these species, a time delay between the introduction of a species to a new area and rapid population growth normally exists (Binggeli 2001; Kowarik 1995). Crooks and Soule (1999) defined this delay as an ‘inherent lag,’ or the normal early period of exponential growth that occurs before the inflection point in the curve of population growth. Prolonged lag phases occur when a species persists in an environment in low numbers for an extended period (Daehler 2009; Rilov et al. 2004). There are two basic types of lags: lags in population growth and lags in population spread, although the two can appear synonymous (Crooks & Soule 1999). To determine whether a lag is ‘prolonged’ (i.e., an extended period of even slower growth than that predicted from exponential growth, which occurs prior to a marked increase in the rate of growth (Aagaard & Lockwood 2014; Crooks 2005), it is necessary to determine whether the observed lag is longer than the inherent lag. I follow these definitions and statistically distinguish between natural exponential population growth and prolonged lags (Aikio et al. 2010; Crooks 2005; Crooks & Soule 1999; Sakai et al. 2001) for ungulate species introduced into non-native ranges.

Prolonged lags can be distinguished using models of expected growth, which can be compared with the observed pattern of growth. If the observed rate of population growth is much lower than predicted in the expected growth model, then the population is experiencing a prolonged lag (Crooks 2005; Hengeveld 1989). Although the idea that a population might experience lag phases longer than those dictated by exponential growth has been recognized for many years, most studies have not tested whether prolonged lags (*sensu stricto*) have occurred (cf., Aagaard & Lockwood 2014; Aikio et al. 2010). Additionally, previous studies that have investigated prolonged lags have focused primarily on invertebrate and plant populations, with little attention given to introduce vertebrates (cf., Aagaard & Lockwood 2014).

A number of factors may influence the length of lag phases in population growth, such as changes in environmental conditions, behavioural plasticity, genetic adaptation, or changes in interactions between the invading species and their surrounding environment (Crooks & Soule 1999; Rilov et al. 2004; Wang & Wang 2006; Witte et al. 2010). There are also lags in the detection of invasive species that can provide incorrect information on initial population growth (e.g., invaders could be present in low numbers before first being detected; Crooks & Soule 1999). Any one, or all of these factors, may impact the population growth of invasive species to different degrees, although this appears to be largely unpredictable (Mack et al. 2000). For example, croton weed (*Areratina adenophora*) is invasive in China and exhibited a lag phase of 20 years before suddenly expanding throughout southern China, potentially due to favourable environmental conditions (Wang & Wang 2006). In invaded regions with favourable conditions for growth, *A. adenophora* has expanded its range at a rate of 20 km/year. In contrast, in less favourable areas, it expanded much more slowly (3.7 km–9.8 km/year). Environmental factors such as rainfall and temperature may also have influenced range expansion both positively and negatively in different areas (Wang & Wang 2006), but little is known about the influence of the environment on the initial population growth of introduced species.

The factors that cause prolonged lag phases, or a species' release from them, may be idiosyncratic and vary among species and populations (Aagaard & Lockwood 2014; Larkin 2012). A wide range of changing interactions between invading species and the surrounding biotic and abiotic environment could potentially enhance the fitness of an invasive species, triggering an increase in its population growth (Crooks & Soule 1999; Rilov et al. 2004; Witte et al. 2010). A species could also increase rapidly following the emergence of new mutations and genotypes more suitable to the new environment (Crooks 2005; Mack et al. 2000). Similarly, an expanding invasive species that suddenly experiences favourable environments may exhibit sudden, rapid population growth, after a period of prolonged lag (Crooks 2005). The Eurasian collared dove (*Streptopelia decaocto*) spreading through Syria and Turkey in the 16th century exhibited a lag phase of approximately 200 years (Crooks & Soule 1999). Its sudden range expansion was attributed to changes in climate, and to an increase in the availability of human-altered environments (Crooks & Soule 1999; Fujisaki et al. 2010; Romagosa & Labisky 2000). Similarly, the fire-adapted heath banksia (*Banksia ericafolia*), introduced to South Africa, remained in a lag phase for over 40 years until several fires caused a sudden and rapid increase in its abundance (Geerts et al. 2013).

Understanding a population's initial growth phase and trying to clarify potential causes of prolonged lags is critical for designing and implementing management strategies for extermination. To determine which populations lagged for periods longer than the inherent lag phase, and to discern which factors may cause prolonged lags in population growth, I used ungulates as a model system. Ungulates have been widely introduced to environments around the world, primarily as a game or food resources, and can be extremely damaging as invasive species (Cote et al. 2004; Forsyth & Hickling 1998; Hernandez et al. 2018; Ikagawa 2013; Riney 1964). Their well-documented introduced populations provide an opportunity to investigate rates of growth post-release in several environments and conditions. Typically, introduced ungulate populations increase rapidly postliberation, usually exceeding their carrying capacity, after which their populations crash (e.g., reindeer *Rangifer* sp.; Scheffer 1951; Riney 1964; Klein 1968). Most population studies of ungulates have focused on investigating the factors causing the crash phase of population growth, while the initial growth phase is often neglected (Forsyth & Caley 2006; Kaji et al. 2004; Riney 1964).

In this study, I used abundance data to (a) distinguish inherent from prolonged lags in published studies of the population growth of introduced ungulates and (b) determine which environmental or life-history factors might have affected the length of the lag phase, or if lag phases are idiosyncratic (i.e., that the factors that influence population growth varied among species and populations). I selected a range of environmental variables that may have contributed to the population growth of introduced species. This included rainfall metrics (total annual rainfall, intra-annual rainfall variance, and the length of the dry season), location information (temperate or tropical environment, island or mainland environment, average annual temperature), and other factors including gestation period, presence of interspecific relationships (predators or competitors), and if the population was reported to be subject to hunting pressure. While all these variables may influence population growth, I thought several would contribute to the occurrence and length of prolonged lags. Considering the environmental conditions that typically reduce reproductive output and mortality in ungulates, I predicted that species with long gestation periods living in areas with more competitors and longer dry seasons would be more likely to exhibit prolonged lags (Coe et al. 1976; Fryxell et al. 1988; Garel et al. 2004). In contrast, I expected species with shorter gestation periods, introduced to areas with no native competitors, and consistent rainfall throughout the year would exhibit earlier, faster population growth.

Methods

I used data from 33 published studies of 25 introduced ungulate species, and 36 populations (Table 2.1). To locate relevant literature, I searched the James Cook University library digital database (https://www.jcu.edu.au/library) and Google Scholar (https://scholar.google.com/) using the following terms: “introduced,” “invasive,” “feral,” “non-native,” “exotic,” “population,” and/or “introduction” followed by “ungulate” or a family name such as “cervid” or “deer.” The reference lists in each publication were checked for any additional publications not on my list. In some cases, publications alluded to, but did not specifically reference an introduced population. In these cases, a specific search was performed. Populations of liberated domestic species were excluded. Studies were retained for analysis if they included information on the founding population size, an estimate of the period of population growth, and a population size at a later date. Studies were also only included when they described a novel introduction or colonization. Populations that were reintroductions to previously inhabited areas were excluded. Many of the studies included here (n = 28) only had two population estimates: the initial size of the founding population and the population size at one point later in time. Populations in this analysis were isolated from other introduced populations so counts could not have been influenced by immigration or emigration. I determined gestation period, age at sexual maturity, maximum number of offspring produced per year, and average maximum age (i.e., adult survival) in the wild for each species for which population data were available (Table 2.1). Where available, I used data specific to each introduced population (i.e., the same data as listed above but specific to each introduced population). In some cases (n = 21), there were insufficient life-history data available for the introduced population, so information from another population in the species' native range was used.

Table 2.1. List of species included in this study

Life history source references: a. Gunn (2016), b. Santiago-Moreno et al. (2005), c. Tomich (1969), d. Robinette et al. (1973), e. Festa-Bianchet (2008), f. Hoffmann et al. (1978), g. McCullough et al. (2009), h. Hedges et al. (2008), i. King (2005), j. Kekkonen et al. (2016), k. Abaigar et al. (2012), l. Asher et al. (1988), m. Garel et al. (2005), n. Riveros et al. (2015), o. Dieckmann et al. (1980), p. Leslie (2011), q. Graf & Nichols (1966), r. Chapple (1989), s. Lauer et al. (1999), t. Boulton & Freeland (1991), u. Pople & McLeod (2010), v. Dubost et al. (2011), w. Bradshaw & Brook (2007)

Species (source)	Location	Growth Period	Initial number	Surveyed number	Weather data source	Life history sources
Rangifer tarandus (St Matthew) (1)	Alaska	19	29	6000	NOAA	a
Rangifer tarandus (Grande-Terre) (2)	Kerguelen Isl.	16	7	2000	MET Office	a
Ovis gmelini musimon (2)	Kerguelen Isl.	12	2	100	MET Office	b
Rangifer tarandus (St George) (3)	Alaska	11	15	222	NOAA	a
Rangifer tarandus (Haute) (2)	Kerguelen Isl.	15	3	115	MET Office	a
Antilocapra americana (4)	Hawai'i	7	38	250	NOAA	c
Odocoileus hemionus (5)	USA	17	22	2000	NOAA	d
Ovis Canadensis (6)	Mexico	18	16	700	CICESE	e
Capreolus capreolus (7)	Germany	20	8	550	Deutscher Wetterdienst	f
Cervus nippon (8)	Japan	12	54	592	Japan Meteorological Agency	g
Cervus timorensis (9)	Australia	21	7	850	Bureau of Meteorology	h
Cervus unicolor (10)	New Zealand	24	2	100	NIWA	i
Odocoileus virginianus (11)	Finland	27	5	1000	Finnish Meteorological Institute	j
Ammotragus lervia (12)	Spain	19	34	2000	Murcia MET	k
Rangifer tarandus (St Paul) (3)	Alaska	27	25	1943	NOAA	a
Ammotragus lervia (13)	USA	10	85	500	NOAA	k
Ovis gmelini (14)	Hawai'i	30	11	2500	NOAA	c
Dama dama (15)	USA	20	28	550	NOAA	l
Ovis gmelini (16)	Canary Isl.	22	11	400	Murcia MET	m
Lama guanicoe (17)	Falkland Isl.	17	15	275	Climate Research Unit	n
Oryx gazella gazelle (18)	USA	24	95	3500	NOAA	o
Ammotragus lervia (16)	Canary Isl.	18	16	250	Murcia MET	k
Rangifer tarandus (19)	South Georgia Isl.	42	10	3000	World Weather Online	a
Rusa timorensis (20)	New Caledonia	70	12	200000	World Weather Online	p
Cervus nippon (21)	USA	42	5	300	NOAA	g
Axis axis (15)	USA	28	36	461	NOAA	q
Hemitragus jemlahicus (22,23)	New Zealand	46	21	710	NIWA	**j**
Axis axis (24,25)	Australia	130	4	44000	Bureau of Meteorology	r
Axis axis (26)	Hawai'i	98	8	6000	NOAA	q
Oreamnos americanus (27)	USA	44	170	2355	NOAA	s
Bubalus bubalis (28)	Australia	142	80	340000	Bureau of Meteorology	t
Camelus dromedarius (29)	Australia	84	4500	600000	Bureau of Meteorology	u
Odocoileus virginianus (30)	Canada	120	220	160000	Government of Canada	j
Hydropotes inermis (31)	England	96	19	4000	MET Office	v
Bos javanicus (32)	Australia	158	20	10000	Bureau of Meteorology	**w**
Cervus nippon (33)	Poland	29	54	121	TuTiempo	g

To create a model of population increase for unrestricted growth, exponential models were generated using the founding population size, average maximum age in the wild, average number of offspring produced by each female per year, average age at sexual maturity, and assuming equal sex ratios. It was these models that were used to calculate the population sizes under exponential growth, and later used to calculate the doubling time assuming exponential growth.

I compared empirical measures of population growth rates with my estimates of maximum possible exponential growth rates. Empirical population growth was determined using the initial and final population sizes found in my literature search (Table 2.2). 95% confidence intervals were then calculated for the empirical growth curve and populations were classified as having exhibited a prolonged lag phase when the slope of a population's exponential curve fell outside 95% confidence intervals of the empirical model (using the method suggested by Crooks & Soule 1999). I used a binary response variable of lag (1) or non-lag (0) to investigate the factors that influenced the likelihood of a population exhibiting a prolonged lag in the statistical models described below.

To estimate the growth rates of these species, I calculated the doubling time using the following formula (Hulting et al. 1990):

$$dt = \log(2)/r$$

where *r* is the annual rate of increase (∆population/∆time). Delta time, as used here, was the same for both empirical and exponential populations. The difference in doubling time between the empirical and exponential models (calculated from population growth in the exponential models) was then calculated and used as a response variable, also described below Table 2.2).

After determining which populations showed significant prolonged lags (n = 17), I examined possible causes of variation in population growth rates using generalized linear models, and a range of different explanatory variables associated with climate and life history (Table 2.3). To determine the degree of lag shown by each lagging population, I calculated the difference between the theoretical population growth rate calculated for each lagging population, and its actual growth rate, and used this difference as the response variable in the models. One disadvantage of this method is that it was not possible to detect population crashes or changes in growth rate between the starting and ending points. In my dataset, there were only eight species with more than two available population estimates. I found that the theoretical growth trajectories in these eight species were largely similar to the empirical data (see Appendix A) and thus concluded that my estimation method reflected biological reality reasonably well.

Climate data were obtained from meteorological databases and public weather stations (including temperature and historic monthly rainfall from weather stations as close as possible to the release site of each population; Table 2.2). The climatic variables for each location included mean annual rainfall (mm) and temperature (°C) (calculated from the entire available weather station dataset). The number of consecutive months with rainfall in the lowest 25% per annum was calculated to estimate the length of the dry season (i.e., the lowest 25% monthly rainfall measurements available from the entire dataset available from the appropriate weather station). A categorical variable: “island” or “mainland” was also included. The gestation period of each species was also determined from the literature and used as an explanatory variable in the model. Other intrinsic variables (e.g., maximum age in wild, age at sexual maturity, etc.) were used to generate models for population growth and, therefore, were not included here. In addition, I classified whether populations were introduced to areas with native natural predators or competitors. A species list was obtained for each area and if there was at least one native potential competitor (mega-herbivore) or predator (medium-to-large carnivore), that population was said to have had potential competition or predation pressure. Finally, I also included if the literature suggested a population was subject to hunting. To account for effects potentially caused by using the same species more than once in the model and among-species differences, species was included as a random effect in the model. I also conducted all analyses with various calculated measures of growth as response rates (annual rate of increase (r) and the slopes of the curves; Appendix B).

All analyses were conducted in R (V3.4.1, R Studio Team 2017) and visualized using the *ggplot2* package (Wickham 2016). I performed model selection based on Akaike's information criterion (AICc) to select the best subset models of population growth. Due to multicollinearity, island, total annual rainfall, and temperature were removed from model selection. I tested all combinations of gestation period, months of consecutive low rainfall, average annual rainfall, and location.

I built generalized linear models and used the ‘dredge’ function from package *MuMIn* (Barton 2018) to perform model selection. I assessed the weight of each model using the delta AICc values (Δi; models were considered significant if the delta AICc value was <2 and the AIC weight close to 1; Burnham & Anderson 2002; Symonds & Moussalli 2011). Model averaging was performed when no single top model could be identified (i.e., Multiple top models with a ΔAICc value < 2).

Table 2.1. Description of variables derived from meteorological databases and primary literature to select candidate models for population growth of introduced ungulates

Variable Name	Variable Description
dry season	the number of consecutive months with rainfall in the lowest 25% of monthly rainfall, correlating with the length of the dry season
gestation	the gestation period of each species (days)
region	a categorical variable indicating if the population was introduced to a tropical or temperate environment
rainfall	the average annual rainfall (mm)
temperature	the average annual temperature (°c)
island	a categorical variable indicating if the population was introduced to an island or the mainland
predators	a categorical variable indicating if the population was introduced to a location with potential predators
competition	a categorical variable indicating if the population was introduced to an area with native competitors
hunting	a categorical variable indicating whether the population was introduced for hunting purposes
variance	average intra-annual rainfall variance

Results

I found a wide range of doubling times for introduced ungulate populations, from nearly exponential growth (with a difference in doubling time of 0.07 years between the theoretical and empirical curves) to large differences (up to 22.54 years) between empirical and exponential growth (Table 2.3).

For 17 populations, the slope calculated for the empirical populations was significantly less than that calculated for theoretical populations, that is, the slope calculated for the theoretical model fell above the 95% confidence intervals for the slope of the empirical curves (i.e., theoretical populations grew faster than real ones, asterisked in Table 2.3). Therefore, in 17/36 (47%) of ungulate populations, growth lagged significantly. None of the factors that I investigated contributed significantly to explain why populations lagged (n = 36, Table 2.4) or the degree of lagging population growth of introduced ungulates (n = 17, Table 2.5).

Table 2.2. Doubling time (DT) of introduced ungulates compared with exponential population models, sorted in descending order from lowest to highest difference in doubling time.

Species (source)	Location	Introduced environment	Observed DT	Exponential DT	Difference
Rangifer tarandus (St Matthew) (1)	Alaska	non-tropical	2.47	2.40	0.07
Rangifer tarandus (Grande-Terre) (2)	Kerguelen Isl.	non-tropical	1.96	1.82	0.14
Ovis gmelini musimon (2)	Kerguelen Isl.	non-tropical	2.13	1.87	0.26
Rangifer tarandus (St George) (3)	Alaska	non-tropical	2.83	2.50	0.33
Rangifer tarandus (Haute) (2)	Kerguelen Isl.	non-tropical	2.85	2.41	0.44
Antilocapra americana (4)	Hawai'i	tropical	2.84	2.33	0.50
Odocoileus hemionus (5)	USA	non-tropical	2.61	1.83	0.78
Ovis canadensis (6)	Mexico	non-tropical	3.30	2.45	0.85
Capreolus capreolis (7)	Germany	non-tropical	3.28	2.42	0.86
Cervus nippon (8)	Japan	non-tropical	3.47	2.43	1.04
Cervus timorensis (9)	Australia	non-tropical	3.03	1.73	1.30
Cervus unicolor (10)	New Zealand	non-tropical	4.25	2.93	1.32
Odocoileus virginianus (11)	Finland	non-tropical	3.53	1.80	1.73
Ammotragus lervia (12)	Spain	non-tropical	3.23	1.46	1.77
Rangifer tarandus (St Paul) (3)	Alaska	non-tropical	4.30	2.50	1.80
Ammotragus lervia* (13) *	**USA**	**non-tropical**	**3.91**	**1.90**	**2.01**
Ovis gmelini (14)	Hawai'i	tropical	3.83	1.80	2.03
Dama dama (15)	USA	non-tropical	4.66	2.40	2.26
Ovis gmelini (16)	Canary Isl.	non-tropical	4.24	1.82	2.42
Lama guanicoe* (17) *	**Falkland Islands**	**non-tropical**	**4.05**	**1.49**	**2.56**
Oryx gazella gazelle* (18) *	**USA**	**non-tropical**	**4.61**	**1.97**	**2.64**
Ammotragus lervia (16)	Canary Isl.	non-tropical	4.54	1.84	2.70
Rangifer tarandus* (19) *	**South Georgia Isl.**	**non-tropical**	**5.10**	**2.37**	**2.73**
Rusa timorensis* (20) *	**New Caledonia**	**tropical**	**5.35**	**2.35**	**3.00**
Cervus nippon* (21) *	**USA**	**non-tropical**	**7.11**	**2.33**	**4.78**
Axis axis* (15) *	**USA**	**non-tropical**	**7.61**	**2.39**	**5.22**
Hemitragus jemlahicus* (22,23) *	**New Zealand**	**non-tropical**	**9.06**	**2.32**	**6.74**
Axis axis* (24,25) *	**Australia**	**tropical**	**9.69**	**2.35**	**7.34**
Axis axis* (26) *	**Hawai'i**	**tropical**	**10.26**	**2.34**	**7.92**
Oreamnos americanus* (27) *	**USA**	**non-tropical**	**11.60**	**2.98**	**8.63**
Bubalus bubalis* (28) *	**Australia**	**tropical**	**11.78**	**2.77**	**9.01**
Camelus dromedarius* (29) *	**Australia**	**tropical**	**11.90**	**2.77**	**9.13**
Odocoileus virginianus* (30) *	**Canada**	**non-tropical**	**12.62**	**1.81**	**10.82**
Hydropotes inermis* (31) *	**England**	**non-tropical**	**12.44**	**1.52**	**10.92**
Bos javanicus* (32) *	**Australia**	**tropical**	**17.62**	**2.87**	**14.75**
Cervus nippon* (33) *	**Poland**	**non-tropical**	**24.91**	**2.37**	**22.54**

Table 2.3. Model averaging results from generalized linear models (GLM) indicating top variables from model selection for factors that affect introduced ungulate population growth (binary response of prolonged (1) or inherent (0) lagging populations) with variables from Table 2.2.

	Estimate	Std. Error	Adjusted SE	z value	2.50%	97.50%	p value
(Intercept)	-2.67	7.58	7.72	0.35	-17.81	12.46	0.729
island	-0.90	0.92	0.94	0.97	-2.99	0.07	0.335
region	1.01	1.10	1.12	0.90	-0.39	3.61	0.370
competition	0.40	0.74	0.75	0.53	-0.11	2.89	0.595
gestation	1.19	3.26	3.32	0.36	-4.26	16.03	0.720
variance	-0.05	0.24	0.25	0.18	-1.91	0.77	0.855

Table 2.4. Model averaging results from generalized linear mixed effect models (GLMM's) indicating top variables from model selection for factors that affect introduced ungulate population growth (difference between observed and exponential doubling time) of lagging populations with variables from Table 2.2.

	Estimate	Std. Error	Adjusted SE	z value	2.50%	97.50%	p value
(Intercept)	16.54	31.42	35.14	0.47	-52.33	85.41	0.638
gestation	-2.52	12.88	14.40	0.18	-34.35	28.13	0.861
island	-3.23	3.31	3.53	0.92	-11.27	1.73	0.359
dry season	-1.64	12.93	14.45	0.11	-32.48	28.65	0.910
hunting	-1.34	2.67	2.87	0.47	-10.96	3.75	0.642
predators	-1.02	2.39	2.53	0.40	-10.56	3.72	0.687
region	0.80	2.39	2.56	0.31	-5.12	11.93	0.754

Discussion

Populations of introduced ungulates often grow exponentially upon release (Riney 1964), which is a pattern I found in 53% of the populations. Of those species that did exhibit a lag, I could not identify any specific intrinsic or extrinsic variables that were significant contributors to delayed population growth. My results are consistent with other studies that examined causes for lag phases in population growth in birds and plants and found no single cause of slow growth (Aagaard & Lockwood 2014; Larkin 2012).

This study is the first to systematically identify and analyse causes of population growth lags in mammals, specifically in introduced ungulates. Large mammals, such as ungulates, have been widely introduced to environments around the world and caused various environmental problems (Cote et al. 2004; Hernandez et al. 2018; Riney 1964). Sika deer (*Cervus nippon*) and muntjac (*Muntiacus reevesi*) are listed in the top 10 worst alien species for Europe when ranked by impact, while chital deer (*Axis axis*), aoudad (*Ammotragus lervia*), white-tailed deer (*Odocoileus virginianus*), and mouflon (*Ovis gmelini*) rank within the top 100 (Nentwig et al. 2018). I found that four of these five species (muntjac were not included in this study) displayed lag phases in parts of their introduced ranges. I thus conclude that many populations of introduced ungulates currently persisting at low numbers may represent significant economic and environmental threats that are yet to be recognized.

Investigations into causes of lag phases in plants and birds show that they are idiosyncratic and that they are not predictable using a given set of explanatory variables, and my results are consistent with these studies (Larkin 2012; Aagaard & Lockwood 2014; Mack et al. 2000). The factors that allow introduced species to break out of lag phases are variable among species and populations (Aagaard & Lockwood 2014). Environmental change may trigger species that are lagging to suddenly grow and spread rapidly (Crooks & Soule 1999; Fisher et al. 2020; Fujisaki et al. 2010; Rilov et al. 2004; Romagosa & Labisky 2000), as they (through climate and/or anthropogenic influences) enable accelerated expansion into previously unoccupied areas (Fisher et al. 2020; Hengeveld 1989; Witte et al. 2010).

One limitation of this study is that very few publications reported multiple population density estimates over time. Only by examining longitudinal data, I can distinguish more fine-scale patterns of population growth. For example, a species that grows slowly may have a growth curve (as defined in this study) that appears similar to that of a species that grows quickly, but experiences frequent population crashes. For these reasons, it would be ideal to have detailed longitudinal datasets of introduced ungulate population densities to use for this study. On the other hand, I found that my estimates of population growth patterns were fairly good for species with available estimates of population size at multiple points, so I feel my estimates were at least partially representative of likely population growth trajectories for many of these species. Another limitation of my study is that several factors, such as parasite load, and the extent of hunting pressure, were not available in the literature (Albrecht et al. 2009; Carey & McLean 1983; Kock et al. 2010; Wade 2007). While hunting was included in the analyses, I can only report on whether a species was hunted or not, and not the degree of hunting (particularly from private hunters). Removal of adult animals by hunters can significantly reduce both population size and growth rate (Festa-

Bianchet 2003). Several of the species in this study likely experienced some level of hunting pressure, given that many of these populations were introduced specifically for the purpose of recreational hunting (n = 28), whereas others were subsequently hunted as trophies (Bender et al. 2019; Bradshaw & Brook 2007; Fuller et al. 2018). If unmeasured factors, such as degree of hunting, predation rates, and population crashes, significantly influenced population growth in much of my dataset, these factors should all lead to longer lag phases. Given that my study still showed species that exhibited exponential growth, or inherent lags, with this population bias, I believe my growth models are an adequate reflection of biological reality. A final limitation is that there may have been methodological differences in the collection of abundance data. While these differences could not be quantified, these populations still provide valuable information on ungulate population growth, provided that the limitations of using these data are recognized.

Since the eradication and containment of introduced species is best done when populations are small, it is important to identify early which species may be in inherent or prolonged lag phases (Buhle et al. 2005; Simberloff 2003). Species introduced to new environments may be present in low numbers now and seem under control for many years, but still have the potential for explosive growth in the future. It is cases such as these in which managers need to be cognizant of the potential for these populations to suddenly increase. With a better understanding of the factors causing prolonged lags, rapidly accelerated population growth can be anticipated, and pre-emptive controls put in place (Fagan et al. 2002). More work is needed to predict how invasive ungulate populations may grow in the future.

Chital deer stag

(drawing by author)

Chapter Three: Proximity to water and soil mineral content determine habitat selection of invasive chital deer

Adapted from: Kelly C.L., Schwarzkopf, L., Gordon, I. J., Pople, A. & Hirsch, B. (2021) Proximity to water and soil mineral content determine habitat selection of invasive chital deer. *Under consideration at Austral Ecology*

Introduction

Ungulates have been introduced, and successfully established worldwide, usually as food or game resources (Mungall & Sheffield 1994; Forsyth & Hickling 1998; Moriarty, 2004; King 2005; Ikagawa 2013; Hess 2016). Some of these introduced ungulate populations have negative economic and social impacts, causing damage to infrastructure, motor vehicle collisions, and competing with livestock for feed (Jesser 2005; McLeod 2009; Kusta et al. 2017). Invasive ungulates can also have serious environmental effects by degrading habitats, competing with native species, and spreading diseases or parasites (Doran & Laffan 2005; Ens et al. 2016; Hess 2016). Control of invasive ungulates is critical to mitigating their impacts, and an understanding of how they behave within their environment can help in these control efforts.

Ungulate habitat selection is often determined by factors such as the availability of water, minerals, forage, cover, and shelter (Grasman & Hellgren 1993; Smit et al. 2007; Treydte et al. 2009; Thaker et al. 2011). Habitat selection by individual animals influences larger scale patterns of a species' distribution. Various geographic barriers can also heavily influence the distribution of species across a landscape (Hobbs 2003, Northrup et al. 2016), thus, understanding the drivers of species' densities at multiple scales is important for predicting where species may occur in the future.

The availability of water greatly influences habitat selection in many mammals (Coe et al. 1976; Smit et al. 2007; Longshore et al. 2008), especially those that live in drier environments (Noy Meir 1973; Bleich et al. 2010; Letnic et al. 2015). Bleich et al. (2010) found that increasing the number of artificial water points could increase the area of suitable habitat for mountain sheep (*Ovis canadensis*) by up to 92%. Likewise, eastern grey kangaroos (*Macropus giganteus*), a major grazer in Australian savannahs, typically shift home ranges in response to increased water availability (Dawson et al. 2006). With increased provision of watering sites for livestock, the range of these kangaroos have shifted westward into more arid regions (Caughley et al. 1984; Dawson et al. 2006). Increasing access to water also increases the density of eastern grey kangaroos, which has had negative economic impacts (Dawson et al. 2006; Descovich et al. 2016). Water availability should thus be considered when examining species distributions, at both local and regional scales.

Ungulate habitat selection can also be influenced by the availability of minerals in plant material or in the soil as licks (Grasman & Hellgren 1993; Mungall & Sheffield 1994; Ayotte et al. 2006; Treydte et al. 2009; Watter et al. 2019). Phosphorus, sodium, and calcium are vital nutrients for ungulates as they are needed for bone mineralisation, which is important for antler growth in deer, as well as sub-cellular processes and genetic coding (Belovsky 1978; Grasman & Hellgren 1993; Mungall & Sheffield 1994; Dryden 2016; Griffith et al. 2017). Soil mineral content depends on factors such as soil drainage, soil pH, land use, and the original mineral content of the parent material (Shaw et al. 1994; Turner et al. 2007; Huang et al. 2017). Weathering reduces soil phosphorus and calcium availability over time, thus geologically older regions such as continental Australia, typically have phosphorous-deficient soils (Gillman & Bell 1978; McKenzie et al. 2004; Rossel & Bui 2016; Huang et al. 2017; Kooyman et al. 2017). Similarly, areas converted to pastureland frequently have higher soil sodium levels due to greater evaporation rates than the original native woodland (Schofield 1992; Thorburn et al. 2002).

Cover and shelter are also important for ungulates, acting as refuge from both harsh environmental conditions and predators (Mysterud & Ostbye 1999; Winnie et al. 2006; Gustine & Parker 2008; Thaker et al. 2011). Increased solar radiation often drives animals to seek shelter under bushes and trees, particularly in savannah systems (Dawson 1972; Vetaas 1992). Many ungulate species select habitat with lower perceived predation risk (e.g., moving to covered areas when not grazing; Winnie et al. 2006; Thaker et al. 2011; Pierce et al. 2015). As canopy cover can influence most abiotic and biotic factors that affect how ungulates use habitat (Elton 1939; Mysterud & Ostbye 1999), it is likely to contribute to habitat selection. Tracks and roads are frequently avoided by deer, as these anthropogenic features often represent areas of high disturbance (Rost & Bailey 1979; Sibbald et al. 2011; Scholten et al. 2018). As such, the presence of such features may shift how deer select and move through habitat. Forage quality and quantity are also important determinants of the physical condition of ungulates (Clutton-Brock 1989; Yokoyama et al. 2000; Acebes et al. 2013). Multiple studies have suggested that the distribution of food resources limits the movement and spread of ungulate populations (Caughley 1970; Coe et al. 1976; Fryxell 1987; Mduma et al. 1999).

The importance of each of these factors (water, minerals, shelter, and food) in determining ungulate habitat use varies depending on the environment in question, as ungulates are influenced by each variable to different degrees in different environments. For example, a species living in an arid environment may be most influenced by the presence of water (Bleich et al. 2010; Letnic et al. 2015), whereas species living in environments with abundant water may have a greater preference for areas with shelter from predation (Mysterud & Ostbye 2006; Kittle et al. 2008). Many ungulates, particularly deer, select edge habitats that provide access to both cover and food (Alverson et al. 1988; Altendorf et al. 2001). To predict the distribution of invasive ungulates at different scales, it is important to determine the influence of these factors on their habitat selection.

Chital deer (also known as axis or spotted deer: *Axis axis*) are a medium-sized cervid native to India, Sri Lanka, Bangladesh, Nepal, and Bhutan (Mattioli 2011; Duckworth et al. 2015). They have been introduced to many countries including the United States (Texas and Hawaii), Argentina, Chile, Croatia, and Australia (Long 2003). In their native range, chital usually inhabit forest edges in grassland and riverine environments (Mishra 1982; Moe & Wegge 1994). Chital habitat use can also be influenced by the presence of native predators such as tigers (*Panthera tigris*), leopards (*Panthera pardus*), jackals (*Canis aureus*), and dhole (*Cuon alpinus*; Moe & Wegge 1994; Sankar and Acharya 2004; Ramesh et al. 2012), and chital will change habitat use in response to predation risk (e.g., use open grass areas for grazing with access to dense vegetation for resting; Mishra 1982; Moe & Wegge 1994). Because habitat selection in their native range is strongly influenced by predators, examining habitat use in an introduced population with fewer predators could reveal other factors important to their distribution.

In 1886, four chital deer were introduced to North Queensland, Australia, and subsequently established and spread (Bentley 1967; Moriarty 2004). Prior to 20 years ago, the North Queensland chital population remained relatively localised, but currently the population is expanding, which is a concern to local landowners and government authorities (Brennan & Pople 2016). Unfortunately, the factors that have facilitated this rapid change in population size and range are poorly understood. Understanding the habitat selection of chital deer in their introduced range should help determine how such populations might grow and spread in the future. In this study, I investigated chital abundance in relation to multiple habitat variables at both local and regional scales. At the local scale, I anticipated chital trapping rate would be negatively correlated with dingo trapping rate due to predator avoidance. Likewise, due to deer avoidance of anthropogenic features such as tracks and roads (Scholten et al. 2018), I expected chital density to increase with increasing distance from tracks and roads. I also expected that areas with high soil phosphorus, close proximity to water, and with more green vegetation should have more chital due to their importance to physiological processes (Watter et al. 2019).

Methods

Local scale

This study was conducted at Spyglass Beef Research Facility, a cattle property covering 38,221 hectares in the Charters Towers district, Queensland, Australia (Figure 3.1). The study area contains grassland that consists of both native grasses, such as black speargrass (*Heteropogon contortus*) and kangaroo grass (*Themeda triandra*), and exotic grasses such as sabi grass (*Urochloa mosanbicensis*), red Natal grass (*Melinis repens*), and buffel grass (*Cenchrus ciliaris*). A variety of overstorey species include silverleaf box (*Eucalyptus pruinosis*), lancewood (*Acacia shirleyi*), bendee (*Acacia catenulata*) with yellowjacket (*Eucalyptus similis*), and ironbark (*Eucalyptus* spp.). Three main seasons are experienced at the study site: wet (October to March), cool dry (April to August) and hot dry (September to October). Troughs and dams are located across Spyglass as permanent water sources for cattle. The Burdekin River runs adjacent to the north-eastern edge of Spyglass and may also serve as a permanent water source for animals. There are three homesteads in the study area, two on Spyglass itself and one on a neighbouring property close to the boundary.

I used camera traps to determine the presence and relative number of chital in different habitats (Appendix C Figure C.1). To select camera trap locations, a grid with points 500m apart was created using ArcGIS (ESRI). To facilitate access to the locations, 118 points of the grid were selected that fell within 400m of a road or track. Bushnell Aggressor^{TM} cameras were placed at these locations for at least one month each between October 2017 and November 2018. Cameras were set to capture three images per trigger, with no delay between consecutive triggers. All images were stamped with the date and time. Cameras were installed approximately 30-50cm above the ground and pointed north or south to avoid the rising or setting sun. Vegetation in front of cameras was clipped to minimise interference and false triggers. Of the 118 cameras installed, 24 failed or the data they collected could not be analysed (e.g., they collected excessive false triggers; Appendix C Table C.1). I therefore had photos from 94 operational cameras, representing 6707 trap days. Images were identified and organised using WildID and ZSL CTap software (Amin et al 2014; TEAM Network 2017).

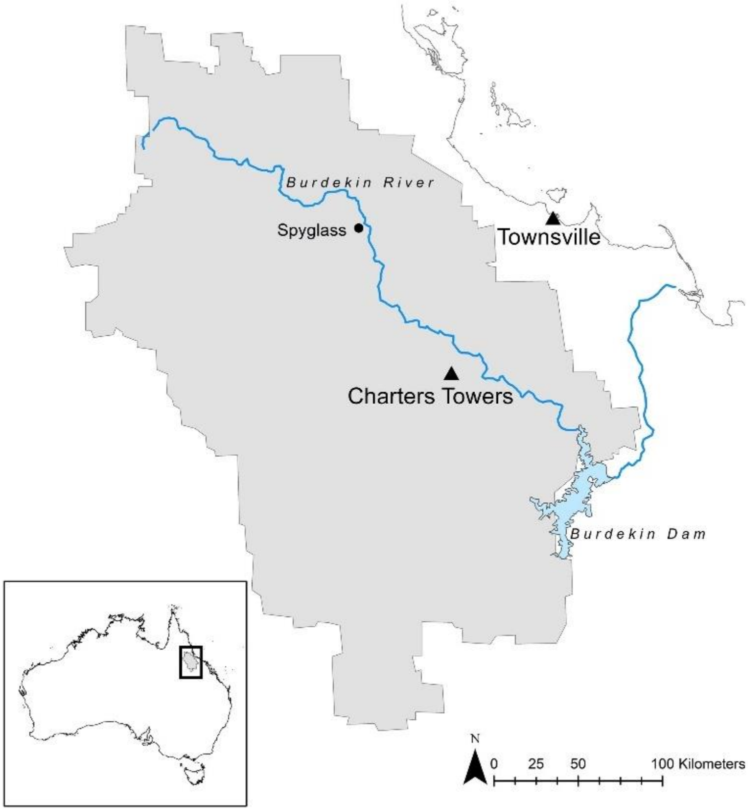

Figure 3.1. Location of fine (Spyglass Beef Research Station; circle) and broad scale (Charters Towers district; grey) areas investigated to determine the factors that drive the distribution of invasive chital deer in North Queensland.

For analysis, an “event” was defined as a sequence of photographs of one species that occurred following the previous sequence of a different species. When there were consecutive events of the same species, I ensured there was one hour or more between events (Bowkett et al. 2007; Amin et al. 2014; Rovero et al. 2017). This time frame was used to avoid repeated counting of the same individuals (Tobler et al. 2009; Rovero et al. 2017; Bruce et al. 2018). I used Moran’s test in ArcGIS to compare the detection rates of chital across all cameras and found no significant spatial autocorrelation in my dataset (Moran’s index: 0.09, p = 0.313).

I calculated spatial covariates for each camera site using geoprocessing tools in ArcGIS (Table 3.1): distance to homesteads, distance to tracks and highways, distance to the nearest water sources (dams, troughs, or the Burdekin River), and average mineral concentrations (phosphorus, sodium, and calcium-magnesium ratios) within the 200m radius of each camera. An average normalized difference vegetation index (NDVI: a measure of vegetation greenness; Pettorelli 2014) was derived for a 250m radius around each camera site using MoveBank's Moderate Resolution Imaging

Spectroradiometer (MODIS) Land V6 product (Wikelski et al. 2020). The NDVI for each site (calculated as the 16-day average for the period each camera was active) was automatically calculated and downloaded. To investigate if soil sodium concentration influenced plant growth, I performed linear regressions between NDVI and average site sodium concentration. Landscape and soil-type maps of Spyglass were obtained from the Department of Agriculture and Fisheries (Bryant et al. 2016), while other maps (Ca:Mg and sodium soil content) were sourced from the "qspatial" (https://qldspatial.information.qld.gov.au) database (Department of Environment and Science 2016). Dingoes are likely an important predator of chital deer (Forsyth et al. 2019), so I calculated a dingo trapping rate using the number of photos of dingoes per camera divided by the number of days the camera was active, multiplied by 100 (Rovero et al. 2014).

Table 3.1. Local scale variables derived from GIS layers and data from site assessments to perform generalized linear mixed models (GLMM) on chital deer habitat selection

Variable Name	Variable Description
Canopy cover	approximate % canopy cover within a 25m radius of site
Canopy height	approximate average canopy height (m)
NDVI	16-day average NDVI measure for each site
Homestead	log distance from the nearest homestead (m)
Highway	log distance from the nearest highway (m)
Track	log distance from nearest track (m)
Water	log distance from nearest permanent water source (m)
Dingo	relative abundance index of dingo per site
Ca:Mg	calcium:magnesium ratio content of soil
P	phosphorus level of soil (very low: <2mg/kg, low: 2-5mg/kg, med: 5-10mg/kg, high:>10mg/kg)
Na	exchangeable sodium concentration of soil (t ha^{-2})

I used a generalised linear mixed model (GLMM) to model relative chital abundance as a function of spatial covariates across the 94 camera sites. My analyses were based on counts (the number of chital photo events at each site). To avoid overdispersion and account for the excess zeros in my data, I used a negative binomial distribution (Lambert 1992; Zuur et al. 2009). The zero-inflated model was constructed using the *glmmTMB* package that allows for both offset and random effect variables (Brooks et al. 2017). I also used effort (the number of days the camera was operating) included as an offset. To account for potential seasonal effects, I included the camera sampling period as a random effect. The camera sampling period was broadly categorised into periods when the camera was active: Period 1 (September 2017 - January 2018; n = 44), Period 2 (February 2018 - May 2018; n = 40), and Period 3 (August 2018-November 2018; n = 10). I used Akaike's Information Criterion (AICc) adjusted for small sample size to select the best models of habitat selection. I calculated delta AICc values (model AICc – minimum AICc), where models with delta AICc values less than 2 are considered most plausible (Burnham & Anderson 2002; Symonds & Moussalli 2011). All analyses were conducted in R (V3.4.1, R Core Team, 2017) and visualised using the *ggplot2* package (Wickham 2016).

Regional scale

To examine larger scale patterns of chital abundance, I used a survey of landowners (Appendix D). Surveys (n = 254) were distributed by the Charters Towers Regional Council over 2018-2019. Landholders were asked to estimate the number of chital deer on their property either as a numerical or categorical estimate (0, 1-50, 51-200, 201-1000, >1000). The estimated number of chital on each property were imported into ArcMap. Property boundaries were derived from property boundary maps supplied by Charters Towers Regional Council, and polygons for each respondent property were created. I divided the number of chital reported by landholders by the size of their property to calculate the number of deer per square kilometre. Properties outside of the potential range of this chital population were excluded from the analyses (properties that fell more than 50km beyond two consecutive properties that reported zero deer).

A number of potential predictors of chital abundance on a regional scale were considered (Table 3.2). As water availability likely influences chital landscape use, I calculated the distance from the nearest major watercourse (those classified by Geoscience Australia 250 000 Topographic Data as being major) to the geometric centre of each property. This was selected over other water metrics as I was unable to determine specific locations on properties where chital were being reported. Average soil mineral concentration (t ha^{-1}) of phosphorus, sodium, and the ratio of calcium:magnesium were calculated for each property using maps obtained from "qspatial" (Department of Environment and Science 2016; Rossel & Bui 2016). The average NDVI (calculated average from 10-year dataset to estimate average station greenness) was also calculated for each property and used as a covariate. To determine if the average soil sodium content influenced plant growth, I performed linear regressions between NDVI and average property sodium concentration.

Due to the potential impact of predators, landholders were also asked if they undertook dog control on the property, however, not every landholder responded to this question. Of the 84 stations that responded, 54 (68%) answered the question of dog control. Of those, 100% responded that they undertook dog control. As such, this variable was excluded from analyses.

Table 3.2. Regional scale variables. Description of variables derived from GIS layers to select candidate models for chital habitat selection at the regional scale

Variable Name	Variable Description
River	average distance from a major watercourse (m)
Slope	average slope of property (degrees)
NDVI	10-year average NDVI measure for each property
Ca:Mg	average calcium:magnesium ratio content of soil
P	average phosphorus concentration of soil (t ha^{-1})
Na	average exchangeable sodium concentration of soil (t ha^{-1})

To investigate predictors of chital abundance per property, I built generalized linear models (GLMs). To avoid overdispersion and account for the excess zeros in my data, I used a negative binomial distribution in my analysis. I used count data (the number of chital reported on each property) with property area included as an offset. As with the fine scale analyses, I calculated delta AICc values where models with delta AICc values less than 2 were considered most plausible (Burnham & Anderson 2002; Symonds & Moussalli 2011). Model averaging was performed when no single best model could be identified (i.e., multiple models with a ΔAICc value less than 2). All analyses were conducted in R (V3.4.1, R Core Team, 2017) and visualised using the *ggplot2* package (Wickham 2016).

Results

Local scale

Cameras recorded an average of 7.96 (+/- 1.73 SE) total chital events, or 0.14 (+/- 0.03 SE) per night (Figure 3.2). A total of 753 chital events were recorded across all camera sites. At the local scale, there were three plausible models (see Appendix C Table C.2), so model averaging was performed.

Chital density increased with decreasing distance to water (p < 0.001; Appendix C Figure C.2). Likewise, high soil phosphorus content (p = 0.001) was significantly correlated with increased chital trapping rates (Appendix C Figure C.3). In contrast, higher soil sodium content correlated with lower deer trapping rates (p < 0.001; Appendix C Figure C.4). High NDVI values, high canopy cover and height, as well as decreasing distance to tracks and highways also correlated with higher deer trapping rates (Table 3.3). Dingo trapping rate (p = 0.273) and calcium:magnesium content of the soil (p = 0.736) were not significant following model averaging. They were, however, present in the top models prior to model averaging (Appendix C Table C.2). Distance from homestead did not appear in the plausible models. There was no significant relationship between average site soil sodium content and NDVI (p = 0.858).

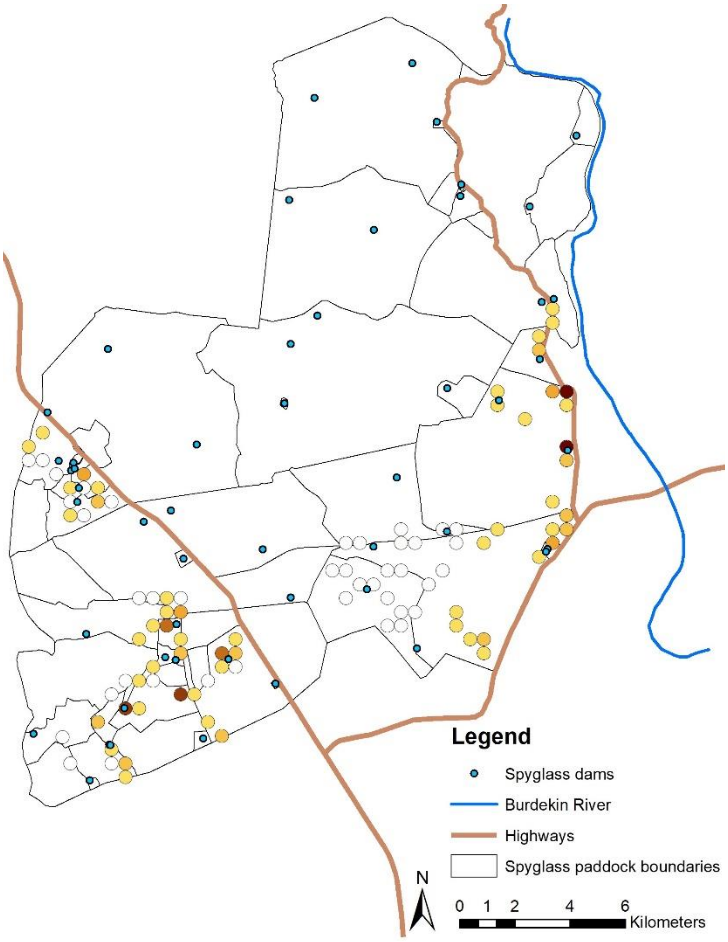

Figure 3.2. Map of chital trapping densities at cameras on Spyglass Beef Research Station. White points represent sites where chital were absent, with increasingly dark points representing increasing chital trapping rate < 0.00 – 1.34 events/day (each shade darker represents an increase in trapping rate of 0.224 events/day).

Table 3.3. Local level analysis. Model averaged parameter estimates from the best (Δ AICc <2) generalized linear models (GLMM) of chital deer habitat selection at a local level with variables from Table 3.1. Camera sampling period was included as random effect.

	Estimate	Std. Error	Adjusted SE	z value	2.50%	97.50%	p value
Intercept	7.19	0.73	0.74	9.72	5.74	8.64	<0.000
Dingo	-4.41	3.99	4.02	1.10	-12.87	0.39	0.273
Ca:Mg	0.05	0.15	0.15	0.34	-0.25	0.74	0.736
Na	-0.06	0.02	0.02	2.96	-0.10	-0.02	0.003
P	0.24	0.07	0.07	3.27	0.10	0.38	0.001
Canopy Cover	0.06	0.01	0.01	9.92	0.05	0.07	<0.000
Canopy Height	0.04	0.01	0.01	7.17	0.03	0.05	<0.000
Highway	-0.71	0.10	0.11	6.74	-0.92	-0.50	<0.000
Track	-1.17	0.10	0.11	10.99	-1.38	-0.96	<0.000
Water	-1.74	0.11	0.11	15.65	-1.96	-1.53	<0.000
NDVI	7.27	1.31	1.33	5.46	4.66	9.88	<0.000

Regional scale

Of 98 returned surveys, 56 reported chital deer on their property, with reported chital populations ranging from 1 to 2000, and an average of 0.64 chital/km^2 (+/- 0.12 SE). At the regional scale, there were two plausible models following model selection (see Appendix C Table C.3), so model averaging was performed; parameter estimates are given in Table 3.4.

As with the local scale analyses, reported chital numbers were positively correlated with decreasing distance to a major watercourse ($p < 0.001$; Appendix C Figure C.5) and with increasing average station soil phosphorus content ($p < 0.001$; Appendix C Figure C.6). Lower sodium levels were also associated with increasing deer numbers ($p < 0.001$; Appendix C Figure C.7). Higher deer numbers were also reported on properties with flatter topography. Reported chital numbers were positively associated with soil Ca:Mg content ($p < 0.001$). Unlike local level analyses, however, chital reported numbers were not influenced by average station NDVI ($p = 0.310$). There was a significant negative relationship between average property soil sodium content and NDVI ($p = 0.002$); increasing sodium content of the station was correlated with an increase in NDVI.

Table 3.4. Regional level analysis. Model averaged parameter estimates from the best (Δ AICc <2) generalized linear models (GLM) of chital deer habitat selection at a regional level with variables from Table 3.2.

	Estimate	Std. Error	Adjusted SE	z value	2.50%	97.50%	Pr(>|z|)
(Intercept)	7.67	2.03	2.05	3.75	3.66	11.68	0.000
Ca:Mg	2.08	0.55	0.56	3.69	0.97	3.18	0.000
Na	-2.55	0.24	0.25	10.34	-3.04	-2.07	0.000
P	35.28	5.70	5.79	6.10	23.93	46.62	0.000
NDVI	-5.29	5.19	5.21	1.02	-15.78	-2.62	0.310
River	<0.00	<0.00	<0.00	5.74	0.00	0.00	0.000
Slope	-0.43	0.08	0.08	5.22	-0.60	-0.27	0.000

Discussion

Chital densities were greater in areas closer to water at both local and regional scales. In their native range, chital predominantly inhabit riverine forest and grassland edges along river courses (Mishra 1982; Moe & Wegge 1994; Bhat & Rawat 1995; Dey 2007). Chital dependence on water has also been reported in their introduced ranges (Graf and Nichols 1966; Mungall & Sheffield 1994; Centore 2016). My results are similar to those of Forsyth et al. (2019) who found that chital were dependent on water points at a local scale within several cattle grazing properties in the Charter Towers region. The region is relatively water limited in the dry season, with available water restricted to artificial water points, major streams, and natural springs (Forsyth et al. 2019). Other species in this region, such as feral pigs (*Sus scrofa*) and eastern grey kangaroos also depend on these water points (Forsyth et al. 2019). It is likely that access to permanent water points has enabled the spread of chital in the Charters Towers region.

Soil sodium content was negatively correlated with deer abundance at both the local and regional scales. Increased sodium content of feed causes an increase in freshwater requirements of deer (Ru et al. 2004). In a water-limited environment, like the Charters Towers region, it may be difficult to offset high sodium diets by increasing water intake. These results differ from other studies where sodium was positively associated with ungulate abundance (McNaughton 1988), including chital in north Queensland (Watter et al. 2020). In their native range, chital use natural licks as a source of sodium due to environmental deficiencies (Moe 1993). The different patterns found in this study are likely due to the moderate to high salinity levels in the Charters Towers region (electrical conductivity of 0.3 -> 1.2 $mScm^{-1}$; Rogers et al. 1999). High salinity levels can reduce plant growth, which could reduce the utility of the habitat to chital. Soil sodium content can be increased by land use changes such as tree clearing (Schofield 1992; Sangha et al. 2005). The Charters Towers district is at particular risk of increased soil salinity as tree clearing is commonly used as a land management tool to increase pasture and thus beef productivity (Williams et al. 1997). The high soil salinity levels in the region have the potential to limit the spread of chital populations, although I predict that deer can overcome these constraints when they have access to permanent water sources.

Chital abundance was positively correlated with high soil phosphorus at both the local and regional scales; local scale results reflect results from previous studies undertaken in the area (Watter et al. 2019). Phosphorus is critical for ungulates (Grasman & Hellgren 1993; Mungall & Sheffield 1994; Dryden 2016) and, in their native range, chital use natural salt licks that are high in phosphate (Schaller, 1967; Moe 1993). In mineralogically-deficient environments, ungulates will actively graze in patches of vegetation where there is higher phosphorus content or salt licks containing higher phosphorus (Moe 1993; McNaughton 1990; Ayotte et al. 2006; Treydte et al. 2009). The Charters Towers region is situated on part of the oldest rock formations in Australia, meaning that deer may be particularly sensitive to phosphorus levels in this deficient environment (Gillman & Bell 1978). The chital population north of Charters Towers are located on an “island” of higher phosphorus (Rossel & Bui 2016), and this could feasibly influence the ability of chital to spread out of this region.

NDVI was positively related to chital abundance at the local scale. NDVI values are greater in areas of higher pasture biomass, as well as areas with significant tree and shrub cover. These results are consistent with chital habitat selection in their native range, where they typically aggregate and forage in grasslands or areas of freshly sprouting grass, but also use areas of dense vegetation (Moe & Wegge 1994; Bhat & Rawat 1995; Ramesh et al. 2012). Likewise, introduced chital in Texas (USA) show a preference for areas with grasses and shoots, either in the understorey or meadows (Mungall & Sheffield 1994). In their native range, chital often use areas with high cover, which serves as protection from predators and shelter from extreme heat and rain (Mishra 1982; Ramesh et al. 2012). In this study, increased canopy cover and canopy height were positively correlated with chital abundance at the local scale. Chital selecting greener areas, with high NDVI and increased cover, indicates that food availability and shelter are potentially major factors that affect home range utilization, but has little effect on large scale abundance patterns. In contrast to the local scale, chital abundance was weakly negatively associated with NDVI at the regional scale. These results suggests that individual deer respond to small scale differences in vegetation, but the amount of green vegetation is not driving the density of deer across the landscape, with other factors (e.g., proximity to watercourses or other factors that are associated with floodout areas and larger watercourses) being more important.

Distance from tracks and highways was also an important driver of chital abundance at the local scale, with greater densities being observed closer to these features. It is possible that anthropogenic clearing in the vicinity of highways and tracks may provide an interface between denser vegetation and open grassland that is favoured by chital. It is also likely that predators such as dingoes also use linear features such as tracks (Vernes & Dennis 2001). Many properties in the Charters Towers region, such as Spyglass Beef research station, undertake regular dingo control (Fleming et al. 2001; Forsyth et al. 2019). As such, their impacts on chital habitat selection and landscape use may be more limited than if dingo control did not occur (Forsyth et al. 2019). My results also differ from those of Forsyth et al. (2019) who reported higher chital abundance in close proximity to homesteads. This discrepancy could possibly be due to the smaller number of homesteads in this study site. In contrast to Forsyth et al.'s (2019) study.

I must acknowledge several limitations of this study. First, a certain degree of trust is placed in landholder responses, and they are analysed assuming that they are accurate. Despite the limitations, these responses still provide valuable information on chital density, provided that the limitations of using these data are recognised. Secondly, camera trapping was undertaken in a single season without replicates. In the future, I would undertake this study with more cameras, and seasonal replications to further enhance my results. This would also allow further discussion of occupancy and seasonal movements. As it stands, my results very closely reflect those of previous studies and are the same at both scales examined (both local and regional), and as such, I feel they are robust.

Several of the variables that influenced local scale abundance of chital were also correlated with density at the regional scale (distance from water, sodium, and phosphorus). It is possible that watercourses in the Charters Towers region have facilitated the spread of chital deer because they provide access to permanent water, as well as cover and food. In addition, increased access to permanent water such as troughs and dams for cattle may serve as potential mechanism that facilitates the spread of chital into areas that may have otherwise been inaccessible (Hunt et al. 2014). Attempts have been made in other systems to control the spread of invasive species by restricting access to water (e.g., kangaroos and cane toads (*Rhinella marina*) in Australia; Underhill et al. 2007; Florance et al. 2011; Letnic et al. 2015). Given the vast geographical scale and large number of water points, and the other animals that need to access water points, restricting access would be exceedingly difficult. Instead, these areas should be the focus of monitoring efforts to identify if, and when, chital invasion has occurred. This will allow immediate action, such as culling, to be taken to minimise the environmental and economic impacts of this invasive species.

Areas with relatively high phosphorus content, relatively low soil sodium content, and ready access to water should be the targets for intensive efforts to reduce the likelihood of future spread of chital deer. Future directions should focus on monitoring the areas that facilitate the spread of chital deer in the Charters Towers region (e.g., major watercourses), thus allowing more effective predictions of chital distribution, and therefore focus areas for management, in the future.

Chital deer stag

(drawing by author)

Chapter Four: Reproductive asynchrony of the sexes in introduced Australian chital deer

Adapted from: Kelly C.L., Schwarzkopf, L., Gordon, I. J., Pople, A., Kelly, D. & Hirsch, B. (2021) Reproductive asynchrony in Australian chital deer: implications for adaptation to climate change. *Under consideration at Oecologia*

Introduction

Many species exhibit seasonal peaks in reproduction. Usually, the physiological reproductive cycles of males and females are triggered by the same environmental factors (O'Brien et al. 2003). In other species, male and female cycles are influenced by different mechanisms, but these events usually occur with enough predictability, or temporal synchrony, that male and female cycles match (Ball & Ketterson 2008). For example, female breeding cycles in many temperate birds are driven by food availability, whereas male cycles are triggered by photoperiod (Moore et al. 2005). In these instances, male and female cycles remain synchronised because days get longer in spring, and food availability also increases in spring (Moore et al. 2005).

When photoperiod does not vary strongly, which often occurs in tropical environments, the signals for reproductive timing may not be robust, which can lead to differences in the physiological breeding season between males and females (Spinage 1973; Bronson 1988; Moore et al. 2005). If the triggers for reproduction become temporally uncorrelated over evolutionary time, then I might expect linking mechanisms like sperm storage or embryonic diapause to evolve (Birkhead & Moller 1993). In species exposed to rapidly changing environments, due to climate change or being introduced to new environments, physiological reproductive cycles of males and females may become unsynchronised (Paoli et al. 2018). Here I define this mismatch as temporal shifts in male and female breeding patterns. Although several studies have examined the causes of among-population asynchrony in male and female breeding cycles (Primack 1980; Post et al. 2001; Moore et al. 2005, Walter et al. 2015; Waddle et al 2019), few have examined reproductive asynchrony between sexes within a population, to distinguish its causes. Particularly lacking in the literature is an examination of populations introduced into novel environments where seasonal cues are different from those experienced in the native environment.

Deer provide an excellent system to study asynchrony in reproductive periods. Deer exhibit wide among-population variation in physiological reproductive cycles, ranging from extremely synchronised to completely asynchronous populations (Asher et al. 2000). For many deer species, the environmental drivers of male and female reproductive cycles are well understood (Mitchell & Lincoln 1973; Bubenik et al. 1991; Clements et al. 2010; Rodriguez-Hidalgo et al. 2010; Asher 2011).

Female reproductive cycles are often strongly influenced by conditions that support pregnancy and offspring survival, such as high food availability, mild weather, or low predation rates (Patterson 1965; Raveling 1978; Wingfield 1984; Asher 2011; Contreras-Moreno et al. 2019; Froy et al. 2019). The degree of synchrony in female receptivity may be influenced by factors such as the length and severity of low resource periods (Bronson 1988). For example, extreme reproductive synchrony (ie., short periods of synchronised female receptivity) may benefit species where there is a narrow window of high-quality resources that allow for the greatest reproductive success (eg., temperate regions), while lower synchrony in female receptivity may benefit species with longer windows (eg., tropical regions; Loe et al. 2005; Ahreshtani et al. 2012).

In contrast to females, reproductive cycles of male deer are often driven by photoperiod (Lee 1970; Lincoln et al. 1984; Bubenik et al. 1987; Asher 2011). In most deer, males undergo a synchronised annual cycle where antlers are grown and then shed (Bubenik et al. 1987; Tomas 1995; Ungerfeld et al. 2008). Antlers are used during confrontations with other males to secure mates, and act as an indication to females of male fitness and condition during a period called the rut (Bubenik et al. 1991; Clements et al. 2010; Vanpe et al. 2010; Heckeberg 2017). During this cycle, males that are without antlers, or still growing antlers (i.e., in velvet), are not competitive with other stags (Gosch & Fisher 1989). In many deer, this period of hard antler is also associated with an increase in testicular volume, and sperm quantity and quality (Lincoln et al. 1984; Loudon & Curlewis 1988; Gosch & Fischer 1989; Willard & Randel 2002; Hernandez-Souza et al. 2013). In some deer, such as fallow (*Dama dama*) and roe deer (*Capreolus capreolus*), males are unable to reproduce out of hard antler (Gosch & Fischer 1989; Goeritz et al. 2003). In others, such as chital (*Axis axis*) and Reeve's muntjac (*Muntiacus reevesi*), males can produce viable sperm regardless of season and antler phase (Loudon & Curlewis 1988; Chapman & Harris 1991; Willard & Randel 2002).

In environments with less variation in day length, such as in tropical habitats, male deer exhibit less dependence on photoperiod (Rutberg 1987; van Mourik & Stelmasiak 1990; Asher 2011; Contreras-Moreno et al. 2019; Pereira et al. 2020). Although ungulate breeding cycles have been extensively examined in relation to latitude (Spinage 1973; Fletcher 1974; Bubenik et al. 1990; Bonenfant et al. 2003; Loe et al. 2005; Asher 2011; English et al. 2012; Pereira et al. 2020), causes of within-population and between-sex asynchrony are seldom addressed (Moyes et al. 2011).

Deer are also a good study taxa to examine reproductive asynchrony because many species have been introduced to new locations and latitudes worldwide. As few studies have examined the causes of reproductive asynchrony in introduced mammals, examining introduced deer allows comparisons of reproductive patterns in the same species exposed to environments with different environmental triggers for reproduction (Fletcher 1974; Bubenik et al. 1990; Asher 2011; Moyes et al. 2011).

Chital deer are a sub-tropical to tropical cervid native to India, Nepal, and Sri Lanka, that have been introduced to locations around the world including Argentina, Chile, Croatia, Hawai'i, and Australia (Long 2003). In their native range, the presence of hard antlers in adult male chital is associated with lengthening photoperiod (Raman 1997; Sankar & Acharya 2004; Ramesh et al. 2012). Female chital have a seasonal peak in conceptions that correlates with peak rutting activity in males, although they can produce fawns throughout the year (Graf & Nichols 1966; Mungall & Sheffield 1994; Ahrestani et al. 2012; Ramesh et al. 2012). This is conserved in their introduced ranges, except for one population (Croatia) where the reproductive seasons have changed, suggesting that chital do have flexible timing of reproduction (Kavcic et al. 2019)

In this study, I examined the reproductive synchrony of male and female chital in a population introduced to tropical Australia in 1886 (Roff 1960). I predicted that, as in their native range, photoperiod would drive male reproductive condition (Willard & Randel 2002). Given the highly seasonal rainfall in this region and the influence of rainfall-driven nutrition on chital body condition and abundance (Watter et al. 2019), I predicted that timing of female reproduction would be heavily influenced by rainfall patterns (Clutton-Brock et al. 1983). I predicted that if males were influenced by photoperiod as a cue for antler formation, and females use rainfall, asynchrony between male and female physiological reproductive cycles may be observed.

Methods

To investigate patterns of antler growth in male chital deer, I collected data between 2014-2019 from camera traps, culls, and incidental observations. Camera traps were deployed at Spyglass Beef Research Facility, a cattle property covering 38,221 hectares in the Charters Towers region, North Queensland, Australia. Three seasons occur at the study site: wet (January to March; 12.55 daylight hours), cool dry (April to August; 11.07 daylight hours), and hot dry (September to December; 12.52 daylight hours), although the timing of rainfall in these seasons can vary. This region is considered semi-arid, experiencing highly seasonal rainfall (average 689mm), with ~75% of the rainfall falling between November and March.

Camera trapping was conducted with 94 Bushnell Aggressor cameras spaced at least 500-m apart (methods detailed in Appendix F). Cameras were deployed for at least one month each between October 2017 and November 2018. Cameras captured three images per trigger, with a 1-

second delay between photos. For analysis, I ensured there was one hour or more between events (Bowkett et al. 2007; Amin et al. 2014; Rovero et al. 2017). This time frame was used to avoid repeated counting of the same individuals, and to minimise pseudoreplication (Tobler et al. 2009; Rovero et al. 2017). All photos were time- and date-stamped. Cameras were installed approximately 30-50cm above and perpendicular to the ground, and faced north or south, to avoid the rising or setting sun. There were three months when cameras were not active (May-July 2018). Images were identified and organised using WildID software and ZSL CTap software (Amin et al 2014; TEAM Network 2017 [https://www.wildlifeinsights.org/team-network]). Records of incidental observations of males were also collected between 2014-2019. In both camera trap images and incidental observations, only stags that could be positively identified were included in analyses. If a stag's antler stage was uncertain or unknown, it was excluded.

Camera trap data and incidental observations were supplemented with data from deer shot from 2014-2019 in the Charters Towers region (20.0770°S, 146.2601°E). Chital were shot from a helicopter on nine properties in the region in October-November 2016 (five properties), November 2017 (three properties), and March 2018 (three properties) as part of a governmental feral animal control program. Research samples were taken from animals shot on two properties (10 males and 10 females on each occasion) in October 2014, March 2015, October 2015, and March 2016 (Watter et al. 2019). Because chital deer are legally declared a pest animal (Queensland's *Biosecurity Act 2014*), no permits were required for culls on private lands. Deer shot for research were under the authorization of the Queensland Department of Agriculture and Fisheries (Ethics permit number: SA 2014/07/475).

Data on female seasonality of reproduction were determined by dissection of shot females and measurement of their foetuses if they were pregnant. I determined the age of foetuses using equations parameterized from prior data (Graf and Nichols 1966; note that in Hawaii, average female chital weight was 44.36kg (Graf and Nichols 1966), while the average female weight in this study was 45.0kg). Graf and Nichols (1966) reported a gestation length of 229 days, and a birth weight of 3690 grams for this species. I used these values to develop age estimates based on foetal size at dissection. Chital foetuses grow exponentially for the first 120 days (when their mass is < 560g), and then growth slows and becomes linear (Graf & Nichols 1966). So, I developed two equations to predict age: one for each growth phase, depending on foetus size at culling. For the initial exponential growth phase, I assumed a weight at day 1 of 1.1396 (g) (Graf and Nichols 1966), and a growth constant of 0.0504. For foetuses < 560g ($R^2 = 0.986$), I calculated age as:

$$age\ (in\ days) = ln\ (Y / 1.3196) / 0.0504$$

Where Y equals foetus weight (g). For foetuses larger than >560g, and in the linear growth phase ($R^2 \sim 1$), I calculated:

age (in days) = (Y – -2832.25) / 27.95

These equations allowed me to determine the date of conception for each pregnant female, by subtracting foetus age in days from the date of dissection. I determined conception date for 117 pregnant females from shot samples. Conception dates were grouped into months to generate monthly conception numbers between 2014-2019. Because no cull was undertaken in early 2017, conception dates from December 2016 to March 2017 are missing.

Analyses

To investigate male seasonality, I calculated the proportion of stags in hard antler from the total number of stags that were observed in each given month. This proportion was analysed using the cosinor function from the *season* package that captures seasonal patterns using a sinusoid, thus accounting for the serial nature of months (Barnett et al. 2021). All analyses were conducted in R (V3.6.2, R Core Team, 2019) and visualised using the *ggplot2* package (Wickham 2016).

To investigate environmental variables that may influence male seasonality in reproduction, I constructed generalised linear models with the proportion of males in hard antler as the response variable, and average monthly absolute day length (58-year average), year and photoperiod interaction (to test for year-to-year differences). Monthly rainfall totals for the region were obtained from the Australian Bureau of Meteorology for months between July 2013 and March 2018. Rainfall totals were calculated for periods zero, one, three, and six months prior to each month (including the month of each antler measure) and used as predictive variables. Predictor variables were scaled prior to analyses by converting to *z* scores. The best model was identified by the lowest AIC value using package *MuMIn* (Anderson et al. 2000; Barton 2019). Where a single top model could not be identified (i.e., there were multiple top models with a $\Delta AIC_c < 2$), model averaging (the practice of using multiple models for making predictions; Banner & Higgs 2017) was performed (Burnham & Anderson 2002). If antler phase in males was related to photoperiod, I expected a significant relationship with photoperiod, with peak hard antler occurring in months with shortening days. If male antler phase was influenced by resources, I expected a relationship between antler phenology and rainfall.

To examine whether conception by females was seasonal, I calculated the proportion of conceptions per month. These proportions were calculated as: the number of conceptions observed in a particular month (determined using the above formulas to age each foetus) divided by the total number of culled females that could have been pregnant during that time period (i.e., back-calculating the age of the oldest foetus from each cull date to provide a total number of females that could be pregnant in a given month). To determine if the females exhibited seasonal patterns in conceptions, I examined the proportion of female conceptions using the cosinor function in the *season* package in a similar manner to the males (Barnett et al. 2021).

To determine the factors that may have influenced the conception rates, I constructed models using a range of biological and environmental variables and sued the number of conceptions in a given month as the response variable with the total number of females included as an offset (to account for the differences in sample size). Because conception in many deer species is related to resource availability, I used rainfall as a proxy for vegetation quality. Rainfall totals were calculated for periods zero (i.e., in the month of conception), one, three, and six months prior to conceptions (including the month of conception). As photoperiod or seasonal factors strongly influence the timing of reproduction in deer, I included average monthly day length (Jan 1993-Dec 2017). Finally, to investigate if conceptions were correlated with male antler phase, I included the number of males in hard antler as the response variable with the total number of males that were sampled in each month included as an offset. If male antler phase and female conceptions were synchronised, I would expect the presence of hard antlers to be positively correlated with conception rate. Generalised linear models (using the *glm* function) were used to examine relationships between the difference in predicted and observed rates of conception and rainfall (0, 1, 3, and 6 months prior to conception), photoperiod, year and photoperiod interaction, and proportion of males in hard antler. As with males, predictor variables were scaled prior to analyses. The most parsimonious models were again determined using AIC and model averaging was performed if there was more than one top model ($\Delta AIC_c < 2$).

Results

I recorded the antler stage of 2397 stags in shot samples (n = 158), incidental observations (n = 1530), and photos from camera trapping (n = 709). Of these, I recorded 923 stags in hard antler (60%). There were seasonal peaks in the number of males in hard antler (May-August every year) with a consistent decline in the number of stags in hard antler from September through to November ($p < 0.05$; Appendix E Table E.1; Figure 4.1). Following model selection (Appendix E Table E.2), there were three top model candidates (rainfall alone ($AIC_c = 0.00$) and rainfall + 6 month rainfall (AICC = 0.58), so model averaging was performed. Peak hard antler phase was best explained by absolute day length only (Table 4.1), which had a negative influence on the proportion of stags in hard antler ($R^2 = 0.570$). Other models examined (rainfall, year, and photoperiod) did not explain more of the variation.

Table 4.1. Model averaged parameter estimates from the best (Δ AICc <2) generalized linear models (GLM) for the proportion of stags in hard antler from Appendix E Table E.2, where daylight is the average hours of daylight for a given month, and 0, 1, and 6 months are the total rainfall in the 0, 1, and 6 months prior to a given month, respectively.

	Estimate	2.50%	97.50%
Intercept	1.94	0.70	3.18
Daylight	-0.20	-0.30	-0.11
6 month	0.00	0.00	0.00
0 month	0.00	0.00	0.00
1 month	0.00	0.00	0.00

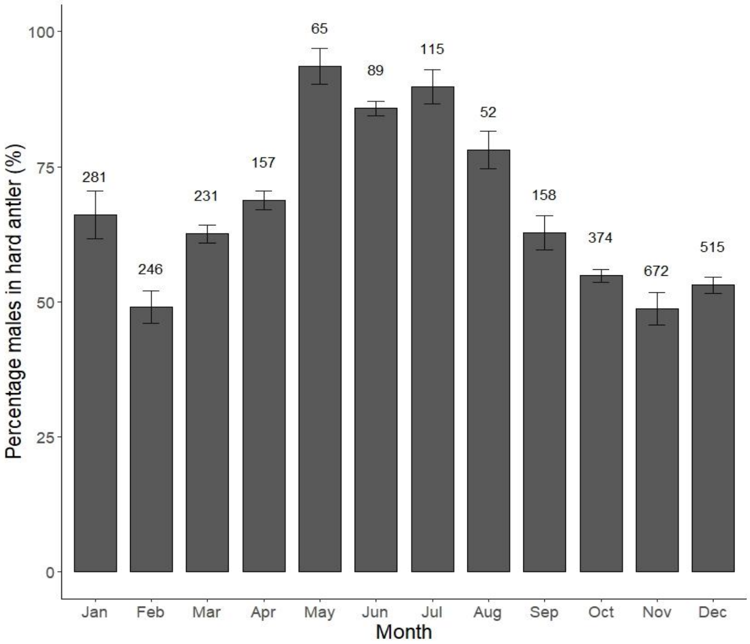

Figure 4.1. Relationship between the percentage of male chital deer in hard antler in any given month over 2014-2019 in north Queensland. Minimum monthly value for the percentage of males in hard antler was 35%.

Similar to the males, I found seasonal peaks in female conceptions, although conceptions also occurred year-round ($p < 0.05$; Appendix E Table E.3, Figure 4.2). Model selection resulted in two top model candidates (Appendix E Table E.4), so model averaging was performed. Female conception rates were best explained by the rainfall 3 months prior to conception, whereby increased rainfall correlated with increased conceptions ($R^2 = 0.299$; Table 4.2, Figure 4.3). Hard antler rate appeared in the top models (Appendix E Table E.4) with a marginally positive relationship with conception rates, but confidence intervals were broad following model averaging. The moderate relationship between rainfall and conception rates was consistent across years, based on a lack of support for models with an interaction between year and rainfall metrics. There was no significant relationship between female age and conception date ($p = 0.185$).

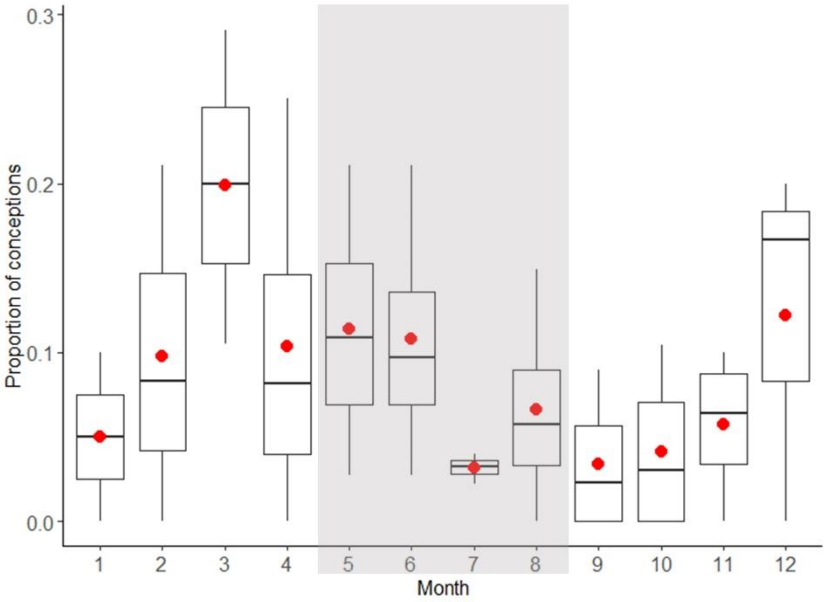

Figure 4.2. Average monthly proportions of conceptions in female chital in the Charters Towers Region, Australia, over 2013-2018. Boxplots show the median proportions per month as horizontal lines and the red points indicate the mean proportion per month. Boxes indicate the 25th and 75th percentiles and the whiskers represent either 1.5 times the interquartile range or the maximum value; values outside of this are plotted as points. The shaded region represents the seasonal period during which males are in peak hard antler, which I predicted would be periods of peak conceptions, should males and females be in synchrony.

Table 4.2. Model averaged parameter estimates from the best (Δ AICc <2) generalized linear models (GLM) for the number of conceptions from Appendix E Table E.4, where 3 months is the total rainfall in the 3 months prior to conception, and hard antler is the % stags in hard antler in the month of conception. The total number of females that could have conceived in each month was included as an offset to account for differences in sample sizes.

	Estimate	2.50%	97.50%
Intercept	-3.24	-5.307	-1.167
3 month	0.00	0.002	0.006
Hard antler	0.00	-0.005	0.023
Daylight	-0.02	-0.403	0.208

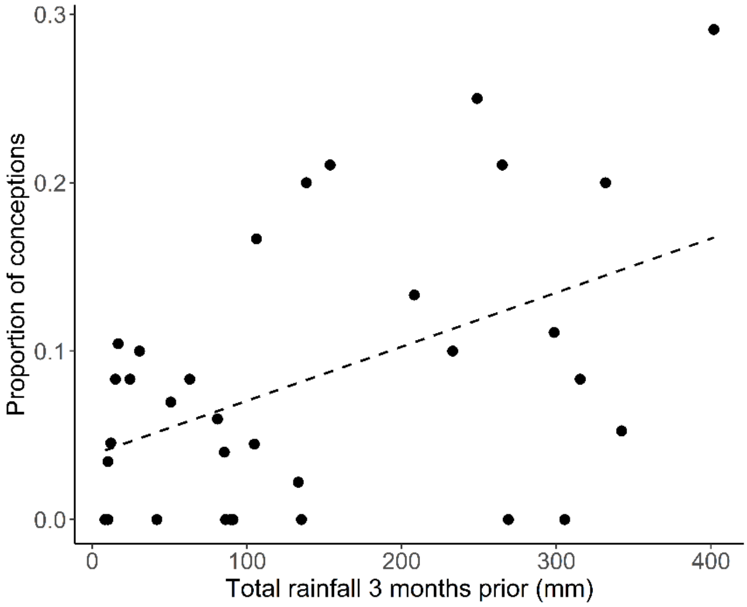

Figure 4.3. Relationship between the monthly proportion of conception rates in chital deer, and the rainfall three months prior to the month of conception.

Discussion

Male chital were more likely to be in hard antler during May-August, exhibiting a strong seasonal pattern in their reproductive physiology. The time when most males were in hard antler in this population was highly correlated with shorter days, and thus it is likely that day length triggers physiological processes associated with reproduction in males. In their native range, the rutting period is also seasonal, except it occurs during the summer (Moe & Wegge 1994; Sankar & Acharya 2004; Umapathy 2007). This means that if daylength is driving the timing of reproduction for male chital in Australia, they have switched their rut from longer to shorter day lengths. The exact manner and timeframe when this switch occurred in the past 130 years is unknown. In India, chital populations closer to the equator have longer rutting periods compared to their northern counterparts (Sankar & Acharya 2004). It is generally believed that male deer living closer to the equator are less sensitive to day length cues, and thus exhibit smaller seasonal peaks in their reproductive cycle (Asher 2011). In the northern Australian chital population, which occurs in tropical latitudes, there are males in hard antler throughout the year. This potentially could have important implications for the mating system in this population. It should be noted that male chital have the potential to breed with females at any antler stage (Graf & Nichols 1966; Willard & Randel 2002), but testes size, sperm volume and quality increase when they are in hard antler (Loudon & Curlewis 1988; Willard & Randel 2002). Given this change in their reproductive physiology, and the use of antlers in male contests, it is likely that there is a close association between reproductive success and antler stage.

Female reproduction was also significantly seasonal in this population although there were females that were able to conceive year-round. Conceptions were positively correlated with the quantity of rainfall in the three months prior to reproduction. In some deer species, females can conceive only when they are in sufficient body condition (Mitchell & Lincoln 1973; Clutton-Brock et al. 1983; Flajsman et al. 2017; Paoli et al. 2018). The pattern exhibited by female chital in this study is consistent with this mechanism driving rates of conception. If seasonal rainfall patterns were predictable, the timing of births in this population would coincide with the end of the dry season. This would mean that the season with high food availability coincides with the period of highest energetic need for reproducing females. Given the semi-arid climate in this region, it is logical that females respond strongly to changes in rainfall. While rain during the wet season (December-March) accounts for almost 75% of the yearly rainfall, there is considerable year-to-year variation in the amount (CV (annual rainfall) = 47%) and timing (range 32-99%) varies tremendously from year to year (SD ± 0.134). In any given year, the timing of female reproduction could diverge widely from what would be expected based on a predictable rainy season.

The different mechanisms driving the timing of reproductive activity in male and female chital deer has led to a mismatch in the timing of reproductive seasonality in this introduced population, a process which may also be relevant to the mating systems of other deer species. Increasing reproductive mismatch may not be deleterious to an abundant invasive species, or to populations that already exhibit an extended breeding period, as shifts are not going to drastically impact the availability of fertile reproductive partners. However, for populations with discrete breeding periods, the effects of asynchrony in reproductive activity between males and females may result in greater variation in reproductive success. Greater reproductive asynchrony should lead to greater reproductive skew, with fewer individuals contributing to the reproductive output of a population (i.e., greater mismatch between available males and females potentially reduces the number of animals receptive at the same time, and therefore, reproducing; Garnier et al. 2001; Ostner et al. 2008; Sukmak et al. 2014). In small populations, increased reproductive skew can lead to lower genetic diversity (Johnstone 2000), thus reproductive asynchrony may be a conservation concern in some species, particularly ones strongly affected by climate change. This prediction of increased reproductive skew may be counter-balanced by a decrease in female spatial aggregation, or an increase in the receptive period of females (effectively reducing the effect of increased mismatch in male-female reproductive activity; Figure 4.4; Perez-Gonzalez & Carranza 2011). In this case, increasing the length of time females are receptive, or reducing female gregariousness, would make it more difficult for individual males to monopolize females, thereby reducing male reproductive skew (Ims 1990; Say et al. 2003). Female chital already exhibit a high degree of receptive asynchrony, in that females may exhibit oestrus during any month of the year (Mylrea et al. 1999; Ahrestani et al. 2012). I have no evidence, however, that the estrous period affects chital grouping patterns, and thus conclude that reproductive asynchrony likely increases reproductive skew in this population. Quantifying patterns of male reproductive fitness in this population, and others, is likely to be a valuable direction for future research.

The pattern described here, in which reproductive asynchrony should lead to higher reproductive skew, may be different for other species with more discrete male reproductive seasonality. For example, in fallow (*Dama dama*) and roe deer (*Capreolus capreolus*), all males are in hard antler over a discrete period, outside of which no males are in hard antler and able to produce functionally competent spermatozoa (Gosch & Fisher 1989; Goeritz et al. 2003). Females coming into oestrus outside of this period of hard antler would not be able to find a viable male. Selection pressure in these systems will be on males to respond to the same cues the females use to come into oestrus or produce active sperm throughout the year. A change in external factors that affect the timing of female oestrus (e.g., rainfall), could have a deleterious effect on reproductive output in these populations.

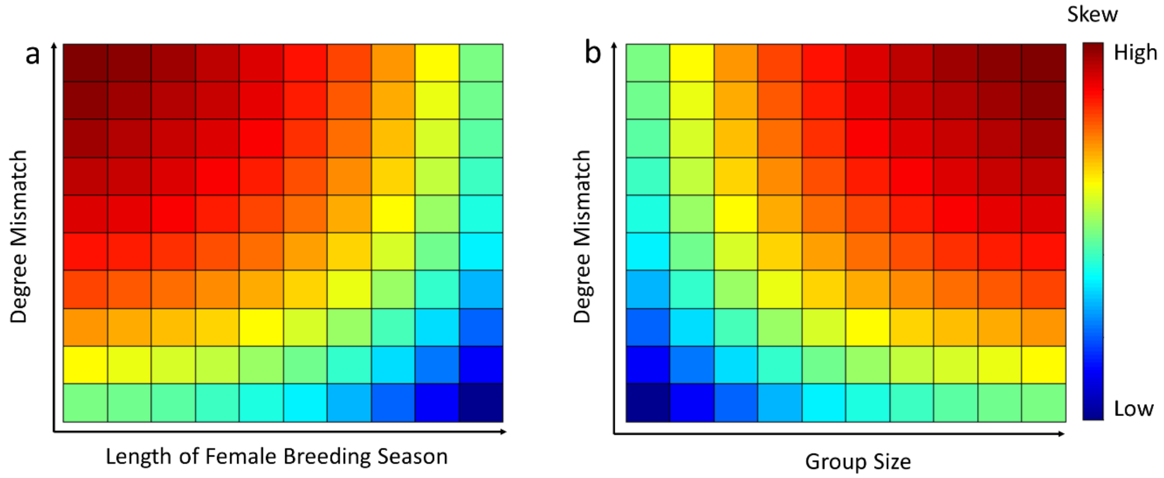

Figure 4.4. Hypothetical visualisation of the degree of reproductive skew (i.e., increasing or decreasing the proportion of individuals of each sex that are available to reproduce) in relation to the interaction between temporal (left; female breeding season) and spatial (right; group size) availability of females. In Figure 4.4a there is an increase in skew with decreasing length of the female breeding season and increasing mismatch (shorter breeding periods mean males can monopolise synchronised females) and in Figure 4.4b, there is a similar increase in skew with increasing group size and an increasing mismatch in peaks of male and female reproductive physiology (larger groups mean dominant males can monopolise them more and increase skew).

Anthropogenic climate change impacts the timing of seasonal behaviours such as reproduction (Bronson 2009; Todd et al. 2011). Much of the research studying changes in the seasonality of reproduction and revealing mismatches between resource availability and behaviors such as migration and reproduction, has focused on the effects of climate change (Rutberg 1987; Visser et al. 1998; Post & Forchhammer 2008; Gaillard et al. 2013; Stopher et al. 2014; Lameris et al. 2017). For example, female red deer (Bonnet et al. 2019), and reindeer (Paoli et al. 2018) have started reproducing earlier. In the current study, asynchrony between male antler phase and female conceptions in chital has occurred because they were introduced to a novel environment. Globally, in introduced ungulates, shifts in reproductive timing may cause reproductive asynchrony in various situations if the sexes use different environmental cues (Post & Forchhammer 2008; Moyes et al. 2011; Gaillard et al. 2013). Shifts in reproductive timing could impact a number of aspects of population biology such as behavior, mating patterns, and population genetics which could lead to long-term consequences for population viability, which may, in turn enhance or impede attempts to control population sizes, depending on the goal of management.

Chital deer hind

(drawing by author)

Chapter Five: Wild deer exhibit niche shifts in an Australian environment: where to from here?

Introduction

Invasive species are one of the leading causes of ecological change and biodiversity loss worldwide (Mack et al. 2000; Doherty et al. 2016). Humans have facilitated the invasion and subsequent spread of non-native species to previously inaccessible areas and niches (Tingley et al. 2014; Hernandez et al. 2018; Da Re et al. 2020). Here, a niche is defined as the range of ecological conditions in which a species can maintain viable populations (Valverde et al. 2011; Guisan et al. 2014; Srivastava et al. 2020). Factors such as propagule pressure can influence the probability of an invasive species' successful establishment in a novel environment, while other mechanisms such as adaptation, reduced competition, and reduced predation, can allow a species to expand its environmental niche (Kolar & Lodge 2001; Simberloff 2009; Lakeman-Fraser & Ewers 2013; Kumar et al. 2015; Tingley et al. 2014). Understanding the degree to which species shift their environmental niche post-introduction provides insights into invasion processes and assists with predicting which areas are vulnerable to future spread (Peterson 2011; Guisan et al. 2014; Braschler et al. 2019).

A species' ability to adapt rapidly to a novel environment can increase their probability of successful invasion and their likelihood of colonisation, as niche characteristics are often different between native and invaded environments (Sakai et al. 2001; Peterson & Nakazama 2008; Gallagher et al. 2010; Guisan et al. 2014). Many species have expanded into conditions that are not present in their native range, thus using more of their potential environmental niche or adapting to new conditions and spreading (Pearman et al. 2008; Beaumont et al. 2009; Blackburn & Duncan 2001; Guisan et al. 2014; Beaumont et al. 2009).

Species Distribution Models (SDMs) are frequently used to predict habitat suitability and invasion risk (Valverde et al. 2011; Tingley et al. 2014; Santamarina et al. 2019). Predicting suitable habitats based on the native distribution (or a limited invaded range) can severely underestimate the potential for an invasive species' establishment or spread in a novel environment (Morehouse & Tobler 2013; Tingley et al. 2014; Ahmed et al. 2017; Srivastava et al. 2020). It is, therefore, beneficial to use a species' global invaded distributions when modelling habitat suitability. Another potential problem with predicting habitat suitability for invasive species is that suitable habitat may occur in areas nowhere near a species' site of introduction (Elith & Leathwick 2009). For this reason, it's important to model habitat suitability along with connectivity (Soberon & Peterson 2005; Dunstan & Johnson 2007; Valverde et al. 2011).

Deer (order Artiodactyla) represent a highly adaptable and diverse family and occupy various niches around the world (Fraser 1996; Hudson & Jeon 2003; Fautley et al. 2012). Deer can have severe impacts on ecosystems through degrading habitats, competing with native species, and spreading diseases and parasites (Doran & Laffan 2005; Dolman & Waber 2008; Ens et al. 2016; Hess 2016). Invasive deer often have significant economic impacts, posing risks to motor vehicles, and competing with livestock for feed (Jesser 2005; McLeod 2009; Kusta et al. 2017). Humans have successfully established populations of deer globally (King 2005). Many deer have broad international introductions (largely as game resources; Forsyth & Hickling 1998) and, like other invasive species introduced to novel environments, have the ability to adapt, spread, and become invasive. Due to these extensive international introductions, calculating their potential niche based on worldwide occurrences is far more informative compared to species rarely found outside of their native range.

Deer were introduced to Australia in the early 1800s by acclimatisation societies (Roff 1960; Bentley 1967). Of the twenty-nine species brought to Australia (Table 1), six have established free-living populations, increasing in both population size and range (Bentley 1967; Moriarty 2004). These species have successfully established in multiple environments across Australia, and many deer are significantly degrading local ecosystems and economies (Jesser 2005; English 2007; Forsyth et al. 2012; Burgin et al. 2014; Davis et al. 2016).

To examine if deer exhibited niche shifts following their introduction into Australia, I compared niche overlap between each species' international and Australian ranges. I predicted that species with broader invasive distributions would exhibit smaller niche shifts between their international range and their Australian distribution compared to those species with limited global distributions. To identify areas vulnerable to future invasion in Australia, I created Species Distribution Models (SDMs) for the native and international ranges of the six successful species of invasive deer in Australia. I quantified niche shifts by comparing the similarity in suitable habitat as predicted by native and Australian ranges. I expected that species whose native range was most similar to available Australian habitat would have the largest potential for spread.

Table 5.1. The 29 species (and subspecies) of deer that were brought to Australia (the six with known wild distributions are in bold), and the states where they occurred.

Species	Latin name	First record	States held in
Barasingha deer	*Cervus duvaucelli*	1864	VIC, NT
Bawean deer	*Axis kuhlii*	1867	VIC
Chinese water deer	*Hydropotes inermis*	1867	VIC, SA
Chital deer	***Axis axis***	**1861**	**VIC, SA, WA, QLD**
Eld's deer (Panolia deer)	*Cervus eldii*	1900	VIC
Fallow deer	***Dama dama***	**1832**	**VIC, SA, WA, NSW, QLD, NT**
Hog deer	***Axis porcinus***	**1860**	**VIC, SA, WA, NSW**
Indian muntjac	*Muntiacus muntjak*	1863	VIC, SA, WA
- Tennasserim muntjac	*Muntiacus feae*	1926	VIC
Mouse deer	*Moschiola meminna*	1878	VIC, SA, QLD
- Java mouse-deer	*Tragulus jaranicus*	1864	SA, NSW
Mule deer	*Odocoileus hemionus*	1863	VIC
- Black-tailed deer	*Odocoileus hemionus columbianus*	1914	VIC
Musk deer	*Moschus moschiferus*	1871	VIC
Pere David's deer	*Elaphurus davidianus*	1903	WA, NSW
Red deer	***Cervus elaphus***	**1865**	**VIC, SA, WA, QLD, NSW**
Reindeer	*Rangifer tarandus*	1891	VIC
Roe deer	*Capreolus capreolus*	1874	VIC
Rusa deer	***Rusa timorensis***	**1865**	**VIC, SA, WA, NSW, QLD, NT**
- Batavia deer (Javan rusa)	*Rusa timorensis russa*	1868	VIC
- Molucca deer	*Rusa timorensis moluccensis*	1891	VIC
Sambar deer	***Cervus unicolor***	**1860**	**VIC, NSW, NT**
- Malay sambar	*Cervus unicolor equinus*	1898	VIC
- Borneo deer	*Cervus unicolor brookei*	1883	VIC, SA
Sika deer	*Cervus nippon*	1868	VIC
- Formosa sika	*Cervus nippon taiouanus*	1863	VIC
Visayan spotted deer	*Rusa alfredi*	1902	WA
Wapiti	*Cervus canadensis*	1886	VIC, SA, WA, NSW
White-tailed deer	*Odocoileus virginianus*	1877	SA

Methods

Species records and bioclimatic data

Species presence data for the six established deer species in Australia were obtained from open-access databases. Native range and international occurrence records were collected from Global Biodiversity Information Facility (GBIF; “GBIF.org”), and Australian occurrence records were collected from Atlas of Living Australia (ALA; "ala.org.au"). I supplemented Australian records with direct observations from "FeralScan", a citizen science platform to track feral deer observation records in Australia ("feralscan.org"). I also supplemented Australian records of chital deer with occurrence records collected from 2017-2020 using direct observations and systematic sampling campaigns (e.g., spotlighting and camera-trap surveys) conducted by the authors (Pople, personal comms). I first filtered imprecise records (precision greater than 10km) and ensured that this left at least 50% of the dataset and at least 20 unique records. I then repeated this at 1 km to ensure locations were as precise as possible while maintaining adequate sample size. I removed duplicates within 1 km^2 cells. This resulted in records for chital (n = 359), fallow (n = 7013), red (n = 16263), sambar (n = 869), rusa (n = 269), and hog (n = 79) deer. I selected 20 environmental variables from the literature likely to be important predictors of deer distributions in Australia (Appendix G Table G.1). I performed variable selection based on each variable's permutation importance, resulting in models using only variables that had a permutation importance of over 1% for each species.

Niche overlap methods

To estimate climatic niche overlap between the native and Australian ranges of the six deer species, I used the *ecospat* package (Broennimann et al. 2021), and R script developed by Di Cola et al. (2017; R Core Team 2017). First, to reduce multicollinearity I removed predictor variables that were highly correlated (Pearson correlation coefficient greater than 0.80) and were left with 16 variables (Appendix G Table G.2). I produced niche overlap plots comparing the deer's international and Australian niches using species records and environmental variables. To investigate how the six deer in Australia exhibited niche shifts between international and Australian ranges, I calculated a kernel density distribution map of each species' occurrence records (Di Cola et al. 2017). For each of the six free-living deer species in Australia, I compared the environmental conditions available in the international (all records outside of Australia) and Australian ranges. I created occurrence density models and determined the contribution of different environmental variables to species distributions. Niche overlap was quantified using Schoener's D index, which varies from 0 (complete dissimilarity) to 1 (complete overlap; Broennimann et al. 2012). I then tested for niche equivalency and similarity between each set of compared ranges, by randomising the occurrence records and calculating Schoener's D 1000 times each. This value was then compared to the observed value. Niche equivalency tests determine whether the niches in two geographic ranges are equivalent by merging the two ranges (international and Australian), and then splitting the resulting merged layer into two (with the same sample size as the original ranges) and comparing the Schoener's D for each pair of datasets (Warren et al. 2008; Carretero & Sillero 2016; Strivastava et al. 2020). However, as niche equivalency tests only examine exact species occurrences, and not the available environmental conditions or spaces, they are often not used. In contrast, niche similarity tests assess whether the species niches are more similar than expected by chance, considering the ecological niche of the two species and accounting for differences in the environment surrounding the records (Broennimann et al. 2012; Da Re et al. 2020). Here, I used the niche similarity test to assess both the niche shifts and the niche conservatism exhibited by deer among different aspects of their range (Strivastava et al. 2020). Rejection of the niche similarity hypothesis ($p < 0.05$) indicates that the occupied environmental conditions in one range are more similar to the conditions occupied in another range, than would be expected by chance.

I then calculated the niche shifts, niche expansion, and the unfilled niche (niche unfilling). Niche stability represents the proportion of one niche with identical conditions as in another range (i.e., determining whether species occupy identical environmental space in both ranges). In contrast, niche expansion represents the non-overlapping environmental space between ranges (i.e., determining if species occur in novel environmental conditions that are not found in their native range; Petitpierre et al. 2012). Finally, an unfilled niche represents the proportion of occurrence records in one range that are present in unused environments in another range (i.e., a species only partially fills its environmental niche in an invaded range; Polidori et al. 2018).

Maxent modelling methods

To model habitat suitability for each of the six deer species in Australia, I constructed species distribution models using maximum entropy (MaxEnt V. 3.4) modelling. MaxEnt uses occurrence records and used a target background that was based on known occurrences of similar species (in my case all global records of deer and Australian records of macropods (*Macpodidae* spp.), buffalo (*Bubalis bubalus*), and goats (*Capra hircus*) since I needed background data in Australia and there are no native deer. As such I used macropods as the Australian native herbivore, and buffaloes/goats as a widespread invasive browser/grazer equivalent. This type of target background corrects for sampling bias (Phillips et al. 2009). to estimate the probability of the presence of a species, generating an index of suitable habitat from 0 (lowest suitability) and 1 (highest suitability; Philips et al. 2006; Elith et al. 2011). I used the selected environmental variables (Appendix G Table G.1) to predict the distributions of the six deer species in Australia. I then used the “Fixed cumulative value 10” threshold, as determined by the MaxEnt output, to set the threshold for discriminating suitable from non-suitable habitat. I used the lowest recommended threshold to avoid underestimating potential suitable habitat, which could be important for invasive species management.

To determine how the six deer species in Australia are likely to spread in the future, I created estimates of present range using α-hull methodology (Burgman & Fox 2003) in the *alphahull* package (Pateiro-Lopez & Rodriguez-Casal 2019). I applied an α-hull value of 1.5 to all species. Using these occurrence records, I generated maps of the deer's present ranges and overlaid those with maps of invasion risk. Invasion risk maps were generated using the suitable habitat layer (established using global occurrence records). I first calculated cost distance from known occurrences using R function accost() from the package *gdistance* (Etten 2017), which calculates the 'accumulated distance' using the habitat suitability as a cost surface. That is, the more suitable a grid cell is, the easier it is for the species to spread across it from a known point of occurrence. Then I used this cost distance from known occurrences to down-weight the initial suitability map. That is, areas that are far away and hard to get to might have a high suitability but the invasion risk here is still quite small. I then scaled these values as 0 (very far and hard to invade) to 1 (close to occurrences, with high invasion risk). To determine the total area where deer could potentially spread, I removed the α-hull polygons from the maps of suitable habitat (i.e., the present range), and then calculated the area remaining.

Finally, to identify dissimilarity in suitability between the native ranges of deer and their range in Australia, I applied Multivariate Environmental Similarity Surface analysis (MESS; Elith et al. 2010). MESS analysis allows visualization of the similarity between pixels that are predicted to be suitable in Australia (as determined from the MaxEnt modelling), compared with conditions at known occurrences in the native range. Here, a positive value represents a pixel where there is high similarity between native and invaded habitat suitability, and a negative value indicates dissimilarity between native and invaded habitat suitability (Elith et al. 2010; Broennimann et al. 2014).

Results

Niche shifts

I found evidence of niche shifts when I made pair-wise comparisons of each species' international and Australian ranges with low niche overlap ($D = 0 – 0.292$; Table 5.2; Appendix G Figures G.1 – G.6). Chital deer exhibited significant similarity between their international and Australian niches ($p < 0.05$). All species, except chital and red deer, exhibited a relatively high degree of niche expansion, undergoing significant changes following introduction to Australia (Figure 5.1; Table 5.2). Chital and red deer in Australia exist within the total niche envelope of their international ranges, thus exhibiting limited niche expansion (0.007 and 0.134, respectively) and high stability (0.993 and 0.866, respectively). Despite this, red deer still exhibited non-significant niche similarity between international and Australian ranges (p = 0.150). Fallow deer also exhibited relatively high niche stability (0.892; Table 5.2), although unlike chital or red deer, fallow deer exhibited some degree of niche expansion (Table 5.2). Hog deer exhibited no niche overlap between international and Australian ranges (Figure 5.1c) and so showed no niche stability (0.000), with high niche expansion (1.000).

Table 5.2. Results of equivalency and similarity testing for niche overlap of the international and Australian distributions of each of the six deer species in Australia.

	Schoener's D	Similarity	Expansion	Stability	Unfilled
Chital	0.087	**0.010**	0.007	0.993	0.799
Fallow	0.292	0.061	0.108	0.892	0.337
Hog	0.000	1.000	1.000	0.000	1.000
Red	0.041	0.150	0.134	0.866	0.725
Rusa	0.317	0.060	0.715	0.285	0.799
Sambar	0.064	0.231	0.082	0.918	0.968

Species niche profiles for each variable were also assessed (Appendix G Figures G.7 – G.12), and several variables (maximum temperature in warmest month, minimum temperature in coldest month, and average annual rainfall) were selected to compare international and Australian ranges of deer. Fallow deer have spread into warmer niches (max temp = 4.04°C and min temp = 4.87°C warmer) in Australia compared to other parts of their international range. Likewise, hog and rusa deer have shifted into drier (average annual rainfall 1288.9mm and 502.45mm less, respectively) and colder ranges following introduction to Australia (max temp = 8.76°C and 3.28°C colder, respectively, min temp = 5.67°C and 9.55°C colder, respectively). Red deer shifted to wetter (135.99mm) and warmer areas (max temp = 4.29°C, min temp = 8.85°C warmer) and sambar are present in colder areas (max temp = 9.32°C, min temp = 9.89°C colder) than those experienced in their international ranges. In contrast, chital inhabit niche profiles in Australia that are very similar to their international range, although the Australian range is drier (average annual rainfall = 534.05mm less in Australia; max temp = 2.46°C, min temp = 0.92°C colder in Australia).

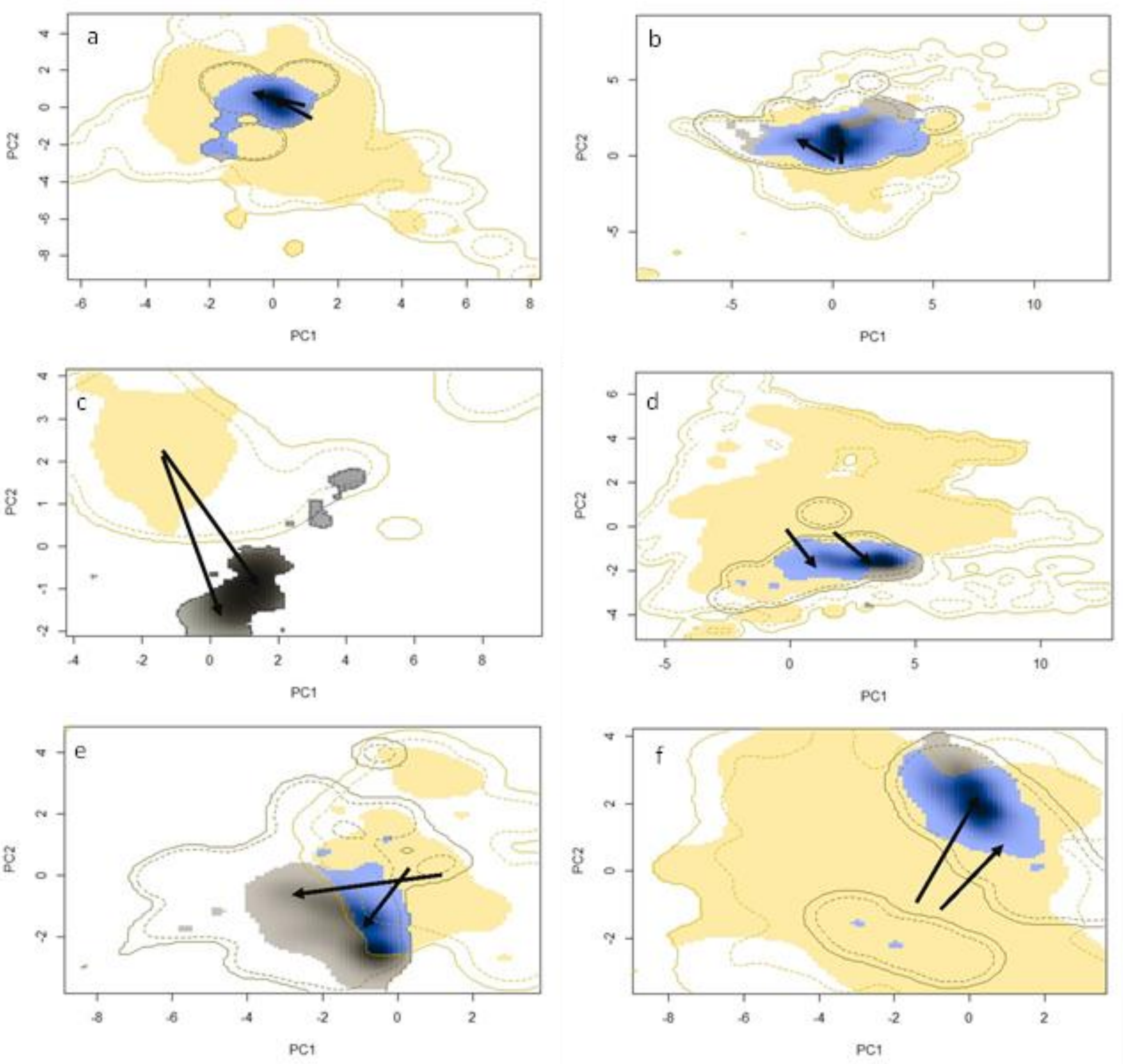

Figure 5.1. Niche overlap (blue) of deer between international range (tan) and Australian range (dark brown; a. chital, b. fallow, c. hog, d. red, e. rusa, and f. sambar). The international range was calculated using all records outside of Australia. The Australian range was modelled using records from Australia only. In all plots, blue areas represent the overlap between the different niches. Darker patches represent the highest population density in both ranges, and solid and dashed contour lines illustrate 100% and 50% of the available environmental space, respectively. Arrows visualise the shift of the centroids between respective distributions.

Habitat suitability modelling and present ranges

My models predicting the future suitable habitat of deer in Australia performed well (AUC values for all species were greater than 0.85; Appendix G Figure G.13). Contributing variables are also presented in Appendix G (Table G.3). Of all deer species examined here, chital and hog had the largest potentially suitable areas that had not yet been invaded, leading to a high percentage difference between areas of presently occupied suitable habitat and areas that had not yet been invaded (4,790% and 1,443%, respectively; Table 5.3). Fallow had the largest area of uninvaded suitable habitat (123,665 km), but because it has invaded such a large area already, this only represented 19% of the area that is presently occupied (654,193 km). Rusa exhibited a relatively small area of potentially suitable habitat not yet invaded (18,668km), however this represented a 73% increase from the area that it presently occupies. Red and sambar both exhibited much smaller areas of uninvaded but potentially suitable habitat (2% and 16% respectively).

Table 5.3. Total area (km^2) that is presently occupied (present range) and uninvaded suitable habitat, calculated from Figure 5.2. The % difference represents the proportion of the area between the present range and the threatened range that has not yet been invaded.

	Present range	Uninvaded	% Difference
Chital	10,667	510,957	4,790
Fallow	654,193	123,655	19
Hog	6,916	99,806	1,443
Red	262,287	5,188	2
Rusa	25,657	18,668	73
Sambar	101,957	15,953	16

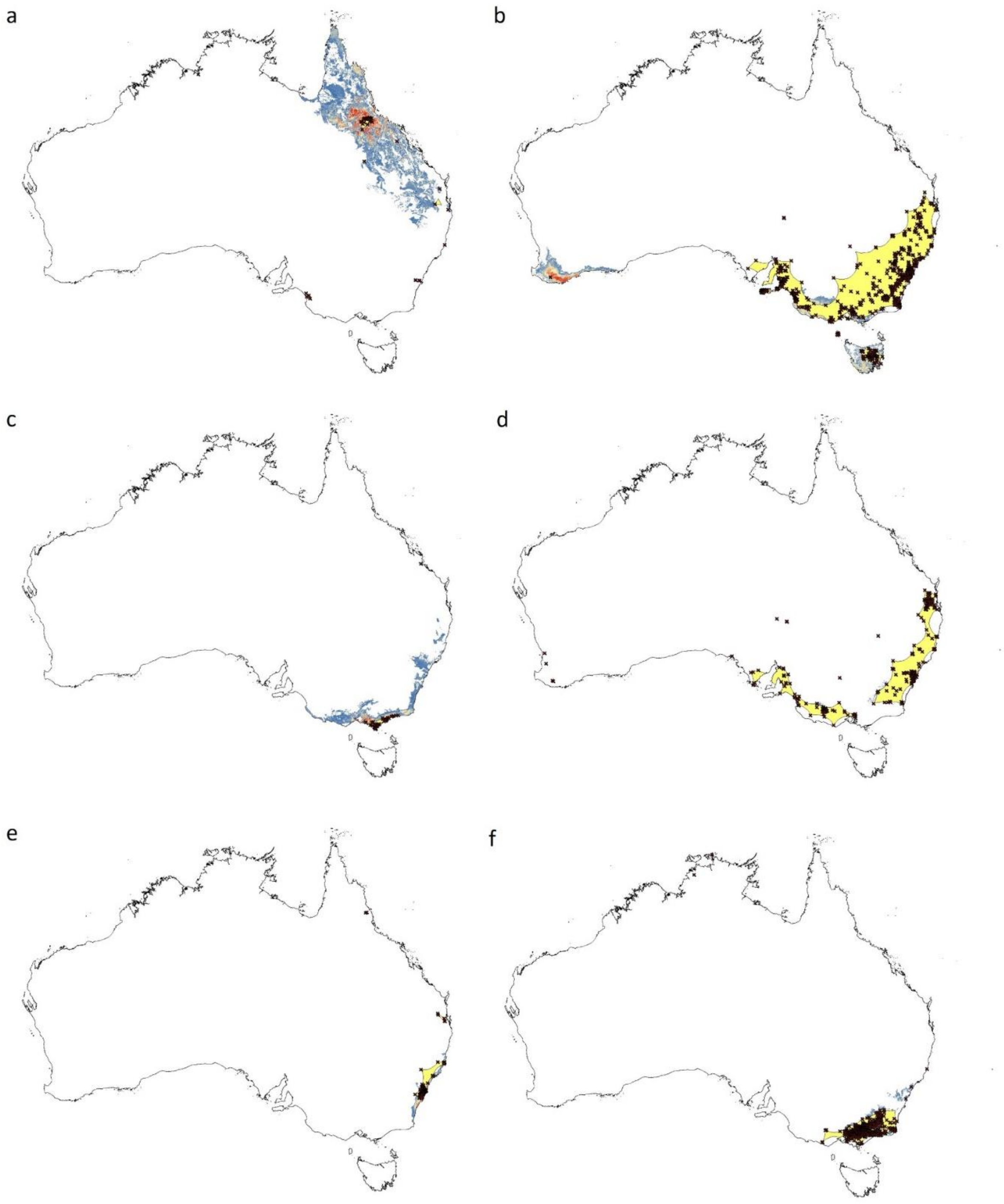

Figure 5.2. Maps of invasible habitat and future spread range from high vulnerability (red) to low vulnerability (blue) as determined by MaxEnt modelling, including the present estimated ranges (yellow) and records (crosses) of the six feral deer species in Australia: a. chital, b. fallow, c. hog, d. red, e. rusa, and f. sambar.

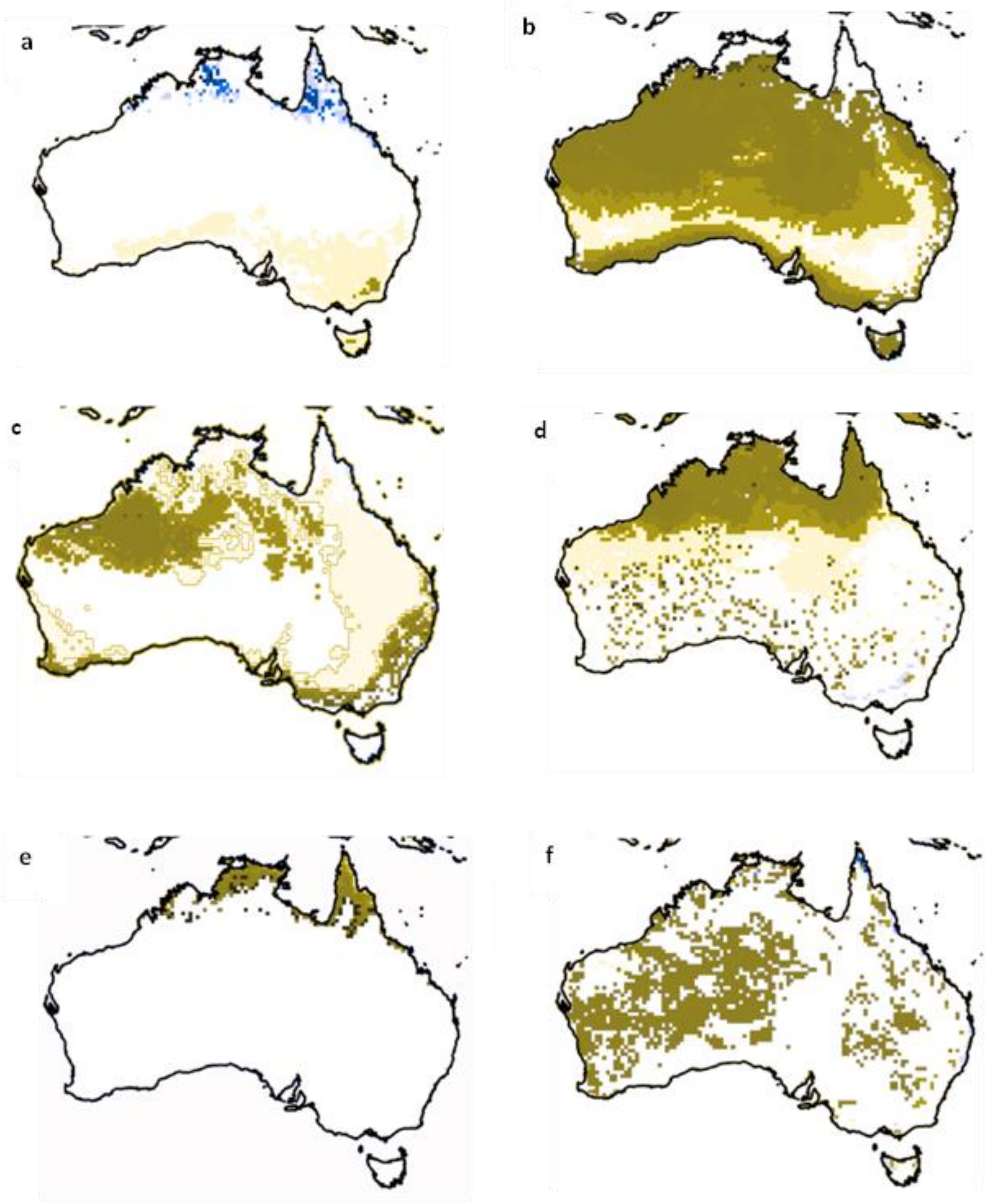

Figure 5.3. Similarity between habitat suitability predicted from native and introduced ranges of the six deer in Australia (a. chital, b. fallow, c. hog, d. red, e. rusa, and f. sambar), dark blue indicates high similarity, dark brown indicates low.

Discussion

Five of the six deer species introduced to Australia have exhibited niche shifts compared to their international niche profiles (fallow, hog, red, rusa, and sambar; Figure 5.1). Range estimate models suggest that fallow, red, and sambar deer have already spread beyond habitat expected to be suitable from modelling. In contrast, chital, hog, and rusa deer have the potential to spread much further than their present distributions. Of all the species examined, chital have the greatest predicted range in Australia, orders of magnitude greater than the other species. As such, chital potentially represent a huge problem in northern and eastern Australia.

In the future, deer in Australia are likely to spread much further than their current distributions or range estimations (Figure 5.2). Fallow deer are currently spreading north from their current distributions in Victoria and New South Wales, beyond habitat predicted to be suitable, and establishing in areas that are warmer than I would expect given the international range they occupy. Likewise, red deer are present in areas that are warmer, but also wetter than where they occur in their international range. Hog and rusa have shifted into drier and colder ranges following introduction to Australia. Hog deer have a high degree of potentially invasible habitat north of their current distribution in Victoria, and it is likely that spread will initially occur into this area. Likewise, rusa ranges are expanding along the south-eastern coast of Australia. Finally, sambar are predicted to spread further along the north-eastern coast of their present range. Many of these invasible areas represent significant agricultural and natural (conservation or native vegetation) areas. Deer in Australia are already competing with livestock for forage and feeding on pastures and crops (Bentley 1998; Davis et al. 2016). Deer invasions into natural areas are likely to cause degradation of water quality through trampling, erosion, and increased nutrient loading (McDowell 2007; McDowell 2008). Impacts of deer are, therefore, likely to increase in these sectors as deer populations continue to grow and spread beyond their present distributions.

As populations increase in size, genetic variation should also increase, which facilitates evolution and adaptation to new environments (Lee 2002; Urban et al. 2007). Meanwhile, population expansion can drive individuals into suboptimal habitats, thus forcing animals to face novel environmental conditions (Hardie & Hutchings 2010; Urban et al. 2007). As these deer species continue to spread, genetic adaptations on the invasion front can enable future spread through niche expansion and evolution (Urban et al. 2007). Even without adaptation, chital, hog, and rusa have the capacity to spread further than their current distributions. Considering the ability of these species to exhibit niche shifts, it is likely that the species with currently limited distributions will exhibit environmental niche expansion in the future. Thus, once chital, hog, and rusa deer in

Australia have filled potentially suitable habitat, it is likely that they will adapt and expand beyond their respective ranges, much like fallow, red, and sambar.

Chital deer in particular have the capacity to spread much further than their present distribution and have the greatest potential of any species to spread further in Australia (Table 5.3). When comparing their niches, there were no significant differences between international and Australian ranges for chital deer, probably because they were introduced to habitat similar to that in their native range (Figure 5.3a). Compared to the other deer species in Australia, chital have not had to adjust to a particularly novel environment (Figure 5.3). Since their present distribution is relatively restricted compared with other deer species in Australia, population spread may be limited by other biotic or abiotic variables (Watter et al. 2019; Kelly et al. 2021). Despite this, chital deer represent a significant risk in the Australian environment, because much of the present habitat adjacent to their current distribution is ecologically similar to their native range.

In contrast to chital, the other five species of deer in Australia have exhibited significant niche shifts since arriving. As many of the deer species in Australia have broad international ranges (except for hog deer), international ranges likely represent something akin to their fundamental niche, and the observed spread into new niche space in the Australian likely represents true niche shifts. Many invasive species undergo rapid evolution following invasion, quickly adapting to conditions in the novel environment (Callaway & Maron 2006; Broennimann et al. 2007; Maron & Alexander 2014), which I believe has likely occurred in several deer species introduced into Australia.

Hog deer have a very limited history of introduction worldwide, and their invaded range is almost completely confined to Australia (Hill et al. 2019). Prins and Gordon (2014) proposed that species will not invade areas with abiotic conditions outside its physiological tolerance levels. If this hypothesis is accepted, then these Australian ecosystems must have fallen within their physiological tolerance. The success of hog deer in Australia demonstrates that species with limited distributions could spread beyond predictions, simply because their physiological tolerances are not known. In addition, physiological tolerances can evolve (Lee et al. 2003; Qu & Wiens 2020), so even given this knowledge, the accuracy of predictions of spread may be limited.

While habitat suitability has likely contributed to the success and spread of invasive deer in Australia, the number of deer introductions, or propagule pressure, has also likely played a role (Forsyth et al. 2004; Fautley et al. 2012). Propagule pressure influences establishment success, as well as subsequent viability of a population (Forsyth & Duncan 2001; Leung et al. 2004; Lockwood et al. 2005; Prins and Gordon 2014). Low propagule pressure seems to have been important in the spread of deer in Australia as well. The chital population in North Queensland arose from four individuals released in 1886, and in the hog deer founding population was comprised of 15 individuals in Victoria, with no subsequent releases (Bentley 1967; Moriarty 2004; Hill et al. 2019). Interestingly, chital and hog have exhibited the least spread from their point of liberation (occupying 10,667 km^2 and 6,916 km^2, respectively) compared to the other four species in Australia (ranging from 25,657 km^2 (rusa) to 654,193 km^2 (fallow); Table 5.3), which all experienced multiple introductions (Bentley 1967). While the sample size is low, this pattern is consistent with the hypothesis that species with more introductions have exhibited larger niche shifts. This is consistent with previous studies that have found that increasing the founding population size increases the number of genes upon which natural selection can work, thus increasing the likelihood of adaptation to local conditions (Lavergne & Molovsky 2007).

The niches of invasive species are capable of shifting over time as they adapt to novel environments (Fitzpatrick et al. 2007; Morehouse & Tobler 2013; Parravincini et al. 2015). Deer have had the opportunity to invade, and subsequently adapt to, areas around the world. As such, it might be expected that many deer species have had the opportunity to fill their entire environmental niche. Here I demonstrate, however, that five of the six deer species introduced to Australia show a shift in their environmental niche, and three have already spread beyond habitat predicted to be suitable. As deer continue to move into different environments, it is likely that they will continue to adapt to previously unavailable niches, thus increasing their potential for future spread, not only in Australia, but worldwide. If this continues, then these pest species will be far more problematic and widespread than would be predicted using SDM models alone.

Chital deer hind

(drawing by author)

Chapter Six: Conclusion

Summary of thesis

Species that are highly adaptable are more likely to become invasive, and, therefore, are often successful following introduction to a novel environment. To understand how an invasive species population may grow and spread, and to achieve better management, we need to understand how different factors or cues influence changes in their ecology. This is particularly important for a species that may be in low densities now but have the potential to rapidly grow and spread in the future. Chital deer in North Queensland are one such species, which have exhibited a significant lag phase prior to an irruption in population growth (Kelly et al. 2021). Here, I examined how chital deer have grown and subsequently spread in Australia, as well as the factors that influence their distribution in the landscape.

In Chapter Two, I investigated the population growth rates of introduced ungulates worldwide and determined if they experienced growth lags. I found that, of the 36 species that were examined, 16 (44%) showed significant lags in population growth. The factors that contributed to these lags were idiosyncratic, i.e., no single factor could be identified as important to all lagging populations. I suggested that while introduced ungulates can, and do, exhibit lags in population growth post liberation, management should take a proactive approach. Species that may be present in low numbers now may not remain that way in the future, and retroactive management is not as efficient or effective as proactive management (Fagan et al. 2002; Crooks 2005).

In Chapter Three, I examined habitat selection by chital deer in North Queensland at two scales (local and regional). I found that chital numbers across both scales are greatest close to water, in areas of high soil phosphorus, and areas of low sodium. At the local scale, high chital densities were also correlated with high NDVI. Due to the high densities of chital present in areas with these features, control efforts should be focused in these areas. Additionally, areas with these features are most vulnerable to future chital invasion, and management should also be focused on preventing chital entering these areas.

In Chapter Four, I investigated synchrony in the reproductive cycles of male and female chital deer in North Queensland. I found that peaks in the timing of reproductive behaviours (hard antlers in males and conception dates in females) are asynchronised. Male chital exhibited reproductive phenology strongly tied to season; typically, the population of stags showed peaks in periods when most males had hard antlers, although there were stags present with hard antlers year-round. In contrast, dates of conception in females were not cyclic and were more strongly related to rainfall rather than male antler phases. Interestingly, peak times when males maintain hard antlers appear to be a relic of their native range, rather than an adaptation to a novel range. Over time, the lack of synchronised reproduction may drive selection for different mating strategies or physiological mechanisms to increase the individual probability of reproductive success, and we may be seeing this action of selection because 50% of males are in hard antler outside of the peak time of females.

Finally, in Chapter Five, using data from the previous chapters, I demonstrated that five of the six deer species introduced to Australia exhibited niche shifts when comparing their international and Australian ranges. Chapter Five mapped their present and potential future distributions. Chital were the only deer species in Australia that did not exhibit a niche shift. This is likely because chital were introduced to an Australian environment very similar their native range. As such, chital have not had to adapt to conditions very different from their native range. In contrast, the other five species of deer (hog, fallow, red, rusa, and sambar deer) did exhibit niche shifts in Australia. When examining potential spread, chital had the greatest predicted potential spread of all deer species in Australia. Hog and rusa still had the capacity to spread beyond their present ranges, while the three other species (fallow, red, and sambar) had already expanded beyond ranges that I predicted would be suitable. As these species' populations continue to grow and spread, it is likely that they will continue to adapt to new, previously unavailable niches.

Management Implications

Invasive ungulate populations are capable of existing at low numbers for an extended period of time. Here, I demonstrated that ungulates are capable of exhibiting lag phases following introduction to a novel environment, but the presence and length of these lag phases can be unpredictable. As such, I emphasized the importance of proactive control for small populations now, as they have the potential for explosive growth in the future.

I identified the variables that drive distribution of chital in the landscape and suggest areas that should be the focus for management or control. Chital are in highest densities close to water with high soil phosphorus and low soil sodium on both fine and broad scales. Management should, therefore, be focused in these areas for two reasons. First, they are likely to contain the greatest densities of deer in the landscape. Secondly, as it is these areas that are likely to be vulnerable to future invasion, as well as act as vectors that facilitate spread between areas of suitable habitat, they should be the focus of pre-emptive measures and control.

As invasive species are highly adaptable, their physiological systems and niches are also subject to change. Cues that drive behaviours may not be in sync in an invaded range (e.g., reproductive behaviours) and as such, invasive species growth and spread can be unpredictable. Likewise, species may exhibit niche shifts following introduction to a novel environment and can likely spread far beyond habitat that would previously have been considered suitable. Species distribution maps can, therefore, underestimate the potential spread of invasive species, particularly when those species have a limited international distribution. As such, managers should exercise caution with invasive species as they can, and do, spread beyond habitats and niches that may be suitable at a particular point in time. Therefore, habitat suitability and species distribution maps should be treated as an absolute minimum of management information, and managers should undertake early control and management of invasive species, before they can spread to unexpected areas.

In my study, three deer species (chital, hog, and rusa) exhibited potential ranges beyond their present distribution. Of those, chital exhibited the largest potential range. As such, chital represent a significant risk in Australia, particularly in northern and eastern Queensland. Meanwhile, the other three species (fallow, red, and sambar) have already spread to habitat that was not within the ‘suitable’ envelop determined from previous distributions. This highlights the ability of these species to adapt to novel conditions, and subsequently spread to areas that may have previously been unsuitable. As these deer continue to move into novel environments, it is likely that they will continue to adapt to novel niches, suggesting that they will be more problematic and widespread than predicted. Management should, therefore, focus on preventing spread by reducing connectivity between different areas of suitable environments.

Directions for Future Research

Like many bodies of research, my thesis has raised several questions that would be fruitful to pursue. In the future, landscape genetic methods should be used to determine gene flow, which will allow researchers to better understand the historic barriers and facilitators of population spread. From this study it seems likely that deer are spreading by following waterways, e.g., the Burdekin River, which is characterised by relatively flat terrain and high phosphorus (Chapter Two). Barriers may include areas with little available water or rougher terrain. A landscape genetics study would help untangle features that have influenced the spread of chital in North Queensland and allow managers to predict where they are likely to spread in the future.

A study examining the genetic diversity of the six established deer species in Australia could help explain why some species have spread further than others. First, the potential for hybridisation is quite high for chital (both with rusa in the Charters Towers region, and also with hog deer prior to introduction to Australia). As deer ranges begin to overlap with further spread, there is also the potential for future hybridisation, which may allow an increase in potential range with adaptations from more than one species. Hybridisation also has conservation implications, in which some deer species in Australia (e.g., hog or chital) serve as potential reservoir populations that could support threatened native populations of those species. Hybridisation could eliminate the possibility of using these populations as reservoirs, thus jeopardising potential conservation measures.

The location, number of introduction events, and founding population size likely influenced the growth and spread of each species. For example, chital were introduced into suitable habitat according to climate envelop models, and a niche very similar to their native range. They have not, however, expanded to fill their potential Australian range, unlike other deer species in Australia. Hog deer have also remained relatively range restricted. Both these species (unlike others in Australia) had only a single introductory event, with low numbers of individuals (4 founding individuals for chital, 15 for hog; Bentley 1967). While all species may be able to adapt and spread, a species with lower genetic diversity from a small founding population size may be less likely to exhibit population growth and spread on the same scale as species with multiple introductions that have greater genetic diversity (Lavergne & Molovsky 2007; Dlugosch & Parker 2008). As such, investigation into the genetic diversity and founding events of the six deer species in Australia could help understand how these species’ populations may have grown in the past and allow us to infer how they may spread in the future.

Future research could help quantify the impact of chital deer in North Queensland on the environment. Deer can impact ecological communities through competition and over-browsing, as well as have economic impacts through competition with sheep or cattle for grazing. Inter-specific interactions were briefly addressed in this thesis, but future research could examine the extent to which deer compete with native species (e.g., macropods, lizard, and plant communities) as well as domestic species (e.g., sheep and cattle) to further quantify their environmental impacts.

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Appendix A

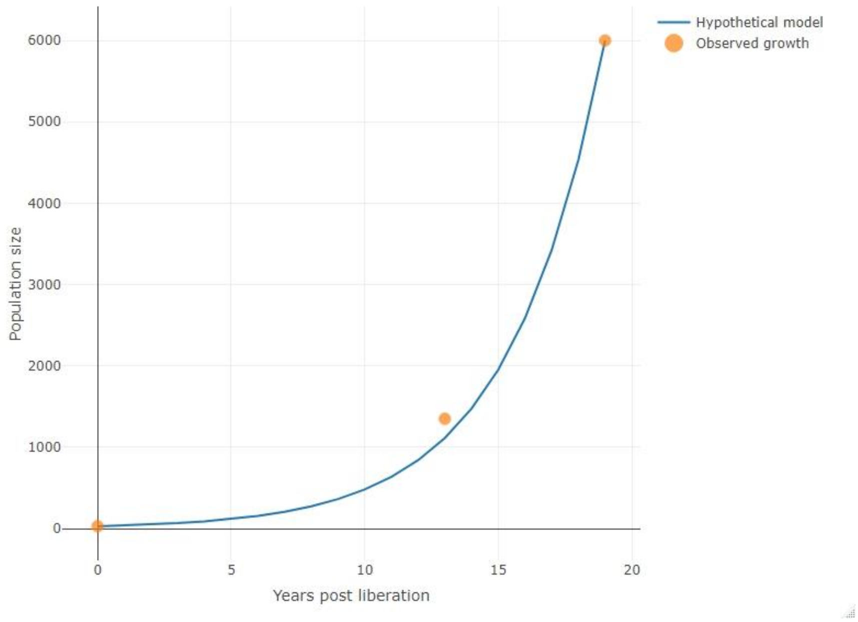


Figure A.1. Observed population size (orange points) plotted against hypothetical curve (blue line) for Rangifer tarandus introduced to St Matthew Island (Alaska; Klein 1968)

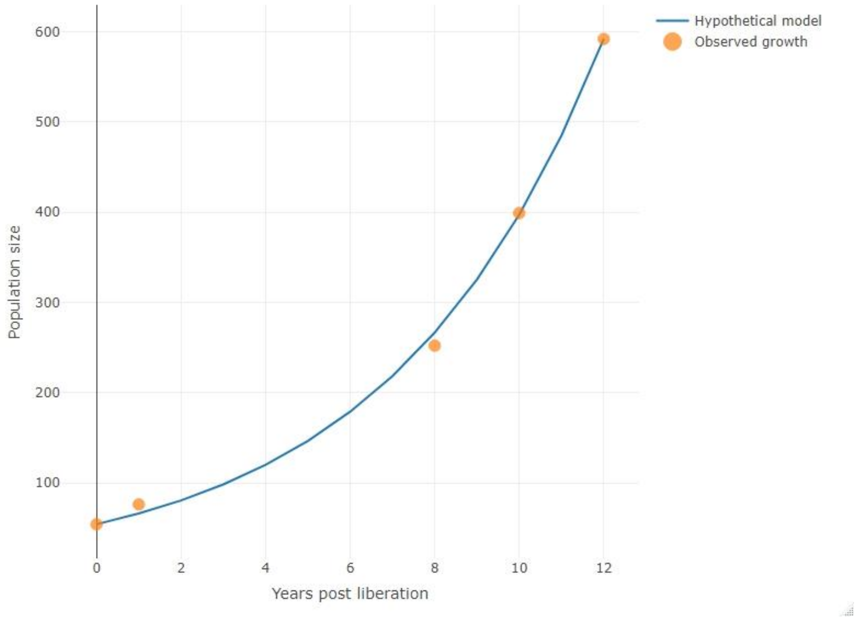


Figure A.2. Observed population size (orange points) plotted against hypothetical curve (blue line) for *Cervus nippon* self-introduced to Japan (Kaji et al. 2004)

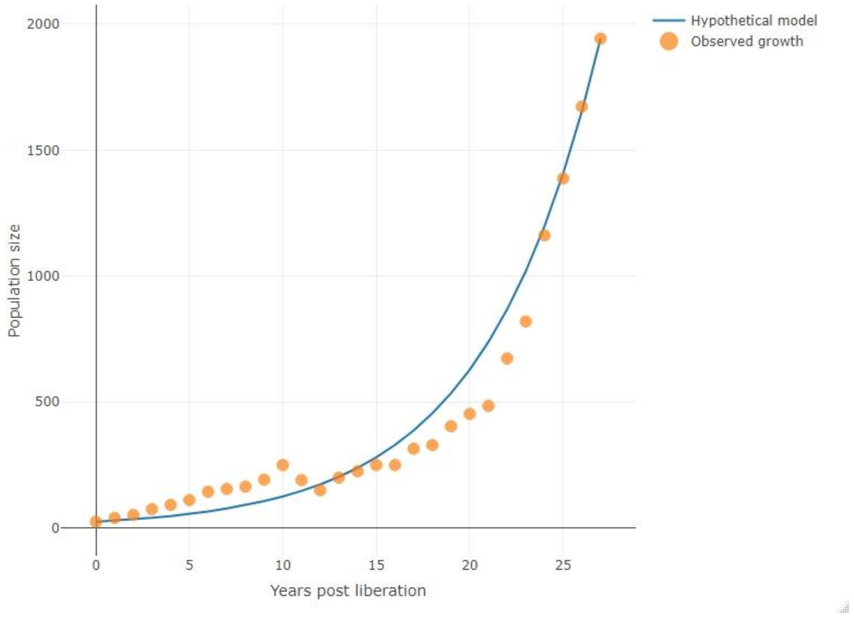


Figure A.3. Observed population size (orange points) plotted against hypothetical curve (blue line) for *Rangifer tarandus* introduced to St Paul Island (Alaska; Scheffer 1951)

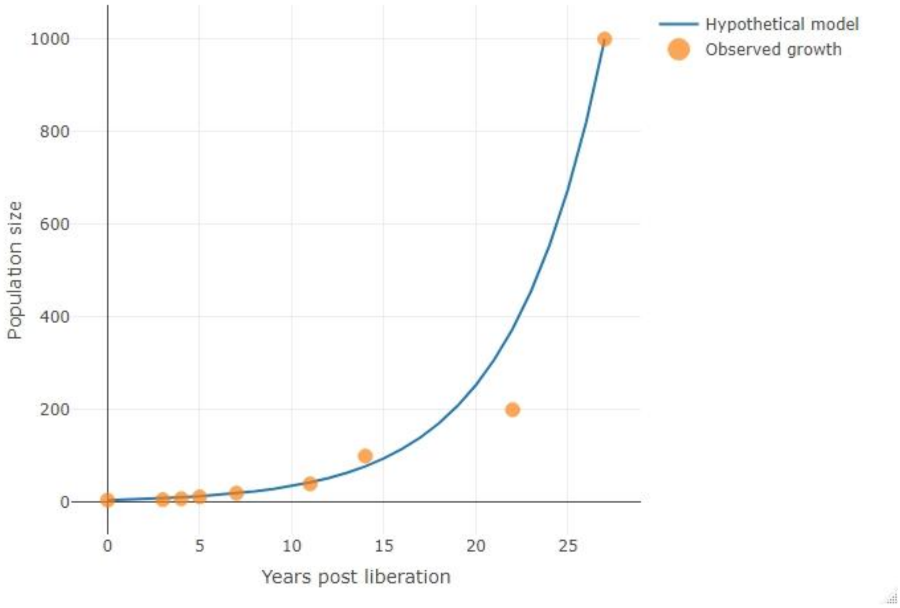


Figure A.4. Observed population size (orange points) plotted against hypothetical curve (blue line) for *Odocoileus virginianus* introduced to Finland (Kekkonen et al. 2012)

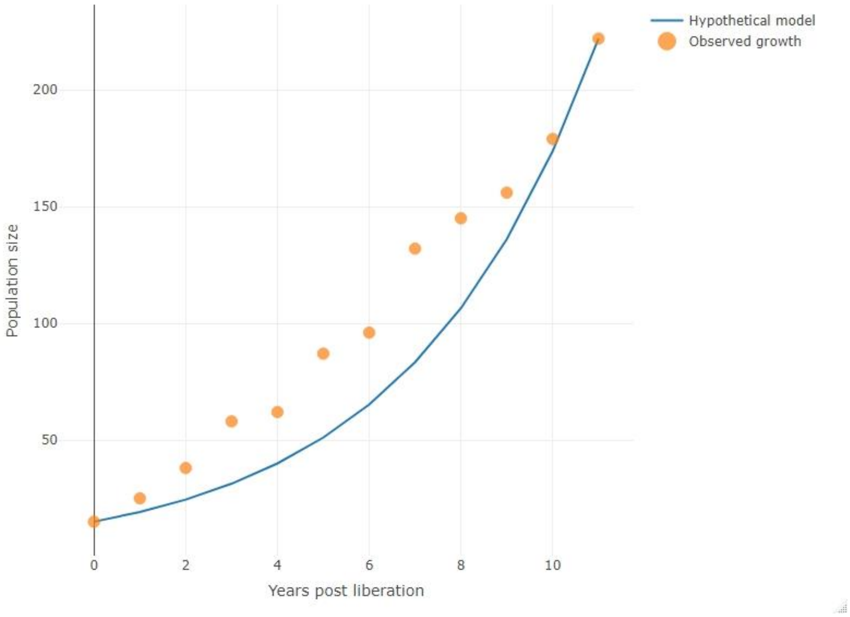


Figure A.5. Observed population size (orange points) plotted against hypothetical curve (blue line) for *Rangifer tarandus* introduced to St George Island (Alaska; Scheffer 1951)

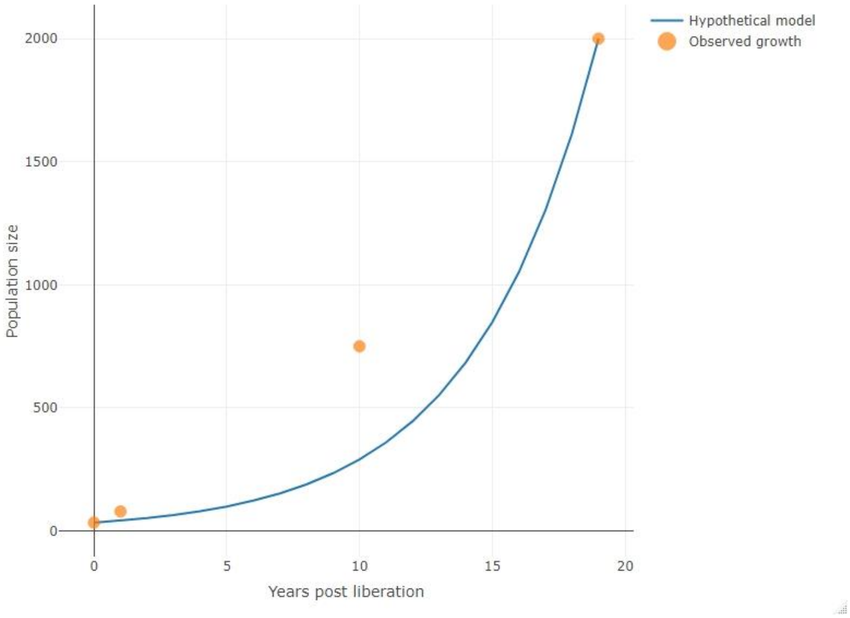


Figure A.6. Observed population size (orange points) plotted against hypothetical curve (blue line) for *Ammotragus lervia* introduced to Spain (Cassinello et al. 2004)

Appendix B

Table B.1. Slopes of introduced ungulates compared with exponential population models, sorted in descending order from lowest to highest difference in slope.
Sources: (1) Klein (1968); (2) Chapui et al. (1994); (3) Scheffer (1951); (4) Tomich (1969); (5) Dvorak & Catalano (2016); (6) Colchero et al. (2009); (7) Steinbach et al. (2018); (8) Kaji et al. (2004); (9) Webley et al. (2004); (10) Thomson (1922); (11) Kekkonen et al. (2012); (12) Cassinello et al. (2004); (13) Cassinello (1998); (14) Judge et al. (2017); (15) Gogan et al. (2001); (16) Nogales et al. (2006); (17) Franklin & Grigione (2005); (18) Bender et al. (2019); (19) Leader-Williams (1980); (20) Barrau & Devambez (1957); (21) McCullough et al. (2009); (22) Caughley (1970); (23) Tustin & Challies (1978); (24) Bentley (1967); (25) Brennan & Pople (2016); (26) Graf & Nichols (1966); (27) Flesch et al. (2016); (28) Boulton & Freeland (1991); (29) Saalfeld & Edwards (2010); (30) Fuller et al. (2018); (31) Cooke (2009); (32) Bradshaw & Brook (2007); (33) Kopij (2017)

** species for which the theoretical exponential growth rate was significantly less than the 95% confidence intervals of empirical exponential growth models.

Species (source)	Location	Introduced environment	Observed slope	Exponential slope	Difference
Cervus unicolor (10)	New Zealand	non-tropical	0.24	0.25	0.01
Rangifer tarandus (St Matthew) (1)	Alaska	non-tropical	0.28	0.30	0.02
Ammotragus lervia (12)	Spain	non-tropical	0.21	0.24	0.03
Cervus timorensis (9)	Australia	non-tropical	0.23	0.26	0.03
Rangifer tarandus (St George) (3)	Alaska	non-tropical	0.25	0.28	0.04
Rangifer tarandus (Haute) (2)	Kerguelen Isl.	non-tropical	0.24	0.29	0.04
Ovis gmelini musimon (2)	Kerguelen Isl.	non-tropical	0.33	0.37	0.05
Cervus nippon (8)	Japan	non-tropical	0.20	0.25	0.05
Ovis gmelini (14)	Hawai'i	tropical	0.18	0.25	0.07
Ovis Canadensis (6)	Mexico	non-tropical	0.21	0.28	0.07
Capreolus capreolis (7)	Germany	non-tropical	0.21	0.29	0.07
Ovis gmelini (16)	Canary Isl.	non-tropical	0.16	0.25	0.09
Ammotragus lervia (16)	Canary Isl.	non-tropical	0.15	0.25	0.10
Odocoileus virginianus (11)	Finland	non-tropical	0.20	0.30	0.11
Rangifer tarandus (Grande-Terre) (2)	Kerguelen Isl.	non-tropical	0.35	0.46	0.11
Odocoileus hemionus (5)	USA	non-tropical	0.27	0.38	0.11
Rangifer tarandus (St Paul) (3)	Alaska	non-tropical	0.16	0.28	0.11
Antilocapra americana (4)	Hawai'i	tropical	0.27	0.41	0.14
Dama dama (15)	USA	non-tropical	0.15	0.29	0.14
Rangifer tarandus (19) **	**South Georgia Isl.**	**non-tropical**	0.14	0.29	0.16
Rusa timorensis (20) **	**New Caledonia**	**tropical**	0.13	0.29	0.17
Cervus nippon (21) **	**USA**	**non-tropical**	0.10	0.27	0.17
Oreamnos americanus (27) **	**USA**	**non-tropical**	0.06	0.23	0.17
Hemitragus jemlahicus (22,23) **	**New Zealand**	**non-tropical**	0.08	0.26	0.18
Ammotragus lervia (13) **	**USA**	**non-tropical**	0.18	0.36	0.19
Camelus dromedarius (29) **	**Australia**	**tropical**	0.06	0.25	0.19
Bubalus bubalis (28) **	**Australia**	**tropical**	0.06	0.25	0.19
Axis axis (15) **	**USA**	**non-tropical**	0.09	0.29	0.20
Oryx gazella gazelle (18) **	**USA**	**non-tropical**	0.15	0.35	0.20
Bos javanicus (32) **	**Australia**	**tropical**	0.04	0.24	0.20
Axis axis (26) **	**Hawai'i**	**tropical**	0.09	0.31	0.22
Axis axis (24,25) **	**Australia**	**tropical**	0.07	0.30	0.23
Cervus nippon (33) **	**Poland**	**non-tropical**	0.03	0.29	0.26
Lama guanicoe (17) **	**Falkland Islands**	**non-tropical**	0.17	0.46	0.29
Odocoileus virginianus (30) **	**Canada**	**non-tropical**	0.05	0.38	0.33
Hydropotes inermis (31) **	**England**	**non-tropical**	0.06	0.46	0.40

Table B.2. Growth rates (r) of introduced ungulates compared with exponential population models, sorted in descending order from lowest to highest difference in r.

** species for which the theoretical exponential growth rate was significantly less than the 95% confidence intervals of empirical exponential growth models.

Species (source)	Location	Introduced environment	Observed r	Exponential r	Difference
Rangifer tarandus (St Matthew) (1)	Alaska	non-tropical	1.32	1.33	0.01
Rangifer tarandus (Grande-Terre) (2)	Kerguelen Isl.	non-tropical	1.42	1.46	0.04
Rangifer tarandus (St George) (3)	Alaska	non-tropical	1.28	1.32	0.04
Ovis gmelini musimon (2)	Kerguelen Isl.	non-tropical	1.39	1.45	0.06
Rangifer tarandus (Haute) (2)	Kerguelen Isl.	non-tropical	1.28	1.33	0.06
Ammotragus lervia (12)	Spain	non-tropical	1.24	1.31	0.07
Ovis Canadensis (6)	Mexico	non-tropical	1.23	1.33	0.09
Capreolus capreolis (7)	Germany	non-tropical	1.24	1.33	0.09
Cervus unicolor (10)	New Zealand	non-tropical	1.18	1.27	0.09
Cervus nippon (8)	Japan	non-tropical	1.22	1.33	0.11
Antilocapra americana (4)	Hawai'i	tropical	1.31	1.43	0.12
Odocoileus hemionus (5)	USA	non-tropical	1.30	1.46	0.16
Rangifer tarandus (St Paul) (3)	Alaska	non-tropical	1.17	1.34	0.16
Dama dama (15)	USA	non-tropical	1.16	1.34	0.18
Rangifer tarandus* (19) *	**South Georgia Isl.**	**non-tropical**	1.15	1.34	0.19
Rusa timorensis* (20) *	**New Caledonia**	**tropical**	1.15	1.34	0.19
Oreamnos americanus* (27) *	**USA**	**non-tropical**	1.06	1.26	0.20
Bubalus bubalis* (28) *	**Australia**	**tropical**	1.08	1.28	0.20
Camelus dromedarius* (29) *	**Australia**	**tropical**	1.06	1.28	0.22
Bos javanicus* (32) *	**Australia**	**tropical**	1.04	1.27	0.23
Cervus timorensis (9)	Australia	non-tropical	1.26	1.49	0.24
Cervus nippon* (21) *	**USA**	**non-tropical**	1.10	1.35	0.24
Axis axis* (15) *	**USA**	**non-tropical**	1.10	1.34	0.24
Odocoileus virginianus (11)	Finland	non-tropical	1.22	1.47	0.25
Ammotragus lervia* (13) *	**USA**	**non-tropical**	1.19	1.44	0.25
Oryx gazella gazelle* (18) *	**USA**	**non-tropical**	1.16	1.42	0.26
Ovis gmelini (14)	Hawai'i	tropical	1.20	1.47	0.27
Axis axis* (24,25) *	**Australia**	**tropical**	1.07	1.34	0.27
Axis axis* (26) *	**Hawai'i**	**tropical**	1.07	1.35	0.28
Ovis gmelini (16)	Canary Isl.	non-tropical	1.18	1.46	0.29
Ammotragus lervia (16)	Canary Isl.	non-tropical	1.16	1.45	0.29
Hemitragus jemlahicus* (22,23) *	**New Zealand**	**non-tropical**	1.06	1.35	0.29
Cervus nippon* (33) *	**Poland**	**non-tropical**	1.03	1.34	0.31
Lama guanicoe* (17) *	**Falkland Islands**	**non-tropical**	1.19	1.59	0.40
Odocoileus virginianus* (30) *	**Canada**	**non-tropical**	1.06	1.47	0.41
Hydropotes inermis* (31) *	**England**	**non-tropical**	1.06	1.58	0.52

Table B.3. AIC model selection top model results from generalized linear mixed effect models (GLMM's) indicating top variables from model selection for factors that affect introduced ungulate population growth (difference between observed and exponential growth rates (r)) of lagging populations

model	Intercept	AICc	Δi	weight	R^2
null	**0.28**	**-23.70**	**0.00**	**0.69**	**0.89**
dry season	0.34	-20.00	3.73	0.11	0.87
gestation	0.64	-19.60	4.17	0.09	0.90
hunting	0.23	-17.40	6.29	0.03	0.90
predators	0.30	-17.40	6.30	0.03	0.82
region	0.29	-15.80	7.97	0.01	0.68
gestation + dry season	0.78	-15.40	8.36	0.01	0.88
island	0.28	-15.00	8.75	0.01	0.87
hunting + dry season	0.30	-13.90	9.85	0.01	0.87
dry season + predation	0.36	-12.90	10.86	0.00	0.86

Table B.4. AIC model selection top model results from generalized linear mixed effect models (GLMM's) indicating top variables from model selection for factors that affect introduced ungulate population growth (difference between observed and exponential slopes) of lagging populations

model	(Int)	AICc	Δi	weight	R^2
null	**0.23**	**-26.30**	**0.00**	**0.75**	**0.74**
dry season	0.26	-21.60	4.72	0.07	0.71
gestation	0.22	-21.40	4.92	0.06	0.76
predators	0.26	-20.60	5.68	0.04	0.67
hunting	0.19	-19.70	6.61	0.03	0.77
region	0.24	-18.70	7.60	0.02	0.07
island	0.22	-17.80	8.52	0.01	0.02
gestation + dry season	0.28	-16.10	10.22	0.00	0.74
gestation + predators	0.13	-15.00	11.31	0.00	0.69
dry season + predators	0.27	-14.90	11.37	0.00	0.67

Appendix C

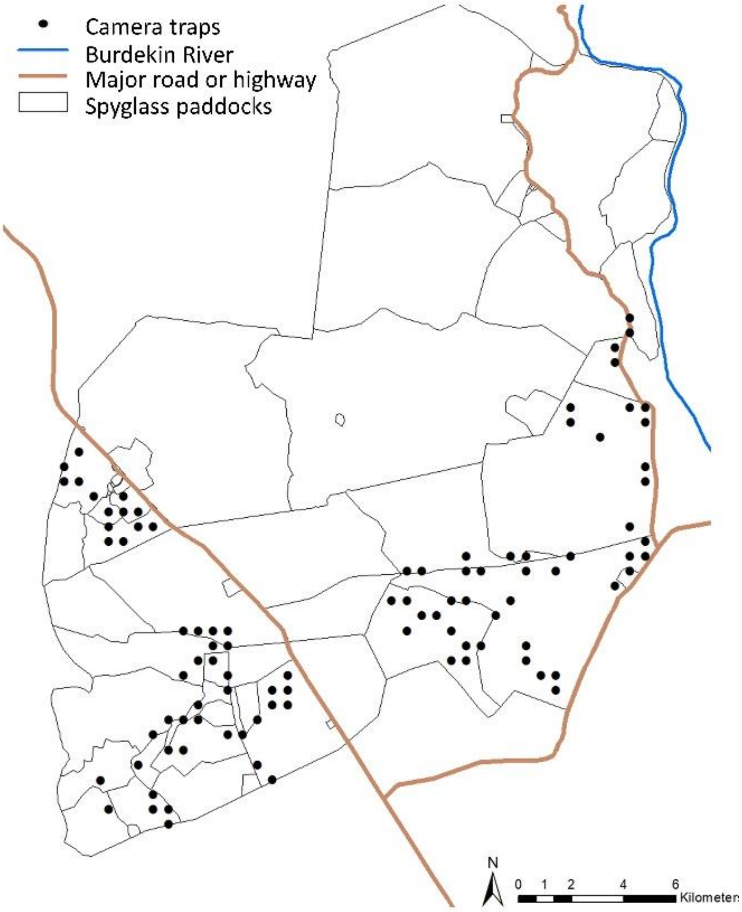


Figure C.1. Map of camera traps on Spyglass Beef Research Station. Black points represent camera sites, thin black lines represent Spyglass paddock boundaries, brown lines represent major roads or highways, and the blue line represents the Burdekin River.

Table C.1. Slopes of introduced ungulates compared with exponential population models, sorted in descending order from lowest to highest difference in slope.

Period	Cameras deployed	Cameras failed	Total used
1	58	14	44
2	45	6	39
3	15	4	11
TOTAL	118	24	94

Table C.2. Slopes of introduced ungulates compared with exponential population models, sorted in descending order from lowest to highest difference in slope.

Model description	df	logLik	AICc	delta	weight
P + canopy cover + canopy height + highway + track + water + Na + NDVI + dingo	12	-355.24	738.33	0.00	0.316
P + canopy cover + canopy height + highway + track + water + Na + NDVI	11	-357.08	739.38	1.05	0.186
P + Ca:Mg + canopy cover + canopy height + highway + track + water + Na + NDVI + dingo	13	-354.75	740.05	1.72	0.133
P + canopy cover + canopy height+ homestead + highway + track + water + Na + NDVI + dingo	13	-354.90	740.35	2.03	0.115
P + canopy cover + canopy height + homestead + highway + track + water + Na + NDVI	12	-356.70	741.25	2.93	0.073
P + Ca:Mg + canopy cover + canopy height + highway + track + water + Na + NDVI + dingo	12	-356.91	741.67	3.34	0.059
P + Ca:Mg + canopy cover + canopy height + homestead + highway + track + water + Na + NDVI + dingo	14	-354.59	742.49	4.16	0.039
P + Ca:Mg + canopy cover + canopy height + homestead + highway + track + water + Na + NDVI	13	-356.63	743.81	5.48	0.020
P + canopy cover + canopy height + highway + track + water + NDVI + dingo	11	-359.46	744.14	5.81	0.017
Ca:Mg + canopy cover + canopy height + highway + track + water + Na + NDVI + dingo	12	-359.03	745.91	7.58	0.007

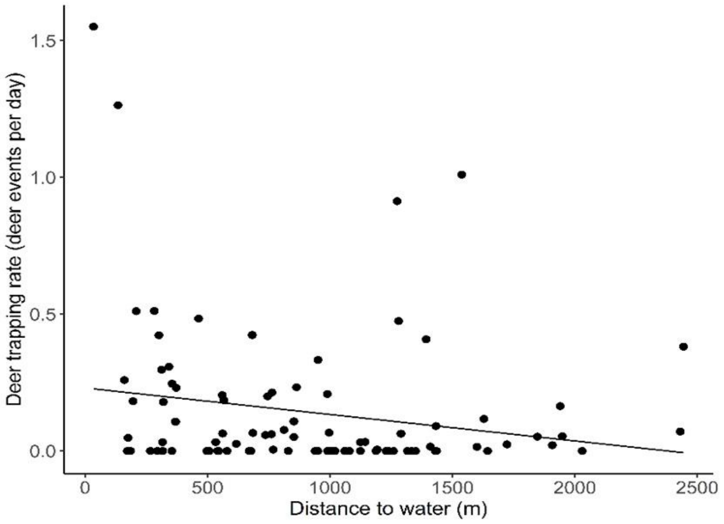


Figure C.2. Relationship between the ‘trapping rate’ of chital deer at a local scale determined from trail cameras (estimated as deer events/ day) and distance from nearest water source (m)

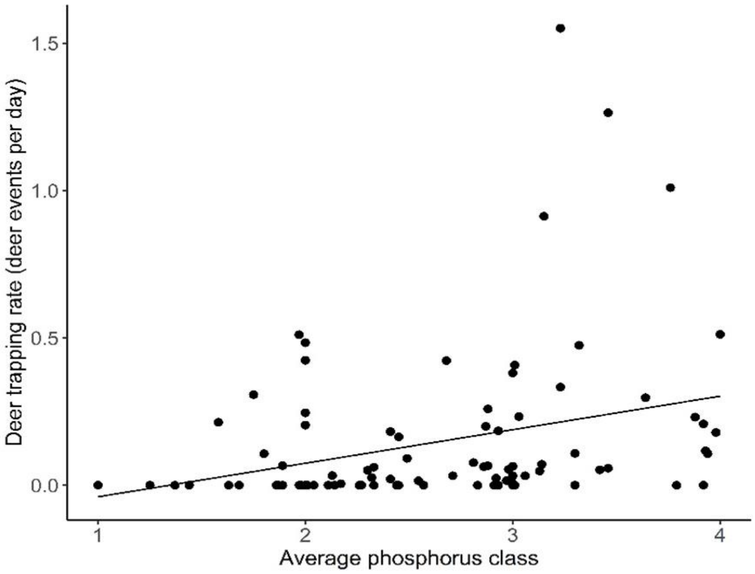


Figure C.3. Relationship between the ‘trapping rate’ of chital deer at a local scale determined from trail cameras (estimated as deer events/ day) and soil phosphorus content (tha-1)

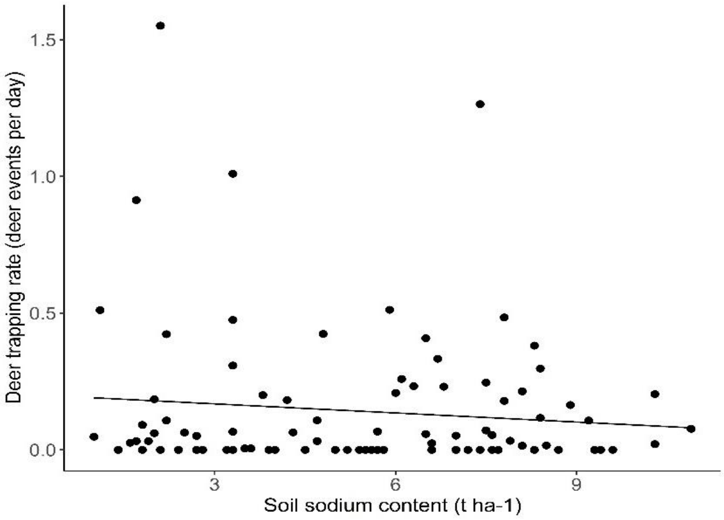


Figure C.4. Relationship between the ‘trapping rate’ of chital deer at a local scale determined from trail cameras (estimated as deer events/ day) and soil sodium content (tha-1)

Table C.3. Slopes of introduced ungulates compared with exponential population models, sorted in descending order from lowest to highest difference in slope.

	df	logLik	AICc	Δ AICc	weight
Ca:Mg + Na + P + NDVI + River + Slope	8	-1868.73	3755.4	0	0.525
Ca:Mg + Na + P + River + Slope	7	-1870.26	3756	0.6	0.388
Na + P + River + Slope	6	-1873.43	3759.9	4.57	0.053
Na + P + NDVI + River + Slope	7	-1873.02	3761.5	6.13	0.024
Ca:Mg + Na + P + NDVI + River	7	-1874.6	3764.7	9.29	0.005
Ca:Mg + Na + P + Slope	6	-1876.78	3766.6	11.27	0.002
Ca:Mg + Na + P + NDVI + Slope	7	-1876.17	3767.8	12.44	0.001
Na + P + Slope	5	-1879.18	3769.1	13.76	0.001
Ca:Mg + Na + River + Slope	6	-1878.58	3770.2	14.88	0
Na + P + NDVI + Slope	6	-1878.91	3770.9	15.53	0

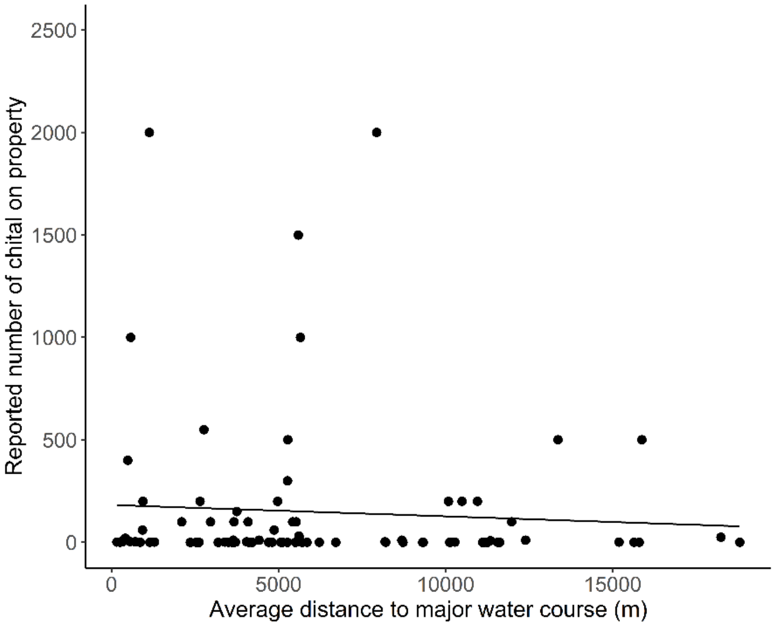


Figure C.5. Relationship between the reported number of deer on properties in the Charters Towers region and distance to nearest major watercourse (m)

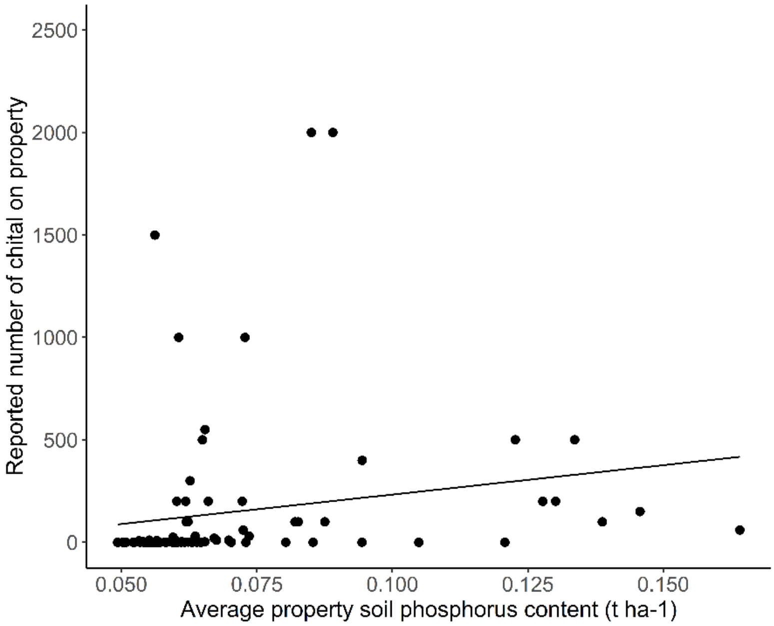


Figure C.6. Relationship between the reported number of deer on properties in the Charters Towers region and average property soil phosphorus content (tha-1)

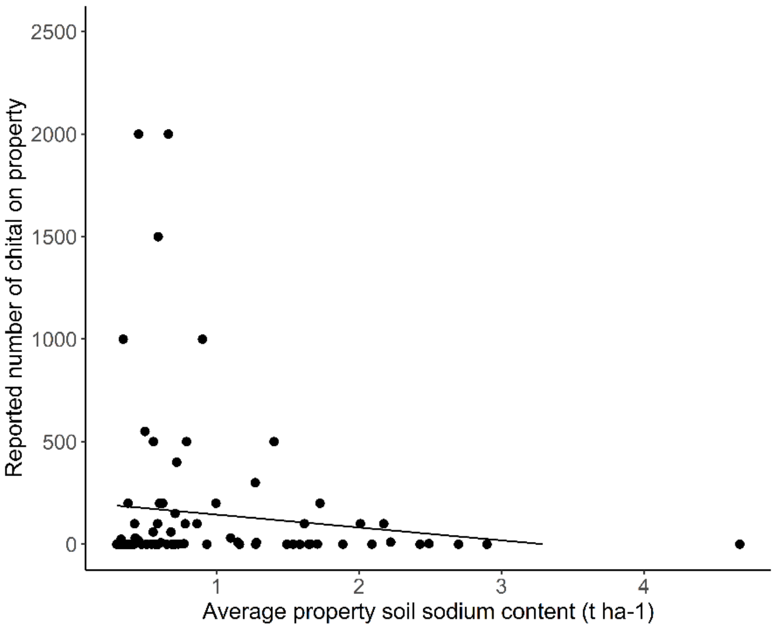


Figure C.7. Relationship between the reported number of deer on properties in the Charters Towers region and average property soil sodium content (tha-1)

Appendix D

Landholder survey distributed by Charters Towers Regional Council

Biosecurity Queensland and Charters Towers Regional Council are conducting research on Chital Deer in their historic range around Charters Towers. A small herd of chital deer were introduced to the area in 1886. We are interested in finding out their current distribution and how fast they are spreading. We would appreciate your assistance with this research by completing the following survey. None of the data will be passed on to others and property and landholder information will remain confidential.

Your name:____________________________**Property Name**:___________________

How many years have you been on this property? _________________________
____
____Years

1. Approximately how many chital deer would you have seen on your property in the past year?
   ☐ None ☐ 1-50 ☐ 51-200 ☐ 201-1000 ☐ More than 1000

2. When did you first notice a permanent chital population on your property?
   ☐ Prior to 1970 ☐ 1970s ☐ 1980s ☐ 1990s ☐ 2000s ☐ 2010-present

   a. If exact date known:____
   b. If prior to 1970's, please provide an approximate date:___________________
3. Please provide an estimate of the chital deer numbers on your property in the corresponding years:
   YearNumber of deer (approx.)

1990	__________________________
2000	__________________________
2010	__________________________
2016	__________________________

4. Where are most chital deer located on your property? Please select **ALL** that apply.

☐ Within 3km of the homestead ☐ Creek flats ☐ Man-made waters (dams, troughs)
☐ Other (please specify) ____
5. Do you have wild dogs on your property?
☐ Yes ☐ No

6. Do you control wild dogs?

☐ Yes ☐ No

7. Has your level of dog control changed or stayed the same in the last 20 years?

☐ Decreased ☐ Stayed the same (no change) ☐ Increased

8. Do you think of chital deer as being harmful (damaging), useful (beneficial) or neutral (neither) on your property?

☐ Harmful ☐ Neutral ☐ Useful

9. What, if any, impacts have you directly experienced from chital deer on your property in the past year? Please select **ALL** that apply.

☐ No negative impacts ☐ Compete with cattle for feed ☐ Trespassing hunters
☐ Damaging trees ☐ Damage to fences
☐ Other – please specify ____

10. Have you ever made an income from chital deer on your property?

☐ No ☐ Paid hunting and safari groups ☐ Venison for pet or game meat
☐ Other (please specify) ____

11. Please rate the following from strongly disagree to strongly agree.

a. Chital deer are part of the local landscape and should be left alone.

☐ Strongly disagree ☐ Disagree ☐ Neither agree nor disagree ☐ Agree ☐ Strongly agree

b. Culling chital deer would be a mistake as they are a source of income/food.

☐ Strongly disagree ☐ Disagree ☐ Neither agree nor disagree ☐ Agree ☐ Strongly agree

c. Controlling chital deer in this area is important for keeping populations under control.

☐ Strongly disagree ☐ Disagree ☐ Neither agree nor disagree ☐ Agree ☐ Strongly agree

12. Have you engaged in any control of chital deer on your property?

☐ Yes ☐ No

If yes, please provide an estimate how many chital deer were removed from your property in the following decades:

Year	**Number of deer removed (approx.)**
1970s	______________________________
1980s	______________________________
1990s	______________________________
2000s	______________________________
2010 – 2017	______________________________

13. Would you agree to being contacted by a researcher to discuss any of the above questions in more detail?

☐ Yes ☐ No

Council appreciates your cooperation in completing this survey. If you have any further comments relating to Chital Deer in the Dry Tropics please note below.

Appendix E

Table E.1. Output from cosinor model examining the seasonal patterns of the proportion of male chital deer in hard antler (reproductively active) between 2013-2018.

	Estimate	Std. Error	t. value	*p*-value
(Intercept)	0.70	0.01	47.92	0.000
cosw	-0.15	0.02	-6.99	0.000
sinw	0.11	0.02	5.39	**0.000**
Significant seasonality based on adjusted significance level of 0.025 = TRUE				

Table E.2. Full set of models from AIC model selection for the proportion of male chital deer in hard antler (reproductively active), as compared with the environmental variables daylength, and 0, 1, 3, and 6 months rainfall prior to sampling including interaction with photoperiod, rainfall, and antler phase.

	df	logLik	AICc	Δ AICc	weight
6 month + daylight	3	-125.80	258.21	0.00	0.36
0 month + daylight	3	-126.01	258.62	0.41	0.29
1 month + daylight	3	-126.14	258.89	0.68	0.26
3 month + daylight	3	-127.65	261.91	3.70	0.06
daylight	2	-129.34	262.96	4.76	0.03
6 month	2	-136.11	276.51	18.31	0.00
6 month * year	10	-130.36	287.40	29.19	0.00
3 month	2	-150.16	304.62	46.41	0.00
3 month * year	10	-140.45	307.57	49.36	0.00
1 month * year	10	-140.76	308.19	49.98	0.00
0 month * year	10	-140.98	308.63	50.42	0.00
1 month	2	-152.55	309.39	51.18	0.00
0 month	2	-153.16	310.61	52.40	0.00

Table E.3. Output from cosinor model examining the seasonal patterns of the proportion of monthly conceptions (reproductively active) between 2013-2018.

	Estimate	Std. Error	t. value	*p*-value
(Intercept)	0.09	0.01	7.79	0.000
cosw	0.02	0.02	1.36	0.181
sinw	0.04	0.02	2.85	**0.007**
Significant seasonality based on adjusted significance level of 0.025 = TRUE				

Table E.4. Full set of models from AIC model selection for the proportion of monthly conceptions (reproductively active), as compared with daylength and the rainfall in the 0, 1, 3, and 6 months prior to conception including interaction with rainfall and year of conception.

Model summary	df	logLik	AICc	delta	weight
3 month	2	-67.33	139.05	0.00	0.43
3 month + hard antler	3	-66.52	139.87	0.82	0.28
3 month + daylength	3	-67.11	141.05	2.00	0.16
3 month + daylength + hard antler	4	-66.44	142.30	3.25	0.08
3 month * year	8	-61.98	145.96	6.90	0.01
6 month + daylength	3	-69.92	146.68	7.62	0.01
6 month	2	-71.18	146.76	7.71	0.01
6 month * year	8	-62.53	147.05	8.00	0.01
6 month + hard antler	3	-70.56	147.96	8.90	0.00
6 month + daylength + hard antler	4	-69.92	149.27	10.22	0.00
hard antler	2	-76.18	156.76	17.71	0.00
1 month	2	-76.26	156.92	17.87	0.00
1 month + hard antler	3	-75.15	157.13	18.08	0.00
0 month	2	-76.85	158.10	19.05	0.00
daylength	2	-76.85	158.10	19.05	0.00
1 month + daylength	3	-75.69	158.21	19.16	0.00
0 month + hard antler	3	-75.92	158.66	19.61	0.00
0 month + daylength	3	-76.52	159.87	20.81	0.00
0 month + daylength + hard antler	4	-75.84	161.11	22.06	0.00
1 month * year	8	-71.64	165.27	26.22	0.00
0 month * year	8	-73.86	169.71	30.66	0.00

Appendix F

This camera trapping portion of this study was conducted at Spyglass Beef Research Facility, a cattle property covering 38,221 hectares in the Charters Towers district, Queensland, Australia (Figure 1). The study area contains grassland that consists of both native grasses, such as black speargrass (*Heteropogon contortus*) and kangaroo grass (*Themeda triandra*), and exotic grasses such as sabi grass (*Urochloa mosanbicensis*), red Natal grass (*Melinis repens*), and buffel grass (*Cenchrus ciliaris*). A variety of overstorey species include silverleaf box (*Eucalyptus pruinosis*), lancewood (*Acacia shirleyi*), bendee (*Acacia catenulata*) with yellowjacket (*Eucalyptus similis*), and ironbark (*Eucalyptus* spp.).

I used camera traps to determine the presence and relative number of chital in different habitats. To select camera trap locations, a grid with points 500m apart was created using ArcGIS (ESRI). To facilitate access to the locations, 124 points of the grid were selected that fell within 400m of a road or track. Bushnell Aggressor^{TM} cameras were placed at these locations for at least one month each between October 2017 and November 2018. Cameras were set to capture three images per trigger, with no delay between consecutive triggers. All images were stamped with the date and time. Cameras were installed approximately 30-50cm above the ground and pointed north or south to avoid the rising or setting sun. Vegetation in front of cameras was clipped to minimise interference and false triggers. Of the 124 cameras installed, 30 failed or the data they collected could not be analysed (e.g., they collected excessive false triggers). I, therefore, had photos from 94 operational cameras, representing 6707 trap days. Images were identified and organised using WildID and ZSL CTap software (Amin et al 2014; TEAM Network 2017). Chital stag antler stage (hard or velvet) was identified from images. Only images that could be positively identified were included in analyses. If a stag's antler stage was uncertain or unknown, it was excluded.

For analysis, an "event" was defined as a sequence of photographs of one species that occurred following the previous sequence of a different species. When there were consecutive events of the same species, I ensured there was one hour or more between events (Bowkett et al. 2007; Amin et al. 2014; Rovero et al. 2017). This time frame was used to avoid repeated counting of the same individuals (Tobler et al. 2009; Rovero et al. 2017). I used Moran's test in ArcGIS to compare the detection rates of chital across all cameras and found no significant spatial autocorrelation in my dataset (Moran's index: 0.09, $p = 0.313$).

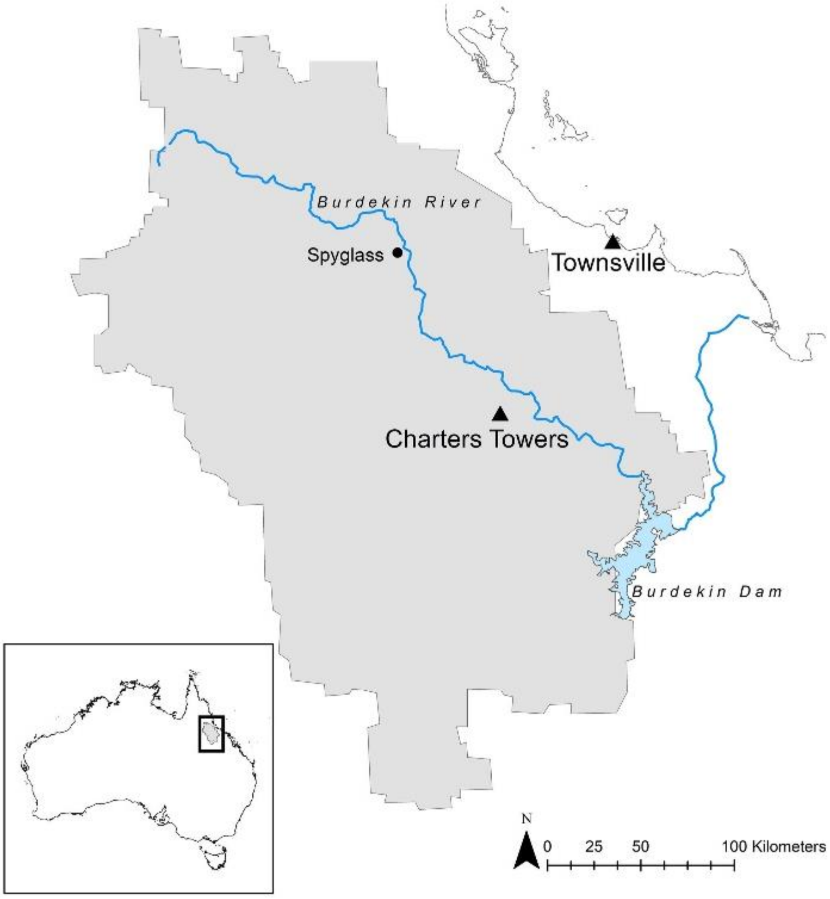


Figure F.1. Location of Spyglass Beef Research Station in relation to the Charters Towers region (the location of the invasive chital population in North Queensland).

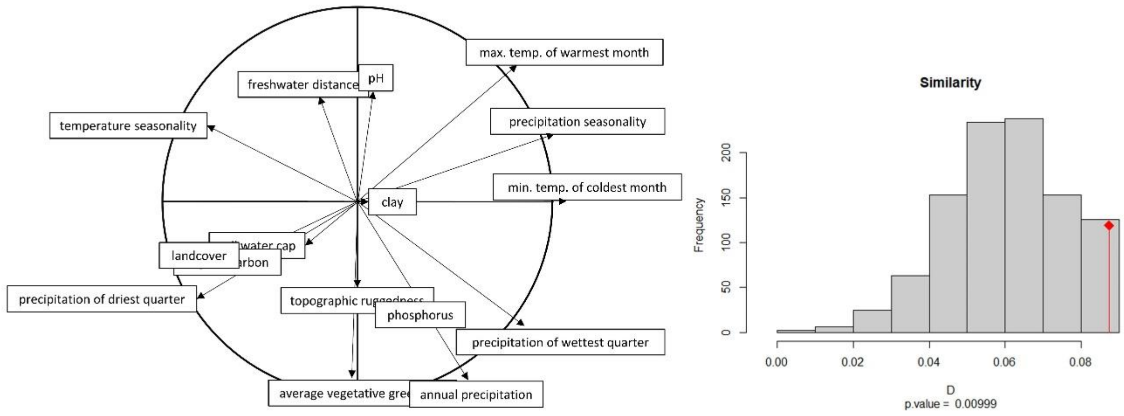
Appendix G

Table G.1. Input variables for MaxEnt modelling

Variable name	Variable description	Source
BIO4	Temperature seasonality (standard deviation x 100)	WorldClim V2.0 datasets: https://www.worldclim.org/
BIO5	Max temperature of warmest month (°C)	"
BIO6	Min temperature of coldest month (°C)	"
BIO12	Annual precipitation (mm)	"
BIO15	Precipitation seasonality (Coefficient of variation)	"
BIO16	Precipitation of wettest quarter (mm)	"
BIO17	Precipitation of driest quarter (mm)	"
landcover	Categorical variable	https://www.esa-landcover-cci.org/
FAPAR mean	Average vegetation greenness	https://land.copernicus.eu/global/products/fapar
FAPAR seasonality	Seasonality in vegetation greenness	https://land.copernicus.eu/global/products/fapar
freshwater distance	Distance to freshwater (m)	https://www.esa-landcover-cci.org/ & https://www.hydrosheds.org/:
topographic ruggedness	Measure of topographic ruggedness	https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/
water cap	Soil water capacity	https://www.isric.org/explore/wise-databases:
organic carbon	Soil organic carbon	"
soil pH	Soil pH	"
clay	Percent clay in soil (%)	https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en
soil bulk density		https://www.isric.org/explore/wise-databases
soil type	Categorical variable	https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en
phosphorus	Soil phosphorus retention class	https://www.isric.org/explore/wise-databases
lithology	dominant lithology	https://agupubs.onlinelibrary.wiley.com/doi/full/10.1029/2012GC004370:

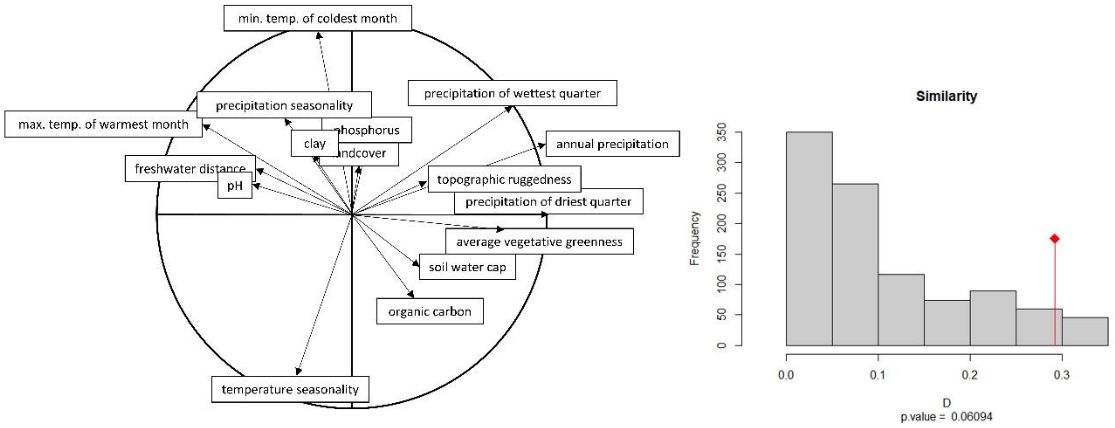
Table G.2. Input variables for niche shift modelling

Variable name	Variable description	Source
BIO4	Temperature seasonality (standard deviation x 100)	WorldClim V2.0 datasets: https://www.worldclim.org/
BIO5	Max temperature of warmest month (°C)	"
BIO6	Min temperature of coldest month (°C)	"
BIO12	Annual precipitation (mm)	"
BIO15	Precipitation seasonality (Coefficient of variation)	"
BIO16	Precipitation of wettest quarter (mm)	"
BIO17	Precipitation of driest quarter (mm)	"
landcover	Categorical variable	https://www.esa-landcover-cci.org/
FAPAR mean	Average vegetation greenness	https://land.copernicus.eu/global/products/fapar
freshwater distance	Distance to freshwater (m)	https://www.esa-landcover-cci.org/ & https://www.hydrosheds.org/:
topographic ruggedness	Measure of topographic ruggedness	https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/
water cap	Soil water capacity	https://www.isric.org/explore/wise-databases:
organic carbon	Soil organic carbon	"
soil pH	Soil pH	"
clay	Percent clay in soil (%)	https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en
phosphorus	Soil phosphorus retention class	https://www.isric.org/explore/wise-databases
lithology	dominant lithology	https://agupubs.onlinelibrary.wiley.com/doi/full/10.1029/2012GC004370:



axis1 = 23.75% axis2 = 18.86%

Figure G.1. Niche of chital deer in both their total range and Australia. Left represents the contribution of each variable to the principal component axis. Right represents the histogram for niche similarity tests between both ranges.



axis1 = 24.29% axis2 = 14.95%

Figure G.2. Niche of fallow deer in both their total range and Australia. Left represents the contribution of each variable to the principal component axis. Right represents the histogram for niche similarity tests between both ranges.

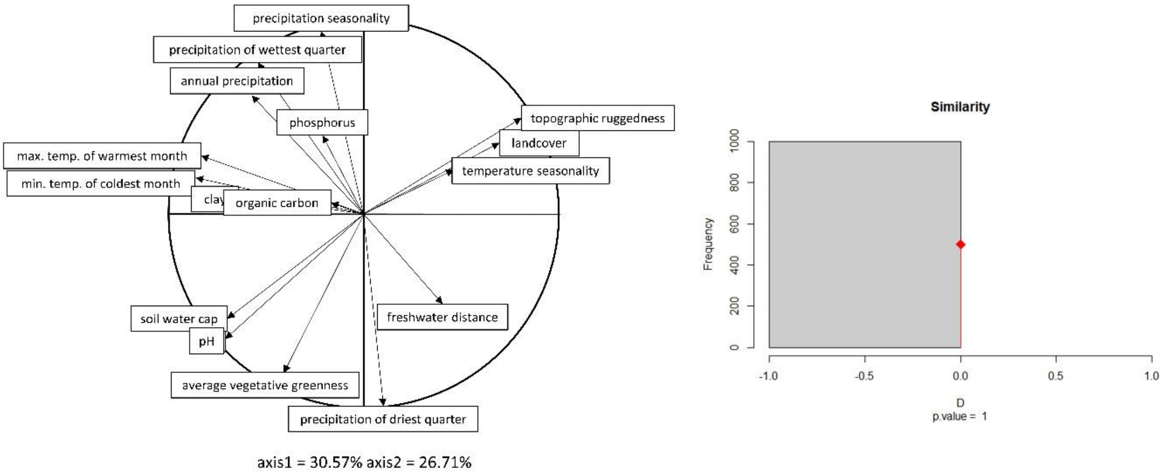


Figure G.3. Niche of hog deer in both their total range and Australia. Left represents the contribution of each variable to the principal component axis. Right represents the histogram for niche similarity tests between both ranges.

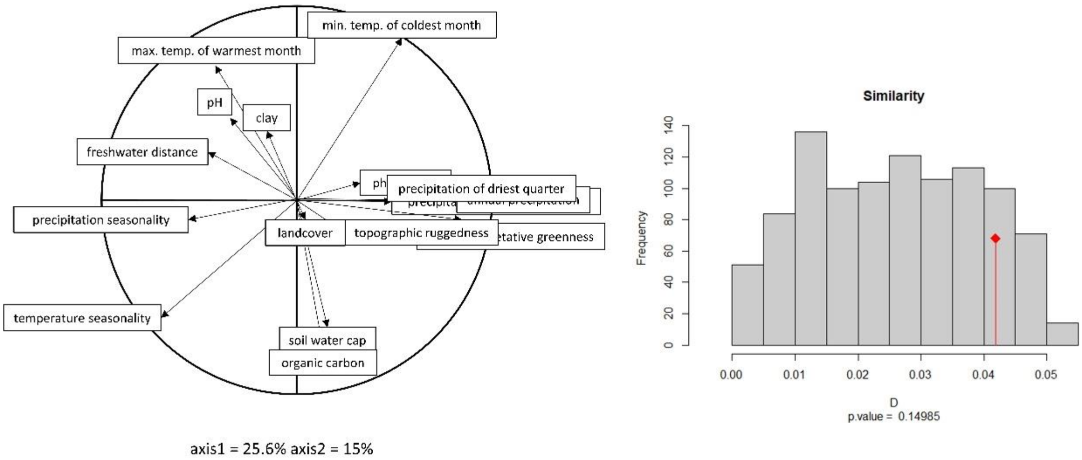


Figure G.4. Niche of red deer in both their total range and Australia. Left represents the contribution of each variable to the principal component axis. Right represents the histogram for niche similarity tests between both ranges.

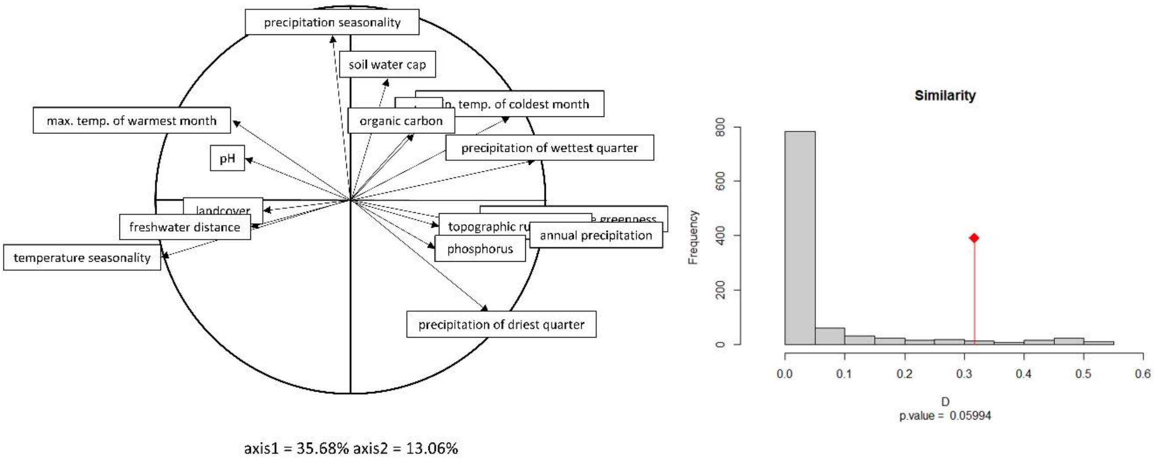


Figure G.5. Niche of rusa deer in both their total range and Australia. Left represents the contribution of each variable to the principal component axis. Right represents the histogram for niche similarity tests between both ranges.

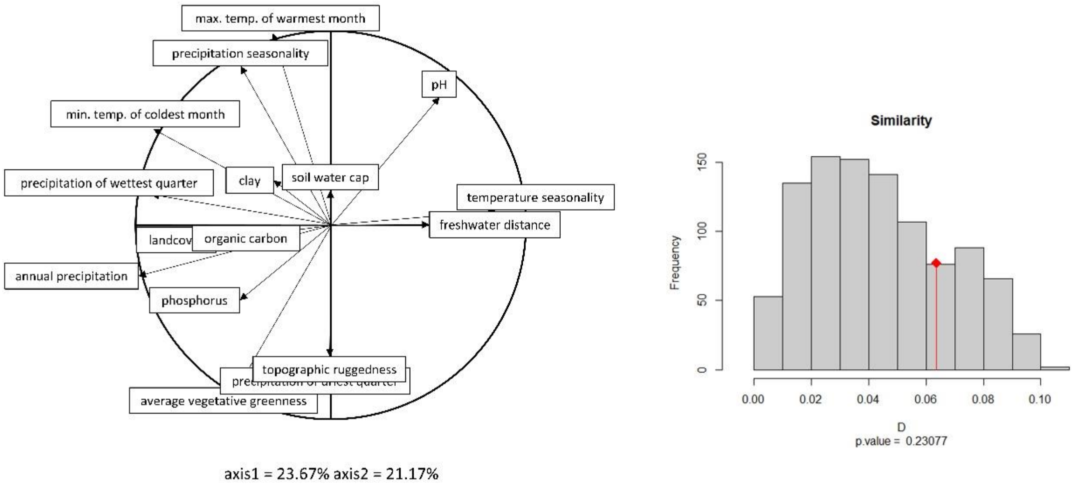
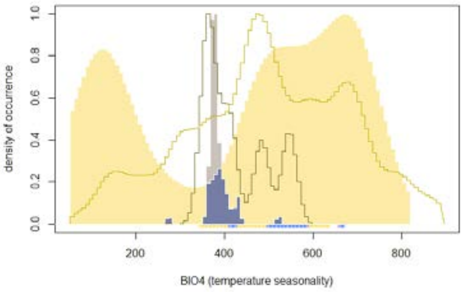
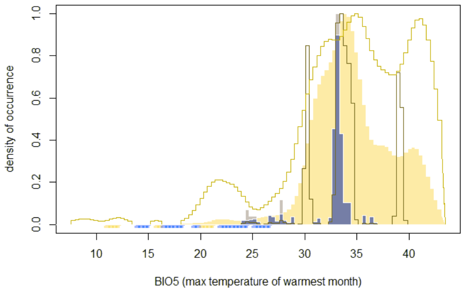
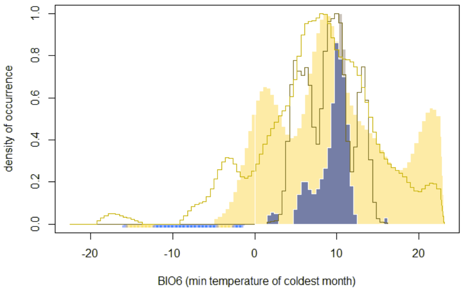
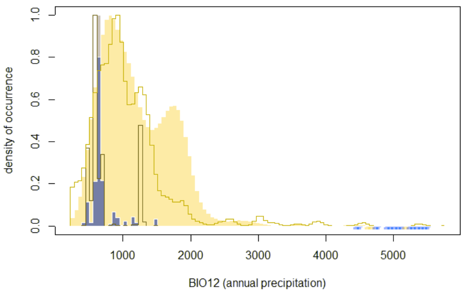


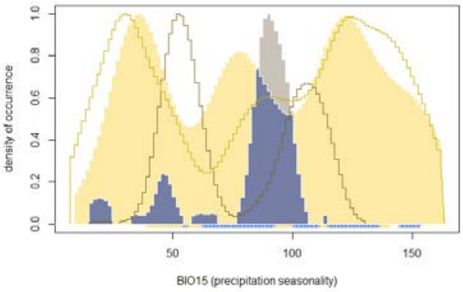
Figure G.6. Niche of sambar deer in both their total range and Australia. Left represents the contribution of each variable to the principal component axis. Right represents the histogram for niche similarity tests between both ranges.

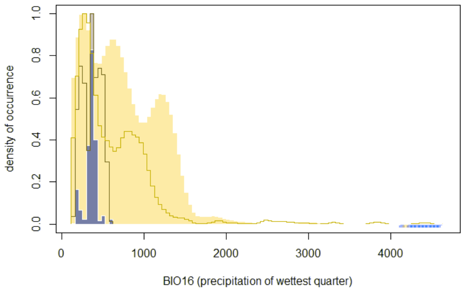

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
200
400
600
800
BIO4 (temperature seasonality)

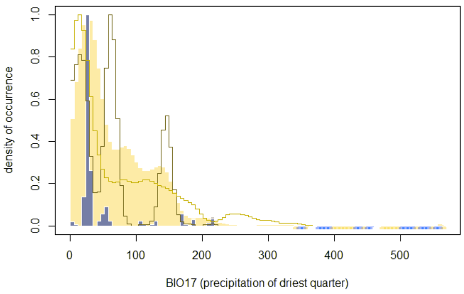

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
10
15
20
25
30
35
40
BIO5 (max temperature of warmest month)

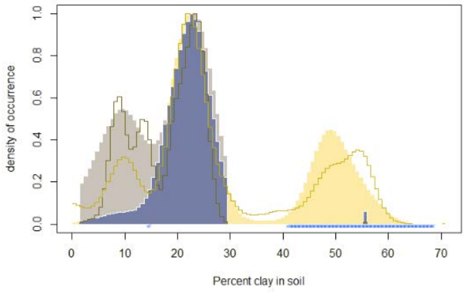

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
-20
-10
0
10
20
BIO6 (min temperature of coldest month)

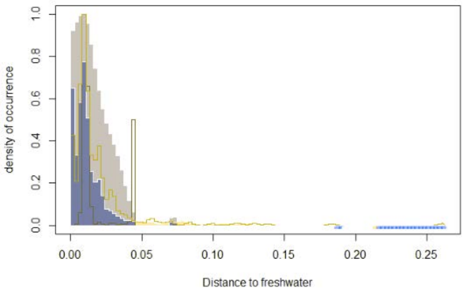

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
1000
2000
3000
4000
5000
BIO12 (annual precipitation)

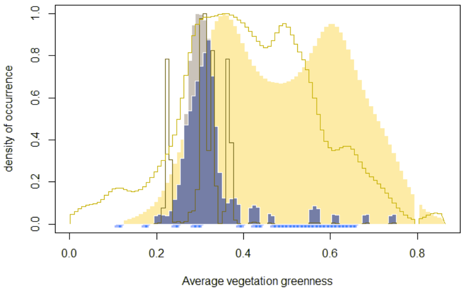

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
50
100
150
BIO15 (precipitation seasonality)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
1000
2000
3000
4000
BIO16 (precipitation of wettest quarter)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
100
200
300
400
500
BIO17 (precipitation of driest quarter)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
60
70
Percent clay in soil


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.00
0.05
0.10
0.15
0.20
0.25
Distance to freshwater


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
0.8
Average vegetation greenness

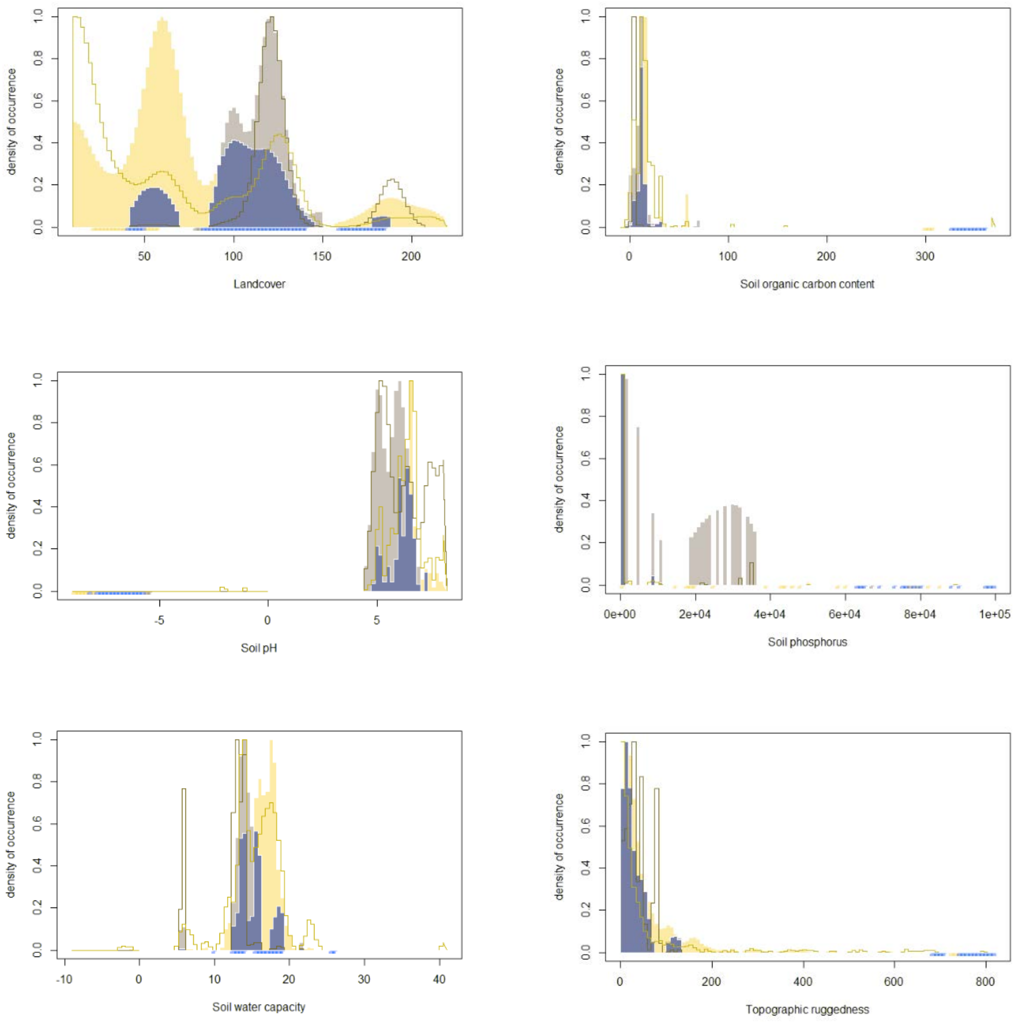
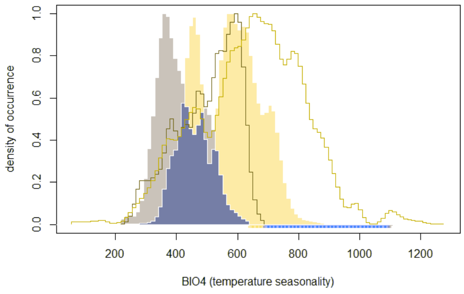


Figure G.7. Chital deer niche occupancy profiles for each variable. Tan represents the total range, and dark brown represents the Australian range. Purple represents the overlap between the two ranges. Overlapping peaks indicate similar variable tolerances. Tan solid lines represent 100% of available space in the total range (sans Australia) and dark brown represents 100% of the available space in the Australian range. Descriptions of variables used, including units, found in Table G.2.


density of occurrence
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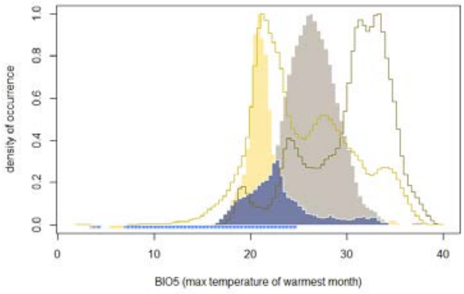
0.4
0.6
0.8
1.0
200
400
600
800
1000
1200
BIO4 (temperature seasonality)


density of occurrence
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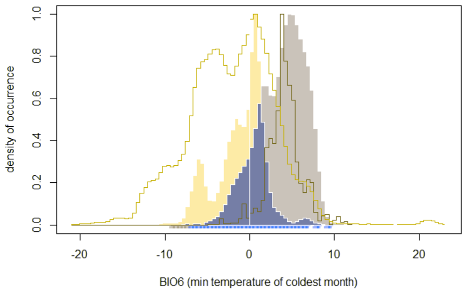
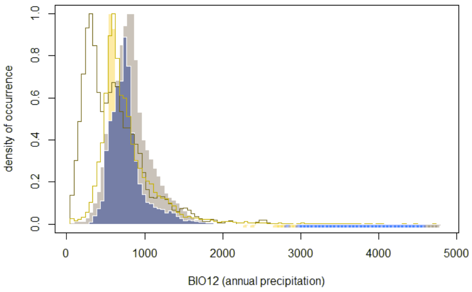
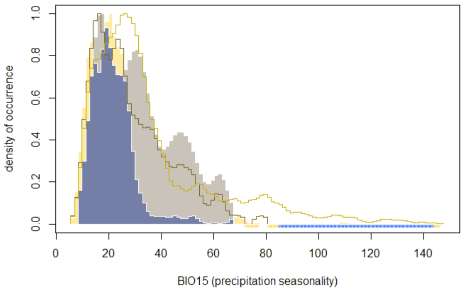
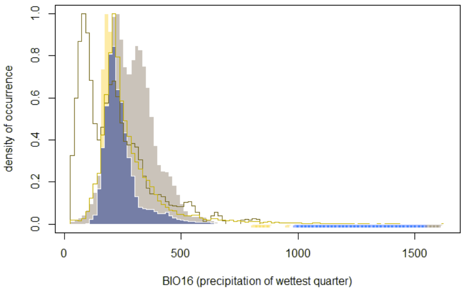
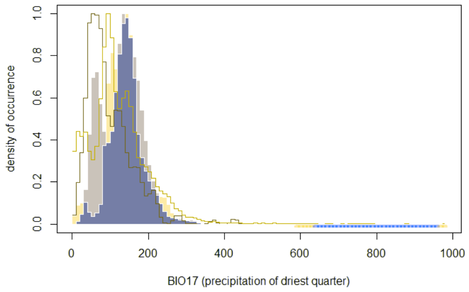
0.4
0.6
0.8
1.0
0
10
20
30
40
BIO5 (max temperature of warmest month)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
-20
-10
0
10
20
BIO6 (min temperature of coldest month)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
1000
2000
3000
4000
5000
BIO12 (annual precipitation)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100
120
140
BIO15 (precipitation seasonality)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
500
1000
1500
BIO16 (precipitation of wettest quarter)


density of occurrence
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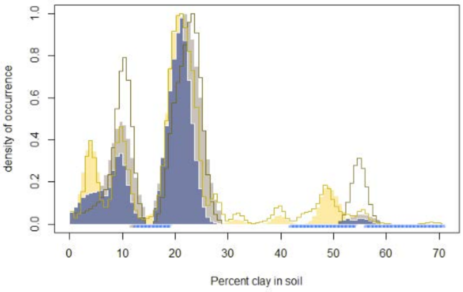
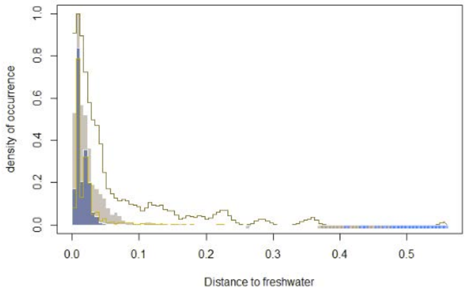
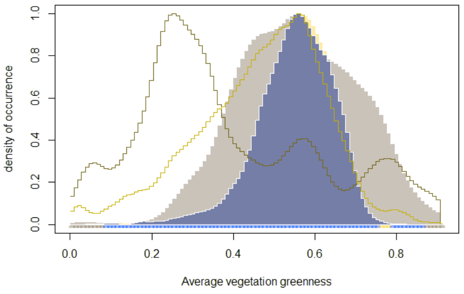
0.2
0.4
0.6
0.8
1.0
0
200
400
600
800
1000
BIO17 (precipitation of driest quarter)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
60
70
Percent clay in soil


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.1
0.2
0.3
0.4
0.5
Distance to freshwater


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
0.8
Average vegetation greenness

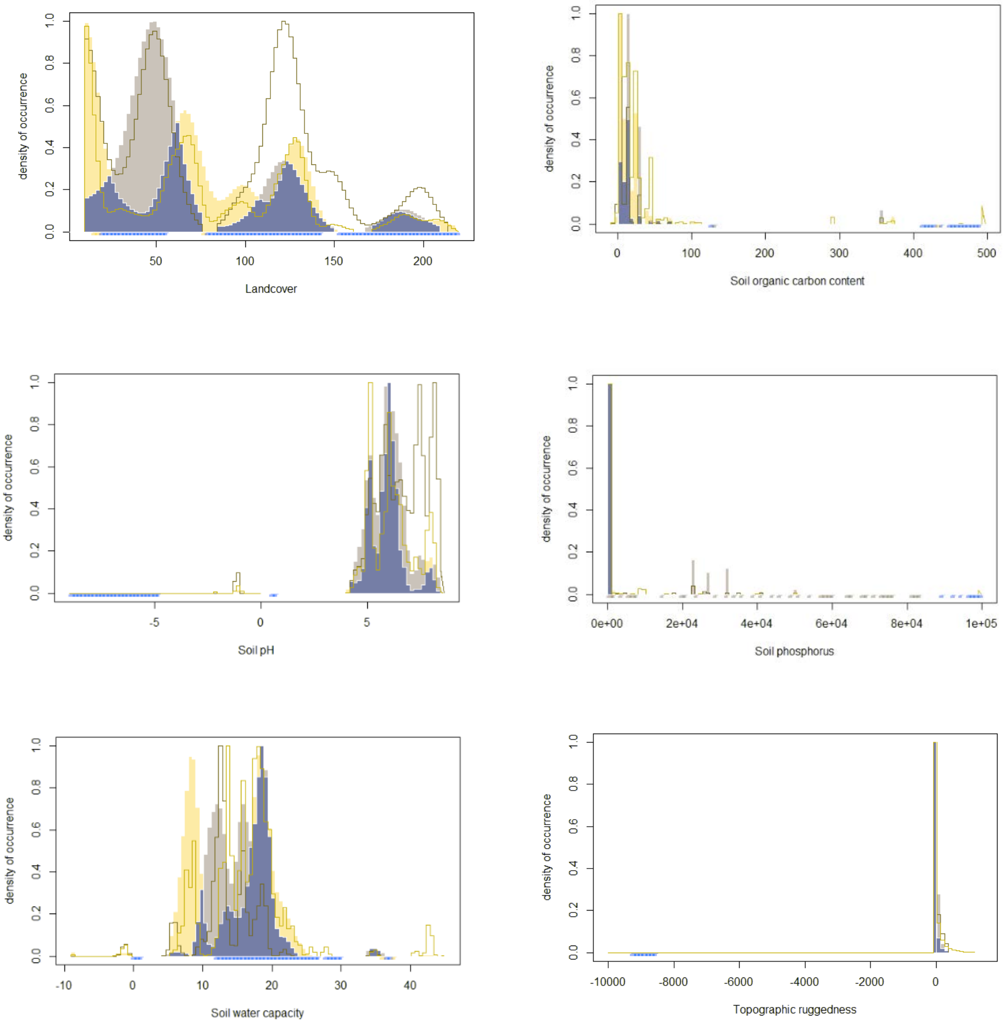
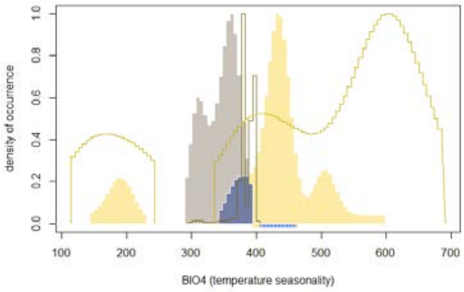
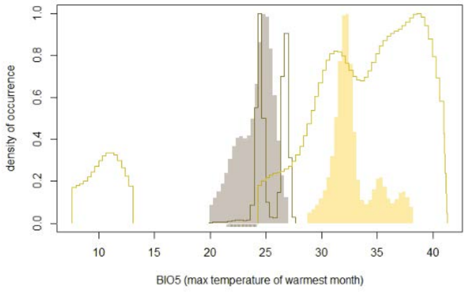
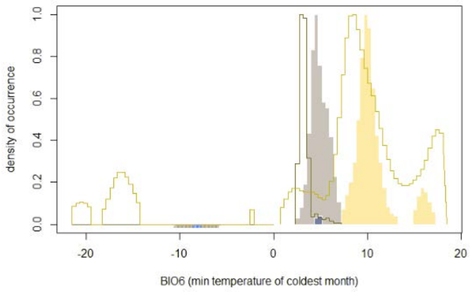
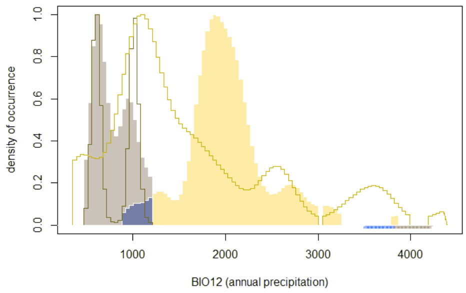


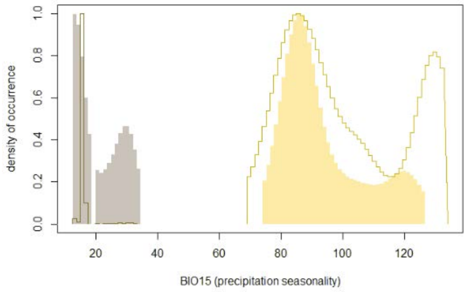
Figure G.8. Fallow deer niche occupancy profiles for each variable. Tan represents the total range, and dark brown represents the Australian range. Purple represents the overlap between the two ranges. Overlapping peaks indicate similar variable tolerances. Tan solid lines represent 100% of available space in the total range (sans Australia) and dark brown represents 100% of the available space in the Australian range. Descriptions of variables used, including units, found in Table G.2.


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
100
200
300
400
500
600
700
BIO4 (temperature seasonality)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
10
15
20
25
30
35
40
BIO5 (max temperature of warmest month)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
-20
-10
0
10
20
BIO6 (min temperature of coldest month)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
1000
2000
3000
4000
BIO12 (annual precipitation)


density of occurrence
0.0
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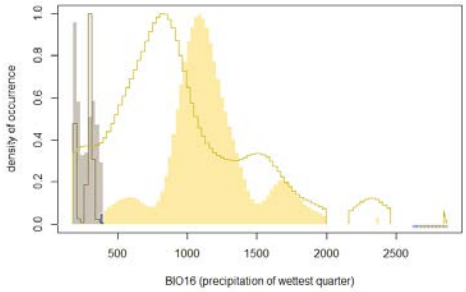
0.4
0.6
0.8
1.0
20
40
60
80
100
120
BIO15 (precipitation seasonality)


density of occurrence
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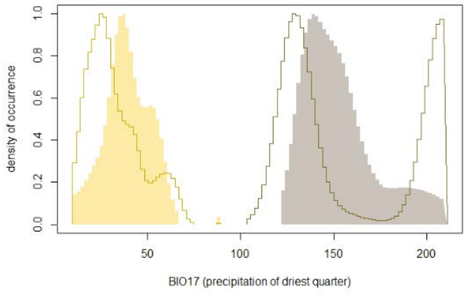
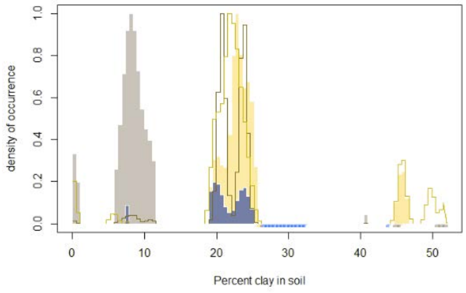
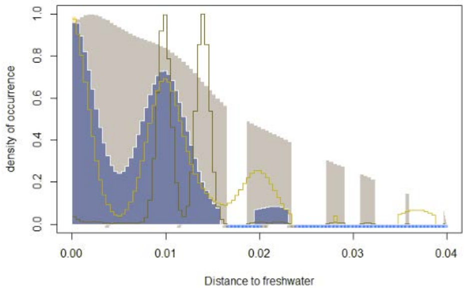
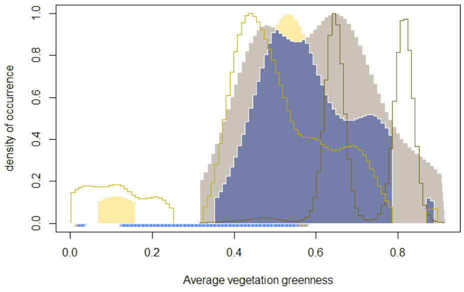
0.2
0.4
0.6
0.8
1.0
500
1000
1500
2000
2500
BIO16 (precipitation of wettest quarter)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
50
100
150
200
BIO17 (precipitation of driest quarter)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
Percent clay in soil


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.00
0.01
0.02
0.03
0.04
Distance to freshwater


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
0.8
Average vegetation greenness

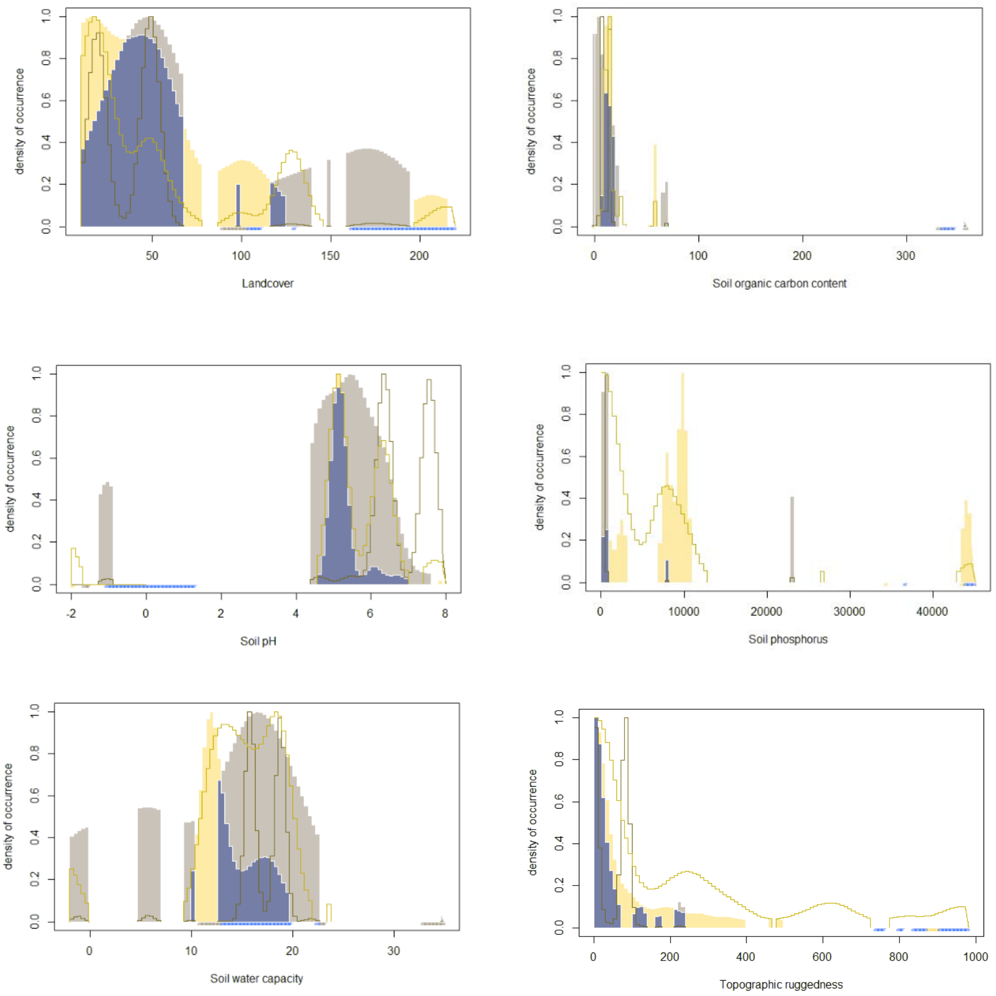
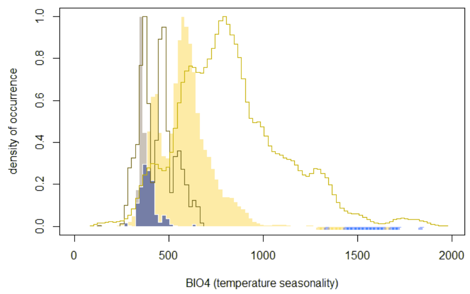
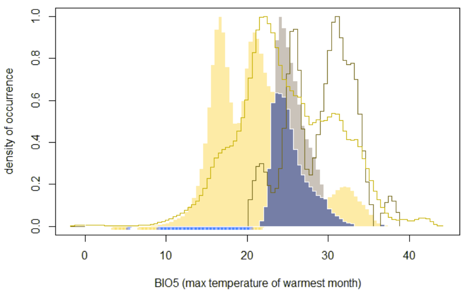
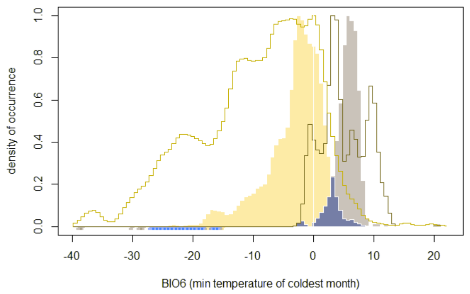
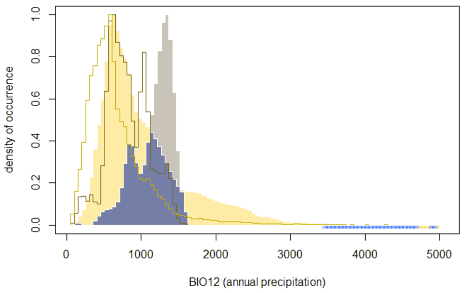


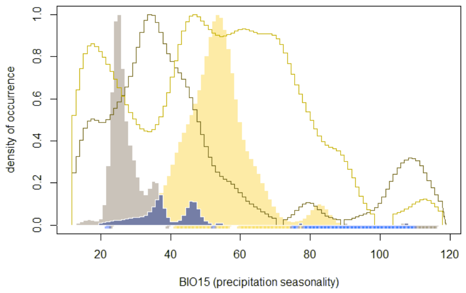
Figure G.9. Hog deer niche occupancy profiles for each variable. Tan represents the total range, and dark brown represents the Australian range. Purple represents the overlap between the two ranges. Overlapping peaks indicate similar variable tolerances. Tan solid lines represent 100% of available space in the total range (sans Australia) and dark brown represents 100% of the available space in the Australian range. Descriptions of variables used, including units, found in Table G.2.

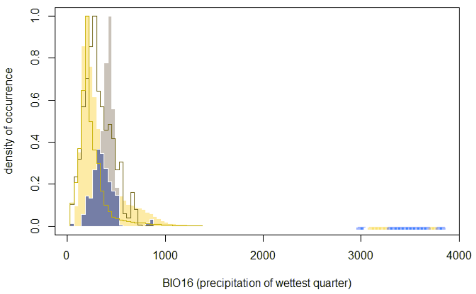

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
500
1000
1500
2000
BIO4 (temperature seasonality)

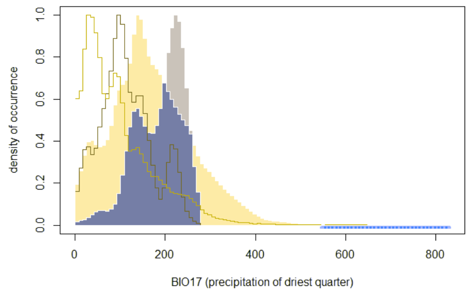

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
BIO5 (max temperature of warmest month)

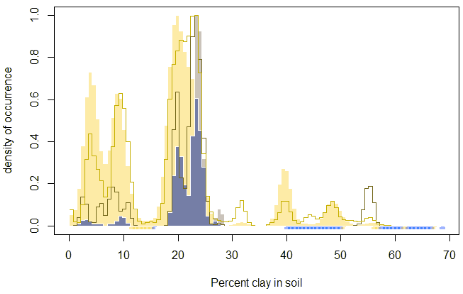

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
-40
-30
-20
-10
0
10
20
BIO6 (min temperature of coldest month)

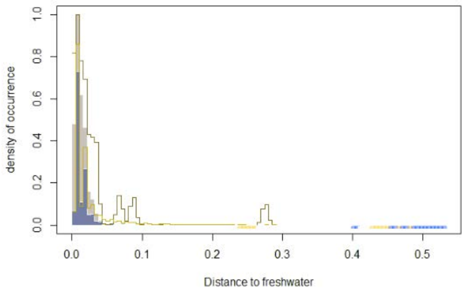

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
1000
2000
3000
4000
5000
BIO12 (annual precipitation)

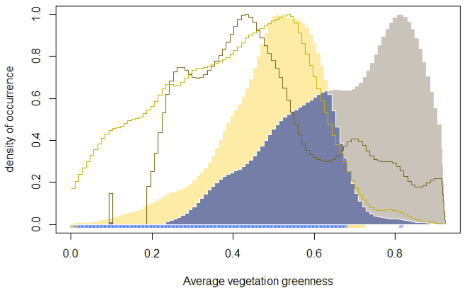

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
20
40
60
80
100
120
BIO15 (precipitation seasonality)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
1000
2000
3000
4000
BIO16 (precipitation of wettest quarter)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
200
400
600
800
BIO17 (precipitation of driest quarter)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
60
70
Percent clay in soil


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.1
0.2
0.3
0.4
0.5
Distance to freshwater


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
0.8
Average vegetation greenness

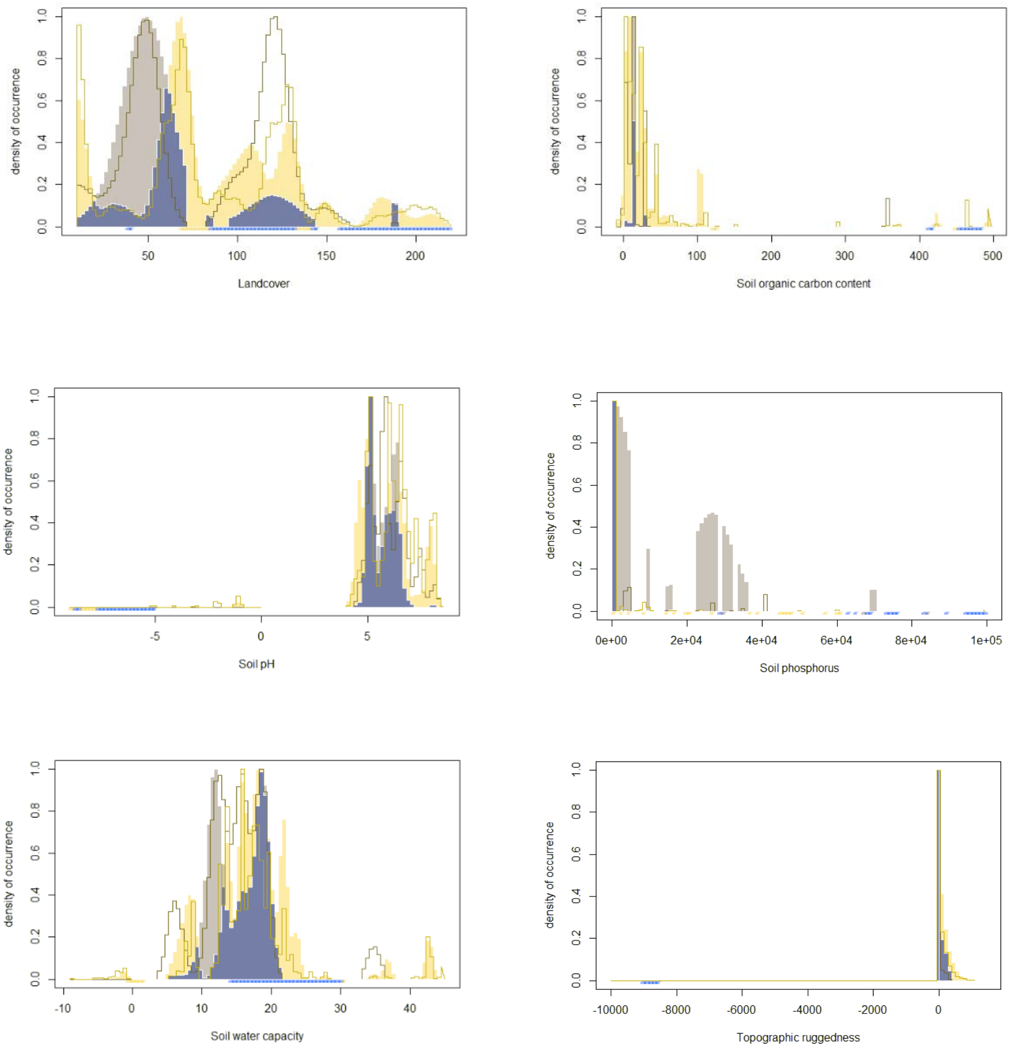
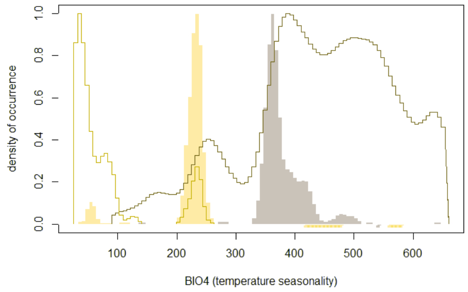
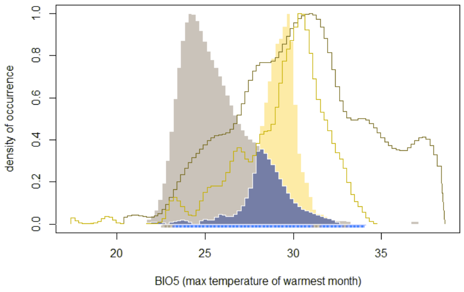
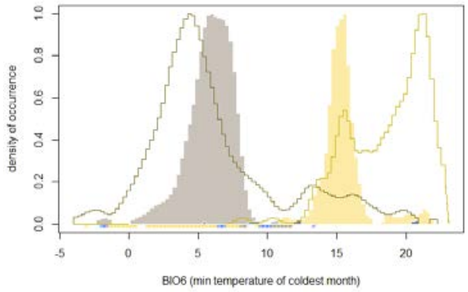
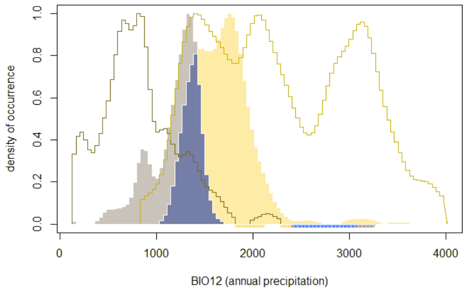


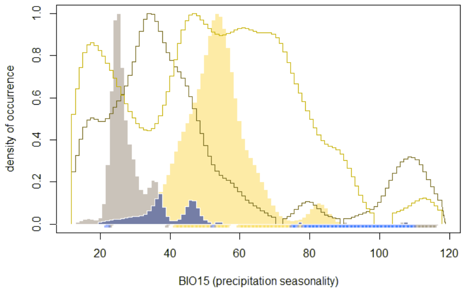
Figure G.10. Red deer niche occupancy profiles for each variable. Tan represents the total range, and dark brown represents the Australian range. Purple represents the overlap between the two ranges. Overlapping peaks indicate similar variable tolerances. Tan solid lines represent 100% of available space in the total range (sans Australia) and dark brown represents 100% of the available space in the Australian range. Descriptions of variables used, including units, found in Table G.2.

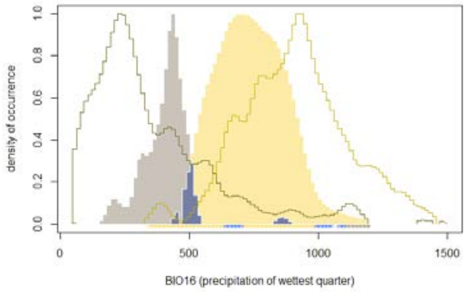

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
100
200
300
400
500
600
BIO4 (temperature seasonality)

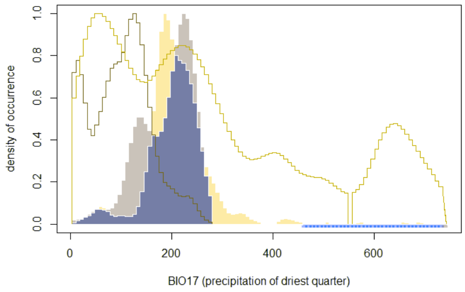

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
20
25
30
35
BIO5 (max temperature of warmest month)

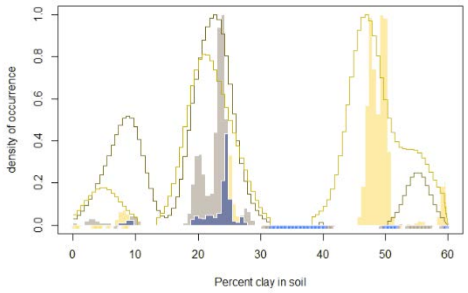

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
-5
0
5
10
15
20
BIO6 (min temperature of coldest month)

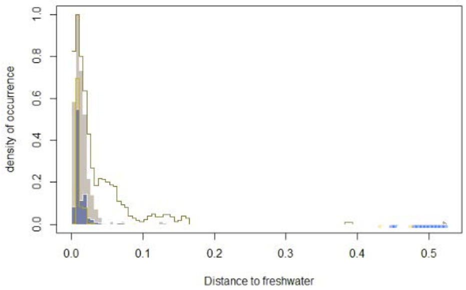

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
1000
2000
3000
4000
BIO12 (annual precipitation)

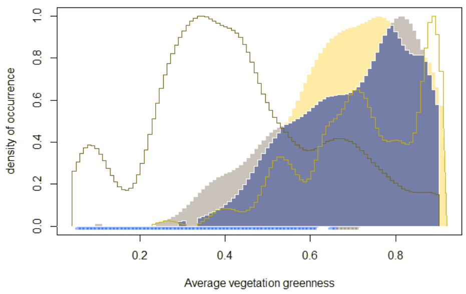

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
20
40
60
80
100
120
BIO15 (precipitation seasonality)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
500
1000
1500
BIO16 (precipitation of wettest quarter)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
200
400
600
BIO17 (precipitation of driest quarter)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
60
Percent clay in soil


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.1
0.2
0.3
0.4
0.5
Distance to freshwater


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.2
0.4
0.6
0.8
Average vegetation greenness

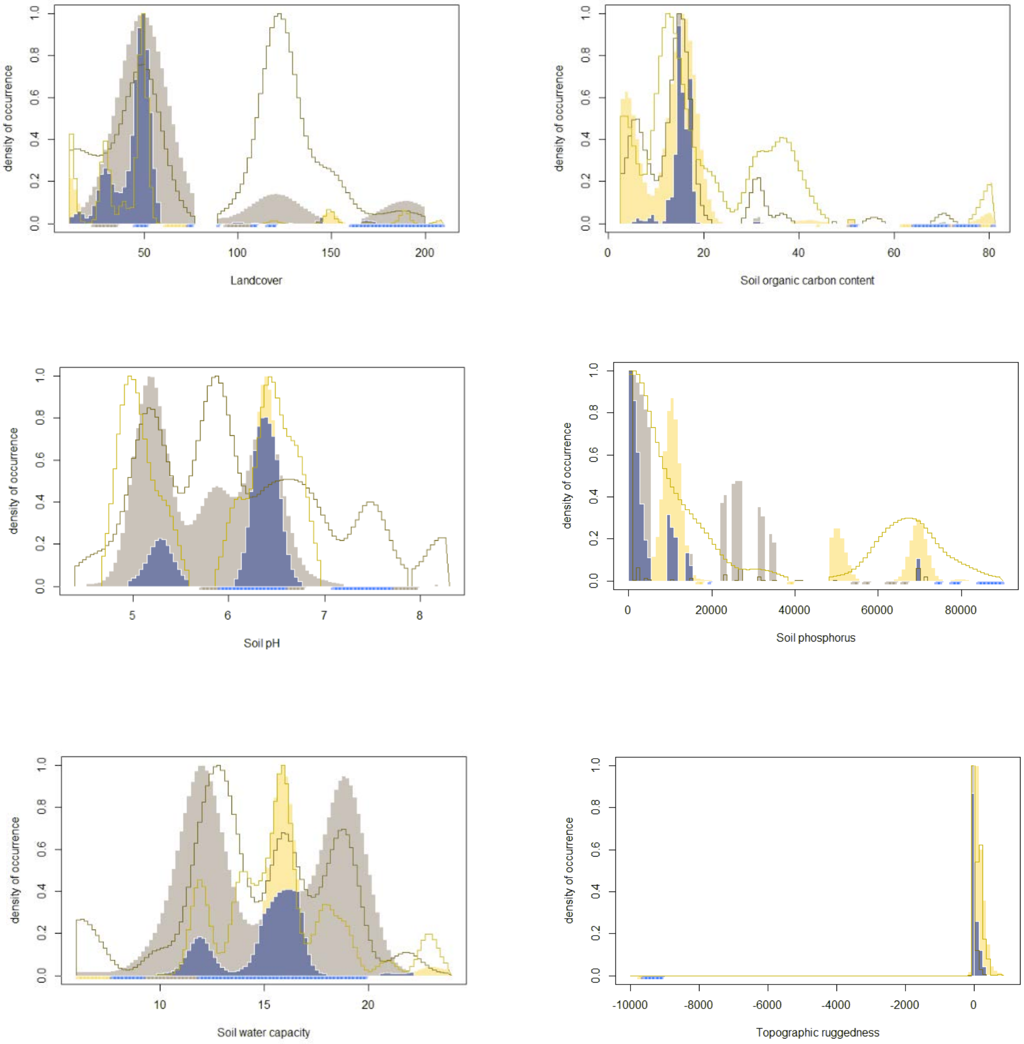
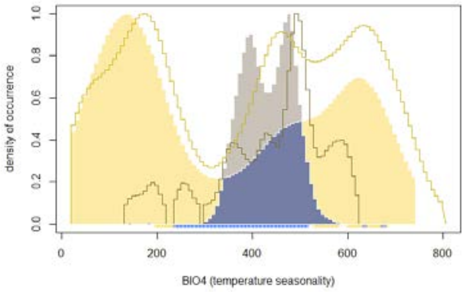
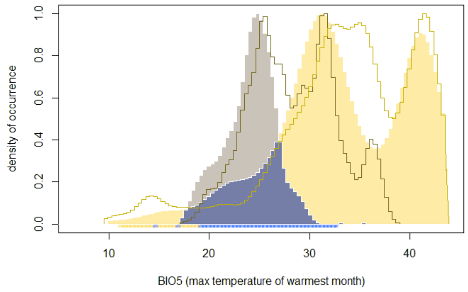
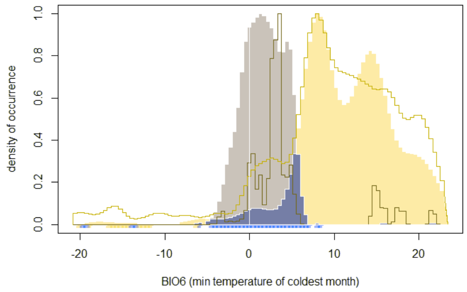
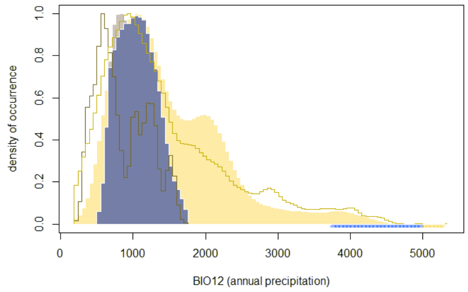


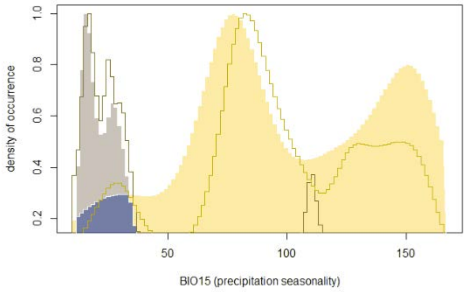
Figure G.11. Rusa deer niche occupancy profiles for each variable. Tan represents the total range, and dark brown represents the Australian range. Purple represents the overlap between the two ranges. Overlapping peaks indicate similar variable tolerances. Tan solid lines represent 100% of available space in the total range (sans Australia) and dark brown represents 100% of the available space in the Australian range. Descriptions of variables used, including units, found in Table G.2.

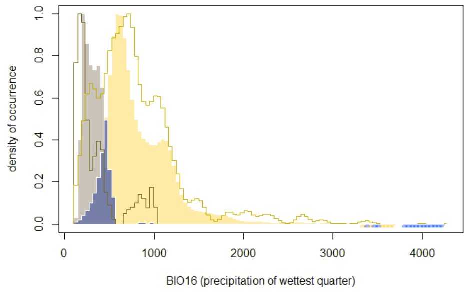

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
200
400
600
800
BIO4 (temperature seasonality)

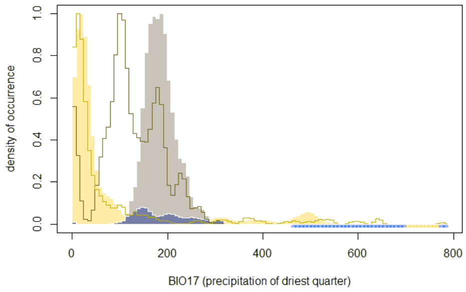

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
10
20
30
40
BIO5 (max temperature of warmest month)

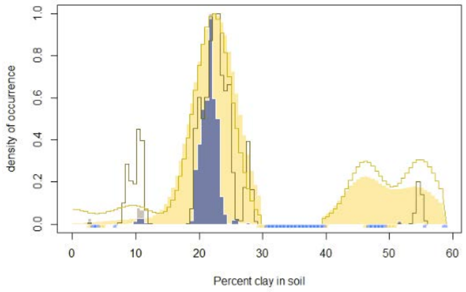

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
-20
-10
0
10
20
BIO6 (min temperature of coldest month)

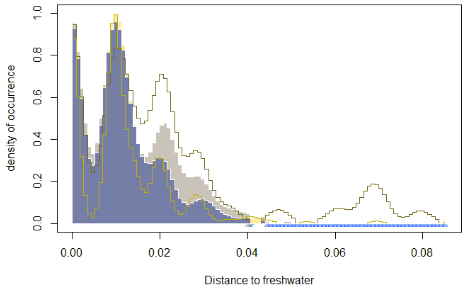

density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
1000
2000
3000
4000
5000
BIO12 (annual precipitation)

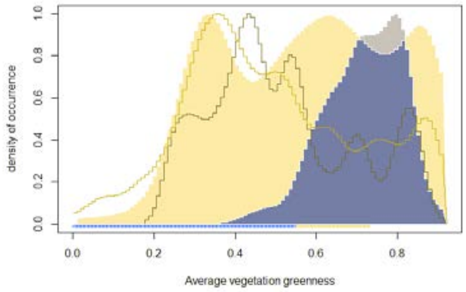

density of occurrence
0.2
0.4
0.6
0.8
1.0
50
100
150
BIO15 (precipitation seasonality)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
1000
2000
3000
4000
BIO16 (precipitation of wettest quarter)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
200
400
600
800
BIO17 (precipitation of driest quarter)


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
60
Percent clay in soil


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.00
0.02
0.04
0.06
0.08
Distance to freshwater


density of occurrence
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
0.8
Average vegetation greenness

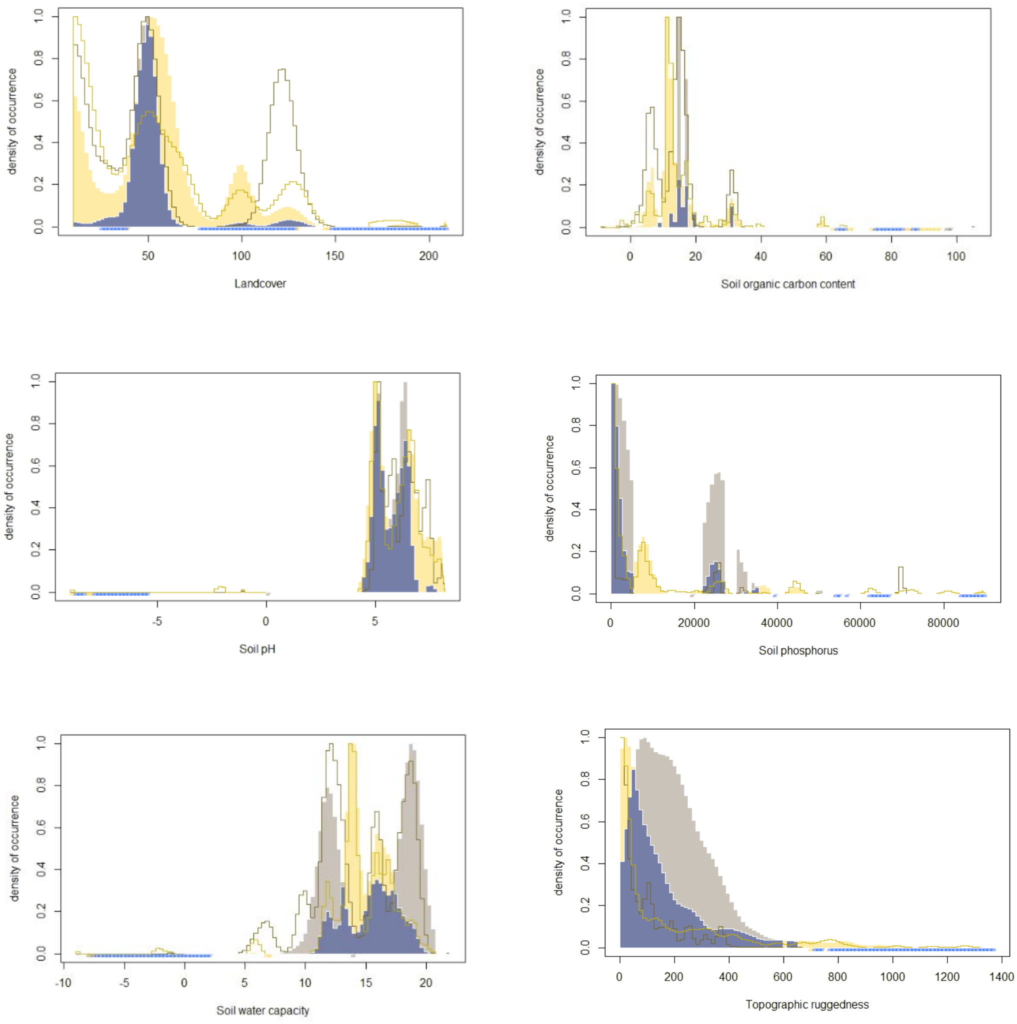
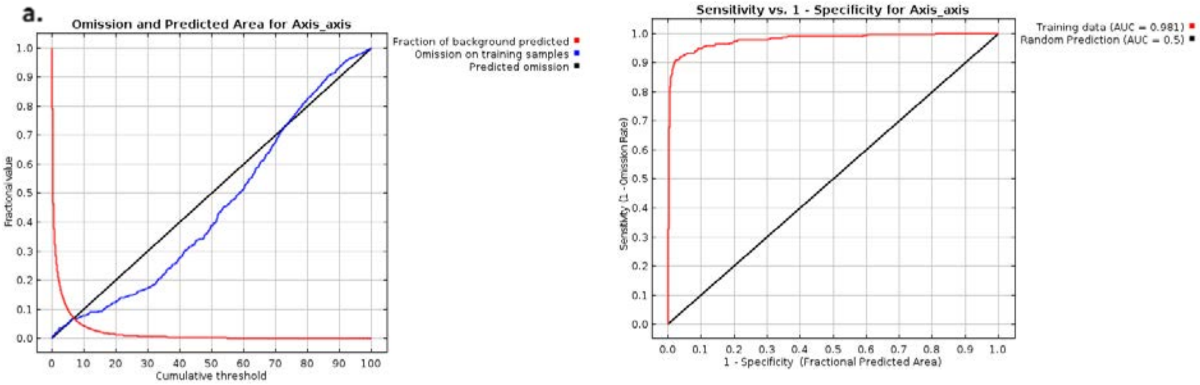
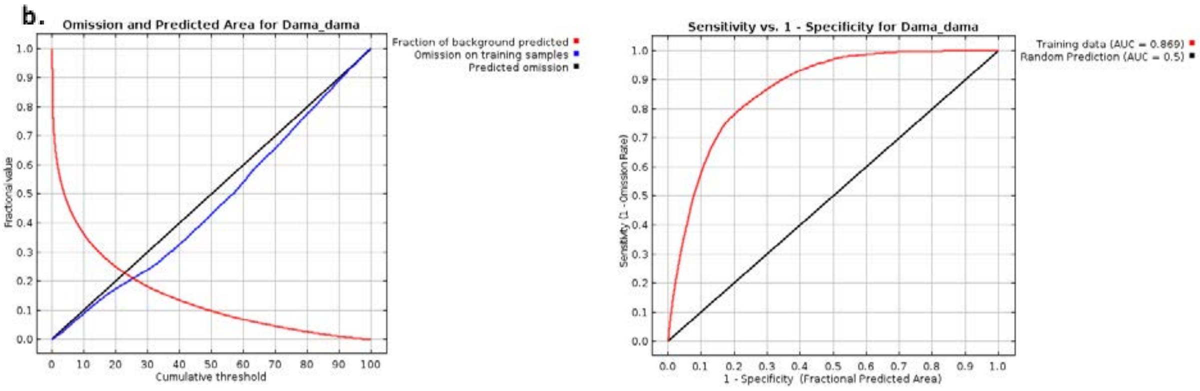
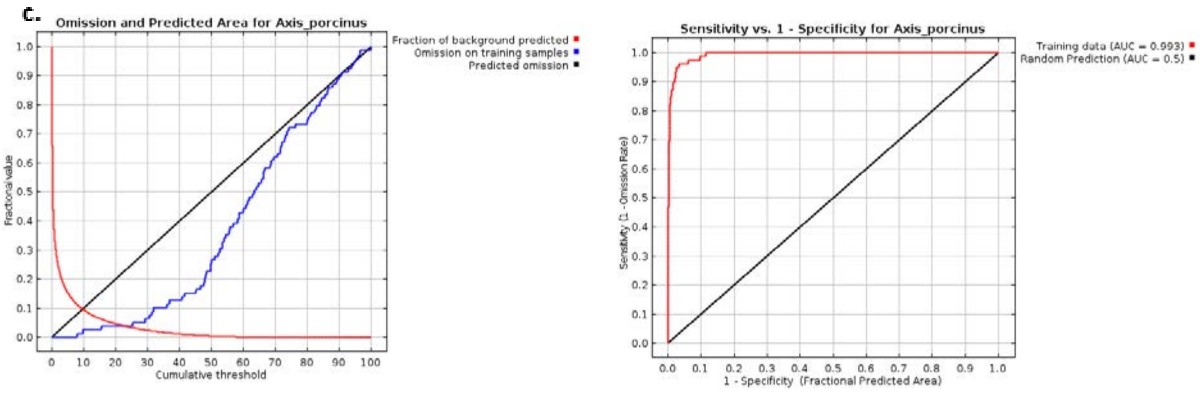
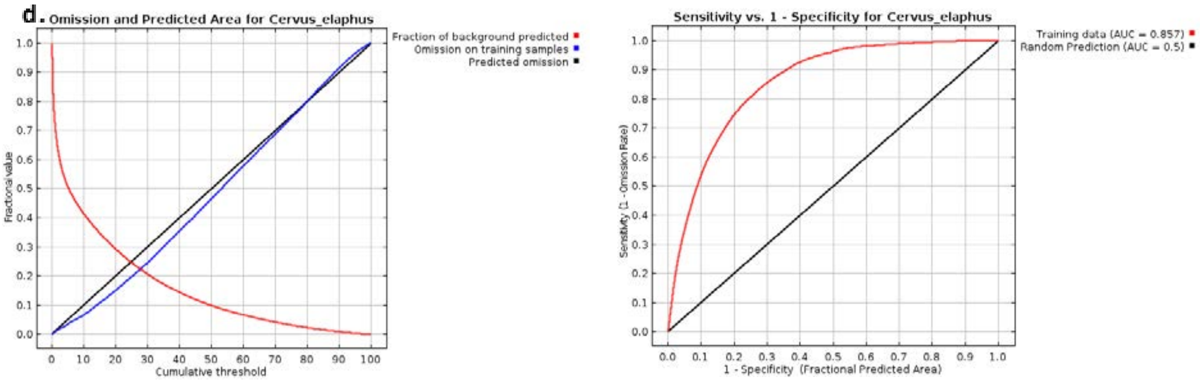


Figure G.12. Sambar deer niche occupancy profiles for each variable. Tan represents the total range, and dark brown represents the Australian range. Purple represents the overlap between the two ranges. Overlapping peaks indicate similar variable tolerances. Tan solid lines represent 100% of available space in the total range (sans Australia) and dark brown represents 100% of the available space in the Australian range. Descriptions of variables used, including units, found in Table G.2.


a.
Omission and Predicted Area for Axis_axis
Fraction of background predicted ■
Omission on training samples ■
Predicted omission ■
Fractional value
Cumulative threshold
0 10 20 30 40 50 60 70 80 90 100
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Sensitivity vs. 1 - Specificity for Axis_axis
Training data (AUC = 0.981) ■
Random Prediction (AUC = 0.5) ■
Sensitivity (1 - Omission Rate)
1 - Specificity (Fractional Predicted Area)


b.
Omission and Predicted Area for Dama_dama
Fraction of background predicted ■
Omission on training samples ■
Predicted omission ■
Fractional value
Cumulative threshold
0 10 20 30 40 50 60 70 80 90 100
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Sensitivity vs. 1 - Specificity for Dama_dama
Training data (AUC = 0.869) ■
Random Prediction (AUC = 0.5) ■
Sensitivity (1 - Omission Rate)
1 - Specificity (Fractional Predicted Area)


c.
Omission and Predicted Area for Axis_porcinus
Fraction of background predicted ■
Omission on training samples ■
Predicted omission ■
Fractional value
Cumulative threshold
0 10 20 30 40 50 60 70 80 90 100
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Sensitivity vs. 1 - Specificity for Axis_porcinus
Training data (AUC = 0.993) ■
Random Prediction (AUC = 0.5) ■
Sensitivity (1 - Omission Rate)
1 - Specificity (Fractional Predicted Area)


d.
Omission and Predicted Area for Cervus_elaphus
Fraction of background predicted ■
Omission on training samples ■
Predicted omission ■
Fractional value
Cumulative threshold
0 10 20 30 40 50 60 70 80 90 100
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Sensitivity vs. 1 - Specificity for Cervus_elaphus
Training data (AUC = 0.857) ■
Random Prediction (AUC = 0.5) ■
Sensitivity (1 - Omission Rate)
1 - Specificity (Fractional Predicted Area)

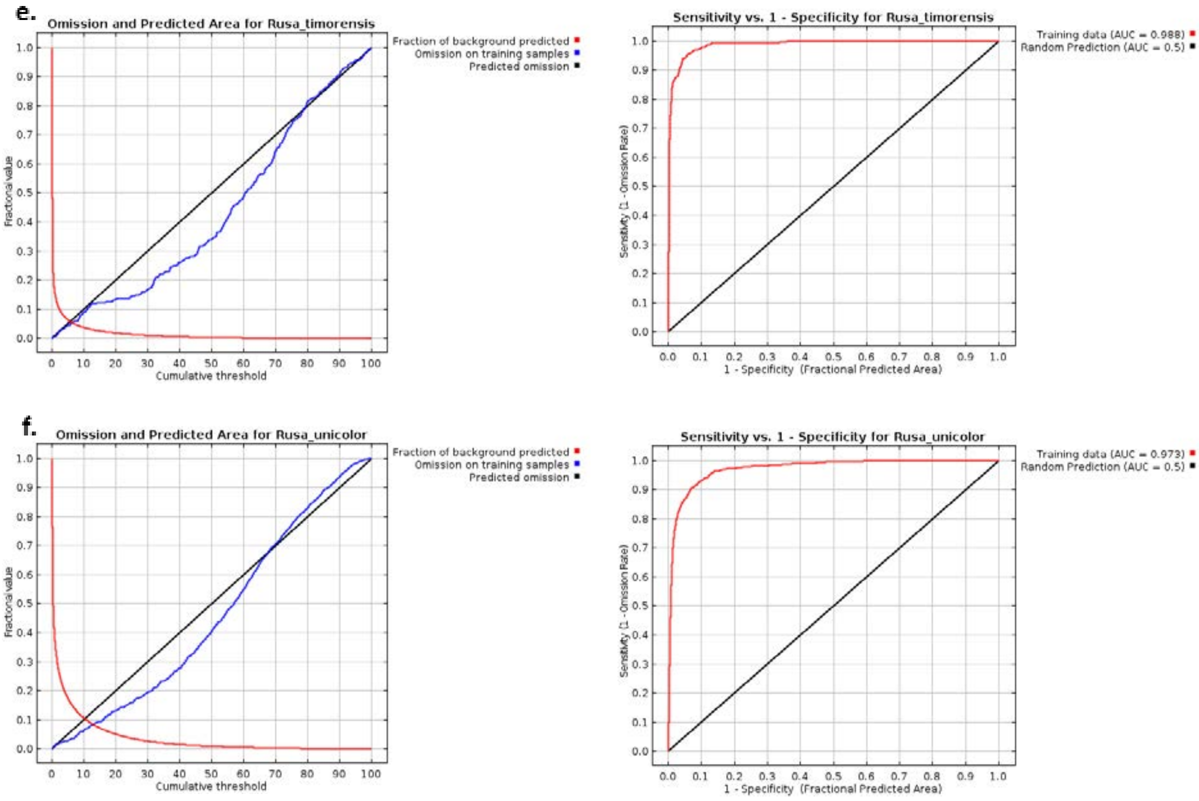


Figure G.13. Maxent output curves for each of the six species of deer in Australia (a. chital, b. fallow, c. hog, d. red, e. rusa, and f. sambar). On the left represents the omission rate and predicted area as a function of the cumulative threshold and on the right represents the receiver operating characteristic (ROC) curve for the same data. The AUC value for each ROC curve is presented on the top right of each plot.

Table G.3. Important variables as determined by MaxEnt modelling for each of the six species of deer in Australia. RC = relative contribution to model, PI =permutational importance. In bold are the two most important variables that contribute to habitat suitability for each species.

	Axis		Fallow		Hog		Red		Rusa		Sambar	
Variable	RC	PI	RC	PI	RC	PI	RC	PI	RC	PI	RC	PI
precipitation seasonality	**21.6**	7.5	2.5	14.3	7.3	11.2	3.6	8.8	13.4	37.3	7	9.1
maximum temperature	**19.4**	5.5	**30.2**	25.2			3.3	4.5	8.8	21.6	1.9	1.3
soil type	13.7	6.4	14.1	5.1	**16.4**	3	**14.9**	8.4	15.4	2	9.2	3.9
minimum temperature	10.5	55	**15.3**	21.1	**39.4**	49.9	14.3	20.5	7.4	14.4		
precipitation of driest quarter	9.5	5	3.4	13.3	12.4	9.7	1.4	12.4	8.7	1.6	3.7	4.4
annual precipitation	9	9.6	0.1	1.8	12.7	25.4	1.1	9	**18.2**	4.3	3.3	7.7
land cover type	7.5	1.7	6.5	1.7	11.7	0.8	32	16.6	**24.2**	2.9	**31.3**	14
dominant lithology	2.3	0.4									2	1
soil pH	1.5	1.4							0.4	5.1		
soil phosphorous retention	1.5	0.1					1.7	1.6			4.4	1.1
average vegetation greenness	1.1	1.1	17	4.7					0.9	2	3	3.8
soil organic carbon	0.9	2.5									0.7	3.3
percent clay in soil	0.7	0.9									9.2	13.2
soil water capacity	0.7	3	7.8	6.1							0.5	3.9
precipitation of wettest quarter			2	5.7					0.2	5.9	0.4	4.3
distance to freshwater			1.1	1.2							1.1	2.7
temperature seasonality							0.8	14.2	2.3	2.8	8.3	13.2
topographic ruggedness							**26.8**	4			**9.4**	2.5
soil bulk density											3.1	4.9
seasonality in vegetation greenness											1.4	5.7