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Understanding population dynamics of feral horses in the Tuan and Toolara State Forest for successful long-term population management

Magdalena Anna Zabek
Bachelor of Equine Science

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Abstract

Feral horses (*Equus caballus)* in Australia are a growing problem despite implementation of management strategies. The increasing number of feral horses within the Tuan and Toolara State Forest (TTSF), a coniferous plantation on the Sunshine Coast, Queensland, and particularly near major public roads, has been recognised as a problem in the last decade. Desensitised to road traffic, horses are a serious distraction for motorists, and have potential to cause serious animal-vehicle accidents.

The primary objective of the study was to characterise the essential demographics of the TTSF feral horses, so that the most suitable methods for long-term population management could be determined. The study was conducted from 2012 – 2014 and determined social structure, reproductive performance and survival, and population growth rate. The estimation of population distribution, abundance and density together with assessment of habitat use and home range size were also addressed.

The studied population did not show significant annual variation in demographics, which is consistent with measurements in other unmanaged feral horse populations in Australia and abroad. The overall size and age composition of social groups remained stable during the study period. The average harem size was estimated as 4.95 (95%CI 4.53-5.41), and usually consisted of 1 stallion, 2 - 3 adult females, and 2 immature offspring (≤ 3 years of age). Males not associated with harems consisted of adult (≥ 3 years old) and sub-adult (2 years old) individuals, either forming groups of 2 – 6 or living by themselves. The population showed a stable age distribution, with adult horses constituting the largest group (68%; n = 247). The sex ratio of adult female to male horses was nearly equal (0.99:1.00).

The mean annual fecundity was 0.23 ± 0.07 SD and was comparable to those obtained for other feral horse populations where the environment imposed nutritional limitations. Adult females were observed to foal on average every second year. The overall nutritional status of the population expressed as body condition score (BCS; 0 - 5) was 2.55 ± 0.51 SD with adult females having poorer scores than other age and gender groups. Survival estimates were consistently high (0.92 – 0.95) across all age groups. The average annual finite rate of population increase (λ) for the three years of the study was 1.088 which was lower than the maximum reported for populations living in the most favourable conditions. Elasticity analysis demonstrated that the TTSF population growth rate was almost seven times more sensitive to changes in adult survival compared with juvenile survival, and almost twice more sensitive than changes in fecundity.

Assessment of the population distribution based on a strip transect survey using horse dung on forest tracks indicated that the majority of the forestry was occupied by horses, with the highest population density being located in the central region of the plantation. Abundance and density of horses were estimated by distance line transect survey of dung counts, dung disappearance rate of 444 (± 150.7 SD) days and individual defecation rates of 7.97 (± 8.74 SD) over 24 hours. The analysis indicated that the TTSF was occupied by 1321 horses (95%CI 940 - 1965), which corresponded to a density of 1.8 horses/km^2.

Habitat use quantified by visual detection of horses, dung counts, and Global Positioning System (GPS) tracking, identified a preference for open habitats of young pine forest and harvested areas, and avoidance of closed canopy habitats of juvenile and mature pine. Home range size determined by GPS tracking was greater than that measured by direct observation (mean ± SD; 16.90 ± 9.11 km^2 and 6.71 ± 3.30 km^2 respectively). All harems were loyal to their home ranges; harem members occupied one core area more than other parts of their range, and home ranges highly overlapped.

The findings of this thesis confirm that there is a gradual increase in feral horse distribution and population size within the TTSF. It is evident that the design and implementation of a program to manage feral horses in the TTSF will need to consider a combination of approaches, which will need to satisfy a number of criteria including efficacy, cost-effectiveness, occupational safety, environmental impacts and animal welfare. Continued monitoring of the population growth is essential to measure the effectiveness of chosen management strategies.

Declaration by author

This thesis *is composed of my original work, and contains* no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted *to qualify for the award of any* other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

Conference abstracts

Zabek MA, Berman DM, and Collins CW (2012). Population growth analysis of feral horses in a coastal forest environment. *Proceedings of the Australian and New Zealand College of Veterinary Scientists*, Gold Coast, p.49.

Zabek MA, Berman DM, and Collins WC (2012). Determination of feral horse density in a forest environment of Toolara State Forest. *Proceedings of the International Wild Equid Conference*, Vienna, p.33.

Zabek MA, Berman DM, Wright J, Blomberg S, and Collins CW (2014). Understanding population dynamics of the feral horse in a coniferous environment in southeast Queensland. *Proceedings of the 16th Australasian Vertebrate Pest Conference*, Brisbane, p.142.

Berman DM, Marshall D, Garrett T, Scriven J, Morgan N, Hosie H, and Zabek MA (2014). Monitoring tools and techniques for intelligent management of vertebrate pests. *Proceedings of the 16th Australasian Vertebrate Pest Conference*, Brisbane, p.84.

Publications

Zabek MA, Wright J, Berman DM, Hampton JO, and Collins CW (2014). Assessing the efficacy of medetomidine and tiletamine-zolazepam for remote immobilisation of feral horses (*Equus caballus*). *Wildlife Research*, 41, 615 - 622.

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Contributions by others to the thesis

The project advisors provided ongoing discussion and feedback on research planning and project design. Dr David Berman taught me how to estimate population distribution, density and abundance by the dung count method; performed remote immobilisation of horses in the field; and offered continuous support and feedback on the study design and content of my written work. Dr Christina W. Collins assisted with the research planning, project design and read through my written work to provide feedback on its content. Dr Simon Blomberg was involved in the design of the algorithm used in habitat use analyses and assisted with statistical analyses included in the thesis. Dr John Wright provided veterinary assistance during remote immobilisation of horses and read through my written work to provide feedback and proof-reading on the content.

Statement of parts of the thesis submitted to qualify for the award of another degree

None

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Keywords

Feral horse, ecology, population dynamic, fecundity, survival, population growth, density, abundance, GPS tracking, home range

Australian and New Zealand Standard Research Classifications (ANZSRC)

ANZSRC code: 060207, Population Ecology, 60%

ANZSRC code: 050103, Invasive Species Ecology, 40%

Fields of Research (FoR) Classification

FoR code: 050103, Invasive Species Ecology, 100%

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List of Abbreviations used in the thesis

A – adult(s)
AIC - Akaike Information Criterion
B – bachelor(s)
BCS – body condition score/s
b.p.m. – beats per minute
cm – centimetres
CRT - capillary refill time
F – foal(s)
F_i - fecundity
FPQ – Forestry Plantations Queensland
GOF - goodness of fit
GPS – Global Positioning System
h – hour(s)
H – harem(s)
HP – harvested pine habitat
HR – heart rate
i.m. – intramuscular
i.v. - intravenous
JP – juvenile pine habitat
km^2 – square kilometre
LT - lateral
LoCoH – local convex hull
m – meter(s)
mm – millimetres
MCP – minimum convex polygon
min – minute(s)
MP – mature pine habitat
MS – multiple stallion harems
NB – native bushland
p – recapture rate
PZP – porcine zona pellucida
r - intrinsic population growth rate
RR – respiratory rate
S – stallion(s)

S_i – survival rate

SA – study area

SB – sub-adult(s)

s.b. – subcutaneous

s.e.m. – standard error of the mean

S_pO_2 - haemoglobin saturation

SS – single stallion harems

TTSF – Tuan and Toolara State Forest

Y – yearling(s)

YP – young pine habitat

vs – versus

ψ – transition probability

λ – finite population growth rate

AIM AND SCOPE OF THE THESIS

It has been proposed that successful control of feral horses in Australia can be achieved by firstly commissioning a detailed scientific study into population distribution and dynamics; secondly by determining population impact on the environment and the economy and society, and finally by identifying appropriate management procedures (Dobbie et al. 1993).

The aim of this thesis is to address the first objective by defining the population ecology of feral horses in the TTSF. The coniferous environment of the TTSF is very different to other Australian ecosystems occupied by feral horses (Dyring 1990; Berman 1991; English 2000; Schott 2004; Dawson and Hone 2012). For that reason, it is crucial to characterise the dynamics of this unique horse population so that better management recommendations can be made. This is the first study in Australia of feral horses in a coniferous forest.

The thesis begins with a description of feral horse ecology both in Australia and elsewhere. The ecological, economic and social impacts of feral horses are emphasised and methods used to reduce population numbers elsewhere in Australia are discussed. Chapter 2 introduces the Tuan and Toolara State Forest; its geography, climate, fauna and flora. This chapter also includes a description of the study design, with results being presented in subsequent chapters.

Chapter 3 describes the structure of the TTSF population by social group, sex ratio and age distribution. The permanency of breeding groups and loyalty of adult individuals to their harems is identified. The characterisation of population structure is an important step in the evaluation of important demographics, such as reproduction ability and survivorship of horses in the various age groups. These factors are discussed in Chapter 4.

The applicability of dung count, dung decomposition and defecation rates on the estimate of horse density and abundance is discussed in Chapter 5. Also examined in Chapter 5 are the long-term abundance trends using the mark-recapture technique. Estimation of horse densities occupying various habitats provides information on population distribution enabling an approximation of the total number of horses in the TTSF.

In Chapter 6, habitat use is investigated using mark-recapture, GPS tracking and dung density counts to assess whether all habitats are used in proportion to their distribution. These findings are important for population management, as they will assist TTSF personnel in the design of harvesting and planting activities, particularly in areas adjacent to the major public roads where there is a high risk of horse-related vehicular accidents. The loyalty of harems to their home ranges and the size of home ranges are assessed in Chapter 7 based on direct observations and GPS-tracking. Chapter 8 outlines the main findings of the study and provides recommendations for population management and future research direction.

CHAPTER 1: LITERATURE REVIEW

1.1. GENERAL INTRODUCTION

The term “wild” or “native” equids refers to seven members of the Equidae family. The African wild ass (*Equus africanus*) inhabits arid and semi-arid bushlands and grasslands of Ethiopia, Eritrea and Somalia and is listed as critically endangered (Moehlman 2002). The Asiatic wild ass (*Equus hemionus*), also known as onager or kulan, is distributed in Mongolia, China, Iran, India and Turkmenistan (Kaczenski 2010a) and is currently listed as endangered (Moehlman 2002). The Kiang (*Equus kiang*) mostly occurs in desert-steppes of India, China, Nepal and Pakistan and its status is listed as least concerned (Schaller 1998). The three species of zebras: Mountain zebra (*Equus zebra*), Common zebra (*Equus burchelli*), and Grevy’s zebra (*Equus grevyi*) are distributed throughout various habitats in Africa (Berger 1986) and are listed as vulnerable, least concerned and endangered respectively (Grubb 2005).

The wild Tarpan horse (*Equus ferus*) became extinct towards the end of the 19th century. The last recorded individual died in captivity in Russia in 1909. The ancestors of today’s domestic horse inhabited areas across Eurasia, from eastern Poland to northern

Turkestan and Mongolia (Grubb 2005). The Przewalski’s horse (*Equus ferus przewalskii*) is the only wild horse saved from extinction and survives to this day in captivity and in the wild (Wakefield et al. 2002; Kaczensky et al. 2008; Kaczensky 2010). The Przewalski’s horse totally disappeared from the Eurasian steppes of Ural and Mongolia, with the last survivors residing in Dzungarian Gobi Desert in Mongolia (Paklina and Pozdnyakova 1989). This closest living wild relative to the domesticated horse has survived in small numbers in captivity because of managed breeding programs (Feh 1988; Kolter and Zimmermann 1988; Van Dierendonck et al. 1996). Starting in 1992, several reserves have been established in Mongolia and China. There are now 308 free-ranging re-introduced and native born Przewalski’s horses in Mongolia (Zimmermann 2011) and 123 in China (Zimmermann 2008).

The term feral refers to all horses living in a wild or free ranging state, whose ancestors were domesticated, regardless of the length of time in a wild state (Berger 1986). Feral horse populations have been living in a wild state or in partially managed reserves throughout the world for decades or centuries. Camargue horses in France (Duncan 1992), Retuertas horses in Spain (Vega-Pla et al. 2006; Brandariz-Fontes et al. 2013), and feral horses in Australia (Berman 1991; Schott 2004), New Zealand (Linklater 2000a; Cameron et al. 2001), Argentina (Scorolli 2007), Northern America (Ransom and Cade 2009), England (Putman 1986) and Japan (Kaseda et al. 1997) are examples of such populations. The term *feral* is sometimes replaced in the literature by *wild* but is incorrect (Berger 1986; Putman 1986; Walter 2002; Roelle et al. 2010). The term feral will be used in this thesis.

1.2. DISTRIBUTION OF FERAL HORSES IN THE WORLD

Feral horses are widely distributed thorough the world (Linklater 2000b), usually in areas that are remote and where people are scarce (Berger 1986; Berman 1991). Feral horses are found in all climate zones except polar circles (cited by Walter 2002), and occupy a broad range of habitats ranging from semi-deserts (Berger 1986; Berman 1991), mountainous regions (Halkett 1996; Cameron et al. 2009), although they are best adapted to grassy plains, such as savannah, shrub or steppe (Dobbie et al. 1993; Linklater 2000b). The majority of populations live in national parks, reserves, and on private land, and some populations are managed (Tyler 1972; Berger 1986; Linklater 2000b; Duncan 1992; Sasimowski et al. 1990a). Management of feral and free-ranging populations has predominantly focused on welfare and health issues such as intestinal parasite control and nutritional supplementation over winter (Sasimowski et al. 1990a), and the occasional removal of young individuals (Kaseda 1983; Duncan 1992) or stallions (Tyler 1972) to control numbers. More radical management has involved fertility control based on castration or immunocontraception (Kaseda 1983; Kirkpatrick and Turner 2003; Nuñez et al. 2009) and lethal control (Berman 1991; Dobbie et al. 1993).

1.3. THE HISTORY AND DISTRIBUTION OF FERAL HORSES IN AUSTRALIA

Domestic horses were brought to Australia by British colonists in 1788 to be used in the pastoral industry (Dobbie et al. 1993). As the industrial revolution gained pace in the 19th century, horses were no longer a necessity and they were often deliberately released into the wild or left behind when farms were abandoned (Dobbie et al. 1993; Walter 2002). Growth of settlements, particularly in extensive cattle-raising areas, expanded feral horse distribution, which was assisted by the lack of fencing and infrequent musters (Csurhes et al. 2009). During World War I, many horses were bred as army remounts but the demand declined after the war, resulting in many being liberated into the wild (Dobbie et al. 1993). Favourable environmental conditions, lack of predators and human intervention, and an absence of diseases facilitated the increase in numbers.

Feral horses were first reported in 1804 (cited by Rolls 1969), and by the 1830's, they became relatively common in the southern states of Australia. In 1860, these horses were designated as feral and officially recognised as pests (cited by Dobbie et al. 1993; Nimmo and Miller 2007). The number of feral horses in Australia has been previously estimated to be in excess of 400,000 with this figure being based on aerial surveys (Dobbie et al. 1993; Dawson et al. 2006) but no coordinated census has been undertaken in the last 25 years. It has been suggested that the current population may be as high as 1 million (cited by Dinn 2012). The USA in comparison has a population of approximately 33,000 feral horses (Lubow and Ransom 2009). In northern New Zealand, there are approximately 1,500 feral horses (Linklater 2000a). In Europe, feral horses live in confined and small populations across many countries, ranging in size from several hundred to several thousand animals (Putman 1986; Sasimowski et al. 1990a; Duncan 1992; Morais et al. 2005; Vega-Pla et al. 2006).

Feral horses have been recorded in the coastal regions of Northern Territory (NT) since the 1820’s and in the inland region of Central Australia since the 1870’s (cited by Dawson et al. 2006). Large groups of feral horses occur in tropical grasslands in the northern part of the NT in the Gulf region, the coastal area between Darwin and Katherine, and on several coastal islands (Dobbie et al. 1993). Major concentrations of horses also inhabit the semi-desert plains and the rocky ranges of Central Australia, south-west of Alice Springs (Berman 1991).

Feral horse populations in Western Australia (WA) are dispersed widely across the state but are predominantly located in the rangelands, which constitute 87% of the state. The highest densities are in the Kimberley, Pilbara and the Goldfields (Dawson et al. 2006). The exact number of feral horses in Western Australia is not known. The pest animal survey performed in 2003 indicated that 1% of the pastoral land of WA is heavily ‘infested’ with feral horses with an additional 5% being moderately ‘infested’ (Woolnough et al. 2005). The survey however, did not accurately identify the densities of feral horses in the affected pastoral lands. In 1976, feral horses were nominated as ‘A5’ category animals under the *Agriculture and Related Resources Protection Act 1976*, which required landholders to reduce and control feral horse numbers (Woolnough et al. 2005).

According to the *Biological Database of South Australia* (SA), the distribution of feral horses is most abundant in the northern and western parts of SA, which are made up of unfenced pastoral lands, cattle stations, national parks, and deserts (cited by Dawson et al. 2006). Aerial surveys performed in the north-western area of SA in 2000 estimated the population size to be 5,000 horses (Last 2001). An aerial survey of the Simpson Desert in 2001 estimated a population of 2,000 horses (Axford et al. 2002). Feral horses were declared a pest species in South Australia under the *Natural Resources Management Act 2004* (Dawson et al. 2006).

In Victoria (VIC), feral horses are considered a major ecological problem; however they are not formally identified as pests. Large numbers of horses occupy the Alpine National Park and its adjacent crown land, the Bogong National Park, the Barmah State Park and adjacent state forest, and east Gippsland (English 2001; Schott 2004; Dawson and Hone 2012). The Australian Alpine National Park, located across NSW and Victoria is the most affected, with numbers reaching 7,000 (Walter 2002). The population in the Bogong National Park has been estimated at around 100 in 2005, and 100 – 150 horses occupy the Barmah State Park (cited by Dawson et al. 2006). There are no figures available for other areas of Victoria.

In New South Wales (NSW) feral horses are distributed across the state with the largest numbers reported in the conservation reserves and state forests on the Great Dividing Range, the Kosciuszko National Park, and the Guy Fawkes River National Park (GFRNP). The total NSW population in 2000 was estimated to be 5,000 to 8,000 horses (English 2001). The highest densities have been reported to be present within isolated catchments of the GFRNP (Freeman 2005).

In Queensland (QLD), feral horses are present in almost all areas that are not intensively managed and are most abundant in the Cape York area, the north-western part of Queensland near the Northern Territory border, and south-western regions bordering South Australia (Dawson et al. 2006). There is also a large population in Carnarvon National Park, estimated to be more than 4,000, with an additional 8,000 on adjacent properties (Lundie-Jenkins et al. 2006), and the forested areas located along the Fraser Coast (Csurhes et al. 2009). The last count of feral horses in Queensland was in 1985, with the estimate being 100,000 (Mitchell et al. 1985). There were no feral horses reported in Tasmania to this date.

1.4. IMPACT OF FERAL HORSES IN AUSTRALIA

As an introduced species, feral horses have adverse effects upon the native environment by trampling indigenous vegetation and changing its structure and composition through erosion and grazing (Berman and Jarman 1988; Dyring 1990; Schott 2004). Horses are very different to Australian native animals because they are large, hoofed and graze congregationally; therefore they change the landscape by destroying grasses that are intolerant to heavy grazing (Dyring 1990; Dobbie et al. 1993). Vegetation destruction causes reduction in biodiversity through loss of natural shelters and food sources for communities of amphibians, reptiles, birds and small mammals (Wharton and Dempster 1981; Ostermann-Kelm et al. 2009). In mountainous areas, feral horses deplete water supplies, and contaminate water with faeces (Schott 2004; Dawson et al. 2006). Horses also cause soil erosion near river banks by mechanical breakdown of soil with their hooves (Dyring 1990; Schott 2004; NSW National Parks and Wildlife Service 2007). Horses grazing and trampling in marsh environments have a negative impact on amphibian reproductive cycles (Hunter et al. 2009) and reduce the abundance of some fish species (Levin et al. 2002). In some national parks, stripping leaves and chewing bark can result in destruction of eucalyptus (Schott 2004; NSW National Parks and Wildlife Service 2007). In semi-arid and arid areas, feral horses accelerate erosion by compacting soil and denuding plant cover (Berman 1991; Dobbie et al. 1993; Ostermann-Kelm et al. 2009).

Feral horses compete with domestic livestock for resources, which negatively impacts on the economy. Their effect on pasture availability for cattle is much more evident during prolonged periods of drought (Dobbie et al. 1993; Dawson et al. 2006). Feral horses have similar nutritional requirements to cattle and therefore in some ecosystems there is direct competition for resources where the two species coexist (Bowman 1987; Dobbie et al. 1993; Loucougaray et al. 2004). A survey performed by Bowman (1987), indicated that competition for forage contributed to a 39% reduction in productivity of cattle. Impact on native wildlife is also a concern in heavily grazed areas. Areas that were grazed by a large number of feral horses and domestic cattle had fewer sightings of macropods (Berman and Jarman 1988). Wharton and Dempster (1981) suggested that feral horses inhabiting forests in Victoria were competing with larger native mammals, like the grey kangaroo (*Macropus giganteus*), by impacting on food, water and shelter. Following removal of horses from the Finke George national Park and the Macdonalds Ranges, an increase in black-footed rock wallabies (*Petrogale lateralis*) and rock-rats (*Zyzomys pedunculatus*) was observed (Matthews et al. 2001; Nano et al. 2003).

The potential of feral horses to pose a threat to human health and safety by causing motor vehicle accidents has been acknowledged (Dobbie et al. 1993; Crittle and Jackson 2004). Feral horses can also spread parasites (Dawson et al. 2006) or be a source of infection for domestic horses, which can be a concern in outbreaks of diseases such as equine influenza (Watson et al. 2011). Also of concern, is the possible involvement of feral horses in the spread of the frequently fatal zoonoses, Hendra virus (Tulsiani et al. 2011).

1.5. FERAL HORSE MANAGEMENT IN AUSTRALIA

There is no unified approach to the management of feral horse populations in Australia. Methods differ between states and territories, and are predominantly influenced by horse numbers, the type and extent of damage, available budgets, and public perception (Nimmo 2005; Dawson et al. 2006; Wilke and Paroz 2006). In the NT, an aerial survey performed in 1986 in the Alice Springs region estimated the population to be about 54,000 feral horses (Graham et al. 1986). Based on this survey, a control program was introduced, using trapping, and helicopter mustering and aerial shooting, which eliminated approximately 33,000 horses (Low and Hewett 1990). In 1999 an aerial survey of the Victoria River District (VRD) west of Katherine estimated that 30,000 feral horses and 70,000 feral donkeys were located in an area totalling 95,000 km^2 (Dawson et al. 2006). Over the next five years, approximately 30,000 horses and 130,000 donkeys were removed from VRD by aerial mustering and shooting but there has been no subsequent control measures undertaken (cited by Dawson et al. 2006). Recently, a helicopter culling operation was performed on Tempe Downs Station, south west of Alice Springs, which resulted in removal of 7000 horses (S Rando 2014, Central Land Council, pers. comm.; Hampton 2013).

The main management methods utilised in WA include aerial shooting of horses and commercial harvesting by muster. Commercial harvesting is only performed when the total cost of implementing the muster is lower than the financial gain from sale of horses for meat (Woolnough et al. 2005; Csurhes et al. 2009). Aerial culling is perceived as the most economical solution as high transportation cost of mustered animals to the closest abattoir is unfeasible and precludes this action. Aerial culling of horses is often performed in conjunction with culling of feral donkeys (Woolnough et al. 2005).

Current control techniques in South Australia combine mustering with aerial or ground shooting (Dawson et al. 2006). Mustering is a preferable option of management in SA as financial gains accrue from the sale of animals. Aerial culling is usually performed concurrently on several neighbouring properties and is coordinated by local stakeholders, land owners, and with the assistance of regional government agencies, while ground culling is usually performed opportunistically (Dawson et al. 2006). Due to remoteness and the rugged landscape, aerial surveys have low precision in estimating population numbers. It has been pointed out that a coordinated national approach that simultaneously targeted feral horses, donkeys, pigs and camels would maximise the cost effectiveness of control programs (Last 2001; Axford et al. 2002).

NSW authorities have developed site-specific strategies to manage feral horse within each national park or reserve to protect native plants and animals (Walter 2002). Despite ecological concerns, feral horses in Victoria are not formally recognised as pests under the *Catchment and Land Protection Act 1994* (Nimmo 2005). The management of feral horses in both states is more complicated than management of other feral vertebrate pests due to the public perception of their historical value (cited by Dawson et al. 2006). Control measures vary between the two states with NSW preferring mustering, trapping and shooting and Victoria showing preference for passive trapping and mustering on horseback (Walter 2002).

In QLD, feral horses historically have been declared a pest species under the *Rural Lands Protection Act 1985*, enforcing landowners to destroy animals and prevent their re-introduction. However, in 2002, horses were no longer perceived as a significant concern and their status changed with the introduction of the *Pest and Stock Route Management Act 2002* (Dawson et al. 2006). Currently, feral horses have no pest status in QLD, despite expressed concerns from various state and federal agencies (Wilke and Paroz 2006). To manage numbers in national parks, several culling operations were conducted between 1980 -1990 resulting in the eradication of 5000 horses (cited by Dawson et al. 2006). Smaller trapping and removal operations were conducted on Fraser Island, and in the Greenbank and Townsville Military Areas (Csurhes et al. 2009).

1.6. PUBLIC PERCEPTION AND FERAL HORSES

Theories on the management of feral horses have led to numerous arguments between focus groups (Symanski 1994; English 2001; Nimmo and Miller 2007). Many Australians see feral horses as an iconic species, which has played an important role in Australia’s development and therefore are entitled to protection (Dawson et al. 2006). Horse significance in tradition and folklore is evidenced in literature, currency (pictured on the $10 bank note) and the opening ceremony of Sydney’s 2000 Olympic Games (Walter 2002; Nimmo and Miller 2007).

Indigenous communities resist lethal control management because they regard feral horses as being a part of their recent past and a part of their cultural heritage, and some view them as an economic resource (Dawson et al. 2006). Animal rights groups are also against culling based on welfare grounds and propose mustering and trapping followed by re-homing or adoption as viable methods of reducing horse numbers (Dobbie et al. 1993). This opinion has intensified after a culling operation in the GFRNP in 2000, which removed 606 horses from the park without consultation with the Royal Society for the Prevention of Cruelty to Animals (RSPCA) and the general public (Chapple 2005). The public outcry following this incident resulted in banning of aerial horse culling in NSW (Chapple 2005; Nimmo and Miller 2007).

Conservationists believe that feral horses (and other introduced ungulates) damage fragile Australian ecosystems, which impacts upon native animal populations, and horses should therefore be removed (Csurhes et al. 2009). Many people who work in the agricultural industry also believe that feral horses should be eradicated from agricultural and pastoral areas because they contribute to land damage and compete with domestic livestock for resources (Berman 1991; Schott 2004).

1.7. MANAGEMENT CONTROL METHODS

If agreement was reached by all that feral horse population control was necessary, the numbers involved and remoteness of the populations pose a massive logistical issue. Past experience indicates that available management techniques should be integrated with individual circumstances as populations differ in size, density, age, gender distribution, and geographical location (Dawson et al. 2006; NSW National Parks and Wildlife Service 2006). The effectiveness of feral horse control is dependent upon a combination of different approaches, which may be implemented separately or in conjunction depending on the ability to implement them (Nimmo and Miller 2007). Of the range of control methods available, those that are mostly used to manage feral horses in Australia are ground and aerial mustering, ground and aerial culling, and trapping (Walter 2002; Dobbie et al. 1993; English 2001; Chapple 2005; Dawson 2005).

Mustering is the most commonly used method of control (English 2001; Walter 2002; Schott 2004). Mustering may involve horses and riders, motor cycles or quad bikes, or aerial transport, such as helicopters, or various combinations of the above depending upon terrain and vegetation. Ground mustering, in general, is most suitable for open and flat environments and requires experienced riders. Helicopters are particularly useful where large areas are involved, where the terrain is rugged or areas are inaccessible to ground-based vehicles (McCosker and Eggington 1986; Dobbie and Berman 1992). Horses are usually mustered into permanent or portable yards and removed in trucks (English 2001). The advantage of mustering is that it is possible to capture a large number of horses in each muster (Dobbie et al. 1993), but the disadvantages include cost, the need for specialised resources and highly trained personnel (English 2001; NSW National Parks and Wildlife Service 2007). Mustering from horse-back involves restraint of an animal by placing a rope around its neck (referred to as roping). This technique is still used in national parks in Victoria but provides very low capture rates in comparison with alternative techniques (Walter 2002).

Mustering and rehoming shows a distinct selection bias towards young and female horses because young horses are easier to catch and train and female horses are less aggressive than stallions (Walter 2002). This selection bias maximises population reduction rates where the population growth rate is the most sensitive to survival of adult females (Walter 2002; Dawson and Hone 2012). However, this method of control may have an impact on the age and sex distribution of the population (Kaseda 1981; Garrott et al. 1991b; Rogers 1991; Duncan 1992). Additionally, if the method is performed in national parks, it may cause damage to fragile ecosystems through the trampling of vegetation by mounted riders (Walter 2002; Schott 2004). For this reason, and because of its limited effectiveness in reducing population numbers, so-called brumby running (mustering and roping from horse-back) is permissible only under a limited permit system in the Alpine National Park in Victoria (Department of Conservation and Environment 1992). Horse mustering was a common method of capturing feral horses in the past but is less popular now, because of strong opposition from animal welfare groups that believe chased and restrained horses are traumatised (Schott 2004; Dobbie et al. 1993; C O’Brien 2012, The Victorian Brumby Association, pers. comm.). It has been quantitatively assessed that horses forced to move towards unfamiliar environment and/or transported by road are subjected to substantial stress (Greer 1989). Similar outcomes were also observed in sheep (Reid and Mills 1962), and Asian elephants (Holger et al. 1992).

Lastly, mustering can be performed on foot. This form of mustering utilises the natural instincts and behaviours of horse thereby minimising stress responses (NSW National Parks and Wildlife Service 2006). The first step involves observation of the group of horses to be mustered permitting assessment of their behaviour, movement pattern and routes of travel when they are placed under pressure (Berman 2013). This knowledge allows construction of a suitable trap site along the group’s travel route. A trap consists of a portable yard equipped with hessian wings that act to funnel horses into the yard opening. Mustering involves walking the horse group on foot in the direction of the trap by applying gentle coersion. This method has been shown to be effective, but is slow and labour intensive and relies on finding a suitable location for the trap to be effective (NSW National Parks and Wildlife Service 2006).

The effective use of passive trapping requires good local knowledge of feral horse behaviour and seasonal movement patterns to select the best location for trap construction and the best time to perform the operation (English 2001). Traps are usually built near water sources (Berman 1991), on high use horse trails, and are equipped with feed or salt licks as an attraction (Nimmo and Miller 2007). Horses passively enter the enclosure through trap gates (Berman 1991; Dobbie et al. 1993); and are then relocated to other sites (Nimmo and Miller 2007) or transported for slaughter, with sick or old individuals being shot in the enclosure (English 2001). The advantage of this method is that horses choose to enter the trap, which reduces the need for specialised personnel (Dobbie et al. 1993). This method can be cost effective if the animals are sold (Dobbie and Berman 1992). The disadvantages of this method are that it can only be used to capture smaller groups of horses, and it is very labour intensive (NSW National Parks and Wildlife Service 2006). Trap yards are also difficult to erect, and horses have to be quickly relocated or provided with water and food (Nimmo and Miller 2007).

Culling from helicopters by trained marksmen is usually performed in areas that are either not accessible by other vehicles or are very remote (Dawson et al. 2006). This control method is generally preferred because it is regarded as the most practical and effective method of removal of introduced ungulates on the landscape scale (Dobbie et al. 1993; Edwards et al. 2004; Hampton 2013). A quantitative analysis of a feral horse aerial cull in central Australia in 2013 assessed wounding rate, instantaneous death rate, and time to death of 1165 horses (Hampton 2013). The analysis concluded that any suffering was of very short duration and adverse animal welfare outcomes were minimal (Hampton 2013). However, the public perception of aerial culling is poor and is widely regarded as being inhumane (Dobbie et al. 1993; Chapple 2005; Nimmo and Miller 2007).

Culling can be also performed from the ground. Ground culling is often combined with mustering and trapping (Walter 2002) for small scale management (Dobbie et al. 1993; NSW National Parks and Wildlife Service 2006). The advantage of ground culling is that animals are shot at close range maximising the likelihood of a rapid kill (English 2000). The disadvantage is that some wounded animals may escape and suffer (Schott 2004).

Fertility control offers non-lethal alternatives for population management and has been successfully used on large herbivores such as deer and camels (Stout et al. 1997; Lauber et al. 2001), as well as feral horse populations in the USA (Liu et al. 1989; Kirkpatrick et al. 1997; Turner et al. 2001; Ransom 2009). Immunocontraception offers many advantages over other methods of population control providing that a cost-effective long-term reduction in fertility can be achieved that is also sensitive to the animal welfare issues centred on stress of administration and social structure disruption (Turner et al. 2001; Ransom 2009). Recent research in immunocontraception has focused on substances that produce an immune response in targeted horses (Nuñez 2009). Porcine zona pellucida (PZP) was experimentally evaluated in a population of feral horses on Assateague Island (Kirkpatrick 1995) and later in other populations in the USA (Liu et al. 1989; Kirkpatrick and Turner 1991; Turner et al. 2001; Killian et al. 2008; Ransom 2009) and in New Zealand (Stafford et al. 2001).

Following vaccination, anti-PZP antibodies attach to the surface of the ovum, and cause the oocyte to produce antibodies, which prevents sperm attachment and fertilisation (Paterson et al. 2000). Since its first application, PZP has been shown to be safe and effective when used in several small populations of feral horses in the USA (Turner et al. 1997; Killian et al. 2004; Kirkpatrick and Turner 2008; Ransom 2009; Gray et al. 2010). It has been shown that recipient females are less fertile in the year following vaccination and additional reductions occur with multiple doses (Kirkpatrick and Turner 2007, 2008). On the other hand, it has been observed that the increase in longevity, increase in body condition among treated females and decrease in foal mortality are directly related to treatment because the lower foaling rate reduces competition (Kirkpatrick and Turner 2007).

Evidence shows, that fertility control can substantially reduce feral horse population growth provided a sufficient number of females are treated (Kirkpatrick and Turner 2008). In populations with growth rates greater than 15%, controlling growth cannot be achieved by contraception alone, horse removal is also necessary (Garrott et al. 1991b). However, in those populations where growth rate does not exceed 15%, contraception effectively reduces population size. On Assateague Island, where every female between two and four years of age was vaccinated with PZP, population growth ceased ($\lambda = 1.00$; 0%) after two years and a 22.8% reduction in the population size was observed after 11 years of the vaccination program (Kirkpatrick and Turner 2008). The effectiveness of fertility control as a management tool needs to be tailored to and trialled in each population, and requires detailed demographic data.

1.8. SOCIAL ORGANISATION OF FERAL HORSES

Harems, also called harem bands (Welsh 1975; Gates 1979), family groups (Klingel 1982), or breeding units (Joubert 1972), refer to groups of horses consisting of both sexes, which live in permanent or semi-permanent associations and form breeding groups. Harem structure usually consists of one dominant stallion, one or more adult mares with their offspring and occasionally one or two subordinate males (Feist and McCullough 1976; Linklater 2000b; Scorolli 2007). The majority of females in harems are not related as both female and male offspring leave the natal group as sub-adults (Berger 1986). In multiple-male harems there is a hierarchical relationship between males based on age, body condition, and reproductive status (Feist and McCullough 1976; Cameron et al. 2009; Rubenstein and Nuñez 2009). Stallions usually express their dominance by controlling interactions with other stallions and groups, preventing subordinate males from interacting with adult females and preventing emigration from their harems by active herding (Feist and McCullough 1976; Salter and Hudson 1982a). The most commonly reported average harem size is five (Feist and McCullough 1976; Perkins et al. 1979; Rubenstein 1981; Berger 1986; Berman 1991; Dobbie et al. 1993); however, larger average harem sizes have been recorded ranging from 7.6 - 12.3 (Keiper 1979; Salter and Hudson 1982a; Rubenstein 1981). Some authors have reported harems as small as two horses and as large as 28 (Gates 1979; Duncan 1992; Linklater 2000b).

It is generally accepted that harems are stable often long-lived social associations (Klingel 1969; Tyler 1972; Duncan et al. 1984; Linklater 2000b). Harem membership is predominantly influenced by births and dispersal of sub-adults (Salter and Hudson 1982a;

Berger 1986), but it can be also affected by occasional ‘migration’ of adults between harems (Berger 1986; Berman 1991; Dobbie et al. 1993). Adult females have been reported to voluntarily leave harems for several days, months or permanently (Berger 1986; Franke Stevens 1990; Scorolli 2007), while harem stallions occasionally separate from their mares for forays outside of the group home range (Linklater 1998; Linklater 2000b).

Various factors may cause harem instability. Low quality of forage in winter and spring months was the main factor influencing harem stability on the salt marsh islands of the Rachel Carson Estuarine Sanctuary (RCES) in North America (Franke Stevens 1990). The increased time required for foraging preceding the breeding season resulted in greater spacing of horses across the landscape, thereby reducing harem cohesion (Franke Stevens 1990). Lack of palatable pasture in winter and low biomass of food in early spring also contributed to frequent disbanding events of adult females in feral horse populations on mainland North America (Nelson 1978; Berger 1986).

In unfavourable conditions, such as drought, there is less available energy for the stallion to maintain and defend his harem and therefore size of the harem influences its stability; in unfavourable conditions, small harems are more likely to remain stable than are large harems (Berman 1991). Berger (1986) concluded that the amount of invested energy by the dominant stallion in harem defence increased proportionally with harem size, which was likely to be detrimental when resources were sparse. These observations indicate that harem size, particularly under unfavourable environmental conditions, has a significant impact on harem stability. The age of the dominant stallion and the presence of other subordinate stallions on the harem periphery have also been found to influence long term harem stability (Miller 1981; Franke Stevens 1990).

The influence of population density on the social stability of feral horses remains unclear. While some authors reported very high levels of social instability in densely populated areas; 35 horses/km^2 (Franke Stevens 1990), other authors reported high social stability despite high density; 31 horses/km^2 (Feh 1999; Duncan 1992). Population confinement to restricted geographical areas has been also suggested to influence social stability and interaction between harems (Rubenstein 1981). Geographically confined populations of feral horses on the Sable and Shackleford Islands (Rubenstein 1981) exhibited reduced social cohesion within harems and bachelor groups, and the population on Cumberland Island showed reduced harem stability (Goodloe et al. 2000).

Adult males, which do not form associations with females, are defined as bachelors, and, if they form groups with other males, these associations are called bachelor groups (Berger 1986; Berman 1991; Linklater 2000b; Walter 2002). Bachelor groups can vary in size between populations and are recognised as being less stable than harems (Miller 1979). The typical size of a bachelor group is two to three (Hall 1972; Feist 1975; Berman and Jarman 1988); however groups of four (Dyring 1990), and five to seven (Berman and Jarman 1988) have been observed. Bachelor groups can constitute up to half of all horse groups in feral populations (Miller 1981; Berger 1986). The home range of bachelor groups is usually larger than those of harems and more distant from permanent water as their nutritional needs are usually smaller than those of harems (Berger 1986; Dobbie et al. 1993). Older males, who do not associate with younger bachelors, are defined as solitary males (Hall 1972; Perkins et al. 1979; Berger 1986; Cameron and Linklater 2000). Various authors have suggested that solitary males were previously harem stallions that have been disposed of their harems (Hall 1972; Perkins et al. 1979). Single males or bachelor groups may live on the harem's periphery and occasionally challenge the dominant male for leadership, particularly during the breeding season (Linklater 2000a).

Mare groups consist of adult females not maintained by a stallion. These groups are usually seen in populations subjected to human management involving the selective removal of males (Tyler 1972; Cameron et al. 2001). In some instances, young females can be temporarily accompanied by bachelors; however, these alliances, known as mixed-sex peer groups, differ from well-defined harem structures because they are unstable and short-lived, lasting from several hours to three months (Waring 1983; Linklater 2000a). The temporary associations of mixed-sex peer groups have also been observed in large feral horse populations, which had not undergone human intervention (Keiper 1976; Linklater 2000a).

Natal dispersal of juveniles from their harems is a feature of wild and free-ranging equidae (Tyler 1972; Berger 1986; Rutberg and Keiper 1993; Monard and Duncan 1996; Kaseda et al. 1997; Linklater 2000a; Khalil et al. 2010). Both young females and males permanently leave their natal harem after reaching maturity, minimising the chances of inbreeding (Dobbie et al. 1993; Monard and Duncan 1996; Khalil et al. 2010). Upon reaching puberty, females disperse from their harems (Tyler 1972; Berger 1986). In mountain zebras (*Equus zebra zebra*), sub-adult females are abducted by non-harem males (Pezhorn 1984), and in feral horses they face reluctance of the sire to mate with them (Berger 1986), or are atracted to unfamiliar males (Monard et al. 1996). In one population of feral horses, young females dispersed because of aggressive behaviour towards them from older mares in their natal harem (Klingel 1982), whereas in other populations of equids young females meet with higher levels of aggression from resident females in their new harems than in their natal harems (Klingel 1967; Pezhorn 1984; Berger 1986; Monard and Duncan 1996). In the first instance, it would appear that young females are driven out of their natal harems to reduce competition for forage, whereas in the second instance, immigrant females are disciplined by established mares to consolidate their hierarchal status (Monard and Duncan 1996). Some females face significant aggression from their own dams prior to the birth of the next sibling (Tyler 1972; Kaseda et al. 1997). Dispersal of young males reflects the limited mating opportunities within the natal harem (Berger 1986). Colts may be actively driven away by dominant stallions, or leave their natal harems voluntarily (Tyler 1972; Welsh 1975; Feist and McCullough 1976). Sometimes dispersal of young males is correlated with the absence of peers in the natal harem (Rutberg and Keiper 1993).

Evidence from previous studies shows that the majority of sub-adult feral horses (both females and males) disperse from their natal harems between 1-3 years of age (Klingel 1969; Tyler 1972; Welsh 1975; Pezhorn 1984; Kirkpatrick and Turner 1986; Goodloe et al. 2000; Roelle et al. 2010) but later dispersal of males at four and five years of age has also been recorded (Roelle et al. 2010). In addition, offspring born to first time mothers develop stronger and longer lasting associations with their dams, which often results in delayed dispersal (Khalil and Kaseda 1997; Khalil et al. 2010). Upon dispersal, fillies move to new harems (Goodloe et al. 2000), while young males form bachelor groups (Berger 1986; Schott 2004). Young horses may also associate with each other and form mixed-sex peer groups (Waring 1983; Linklater 2000a).

The overall proportions of females and males at birth are usually equal in feral and free-ranging horse populations (Berger 1986; Goodloe et al. 2000; Roelle et al. 2010), with insignificant fluctuations occurring from year to year (Keiper and Houpt 1984; Berman 1991). These fluctuations usually arise due to natural reasons, such as the availability of resources, which impacts on the survival of neonates (Berman 1991) and mare fertility. It has been reported that mares with high body condition scores are more likely to produce male offspring (Keiper and Houpt 1984; Cameron and Linklater 2000).

Despite an equal gender ratio at birth (Monard et al. 1997; Roelle et al. 2010), most adult feral horse populations show gender asymmetry with females being in the majority (Greger and Romney 1999; Goodloe et al. 2000; Cameron et al. 2001), although an equal adult gender ratio has been noted in khulans (*Equus hemionus,* Feh et al. 2001). Adult age group mortality is usually the result of injuries sustained in males when competing for females and in females because of the demands of reproduction (Welsh 1973; Berger 1986; Garrott and Taylor 1990). Environmental changes may also affect adult gender distribution in some feral horse populations, as gender may influence adaptability to sudden changes in climatic conditions (Scorolli et al. 2006). For example, a violent storm in the Tornquist National Park in Argentina caused high mortality in adult females following prolonged exposure to rain, wind and cold (Scorolli et al. 2006). At the time of the survey the population was approaching carrying capacity and the majority of adult females were in significantly poorer body condition than stallions because of the demands of pregnancy and lactation (Scorolli 2012).

Asymmetry of gender in feral horse populations could also be the result of human management that focuses on removal of one sex (Ganskopp and Vavra 1986; Garrott and Taylor 1990; Duncan 1992), or the introduction of new individuals predominantly of one sex (Gates 1979; Walzer et al. 2006). Removal of bachelor and sub-adult males often occurs in managed small and confined populations (Duncan 1992), while removal of adult females is common in populations where the main aim is to decrease the population growth rate (Garrott et al. 1991b; Rogers 1991). Management practices focusing on removal of both sexes in adults (Scorolli and Lopez Cazorla 2010a) or young horses (Keiper and Houpt 1984), attempt to maintain a balanced sex ratio. Other management methods, which focus on the protection of existing animal numbers and maintaining the population’s pure-breed status, rely on the introduction of new individuals of both sex (Gates 1979; Walzer et al. 2006).

Large herbivore populations show well-defined age classes. Juveniles are usually born at a well-defined time of the year, and, if they survive, they are classified as yearlings at the beginning of the next biological year (Gaillard et al. 2000a; Scorolli and Lopez Cazorla 2010a). Subsequent age classes are defined as sub-adults (generally 2 - 3 years of age), and adults, in which several distinct sub-classes (young adults, prime-aged adults, and senescent-aged adults) can be recognised (Gaillard et al. 2000a; Cameron et al. 2001). Population studies of wild and feral equids often differ in age group classification because of the variability that exists in determining the ages of horses being studied (Cameron et al. 2001; Roelle et al. 2010). In some studies, birth dates were available, which obviously provided an exact age and, as there is a close correlation between dental characteristics and age, this allowed observers (where the mouth could be examined) to determine with considerable accuracy the animal’s age (Cameron et al. 2001; Garrott 1991b; Grange et al. 2009). Those studies that visually estimated age based on size and behaviour were limited to broad age classifications such as foals, yearlings, adults, and occasionally sub-adults (Feh et al. 2001; Walter 2002; Scorolli 2007).

Populations of feral horses, which did not undergo human management are characterised by a higher prevalence of adults, sometimes constituting two thirds of the population (Welsh 1973; Feist and McCullough 1976; Garrott and Taylor 1990; Cameron et al. 2001). Age structure may vary from year to year within a population, but usually is most stable amongst adults, and more dynamic in the younger age groups (Garrott and Taylor 1990; Cameron et al. 2001). The ratio of foals can vary largely between populations from 7.7 – 20.2% (Wolfe 1980); 17 – 20.3% (Garrott 1991b), and within a population from 9.2 - 19.0% (Scorolli 2007). Similarly, the ratio of yearlings often differs between populations: 10.3 – 15.9% (Garrott 1991b), and 7.3 – 10.2% (Wolfe 1980), and within the same population over several years: 7.4 – 17.3% (Scorolli 2007). The percentage of sub-adults can also fluctuate between (Garrott 1991b) and within populations (Scorolli 2007).

A change in population age structure is known to affect population dynamics of feral horses by altering reproductive performance, mortality patterns, and population growth rates (Gaillard et al. 2000a; Bender 2008). For instance, a large proportion of adults of prime reproductive age would increase the breeding success of a population and therefore increase the population growth rate (Gaillard et al. 1998). As feral horse management programs frequently focus on decreasing the population growth rate, their focus is on the removal of adult horses. The removal of bachelors and/or sub-adult males is practised in confined populations of Camargue feral horses (Duncan 1992), Misaki horses (Kaseda 1981), and several feral horse populations in North America (Tyler 1972; Keiper 1976). The removal of adult horses of both sexes is also performed in populations where the aim is to reduce the population size (Garrott et al. 1991b; Scorolli and Lopez Cazorla 2010a).

Sometimes, removal management focuses on specific groups such as foals and adults (Keiper and Houpt 1984) or more broadly on all age groups (Roelle et al. 2010). Despite being widely adopted, selective removal practices have an impact on the distribution of age groups, and skew the male to female ratio, which may have consequences on population dynamics (Garrott et al. 1991b; Rogers 1991).

1.9 POPULATION DYNAMICS OF FERAL HORSES

Feral horses are seasonal breeders with foaling starting in early spring and continuing until autumn, with a clear peak in late spring and summer months, and is usually associated with availability of forage (Keiper and Houpt 1984; Duncan 1992). During the breeding season mares ovulate at 21 day intervals (McKinnon et al. 2011). During ovulation, which ranges from 2 – 8 days, mares are receptive to stallions (McKinnon et al. 2011).The onset of cyclicity is correlated with increasing day length and ambient temperature, however, nutritional status and body condition are thought to also play an important role (McKinnon et al. 2011). In autumn months, ovarian activity of mares diminishes and winter is characterised by anoestrus (McKinnon et al. 2011). Where day length does not vary greatly throughout the year, such as in sub-tropical and tropical zones, mares may show cyclical ovarian activity thorough the year (Berger 1986) or show a more prolonged foaling season (Keiper and Houpt 1984; Duncan 1992). In the southern hemisphere, breeding season in feral horses occurs between August and April (Berman 1991; Cameron et al. 2001; Walter 2002; Scorolli and Lopez Cazorla 2010a), while in the northern hemisphere it is usually between March and September (Keiper and Houpt 1984; Duncan 1992; Greger and Romney 1999).

Feral horse females usually begin cycling in their second year, and if served, give birth to their first foal at three years of age (Feist 1975; Keiper and Houpt 1984; Garrott and Taylor 1990; Goodloe et al. 2000). In areas where horse density was low and pasture was of a high quality, mares successfully foaled at two years of age (Berger 1986; Duncan 1992; Roelle et al. 2010). Gestation period in wild and feral horses on average is 336 (range 331 – 352) days and only one young is born (Monfort et al. 1991; Duncan 1992; Cameron et al. 2001; Walter 2002). Female fertility gradually increases with age, reaching its peak between 6-10 years of age (Keiper and Houpt 1984; Berger 1986; Duncan 1992; Cameron et al. 2001), with a gradual reduction in fertility until the onset of senescence at about 15-20 years of age (Eberhardt et al. 1982; Garrott and Taylor 1990; Garrott et al. 1991a).

Theoretically, female horses are capable of foaling each year (Berger 1986; Berman 1991; Duncan 1992) but various factors may impact on fertility and annual individual mare foaling in many feral horse populations is uncommon (Keiper and Houpt 1984; Dawson and Hone 2012). During unfavourable climatic conditions, fecundity usually decreases, as lack of forage limits the protein and energy necessary for cyclicity, and pregnancy and lactation (Keiper and Houpt 1984; Berman 1991; Lucas et al. 1991; Scaramuzzi and Martin 2008; Ransom 2009). Mares in poor condition are not able to reproduce (Berman and Jarman 1988; Duncan 1992; Scorolli 2012). Frequent changes to harem composition have also been reported to negatively influence foaling rates (Kaseda et al. 1995; Goodloe et al. 2000; Gray et al. 2012).

Visual assessment of body fat storage has been described as an objective and reliable indicator of body condition of horses, as it indirectly reflects the population nutritional status and health, and may offer an insight into population reproduction performance (Henneke et al. 1983; Carroll and Huntington 1988; Rudman and Keiper 1991; Scorolli 2012). Body condition of feral horses usually varies with gender, with stallions showing higher BCSs than mares (Berman 1991; Scorolli 2012). Horses tend to have lower BCSs in winter months and higher in summer months, corresponding to the greater availability of forage (Rudman and Keiper 1991; Duncan 1992; Walter 2002).

Feral horse populations living in areas with variable forage availability experience greater annual fluctuations in reproduction rates (Gaillard et al. 2000a). The average foaling rates in feral populations have been reported to be low as 27-36% (Siniff et al. 1986; Cameron et al. 2001), and moderate 40-65% (Welsh 1975; Keiper and Houpt 1984; Berger 1986; Goodloe et al. 2000; Scorolli and Lopez Cazorla 2010a). Very high rates of 80-90% have been reported in females of prime age (Garrott et al. 1991b).

One of the main factors shaping age distribution within a population is mortality rate. Severe weather conditions, drastic and prolonged reduction of pasture availability, and predation, are recognised as the major causes of mortality in unmanaged feral horses (Garrott and Taylor 1990; Berman 1991; Lucas et al. 1991; Greger and Romney 1999; Goodloe et al. 2000; Scorolli et al. 2006). Severe winters cause nutritional stress in lactating mares that are pregnant, sometimes resulting in abortion (Lucas et al. 1991). Prolonged drought increases mortality through starvation, thirst and forced consumption of toxic plants (Berman 1991; Dobbie et al. 1993; Walter 2002). Predator activity potentially can kill many juveniles (Greger and Romney 1999; Lagos and Barcena 2012) and occasionally adults (Feh et al. 2001). In a population of khulans, adult females were more often exposed to attacks from wolves while giving birth, and male mortality often followed injuries acquired from previous fights with predators (Feh et al. 2001).

In the absence of predation and during favourable environmental conditions, feral horses show a consistent pattern of high adult survivorship with very low annual variation. Adults in the prime reproductive age group have high survival rates ranging from 92 – 99% (Ganskopp and Vavra 1986; Garrott and Taylor 1990; Turner et al. 1992; Goodloe et al. 2000; Roelle et al. 2010), whereas aged, senescent adults have been shown to have survival rates as low as 80% (Roelle et al. 2010).

Gender specific survival rates are generally equal in horses over two years of age (Goodloe et al. 2000; Cameron et al. 2001; Keiper and Houpt 1984) but higher adult male mortality rates have been reported (Berger 1986; Garrott and Taylor 1990). Elevated male mortality is probably due to the higher energy costs associated with obtaining and maintaining a harem, fighting injuries (Berger 1986; Garrott and Taylor 1990) or predator-acquired injuries (Feh et al. 2001). Survivorship of foals is considerably lower and more variable than in adults: 50% (Welsh 1975); 67% (Goodloe et al. 2000); 69% (Roelle et al. 2010); 84% (Cameron et al. 2001); 88% (Keiper and Houpt 1984); 90% (Scorolli and Lopez Cazorla 2010a), and 95% (Garrott 1991a).

Different environments impose different stressors on feral horse populations, and these in turn influence population growth rates (Berger 1986). While growth rates in some populations are limited by human management (Gates 1979; Eberhardt et al. 1982; Putman 1986; Garrott and Taylor 1990; Linklater et al. 2004), in a majority of populations, food limitation and predation are believed to be the most important factor driving the rate of population change over time (Keiper and Houpt 1984; Greger and Romney 1999; Goodloe et al. 2000; Dawson and Hone 2012). Observed population growth rates vary significantly between studies with negative rates (<1.0) being recorded by Greger and Romney (1999), slow (1.03 – 1.09) by Goodloe et al. (2000); Cameron et al. (2001); Dawson and Hone (2011); Keiper and Houpt (1984), moderate (1.12 – 1.20) by Garrott and Taylor (1990); Garrott et al. (1991a); Berger (1983); Eberhardt (1982), and rapid (>1.20) by Scorolli and Lopez (2010), and Duncan (1992). These variations were due to differences in annual survival and fecundity influenced by climatic conditions, predation or its absence, human management, and removal of domestic stock, which reduced competition for resources.

CHAPTER 2: TUAN AND TOOLARA STATE FOREST

The Tuan and Toolara State Forest (TTSF) forms a contiguous coniferous plantation owned by Forestry Plantation Queensland (FPQ). The fundamental aim of the forest management is to produce timber for various industrial sectors (Wang 2008). The plantation stretches from the coastal lowlands of the Great Sandy Straight, to the Great Dividing Range, covering an area of approximately 1000 km^2. The plantation is located east of Gympie, south of Maryborough, and west of Rainbow Beach (**Figure 2.1**). Two main roads divide the plantation; the Maryborough-Cooloola road divides the forest into western and eastern sections, and Tin Can Bay Road divides the forest into northern and southern sections.

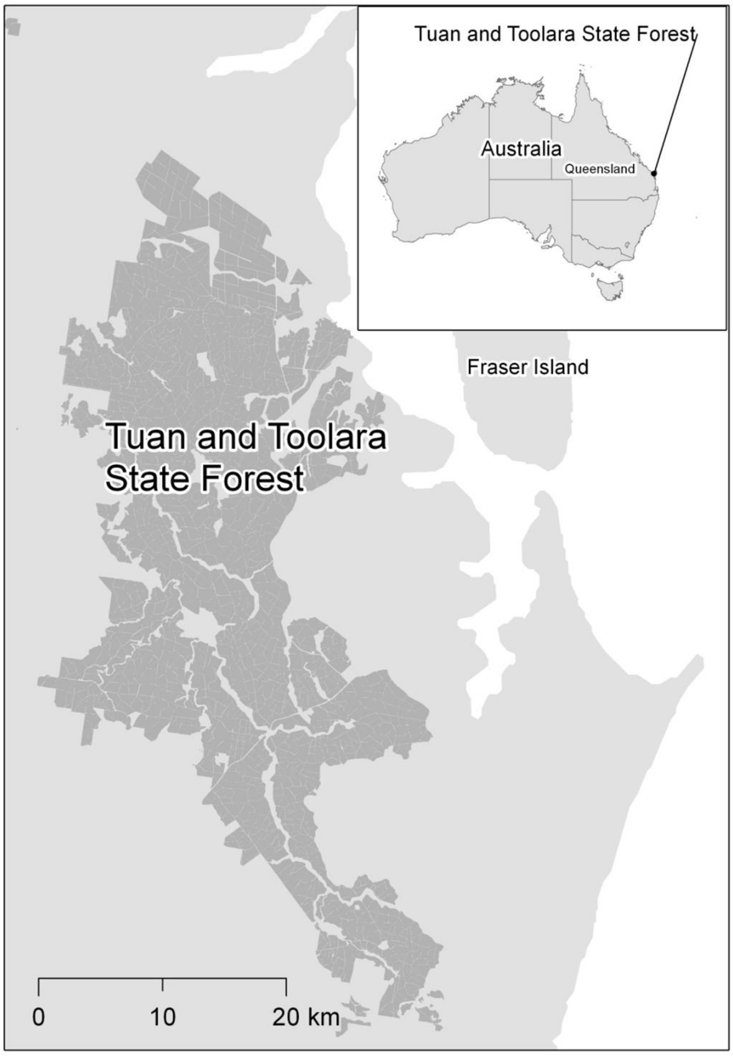

Figure 2.1: The location of the Tuan and Toolara State Forest in southeast Queensland.

The literature reveals very little about the origin of feral horses in the TTSF and surrounding region. First reports of unclaimed horses by local residents occurred in the 1990s (cited by Dobbie et al. 1993), however anecdotal evidence suggests that feral horses have been present in TTSF and surrounding areas since the early 1940s; being liberated as a result of mechanisation of the forest industry (Crittle and Jackson 2004). Since that time, additional deliberate releases of unwanted domestic horses have apparently occurred (Forestry Plantation Queensland personnel 2012, pers. comm.). Lack of feral horse management in association with wild dog eradication programs in 2003, have increased the survival of younger horses and accelerated population growth (Crittle and Jackson 2004).

Feral horses have been recognised as a problem in the TTSF over the last decade. In 2002 a brief survey was undertaken by the Department of Primary Industries and Fisheries (DPI&F), which roughly estimated the population to be 181 animals (Crittle and Jackson 2004). In 2009, a more comprehensive survey was undertaken, which was carried out over an area of 430 km^2. The survey applied a distance sampling technique based on observed animals and estimated the population size for the surveyed area to be 995 horses (95% CI 583 to 1691), with an average density/km^2 of 1.9 horses (Berman 2013).

Both surveys identified feral horses as a serious distraction for motorists, and identified the potential for serious animal-vehicle accidents. The lack of fencing along public roads meant that horses became desensitised to road traffic and crossed roads singly or in groups, resulting in near-collisions and collisions with vehicles, horse deaths and vehicle damage (Crittle and Jackson 2004; Berman 2013; pers. obs.). The incidence of vehicle collisions with horses on the major public roads traversing TTSF have risen in part due to increased vehicular traffic (in excess of 6000 movements per day) as the human population grows in the regions surrounding the TTSF but also because of the unmeasured but obvious increase in horse numbers (Crittle and Jackson 2004; Fraser Coast Chronicle 2012). Accidents attributed to horses have only recently been recorded separately from other causes but in the initial 12 months of recording, six horses were fatally injured in collisions and at least a further 10 near-misses were reported. There is little doubt that minor collisions and most near misses go unreported (Crittle and Jackson 2004). Horses are frequently observed on internal plantation roads where there are in excess of 100 logging trucks movement per day, which constitutes a serious workplace health and safety issue (Fraser Coast Workplace Health and Safety Report 2012). The increasing number of horses within the plantation and particularly near major public roads demanded that a comprehensive risk assessment be urgently undertaken.

The risk of logging vehicles colliding with feral horses within the plantation was assessed as high and collisions with motorists on the major public roads as very high (Crittle and Jackson 2004; Fraser Coast Workplace Health and Safety Report 2012). To reduce the danger of animal-vehicle collisions, risk minimisation protocols were implemented, which included installation of warning signs along the major public roads running through the forest, and removal of horses from the forested areas bordering public roads. At the time of writing, this management plan has resulted in the capture and removal of 77 feral horses, and reduction in vehicle collisions by 68% (Berman 2013). Although control by removal is currently effective, increasing horse numbers will reduce the efficacy of this measure (Berman 2013). Public opinion is antagonistic to removals of any magnitude but particularly large scale removals (Fraser Coast Chronicle 2012; pers. comm. South East Queensland Brumby Association 2013).

Multiple aspects of feral horse ecology need to be identified to facilitate long-term management of the population (Walter 2002). Knowledge of population distribution and abundance would assist in targeting areas where control measures are likely to be of greatest benefit. Estimation of population birth rate, age specific survival and annual population growth rate would assist in making decision on the number of animals to be removed and the age cohort to target to achieve the best outcome (Lande 1988). For management to consider using suppression of fertility to control population size, it is vital to first determine the social stability of the population and its reproductive performance. This study was designed to use new and known methodologies to provide information on feral horse population ecology within the TTSF and subsequently to develop measurable long-term population management strategies.

2.1. THE TTSF ENVIRONMENT

The TTSF landscape is dominated by plains in the north and hills in the central and southern parts of the forest. The average elevation above sea-level is 45 meters; ranging from 0 - 134 meters (Wang 2008). The area is well drained by many ephemeral streams and creeks and permanent waterholes. Springs are sparser in the northern part of the plantation. In many places where springs occur together, swamps occur nearby (Wang 2008).

The climate is sub-tropical but annual rainfall variability can be considerable due to two weather systems: the tropical system to the north and the temperate system to the south (Wang 2008). Weather information, which includes rainfall, maximum and minimum temperature, and solar radiation, is available from the Bureau of Meteorology Australia (BOM), based on data collected at the Toolara-Kelly Station[1] (Site number: 40555; Latitude: 25.97S; Longitude: 152.86E; elevation: 143m). The average annual rainfall for 1998-2013 was 1314.8 mm (**Figure 2.2**), and summers were considerably wetter than winters (**Figure 2.3**).

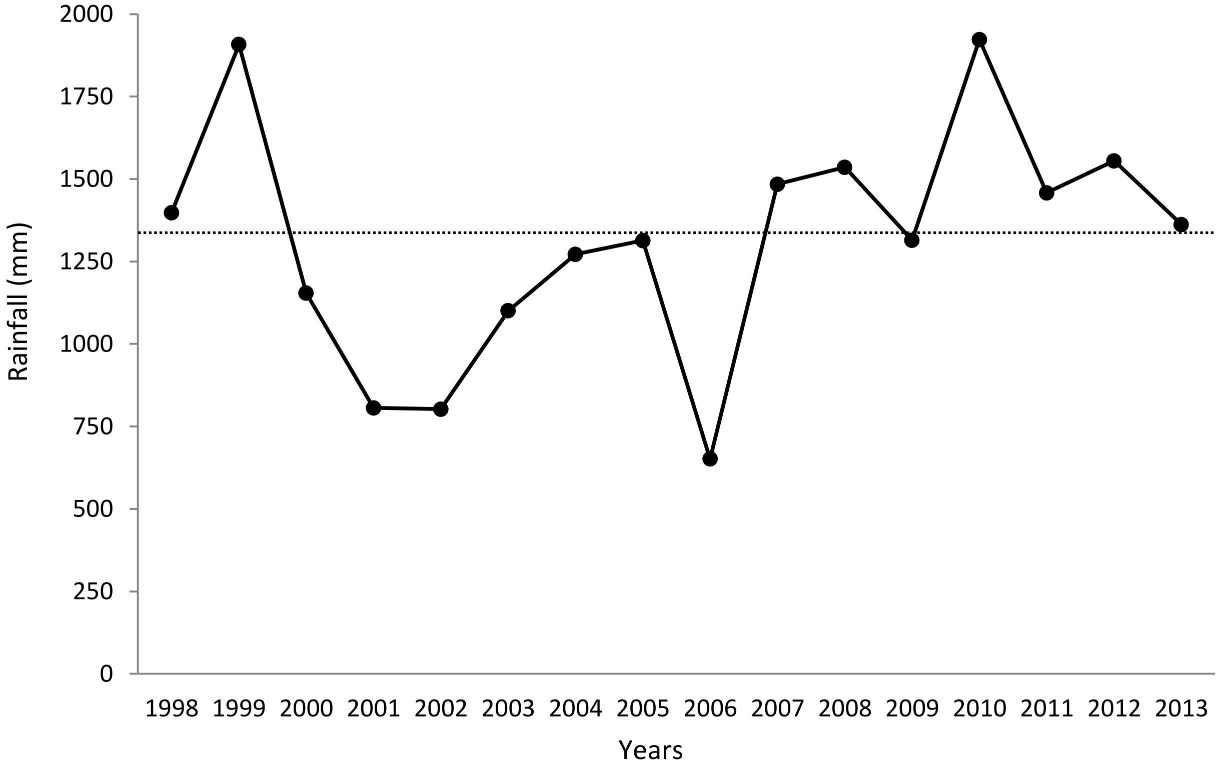

Figure 2.2: Annual precipitation (mm) from 1998 – 2013 with the mean value ($\bar{x}$=1314.8mm) for the period (BOM).

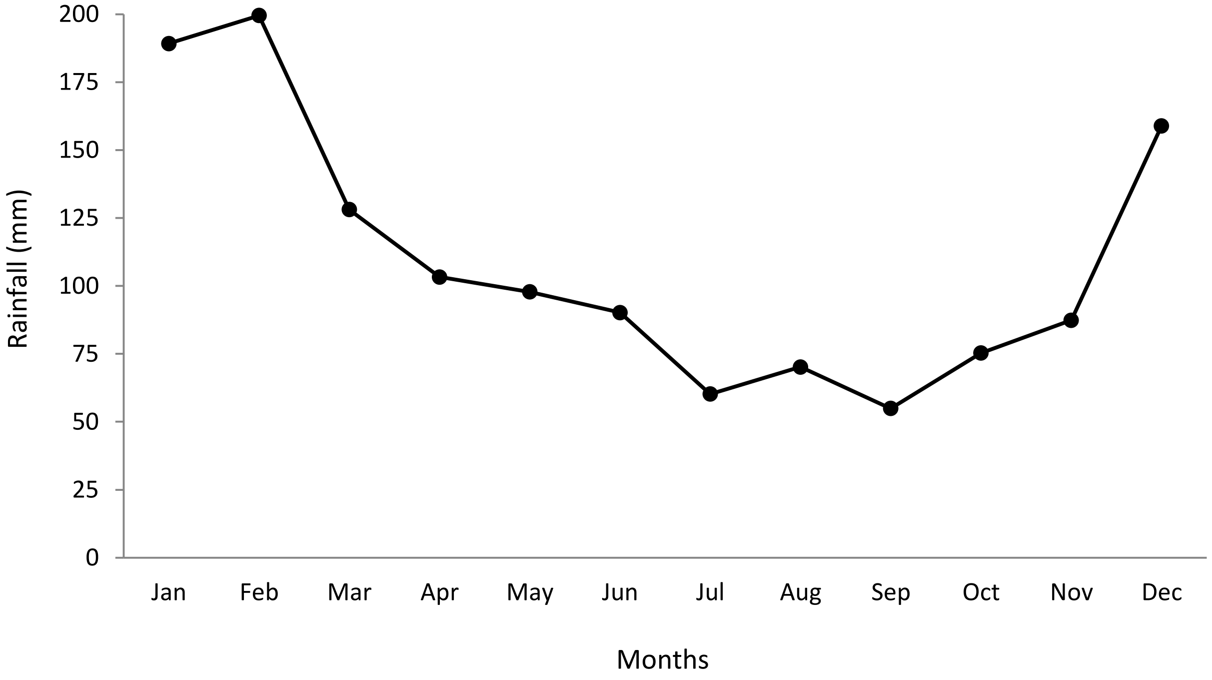

Figure 2.3: Mean monthly rainfall (mm) from 1998 – 2013 (BOM).

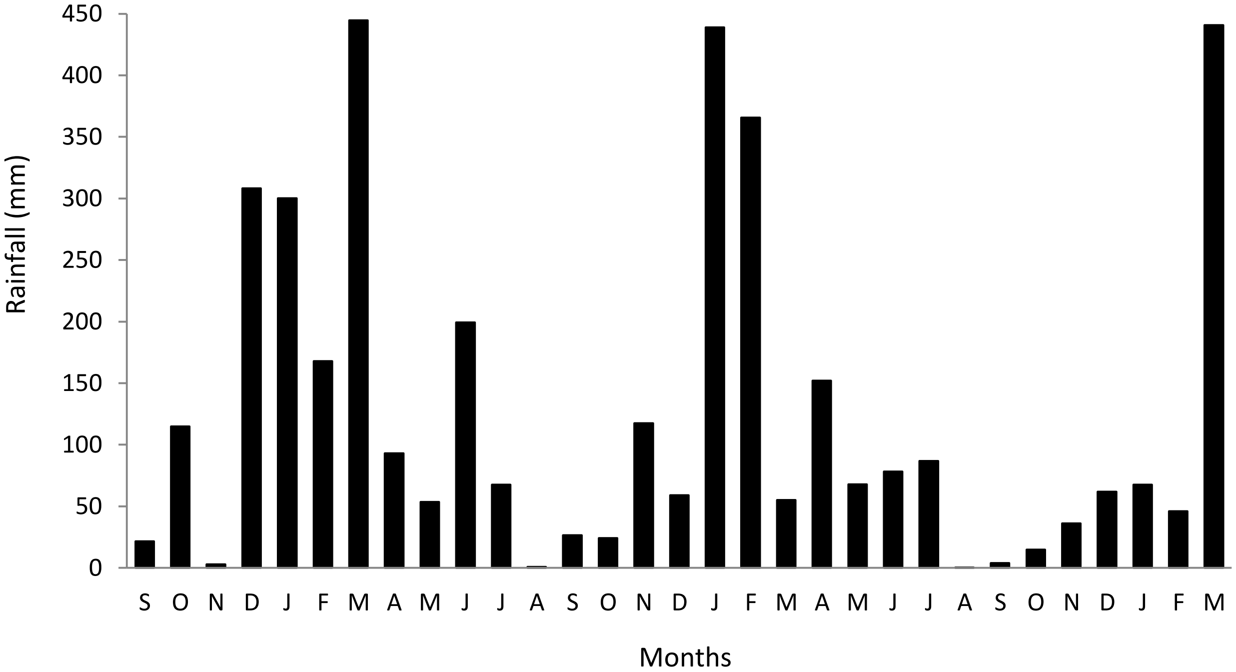

Figure 2.4: Total monthly rainfall for the duration of the study: September 2011 – March 2014 (BOM).

Mean temperature was 22.2C in winter (June - August) and 30.9C in summer (December - February, **Figure 2.5)**.

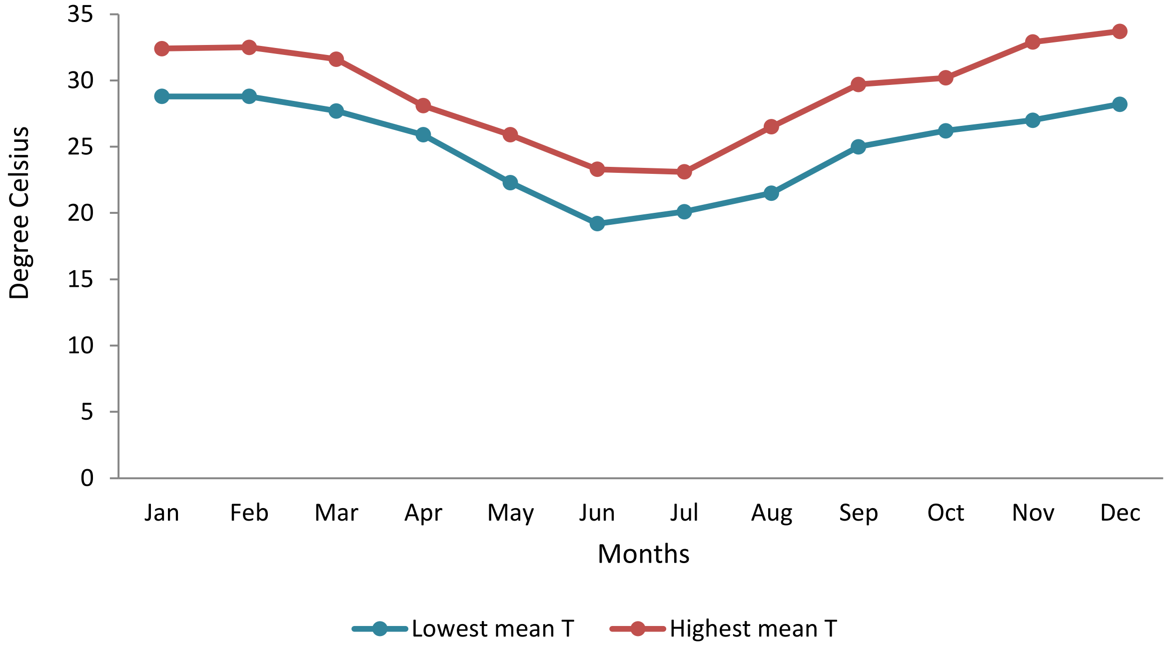

Figure 2.5: Lowest mean (blue) and highest mean (red) monthly temperature in degrees Celsius for the study period (BOM).

2.1.1. FAUNA

Numerous species of amphibians, birds, reptiles and mammals inhabit the forest area. The majority of wildlife occupies native shrubland and heathland areas. Common amphibians are: the wallum froglet (*Crinia tinnula*); the spotted grassfrog (*Limnodynastes tasmaniensis*); and the wallum sedgefrog (*Litoria olongburensis*); all being adapted to the acidic waters of the wallum swamps and marches. The waterlogged wallum habitats are home to rare and threatened bird species, including the eastern ground parrot (*Pezoporus wallicus wallicus*); the glossy black cockatoo (*Calyptorhynchus lathami*); the powerful owl (*Ninox strenua*); the grey goshawk (*Accipiter novaehollandiae*); and the eastern curlew (*Numenius madagascariensis*). Communities of native mammals include the eastern grey kangaroo (*Macropus giganteus*); the red-necked wallaby (*Macropus rufogriseus*); the emu (*Dromaius novaehollandiae*); and the water mouse (*Xeromys myoides*) (DERM 2011). Introduced mammals include pigs, deer, dogs, and some rodents (Holzworth 2010), and horses (Berman and Robinson 2011). Several herds of domestic cattle are grazed in the south-eastern part of the plantation.

2.1.2. FLORA

The vegetation in the forest is quite different to that of other state forests in the region due to FPQ management practices. The majority of the forest is dominated by three pine species: Caribbean pine (*Pinus caribae),* Slash pine *(Pinus elliottii)* and the hybrid of the two species (*Pinus elliotti var. elliotti x Pinus caribaea var. handurensis)* (Wang 2008; Hoey 2009). The plantation is divided into numerous logging areas with each containing an assortment of pine stands of differing age and size (Wang 2008). Classification of the habitat type recognizes four growth stages of coniferous vegetation based on tree height, proportion of canopy cover, and the composition of the ground vegetation.

At the beginning of the study, 28.8 km^2 of the plantation area was clear-felled; an area that had undergone clearing activities, and is referred in this thesis as *HARVESTED PINE (HP)* habitat. The size of this habitat varied as harvesting progressed. The ground cover in recently harvested pine habitat is dominated by harvested timber remnants, and was usually abundant in annual vegetation, such as graminoids and forbs (**Figure 2.6A**). The *YOUNG PINE (YP)* habitat class is characterized by small pine seedlings ranging from 0-2 years of age and about 0.5-2 meters in height. The young pine area was approximately 195.2 km^2 but fluctuated due to forestry planting activities. The small size of the seedlings permitted the establishment of copious palatable ground cover such as grasses, herbs and bushes (**Figure 2.6B**).

The *JUVENILE PINE (JP)* habitat consisted of immature forest, aged 3-10 years. Juvenile pine occupied about 205.1 km^2 and was distributed through the entire plantation. This habitat is characterised by tree canopy height above two meters (which is taller than a horse). The JP habitat is often interspersed with abundant lantana (*Lantana camara*) and other weeds. The uniformity of the canopy makes it very difficult for vascular plants to survive at the ground level, except beneath canopy gaps or at stand edges (**Figure 2.6C**). Thinning of the juvenile forest at eight years and controlled burning at nine years slightly reduces tree density, and frees the habitat from overgrowing shrubs. Canopy closure occurs at the end of the juvenile stage and persists through the mature stage. The remainder of the plantation area, approximately 326.7 km^2, was occupied by the *MATURE PINE (MP)* habitat, with the age of the old stands exceeding 11 years (Wang 2008). This well established forest was seldom populated by other plants due to its dense and closed canopy cover (**Figure 2.6D**).

Very little of the TTSF vegetation was natural, with most native areas having been subjected to some human management such as drainage, clearing, and burning. *NATIVE BUSHLAND (NB)* occupied an area of 157.8 km^2, which was usually restricted to drainage zones, streams and creeks and swamps (**Figure 2.6E**). Native vegetation communities were generally dominated by spotted gum (*Corymbia Citriorora* ssp. *variegata* and ssp. *Henryii)*, and western white gum *(Eucalyptus argophioia)*, interrupted with patches of scribbly gum (*Eucalyptus signata*), which is well adapted to the phosphorus deficient soils (Baynes 2004). Open woodland and forest margins are covered by grassland, often dominated by cockatoo grass (*Alloteropsis semialata*) and kangaroo grass (*Themeda triandra*), while harvested areas are abundantly invaded by blady grass (*Imperata cylindrica*) (DERM 2011). Seasonal swamps, known as “wallum swamps” contained abundant plant growth, dominated by high shrubs such as wallum banksia (*Banksia aemula*) and wallum grevillea (*Grevillea plurinervia*) and were interspersed with swamp grasstree (*Xanthorrhoea fulva*) and several species of endemic heath (Baynes 2004; Wang 2008; DERM 2011). More wet and fertile areas of the native bushland are occupied by eucalypt species, such as bloodwood (*Corymbia intermedia*), while on well drained sands, blackbutt (*Eucalyptus pilularis*) and in wet gullies, rose gum (*Eucalyptus grandis*) are found. Spotted gum (*Corymbia Citriorora ssp. variegata*) and Gympie messmate (*Eucalyptus cloeziana*) form a tall and open forest on dry and sandy ridges, sparsely located within the plantation (Baynes 2004).


B


C


D

Figure 2.6: Habitat classification in the Tuan and Toolara State Forest: A - harvested pine; B – young pine; C – juvenile pine; D – mature pine, and E – native bushland.

2.1.3. HABITAT DISTRIBUTION

Habitat distribution in the TTSF is presented in **Figure 2.8**. The distribution of habitats was compiled over several years (2011 - 2014) from the FPQ data base. Topographical maps (scale 1:50 000) contained information on plantation boundaries, logging area size, habitat classification, water points, creeks, drainage zones, and internal roads. Determination of the exact size and distribution of habitats over the study period was difficult due to constant harvesting and planting activities. For this reason, only an approximation of habitat size and distribution in the TTSF was possible but this agreed well with the habitat distribution data obtained from FPQ topographical maps from June - August 2012.

Evaluation of topographical maps and concurrent interviews with forestry personnel provided early data on feral horse distribution within the plantation. The extensive area of the TTSF meant that the entire plantation could not be surveyed, for that reason a smaller area approximating 99.1 km^2 was selected as the *STUDY AREA (SA)*. The study area was centrally located within the plantation, and contained comparable proportions of open and closed canopy habitats to the entire TTSF (**Figures 2.7 and 2.8**), and no horses were scheduled to be removed during the study.

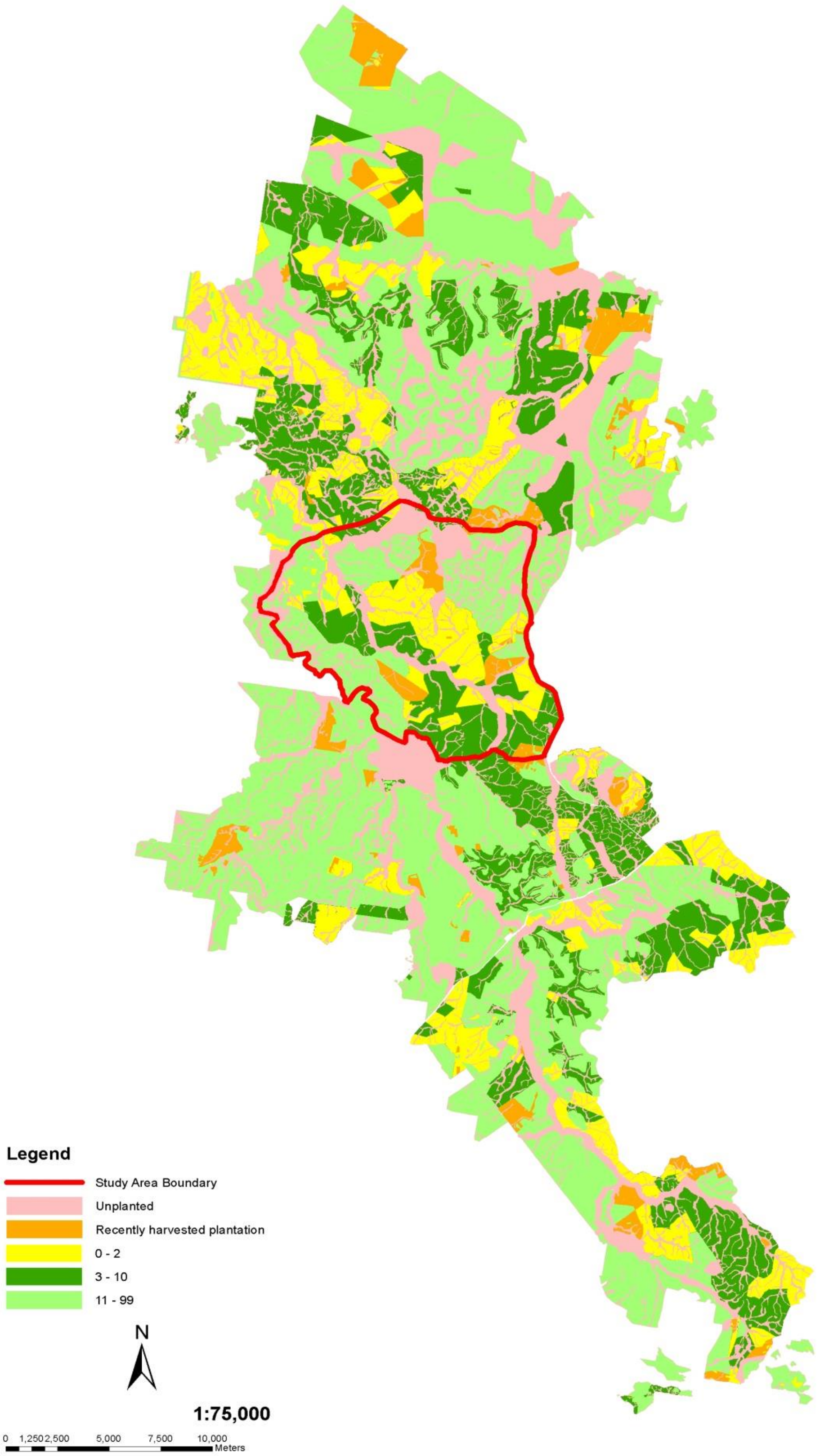

Figure 2.7: Habitat distribution in the study area and in the entire TTSF in 2012: red line – study area boundary; orange - harvested pine; yellow - young pine; dark green - juvenile pine; light green - mature pine, and pink - native bushland.

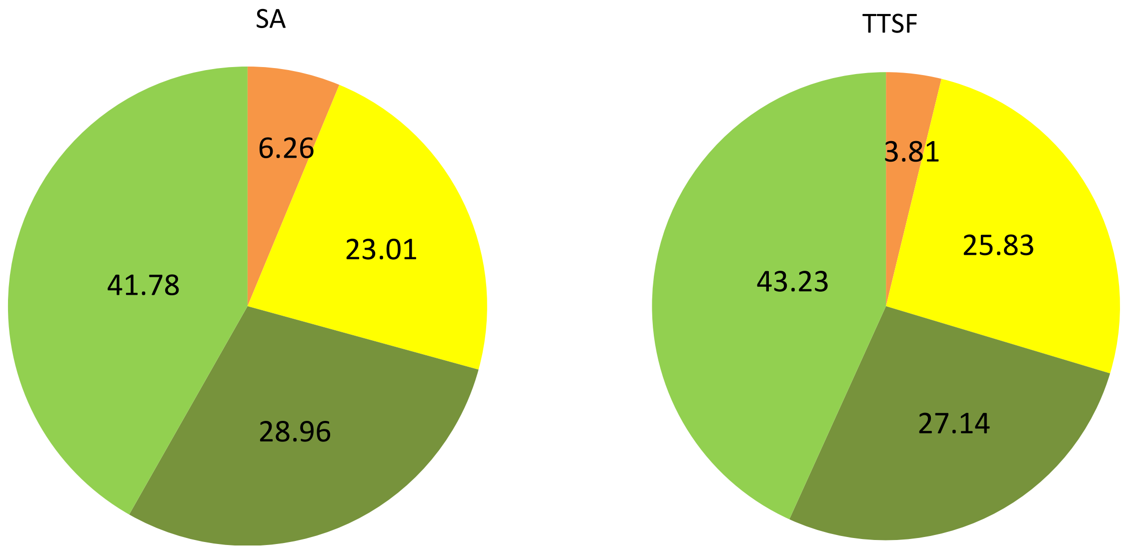

Figure 2.8: Area (km^2) of the four pine habitat types in the study area and in the entire Tuan and Toolara State Forest estimated in June - August 2012: orange - harvested pine; yellow - young pine; dark green - juvenile pine, and light green - mature pine.

The western and eastern borders of the study area were delineated by the plantation boundaries. An extensive corridor of native vegetation to the north, and the wide, permanent *Big Sandy Creek* to the south were considered to be natural barriers to horse movement and were therefore used to define the other two boundaries of the SA. A pilot survey was conducted in September 2011 to test equipment and techniques and to evaluate the suitability of the SA. The pilot study identified that the area could be traversed by a vehicle in one day and enabled mapping of vantage points and habitat distribution.

2.2. GENERAL SURVEY DESIGN

A detailed description of methodology used to quantify demographic parameters is presented separately in subsequent chapters. Data presented in Chapters 3 and 4, and predominantly in Chapters 5 – 7, were collected by direct observation of horses using a modified mark-recapture technique following the structure of the Pollock's Robust Design (Pollock 1982). The Pollock Robust Design incorporates primary and secondary sampling periods, where the primary sampling periods consist of several secondary sampling periods (sometimes referred to as sampling occasions), which are usually undertaken over several consecutive days (**Figure 2.9**). In the current study, primary sampling periods were represented by successive months, and secondary sampling periods by 2 – 6 consecutive days. In total, the observations were collected over 29 primary and 129 secondary periods from September 2011 - March 2014. Survey dates are presented in **Table 2.1**.

In its original form, the mark-recapture technique involves capturing of animals and marking them in a way that allows subsequent identification (e.g. attachment of tags, VHF beacons, GPS data loggers and toe clipping) when the animals are returned to the population (Seber 1992; Blomberg and Shine 2001). In this study, individual horses were identified by body size and colour, markings, gender and group associations, which were used to determine whether a horse was identified in ‘mark’ and ‘recapture’ events (Seber 1992; Walter 2002). This method of identification has been used previously in feral horses (Walter 2002; Cameron et al. 2001; Scorolli 2007) and other wildlife species (Wells and Scott 1990; Stevick et al. 2001; Jackson et al. 2006). Each time a new individual was observed, it was denoted as newly ‘marked’, and when identified in subsequent surveys, was denoted as ‘re-captured’.

Observations of horses were only considered valid when collected during daylight hours with good visibility. The observer was either on foot or in a vehicle travelling at an average speed of 20km/h (range 10 - 30km). For each survey day, the entire study area was surveyed to maximize ‘capture rate’. The observer-horse distance was usually between 200 to 600 metres. Greater distance or limited line of sight observations were facilitated by the use of 10 - 22x binoculars (Nikon Corporation, Tokyo, Japan). A digital DSLR photographic and/or video camera with 400mm lens (Canon Incorporation, Tokyo, Japan) was used to capture (record) the distinctive characteristics of individual animals, and images were stored in digital form on a portable hard-drive for later assessment. Horses were observed until complete identification was possible. Identified horses were assigned a unique number and sighting history including date, geographical location (latitude and longitude), group affiliation and habitat type; these data were entered into a database (Access, Microsoft Corporation, Redmond, Washington, USA).

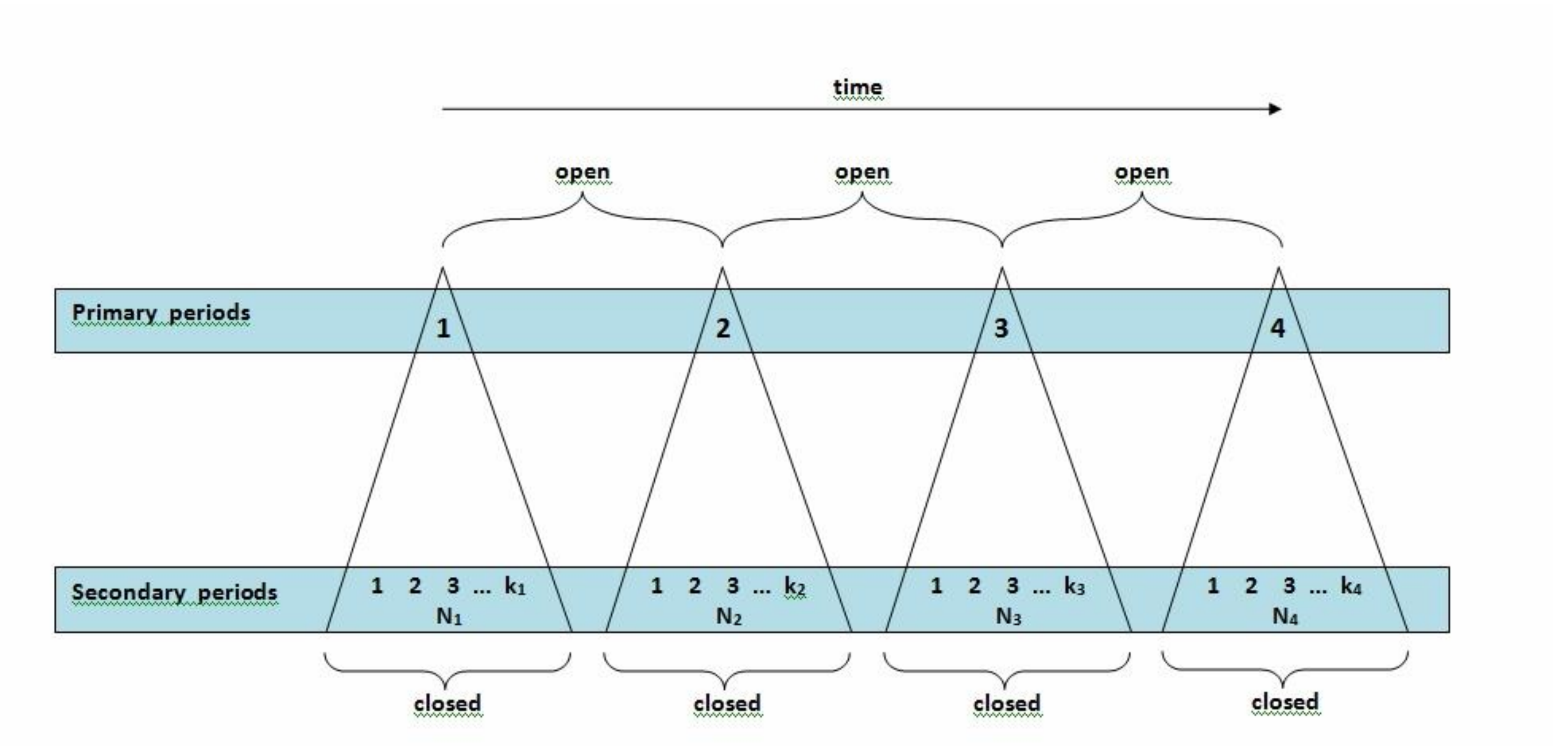

Figure 2.9: The mark-recapture Pollock Robust Design used to record capture events during primary periods (months), and secondary periods (days) in each survey. There were a total of 29 primary periods (four shown in the figure) and within each primary period there were 2 - 5 secondary periods. Population was considered ‘open’ between primary periods and ‘closed’ within secondary periods.

Season	Months	Days	
Spring	Sep	19th - 23rd	2012 year
	Oct	14th – 18th	
	Nov	-*	
Summer	Dec	4rd – 8th	
	Jan 2012	10th – 14th	
	Feb	6th – 10th	
Autumn	Mar	28th – 29th	
	Apr	10th – 14th	
	May	10th – 14th	
Winter	Jun	10th – 14th	
	Jul	10th – 14th	
	Aug	6th – 10th	2013 year
Spring	Sep	4th – 8th	
	Oct	22nd – 26th	
	Nov	19th – 23rd	
Summer	Dec	14th – 18th	
	Jan 2013	15th – 19th	
	Feb	10th - 14th	
Autumn	Mar	15th – 18th	
	Apr	12th – 15th	
	May	10th – 13th	
Winter	Jun	14th – 17th	
	Jul	-*	
	Aug	16th – 19th	2014 year
Spring	Sep	13th – 16th	
	Oct	9th – 13th	
	Nov	14th – 17th	
Summer	Dec	13th – 16th	
	Jan 2014	15th – 18th	
	Feb	21st – 22nd	
Autumn	Mar	21st – 24th	

Table 2.1: Monthly surveys (primary periods), and daily surveys (secondary periods) performed in the study area of the TTSF between September 2011 and March 2014.

* survey was not performed

CHAPTER 3: SOCIAL ORGANISATION AND POPULATION STRUCTURE

3.1. INTRODUCTION

Basic population attributes of large mammalian herbivores are described by parameters such as group size and composition, sex ratio, birth rate, survival, distribution, feeding and movement patterns, and mating systems (Clutton-Brock et al. 1987; Lloyd and Rasa 1989; Kojola 1993; Linklater 2000b; Skalski et al. 2005). Characterisation of demographic parameters provides information on the state of the population and its ability to adjust to environmental and geographic conditions, and natural selection, and this in turn may have implications on management, whether aiming to reduce, or maintain, or protect the status of the population (Berger 1986; Clutton-Brock et al. 1987; Cameron et al. 2001; Walter 2002).

Observational studies have shown that in large herbivores the size of social groups directly relates to availability and quality of pasture (Jarman 1974; Nelson 1978; Franke Stevens

1990; Berman 1991). In environments, where food availability was compromised due to drought, female kudu (*Tragelaphus strepsiceros*) group size decreased (Spinage 1986). In feral horses, harem stallions have higher energy costs associated with harem maintenance during periods of forage scarcity and the number of mares that stallions are able to maintain decreases (Berman 1991). At the end of winter, which coincided with sparsely distributed pasture, stallions spent more time grazing and less time interacting with harem females: this reduced social bonding and lead to social instability (Franke Stevens 1990).

Feral stallions defend harems throughout the year and lifetime reproductive success is dependent on their ability to retain females and maintain harem stability (Franke Stevens 1990). Stability of breeding groups also contributes to the overall well-being of females, which influences foaling rates (Kaseda et al. 1995). Harem instability of Misaki mares was found to correlate negatively with foaling rates during their reproductive life (Kaseda et al. 1995). High levels of social instability were also observed in feral horses on Cumberland Island, which was ascribed to the high level of home range overlap and the large number of bachelors present in the population (Goodloe et al. 2000).

Gender bias in feral horse populations is either the result of bias generated at birth or different survival rates of the two sexes (Berger 1986; Garrott and Taylor 1990; Roelle et al. 2010). Differences in survivability can occur due to unfavourable climatic conditions (Sasimowski et al. 1990a; Lucas et al. 1991; Scorolli et al. 2006), predation (Greger and Romney 1999; Feh et al. 2001; Lagos and Barcena 2012), sex specific behaviour leading to higher mortality of one gender (Berger 1986; Garrott and Taylor 1990), and human management selecting one gender preferentially (Ganskopp and Vavra 1986; Garrott and Taylor 1990; Duncan 1992).

In general, high ratio of adults to juveniles, and/or high number of females of reproductive age, is likely to increase the reproductive success of a population, the result being an expansion in the population growth rate (Garrott et al. 1991b; Scorolli and Lopez Cazorla 2010a). If the management plan is to diminish the size of the population or reduce its reproduction rate, a greater effort should be made to remove adult females (Gaillard et al. 1998). Survival may differ between sexes in any age group (Sapir et al. 2008), and this may alter both the sex ratio and age distribution of the population, which will be reflected in the rate of change of population growth (Gaillard et al. 2000a; Sapir et al. 2008).

Documentation of demographic parameters is essential when determining long-term population management strategies (Garrott et al. 1991b; Scorolli and Lopez Cazorla 2010a).

Concurrently, the effects of management on the social organisation of feral horses should be considered (Cameron et al. 2001). Removal of animals of particular sex or age is likely to alter the sex ratio and age distribution of a population. This has been shown in feral horse populations, where males were selectively removed (Ganskopp and Vavra 1986; Sasimowski et al. 1990a). Confinement of a population to a small area may disrupt natural social behaviour of feral horses by altering social structure, increasing animal density, decreasing home range size and restricting seasonal movements (Goodloe et al. 2000; Linklater 2000a).

Demographic information can be of a considerable importance for managers aiming to control or reduce the population size supressing fertility (Goodloe et al. 2000). In a population whose sex ratio is biased towards males or where a large number of harems are maintained by multiple stallions, male-based contraception will be ineffective (Goodloe et al. 2000). On the other hand, female contraception based on the administration of porcine zona pellucida (PZP) on populations where harem stability is already compromised, may have potentially serious welfare implications as it has been shown that treatment with the PZP decreases social fidelity of contracepted mares and extend their reproductive activity beyond the normal foaling season (Nuñez et al. 2009).

Numerous studies have documented social organisation of feral horses world–wide (Feist and McCullough 1976; Kaseda 1981; Franke Stevens 1990; Duncan 1992; Goodloe et al. 2000; Cameron et al. 2001; Scorolli 2007; Roelle et al. 2010). Although Australia has the world’s largest population of feral horses (Dobbie et al. 1993; Dawson et al. 2006), there have been few studies documenting feral horse demographics. The most recent Australian studies have focussed on population distribution, density and abundance (Dyring 1990; Walter 2002; Schott 2004; Lundie-Jenkins et al. 2006; Vernes et al. 2009), habitat use (Schott 2004), horse impact on the environment (Dyring 1990), and population dynamics (Walter 2002); all were conducted in natural ecosystems within national parks. The only study on social organisation of feral horses in Australia was performed in the Northern Territory in the late 1980s (Berman 1991).

Tuan and Toolara State Forest is an artificial ecosystem, with sparsely distributed natural habitats, therefore being unique to ecosystems occupied by feral horses in Australia. As differences in demographic parameters of feral horses are usually attributed to environmental and ecological factors (Berman 1991; Roelle et al. 2010; Dawson and Hone 2012), the uniqueness of this environment may influence demographics. Although it is expected that the social organisation of the TTSF feral horse population will be similar to other populations of feral horses in Australia (Berman 1991; Walter 2002; Schott 2004), this assumption needs testing. Determination of social structure can assist in the evaluation of vital rates, such as fecundity and survival, and determination of age distribution and sex ratio can be used to define population growth rate. Understanding the processes that drive population dynamics is vital to the management of feral horse populations (Bolen and Robinson 2003; Dawson and Hone 2012). This chapter describes the methodologies used to define the social organisation and population structure of feral horses in the TTSF and discusses data obtained using these methodologies.

AIMS AND OBJECTIVES

1. To characterise the social structure of the TTSF feral horses;
2. To determine the age distribution and sex ratio of the population, and
3. To investigate social stability of breeding groups and how that impacts on reproductive performance of adult females.

HYPOTHESES

1. The social structure of the feral horse population in the TTSF consists of well-defined breeding groups (harems) and bachelor (male only) groups;
2. The population is characterised by a stable age distribution;
3. The adult female to male sex ratio is not different from parity, and
4. The breeding groups are characterised by permanence and a high level of stability expressed by loyalty of adult group members to their harems.

3.2. METHODS

Data pertaining to the demographics of feral horses in the TTSF were collected from September 2011 to August 2013 in the study area. Observations were collected during scheduled monthly surveys of 4 - 5 days duration and at other times through opportunistic sightings while doing other research activities. Observations were collected during daylight hours and the observer was either on foot or in a slowly travelling vehicle. Sightings were not confirmed until identification was absolute, which was based on body colour, markings, gender and group associations (Roelle et al. 2010).

3.2.1. GROUP COMPOSITION

A harem was considered to be a group of adult horses consisting of at least one dominant stallion and one mare, with or without offspring. If a group of adult or sub-adult stallions was observed, it was classified as a bachelor group, while single stallions were recorded as single bachelors (Cameron et al. 2001; Roelle et al. 2010). Age groups were defined as: foal (≤ 1 year old); yearling (1 to 2 years); sub-adult (2 to 3 years of age) and adult (≥ 3 years of age) (Feist and McCullough 1976; Goodloe et al. 2000; Scorolli and Lopez Cazorla 2010a). Dependent foals were identified by their small body size, strong attachment to their dams and frequent suckling events (Goodloe et al. 2000). Yearlings were taller and of larger body, and with longer mane and tail than foals (Goodloe et al. 2000). Yearlings were more independent than foals, which was manifested by increased separation distances from their dams when grazing and playing. The remainder of the immature horses were classified as sub-adults. Sub-adults have a larger, more muscular body than yearlings but smaller than adults (Goodloe et al. 2000). Gender was determined by observation of genitalia and supported by behaviour. Harem stallions were additionally identified when mating with females, herding harem females away from other males, and scent marking (Feist and McCullough 1976; Berger 1986). Dams and their foals were identified by suckling behaviour. Pregnant mares were distinguished by their appearance in late gestation (Perryman and Muchlinski 1987; Goodloe et al. 2000).

3.2.2. DISPERSAL

A dispersal event was determined to have occurred when there was a departure of a juvenile male or female from its natal harem and the individual was later observed alone or with other horses (Kirkpatrick and Turner 1986; Goodloe et al. 2000; Roelle et al. 2010). Dates of dispersal of juvenile horses were taken as being the date on which they were last observed with their natal harem.

3.2.3. SOCIAL STABILITY

Disbanding events by adult mares were recorded, as were returns to the original harem (Roelle et al. 2010). Harem instability was determined by assessing the number of disbanding and acquisition events performed by adult females per harem per year. Disbanding was classified as an occasion when an adult female temporarily or permanently left the harem and joined another harem or group of bachelors, while acquisition was classified as attainment of a new (or previously disbanded) adult female to the harem. Stable harems were those in which females remained loyal (‘loyal females’) to their harem stallion in a given year. Unstable harems were those in which at least one female disbanded (‘transient female’) from the harem on at least one occasion.

3.2.4. DATA ANALYSES

All analyses were conducted on the basis of a biological year, starting August 1st in one year and ending 31st July the next year. The beginning of the biological year was synchronised with the beginning of the foaling season. To simplify the presentation of results, the 2011 - 2012 year is referred as 2012, and 2012 - 2013 as 2013. Horse group composition was recorded monthly into Microsoft Excel® and Access (Microsoft Corporation, Redmond, Washington USA). Each record listed the presence/absence of horses by age, gender and social grouping. The generalised linear mixed model (GLMM), which employed a truncated Poisson model, was used to determine possible effects of a year on the size and composition of harems and bachelor groups. The model incorporated group (H_i = harems; B_i = bachelors), and individual (AS = adult stallion; AFe = adult female; SB = sub-adult; Y = yearling, and F = foal) identification codes as random effects, which allowed for repeated measurement of both groups and individuals (Zuur et al. 2009).

Sex ratio of the adult component of the population was expressed as $R_{F/M} = N_F/N_M$, where N_F is the number of adult females, and N_M is the number of adult males. This formula was employed because it is in common usage and therefore facilitated comparisons between the current study and other studies that had investigated feral horse populations elsewhere (Goodloe et al. 2000; Linklater 2000b). The sex ratio was defined using the following assumptions: female and male individuals have a constant survival rate across all ages in their gender group; there is equal recruitment of both sexes into the population, and the population characterizes a stable age and sex structure (Skalski et al. 2005). Juvenile horses were not included in the estimate as the gender was not determined in a sufficient number of individuals.

Social stability was calculated only for adult females in harems that were observed at least bi-monthly between September 2011 and August 2013. Harem stability was expressed as a ratio of stable to unstable harems in a given year. The annual number of disbanding and acquisition events per harem was also calculated. Annual and biannual loyalty of females was presented as a percentage ratio of loyal to transient females in a given time period.

The Mann-Whitney (W) test was used to determine if the mean annual size of harems and the mean annual female body condition score (BCS) influenced annual harem loyalty. The analysis took into account that evaluated females were measured repeatedly over two years. Calculations were performed annually, because variables such as fidelity, harem size and body condition of feral horses often vary annually (Ransom et al. 2010).

The effect of social instability on foaling rates was analysed by comparing the number of adult females that changed harems with the number of adult females that were loyal to their harems, and their respective foaling events in a given year. Loyalty and fecundity parameters were coded as binary variables: ‘1’ for loyal and for the presence of a foal, and ‘0’ for transient and absence of a foal. The significance between the measured variables was determined by the Pearson contingency table.

Group sizes and composition were analysed using R 3.0.1 (R, Developmental Core Team, 2012), and are presented as mean, and 95% confidence intervals (CI). Sex ratio, age distribution and harem stability were analysed using Microsoft Excel®, and are presented as ratios, and female loyalty as ratios and mean ± SD. To test whether there were annual differences in group composition, sex ratio, age distribution, stability of harems, and loyalty of mares, the Pearson X^2 test was used. All statistical calculations were performed with a significance level of $P = 0.05$.

3.3. RESULTS

Data were obtained from 522 identifiable individual horses between September 2011 and July 2013 (**Table 3.1**). In the first year of the study, 344 horses were observed and the number increased to 522 in the second year. Some horses were observed in both years, and some were observed in the first year only, others in the second year only.

Social group types	Total horses and groups identified 2012 - 2013		Observed in 2012		Observed in 2013	
	Groups (n)	Horses (n)	Groups (n)	Horses (n)	Groups (n)	Horses (n)
Harems	72	443	49	281	50 (27)	328 (166)
Bachelors	29	77	21	61	19 (11)	49 (33)
Mare groups	1	2	1	2	-	-
Total	102	522	71	344	69 (38)	377 (199)

Table 3.1: Presented are the number of groups and individual horses identified throughout the study period. Certain groups and individuals were identified in 2012 only, 2013 only, or in both (numbers in brackets) years of the study.

3.3.1. HAREMS

Analysis of 72 harems observed on 339 occasions during the study showed there was no significant difference in harem size between 2012 and 2013 (**Table 3.2**).

Parameter	GLMM estimate	SE	Z-value	*P*-value
Intercept	1.5767	0.0532	29.64	*P* < 0.001
Year effect	0.0393	0.0479	0.82	0.41

Table 3.2: Effect of year on harem group size estimated using generalised linear mixed models (GLMM) within the study period.

Harem size distribution is presented in **Figure 3.1**. The mean harem size (inclusive of stallions, mares and their offspring) in 2012 was 4.83 (95%CI 4.53 - 5.817) horses, which increased to 5.03 (95%CI 4.37-5.79) in 2013. The mean harem size for the two years of the study was estimated to be 4.95 (95%CI 4.53-5.41; range 2 – 11 horses).

Figure 3.1: Harem size distribution year by year within the study period; values above the bars indicate the number of harems.

The mean annual harem size and composition with 95% confidence intervals are presented in **Figure 3.2**. No significant differences were observed in annual harem composition over the study period ($\chi^2 = 1.698$, df = 1, *P* = 0.193) (**Table 3.3**).

Parameter	Chi-square	df	*P*-value
Year effect	1.698	1	0.193
Age by Year interaction	8.993	4	0.061

Table 3.3: Effect of year on the composition of harems estimated using generalised linear mixed models (GLMM) year by year within the study period.

The mean number of stallions (1.07, 95%CI 0.96 - 1.21 in 2012; and 1.08, 95%CI 0.93 - 1.23 in 2013) and mares (2.12, 95%CI 1.92 - 2.35 in 2012; and 2.13, 95%CI 1.96 - 2.31 in 2013) was constant over the two years. The number of yearlings in harems was higher in 2013 (0.54, 95%CI 0.46 - 0.64) than in 2012 (0.47, 95%CI 0.38 - 0.58) but the difference was not significant (slope = 0.136 ± 0.15 SEM, *P* = 0.37). The sub-adult group was the least numerous and ranged from 0.48 (95%CI 0.39 - 0.60) in 2012 to 0.45 (95%CI 0.37 - 0.53) in 2013. Foal numbers showed a significant increase in 2013 (slope = 0.342 ± 0.13 SEM, *P*<0.008), and varied from 0.66 (95%CI 0.56 - 0.79) in 2012 to 0.94 (95%CI 0.83 - 1.06) in 2013 (**Figure 3.2**).

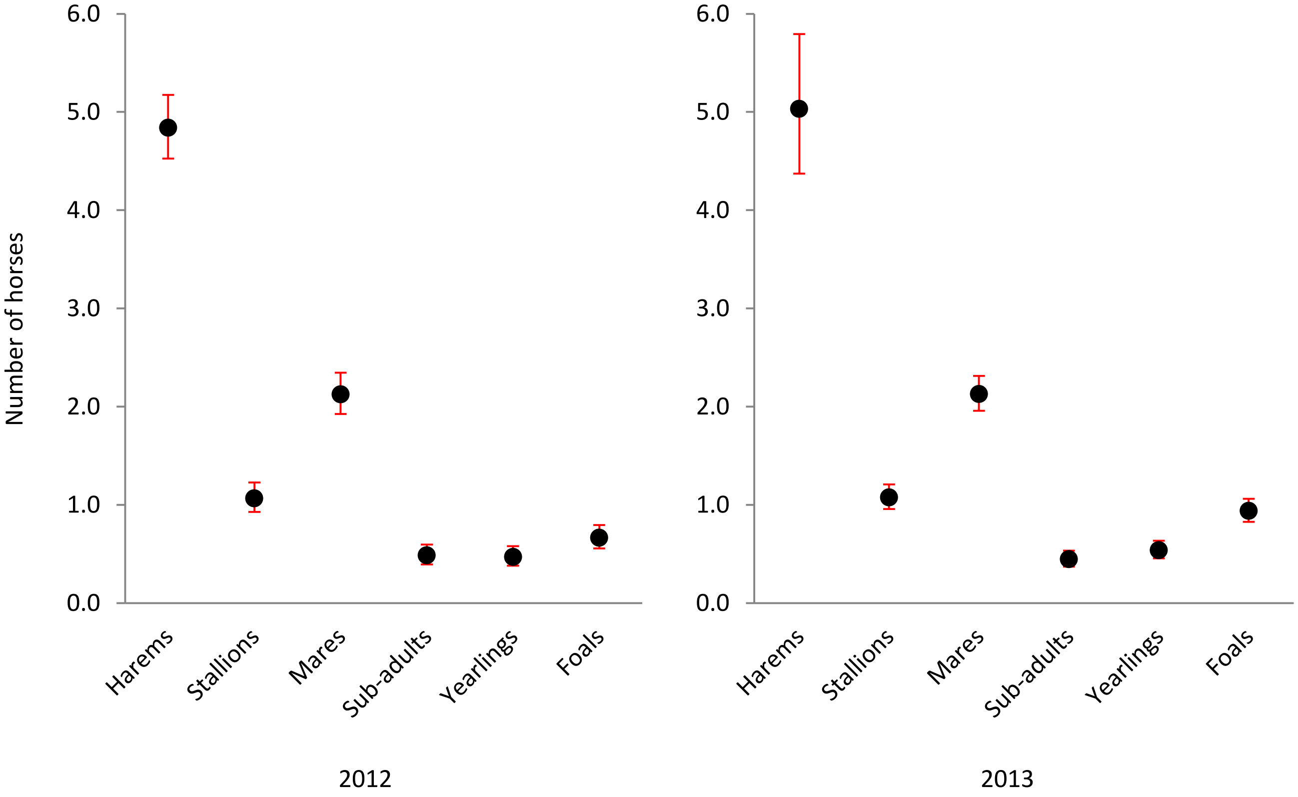

Figure 3.2: Mean (± 95%CI) harem size, number of male and female adults, and number of offspring in harems over the study period.

The numbers of stallions in harems are presented in **Table 3.4**. In 2012, 12.2% (n = 6) harems had two stallions. In 2013, the number fell to 5 harems (10.0%) following the disbanding of three stallions from their respective harems and identification of two new harems each having two stallions. At any given time, the maximum number of stallions in stallion groups was two.

Year	SS harems		MS harems		Total harems
	n	%	n	%	n
2012	43	87.8	6	12.2	49
2013	45	90.0	5	10.0	50

Table 3.4: The number and percentage of harems maintained by single stallions (SS) and multiple stallions (MS), and the total number of harems (n) year by year within the study period.

3.3.2. BACHELORS

Males not associated with harems consisted of adults and sub-adults, and in two instances, yearlings. During two years of observations, 71 bachelors formed 29 groups, ranging from 2 to 6 individuals. Six bachelors remained solitary. The GLMM analysis indicated that bachelor groups did not significantly differ between the two years (slope = -0.341 ± 0.186, $P = 0.068$; **Table 3.5**). The mean bachelor group size in 2012 was 2.20 (95%CI 1.54 - 3.13) and in 2013 was 1.56 (95%CI 0.91 - 2.69). Bachelor group size distribution is presented in **Figure 3.3**.

Parameter	GLMM estimate	SE	Z-value	*P*-value
Intercept	0.788	0.180	4.38	$P < 0.001$
Year effect	-0.341	0.186	1.83	0.068

Table 3.5: Effect of a year on bachelor group size estimated using generalised linear mixed models (GLMM) over the study period.

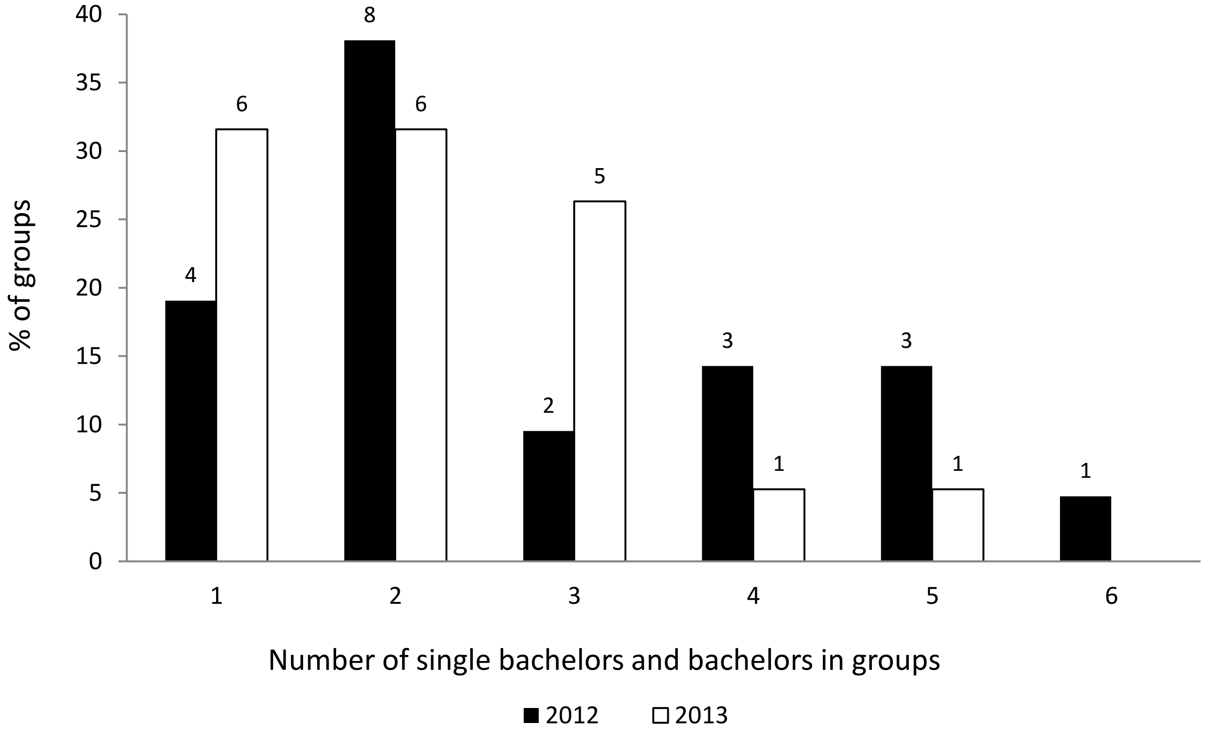

Figure 3.3: Single bachelor and bachelor group size distribution year by year within the study period. Values above the bars indicate the number of single bachelors and groups.

Solitary males were observed infrequently (n = 6, 8.45%) and were sub-adults (n = 2), or mature adults (n = 4). The sub-adults were later observed to join bachelor groups. One solitary adult was injured and, after regaining fitness, formed a harem. Another older male lost his harem in a combat and was solitary for several months. At the end of winter 2013, he acquired a sub-adult female and started a new harem. Other bachelors remained solitary. No sub-adult males were observed to establish their own harem during the study. In general, bachelor groups showed a high degree of social mobility, as they were often observed to change their group composition (n = 22). The observed groupings were usually of short duration and lasted from one day to four weeks; however, two long term associations were also observed lasting eight and 12 months respectively.

3.3.3. DISPERSAL

Of 22 offspring that left their natal harems, nine were observed on subsequent occasions (40.91%). One sub-adult male was transient between several bachelor groups or was observed on his own; four sub-adult males joined pre-existing bachelor groups, and one sub-adult male paired with a yearling male. Three of the dispersed sub-adult and yearling fillies formed a stable relationship with a former mature bachelor. All nine horses were observed to occupy the home range or in close proximity (± 3km) to the home range of their natal harems. The majority (n = 17; 77.27%) of dispersal events occurred in early spring and summer (August – December), and the mean age of dispersed horses was 2.0 ± 0.8 SD years (range 1 – 3 years).

3.3.4. SEX RATIO

The gender of all foals, yearlings and sub-adult horses could not be accurately assessed and therefore, the sex ratio was based only on the adult component of the population. The sex ratio of females to males in both years was not significantly different from parity, and in 2012 was 0.96:1.00 ($\chi^2 = 0.106$, df = 1, $P = 0.744$) based on 115 females and 120 males; and in 2013 was 1.11:1.00 ($\chi^2 = 0.760$, df = 1, $P = 0.383$) based on 136 females and 122 males. The overall gender ratio of all adult horses identified during the study, including sub-adults of known gender in 2012 that survived to adulthood in 2013, was not significantly different from parity ($\chi^2 = 0.820$, df = 2, $P = 0.664$) and was 0.99:1.00.

3.3.5. AGE DISTRIBUTION

The age structure of the population did not alter significantly during the two years of the study. Minor variations were noted in the size of the foal and sub-adult age groups ($\chi^2 = 3.79$, df = 3, $P = 0.285$; **Table 3.6**). Adult horses constituted the largest and least variable age group (68.3 - 68.4%), and sub-adults, yearlings and foals constituted the remainder of horses in the population and their numbers fluctuated annually.

Age group	2012		2013	
Adult	68.3%	(n = 235)	68.4%	(n = 258)
Sub-adult	10.8%	(n = 37)	7.2%	(n = 27)
Yearling	7.6%	(n = 26)	8.0%	(n = 30)
Foal	13.4%	(n = 46)	16.4%	(n = 62)
Total	100%	(n = 344)	100%	(n = 377)

Table 3.6: Age distribution of the feral horse population in each year of the study period.

3.3.6. HAREM STABILITY

Some harems were observed repeatedly over the course of two years while others were only observed occasionally or in one year and not the other. As a result, a total of 27 harems containing 67 adult females and 30 stallions were analysed for harem stability. At completion of the study, 44.4% (n = 12) of harems maintained the same adult mare composition and 55.6% (n = 15) had undergone membership changes at some point in time. The mean number of membership changes in unstable harems in 2012 was 4.0 ± 6.71 SD (range 1 - 14), but this was influenced particularly by one harem (Harem 7) that underwent 14 disbanding and acquisition events. Excluding Harem 7 from the analysis, the mean number of membership changes was 2.75 ± 1.91 SD (range 1 - 5). The mean number of changes in 2013 was 2.07 ± 1.56 SD (range 1 - 4). The mean number of changes over the two years was 4.08 ± 7.78 SD (range 1 - 17), including Harem 7, which underwent 17 changes during that time (**Figure 3.4**). All observed harems were maintained by the same single (n = 24) or multiple stallions (n = 3) for the duration of the study.

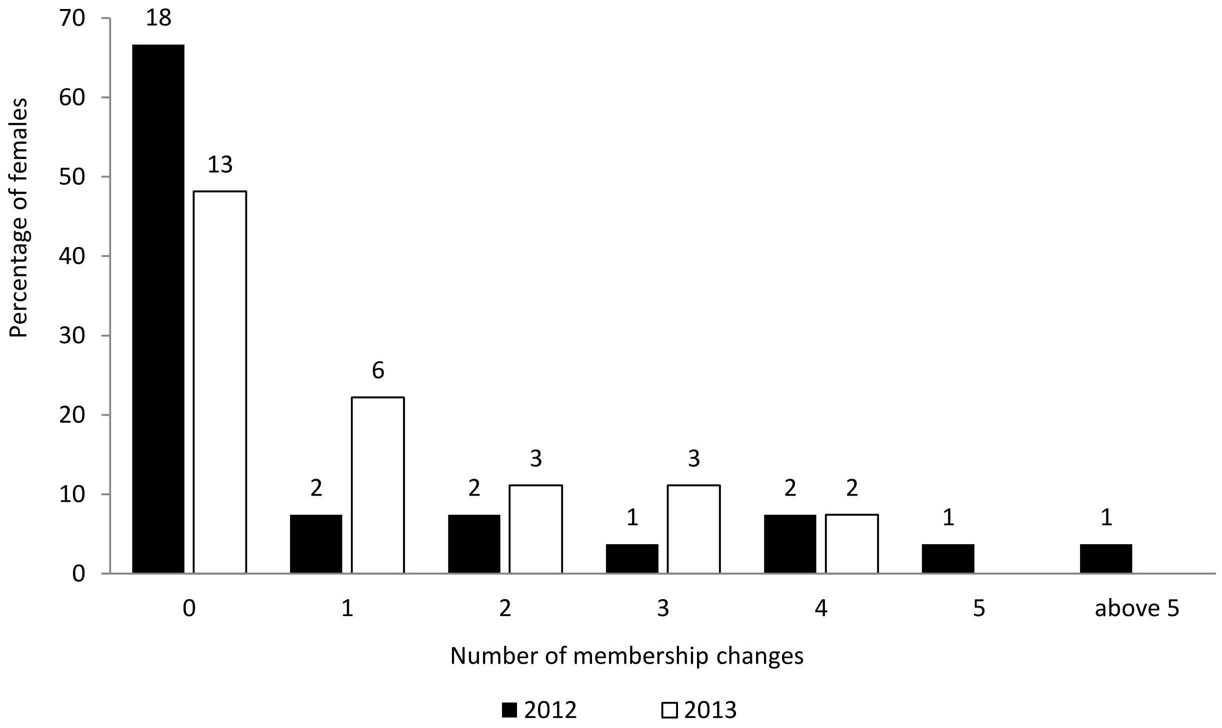

Figure 3.4: Percentage of adult females in 27 harems that underwent annual membership changes year by year within the study period. Values above the bars indicate the number of females.

3.3.7. FEMALE LOYALTY

Of the 67 adult females in 27 harems observed from 2012 - 2013, 49.25% (n = 33) remained loyal to their harems. The remainder (50.75%, n = 34) changed their harem membership at least once, and on average 1.91 ± 0.70 SD (range 1 - 4; **Table 3.7**). There was no significant difference in the annual proportion of loyal and transient females (χ^2 = 0.135, df = 1, *P* = 0.713) over the study period. Analysis of the overall data for the two years is shown in **Figure 3.5**.

Year	Loyal females		Transient females		Total (n)
	%	n	%	n	
2012	68.66	46	31.44	21	67
2013	65.67	43	34.33	24	67
2012 - 2013	49.25	33	50.75	34	67

Table 3.7: Annual and overall number (n) and ratio (%) of loyal and transient adult females in 27 harems year by year within the study period.

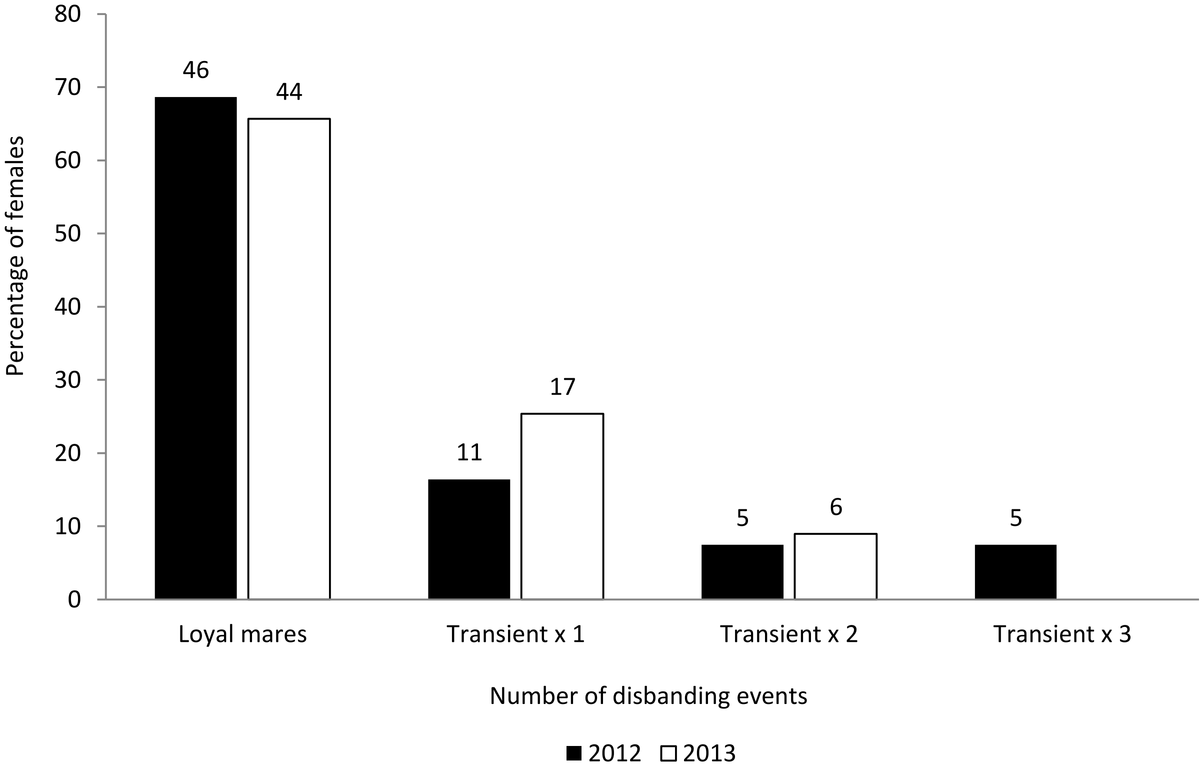

Figure 3.5: Numbers of loyal and transient adult females in 27 harems year by year within the study period. Values above the bars indicate the number of females.

Harem size and the number of loyal and transient mares did not alter significantly over the study period, nor between 2012 and 2013 (**Table 3.8**). The body condition score of loyal and transient mares did not alter significantly over the study period, nor between 2012 and 2013 (**Table 3.8**).

	Loyal females Mean ± SD (N)	Transient females Mean ± SD (N)	W-Test statistics
Mean harem size			
2012	6.29 ± 2.16 (46)	5.89 ± 1.47 (21)	W=530.5, *P*=0.52
2013	6.78 ± 2.43 (43)	6.55 ± 1.96 (24)	W=517.0, *P*=0.89
Overall	6.53 ± 1.84 (33)	6.22 ± 2.04 (34)	W=630.5, *P*=0.38
Mean BCS			
2012	2.32 ± 0.47 (46)	2.07 ± 0.41 (21)	W=593.5, *P*=0.11
2013	2.33 ± 0.46 (43)	2.25 ± 0.49 (24)	W=508.5, *P*=0.98
Overall	2.33 ± 0.40 (33)	2.16 ± 0.58 (34)	W=624.5, *P*=0.41

Table 3.8: Descriptive statistics of loyal and transient females in 27 harems observed over the entire study period, and in each year of the study period.

No significant relationship was found between harem loyalty of adult females and number of foals born annually (2012: χ^2 = 0.533, df = 1, *P* = 0.465; 2013: χ^2 = 1.32, df = 1, *P* = 0.250) (**Table 3.9**). Over two years of the study, 33 loyal females produced 38 foals, and 34 transient females produced 27 foals, but the difference in the number of foals between the two groups was not significant (χ^2 = 1.13, df = 1, *P* = 0.289).

Year	Loyal females			Transient females			Total females (n)	Chi-square statistics
	with foals	without foals	total	with foals	without foals	total		
2012	15	31	46	5	16	21	67	χ^2 = 0.533, df = 1, P = 0.465
2013	31	12	43	14	10	24	67	χ^2 = 1.32, df = 1, P = 0.250

Table 3.9: Number of foals born year by year within the study period to loyal and transient females in 27 harems.

3.4. DISCUSSION

The social structure of feral horses in the TTSF was similar to that described in previous studies of feral horse populations in Australia (Berman 1991; Dawson and Hone 2012) and various parts of the world, (Feist 1975; Berger 1977; Miller 1981; Goodloe et al. 2000; Cameron et al. 2001; Scorolli and Lopez Cazorla 2010a). It was characterised by well-defined breeding groups (harems), which involved the majority of the population, with unattached sub-adult and adult males often forming bachelor groups. The overall size and age composition of harems remained stable during the study period and were consistent with patterns reported for other large mammalian herbivores (Gaillard et al. 2000a). The average number of adult females in harems in the current study was similar to that reported for the feral horse population in Argentina (Scorolli and Lopez Cazorla 2010a), where adult females were defined as ≥ 3 years of age, and populations in North America (Goodloe et al. 2000; Roelle and Ransom 2009), and Australia (Berman 1991), where adult females were defined as ≥ 2 years of age.

The mean harem size in the TTSF was similar to that reported in Australia (Berman 1991; Dawson and Hone 2012) and outside Australia (Welsh 1975; Feist and McCullough 1976; Berger 1977). Slightly lower values were reported by Goodloe *et al*. (2000) and Ransom (2009), and markedly higher values were reported by Keiper (1976) and Rubenstein (1981).

Harem size is usually influenced by high population densities or environmental conditions, which limit forage availability. The mean harem size in central Australia showed seasonal variation reducing from 6.6 horses in autumn to 4.3 horses in spring because the reduction in pasture biomass over the winter meant that stallions lost body condition and could no longer defend their mares and therefore maintain harem stability (Berman 1991). The lower mean values reported for Pryor Mountain and Little Book Cliffs populations can be ascribed to closed canopy habitats that were characterised by dense vegetation; such habitats are associated with a reduced risk of predation but conversely are associated with low forage availability (Ransom 2009). In contrast, the population occupying the open steppe of McCullough Peaks, where the risk of predation was higher, formed larger harems (Ransom 2009).

In general, multiple stallion harems are found in feral horse populations that have not undergone forced removal of male horses (Berger 1986; Scorolli and Lopez Cazorla 2010a), or in populations in which fertility was not artificially controlled (Goodloe et al. 2000). In the TTSF, the majority of harems had one stallion only who maintained and defended his group members throughout the entire study period, and on average, 11.1% of harems contained two stallions. These values are similar to that determined by Nelson (1978); Berger (1986); Berman (1991) and Goodloe *et al*. (2000). Studies of short duration or involving a small sample size may sometimes underestimate the number of multiple stallion harems due to inconsistent detection (Linklater et al. 2001). Populations that are biased towards males are associated with an increase in the number of harems with co-dominant stallions (Kirkpatrick and Turner 1986) whereas a gradual increase in population density increases stallion competition for females (Scorolli and Lopez Cazorla 2010a). Over-reporting of stallion numbers may occur when sub-adult males are mistaken for stallions (Garrott 1991b; Roelle et al. 2010).

The mean of the bachelor group size was similar to that observed in feral horse populations elsewhere (Welsh 1973; Feist and McCullough 1976; Rubenstein 1981; Berman 1991; Linklater 2000a). Bachelor group size and membership fluctuated in the current study and the majority of these associations were temporary ranging from one day to four weeks, with one lasting eight months. Relationships of longer and shorter duration have been reported in other studies (Miller 1979; Linklater 2000b; Roelle et al. 2010) suggesting that the difference in the bachelor group permanency is a characteristic of feral horse populations.

Of the 22 offspring that dispersed their natal harems, six males and three females were followed for variable periods of time from several months (n = 5) to 1.5 years (n = 4). The males joined existing bachelor groups whereas the females were acquired by a bachelor and formed a harem. The fate of 13 horses that dispersed from their natal harem is unknown; but it can be presumed that the majority of horses emigrated from their natal home range after dispersal. Emigration of dispersed offspring is a common feature in feral horses and is a natural response to increasing (or already high) horse densities in their natal home range (Berger 1986; Kaseda et al. 1997). Emigration of young males is often influenced by there being less males elsewhere (Kaseda et al. 1997). In the TTSF, the horse density in the study area was estimated in 2012 as being twice that (2.9 horses/km^2) of the remaining plantation area.

Previous studies have shown that a majority of horses leave their natal harem at 2 - 3 years of age (Kirkpatrick and Turner 1986; Goodloe et al. 2000; Scorolli 2007; Roelle et al. 2010), and rarely at one, or four, or five years of age (Roelle et al. 2010). This was the case in the current study with dispersal occurring predominantly between 2 - 3 years of age. A small number of yearlings and three year old horses were observed to disperse over the study period with the average age of dispersal being two years of age. The majority of dispersed horses left their natal harems between August and December, which correlated with the onset of the foaling season. Apparently, the birth of a sibling weakens the bond between the dam and the previous sibling, which results in the older sibling leaving the natal group (Kaseda et al. 1997; Linklater 1998; Cameron et al. 2001).

The adult sex ratio was similar to that found in other unmanaged feral horse populations. A comparable relationship, but slightly skewed towards females, was reported in the studies of Berger (1986) and Greger and Romney (1999) in the USA, and in New Zealand of Cameron et al. (2001); despite differences between studies in the age at which female horses were classified as adults (two years and one year of age for the USA and NZ studies respectively). A markedly higher female to male ratio was reported by Garrott and Taylor (1990), which was due to lower male survival rates and managed removal of stallions. The preponderance of adult males noted by Goodloe et al. (2000) was due to disproportionately high number of bachelors in the population. Although the author does not provide an explanation for the skewed adult sex ratio, the restricted area in which the population was contained prevented emigration of males. Emigration is a characteristic feature of large ungulate populations unrestricted by area (Berger 1986; Kaseda et al. 1997). The most likely reason for the equal adult sex ratio in the TTSF feral horse population was that the population was unmanaged and therefore no artificial manipulation of the sex ratio had occurred. An equal sex ratio also suggests identical survivorship in adult female and male horses.

The inclusion of an additional 51 (32.5%) foals may have influenced the results presented here for the sex ratio of the TTSF population but their gender could not be determined. Annual changes in the proportion of male and female foals entering the population have been reported (Garrott 1991a; Cameron et al. 1999; Roelle et al. 2010); however over the long term, foal sex ratio does not differ from parity in unmanaged feral horse populations (Feist 1975; Berman 1991; Garrott 1991a; Roelle et al. 2010). A comprehensive study in the USA involving 10,000 foals assessed foal sex ratios and observed a consistent sex ratio of 1:1 in 65 out of 74 populations (Garrott 1991a).

The age distribution of the TTSF feral horse population was stable across the entire study period and within all years and this is in accord with previous reports of unmanaged feral horse populations (Welsh 1973; Rubenstein 1981; Garrott and Taylor 1990; Cameron et al. 2001).The adult group was the largest; the foal group was similar to that reported by others (Welsh 1973; Wolfe 1980; Salter and Hudson 1982a; Rogers 1991; Cameron et al. 2001), and the yearling and sub-adult numbers were slightly lower than those reported in other studies (Feist and McCullough 1976; Salter and Hudson 1982a; Garrott 1991b).

The differences in age ratios between the various studies would appear to be a function of definition. In the current study, adult horses were defined as being ≥3 years of age, which is in agreement with Salter and Hudson (1982). However, several investigators defined adult horses as being older than five years (Garrott and Taylor 1990; Cameron et al. 2001), while others defined adults as being older than one year (Linklater 2000a; Roelle et al. 2010), or two years (Berman 1991). Despite these differences in definition, usually 50 – 66% of an unmanaged feral horse population are adults (Welsh 1973; Feist and McCullough 1976; Garrott and Taylor 1990; Berman 1991; Cameron et al. 2001). A preponderance of adults in long-lived large herbivore populations has been attributed to moderate to high fecundity and high survival (Gaillard et al. 2000a; Grange et al. 2009). As the fecundity of the TTSF population was low (23%) and survival was high (95%), it can be concluded that long term survival was most likely responsible for the preponderance of adult horses in the studied population.

Methods used to age horses are subjective unless birth dates are known (Garrott 1991b). When feral horses in a population are regularly captured and aged using a standardised dental examination, the age distribution of the population can be accurately ascertained (Berman 1991; Garrott 1991b; Baker and Easley 1999). As the age distribution of the TTSF feral horses was based on the individual identification of 522 horses, and was similar to that of other published studies, there is no reason to believe that the method used to allocate horse age was significantly biased.

In The TTSF, social stability of studied harems was variable. In some harems (49%) the adult composition remained unchanged over the two years of the study, in others (51%), it changed sometimes several times. The percentage of adult females that changed harems annually was higher than that reported by Scorolli and Lopez (2010b), but comparable to Goodloe *et al*. (2000), and Franke-Stephens (1990). Harem instability may have negative effects on the reproductive success of feral horse populations (Franke Stevens 1990; Kaseda et al. 1995; Cameron et al. 1999). It has been shown that mares that changed harems or those which were taken over by a new stallion had lower probability of foaling than mares that did not (Berger 1983; Kaseda et al. 1995; Goodloe et al. 2000).

Pregnancy and presence of foals were reported to be vital to harem stability, and non-pregnant mares were more likely to be transient harem members (Nuñez et al. 2009). Female membership changes were tested against foaling events in the TTSF population and contrary to previous reports the results did not show any relationship between these two variables with the number of foals produced by transient females being not significantly different to the number of foals produced by loyal females. Perhaps in the current study, sample size was too small and the duration too short as those studies demonstrating negative correlation between transiency and pregnancy were of considerably longer duration (Berger 1983; Kaseda et al. 1995; Goodloe et al. 2000).

It has been postulated that harem stability may also be influenced by the size of harems and/or number of stallions maintaining them (Franke Stevens 1990). Generally, it is thought that harem stallions find it more difficult to maintain a larger number of females; therefore, larger harems would experience higher transiency (Franke Stevens 1990; Berman 1991). In the current study, the mean size of harems of loyal females was slightly higher than that of transient females but the difference was not significant. In Franke-Stevens (1990) study of a similar duration, harem size did not have an effect on loyalty of adult females. This suggests that there may be other factors influencing the movement of females, or the studies were not of sufficient length to adequately identify time-related effects.

Body condition score also did not appear to influence whether a mare was loyal or transient. On average, transient females had lower body condition scores than loyal females but this difference, although consistent in both years of the study, was not statistically significant. Berman (1991) found that harem stallions with lower body condition lost more mares than harem stallions in better condition. The author suggested that a decrease in pasture volume and quality was responsible for the loss of body condition of stallions and this in turn reduced their ability to manage larger harems. In the current study, stallion BCS was usually good and this may have contributed to the high level of harem stability.

Harem stability may be also influenced by availability and quality of forage (Franke Stevens 1990). Sparsely located pasture requires longer foraging time, which often leads to increased distances between harem members, thereby increasing the risk of disjoining (Franke Stevens 1990). The lower frequency of behavioural interactions may reduce group cohesion (Nelson 1978; Duncan 1980; Berger 1986; Franke Stevens 1990). Pasture quality, quantity and availability were not directly addressed in the current study but observational evidence suggested that feral horses in the TTSF were subjected to nutritional stress. The forest is situated on sandy and phosphorous-deficient soils of low fertility (Baynes 2004), and appears to be scarce in good quality food sources for large herbivores. The main three species of grasses found in the TTSF are of low nutritional value (Karue 1975; Falvey 1981; DERM 2011).

The role of population density in the social stability of feral horses remains unclear. Franke-Stephens (1990) reported high level of social instability in a very dense population of 35 horses/km^2. In contrast, Duncan (1992) and Feh (1999) reported very high social stability despite high population densities (31 horses/km^2). Scorolli and Lopez Cazorla (2010b) found no significant relationship between social instability and high population density. Interestingly, a geographically confined population of much lower density showed elevated social instability (Goodloe et al. 2000). The average horse density within the TTSF study area of 2.9 horses/km^2 was considerably lower than that reported in most other studies, suggesting that population density alone is not the only factor influencing harem instability.

3.5. CONCLUSION

Detailed demographic studies of large, wild herbivores enable ecologists and managers to assess the character of specific populations and develop long-term management plans, which is not always possible if using data interpolated from other studies. The current study provided a detailed characterisation of the social organisation and population structure of feral horses in the TTSF. Although environmentally and ecologically different, the social structure, gender ratio, age distribution and social stability of the TTSF feral horse population were very similar to unmanaged feral horse populations found in Australia and elsewhere.

CHAPTER 4: POPULATION DYNAMICS

4.1. INTRODUCTION

The dynamics of large herbivore populations are shaped by seasonality, which contributes to variability in the availability of food and water, and shelter (Gaillard et al. 2000a). Seasonal breeders adjust their reproductive activity to the most favourable conditions thereby maximising survival of their offspring (Gaillard et al. 2000a; Grange et al. 2009). Prolonged and unfavourable conditions may limit the availability of nutrients causing increased competition for resources (Gaillard et al. 1998). As a result, females lose body condition, which in turn decreases offspring survival and female fertility (Nuñez et al. 2010). Puberty may be delayed and, in severe circumstances, female reproductive cyclic activity may cease, and increased adult mortality may occur (Gaillard et al. 2000a). Depending on population size, density-dependent resource limitations may negatively impact on survival and population growth (Gaillard et al. 2000a). Other factors influencing survival are disease, parasite infestations, and predator activity (Begon et al. 1990; Saether et al. 2001).

Long-term observational studies performed on herbivore populations can offer an insight into the population’s vital rates and their variability (Lebreton et al. 1992). Studies, which are shorter in duration, or are performed at one point in time, have their shortcomings as the annual variability in demographics may not always be detected (Dawson and Hone 2012). Monitoring programs, which aim to estimate population growth rates, must be designed with an adequate sampling frequency so that sampling is representative and identifies years with coincidently low or high recruitment (Cameron et al. 2001). The inclusion of age ordered data allows for a satisfactory estimation of vital rates by applying age structured population models (Lande 1988; Gaillard et al. 1998). Studies that estimate survival parameters of individually identifiable animals by accounting for differences in their detection probability are of the highest quality (Gaillard et al. 2000a).

To establish the relationship between age specific survival, fecundity and the rate of population increase, the elasticity analysis can be used (Gaillard et al. 1998). The measure of elasticity can identify changes in vital rates due to natural changes in the environment or these imposed by management. Quantifying the effects of changes in survival and reproduction assists in selecting that part of the population to target when considering population management (Lande 1988). In large herbivores, elasticity analysis has demonstrated that adult survival has significantly greater influence on population growth than does juvenile survival, and population growth is moderately sensitive to changes in fecundity (Gaillard et al. 2000a).

While feral horse population dynamics have been studied in a range of environments outside Australia (Garrott et al. 1991b; Goodloe et al. 2000; Linklater et al. 2004; Scorolli and Lopez Cazorla 2010a), most Australian studies have focused on social organisation, estimating population abundance and assessing environmental and economic impacts (Hoffmann 1983; Dyring 1990; Walter and Hone 2003; Schott 2004; Dawson et al. 2006; Lundie-Jenkins et al. 2006; Nimmo and Miller 2007; Vernes et al. 2009). Little is known about population dynamics with regards to reproductive performance (fecundity), mortality and the rate of population change.

There are only two Australian studies describing these parameters; one in a semi-arid environment (Berman 1991), the other in a subalpine environment (Dawson and Hone 2012). As the TTSF is located in the sub-tropical zone and is a highly managed ecosystem, it is very different to those ecosystems occupied by feral horses elsewhere in Australia (Dyring 1990; Berman 1991; English 2001; Walter 2002).

Understanding population dynamics of introduced species is crucial for the development of management strategies in Australia. Feral horses are highly invasive, often with substantial deleterious environmental effects, particularly on fragile native ecosystems (Dyring 1990; Schott 2004; Nimmo and Miller 2007; Dawson and Hone 2012), economy (Dobbie et al. 1993; Dawson et al. 2006), and human safety (Crittle and Jackson 2004). The population dynamics of the TTSF feral horses have not been fully elucidated. Therefore, the study was designed to characterise the major vital parameters of this population, and, using these data, develop a long term management plan for the control of the population.

AIMS AND OBJECTIVES

The aim of the present study was to develop an understanding of the major vital parameters of the TTSF feral horse population so that strategies could be developed to manage population size and growth. The primary objectives were to characterise fecundity and age specific survival, which enabled the annual rate of population growth to be determined. Data were subjected to elasticity analysis, which assessed the sensitivity of the rate of population increase to changes in survival and fecundity to determine how elements of the population contributed to population growth. Outcomes were compared with other unmanaged feral horse populations in Australia and elsewhere to test whether the unique TTSF habitat imposed demographic differences

HYPOTHESES

1. Survival will show discrepancy between the age groups and will be lowest in foals and highest in adults;
2. The population reproduction rate is higher than the mortality rate, and contributes positively to the increase in population size, and
3. Population increases slowly at a rate of 1.03 – 1.09 per year.

4.2. METHODS

Population dynamics of feral horses in the TTSF were studied over two and half years from September 2011 to March 2014, using a mark-recapture technique of individually identified horses (Pollock 1982). Since feral horses have been defined as seasonal breeders (Caughley 1977), the study involved three foaling seasons. The study area was surveyed monthly, giving a total of 29 ‘marking events’ and 522 sighting histories of individual horses. Survey design and dates are summarised in **Tables 2.1 – 2.2**. Horses were observed until identification was unequivocal, based on body colour, head and leg markings, gender and group associations (Roelle et al. 2010). Approximation of age (F - foal, Y - yearling, SA – sub-adult, and A - adult) was also determined visually. Identification of foals was additionally based on observing an attachment of a foal to its dam, and suckling behaviour. Gestational status of mares was assessed visually and repeated observations identified pregnancy and approximate foaling dates.

Body condition was assessed visually on the basis of body fat distribution and was evaluated at the end of each season from spring 2011 to winter 2013 for each of the four age cohorts and both sexes. Body condition score (BCS) was assessed only of individuals that were observed within 100 meters and with the aid of 10 - 22x binoculars (Nikon Corporation, Tokyo, Japan). BCS assesses body fat deposition of the neck, back and rump using a five points scale (Carroll and Huntington 1988; Rudman and Keiper 1991), but may incorporate a 0.5 point scale to allow more precise estimation (Cameron and Linklater 2000). Horses with a BCS ≤ 2.0 were considered to be in a poor condition, between 2 - 2.5 in a moderate condition, and those with BCS ≥ 3.0 were considered to be in good condition (**Table 4.1**).

BCS	Description
Very poor (0)	Deep cavity under tail and either side of croup, very visible and angular point of pelvis, skin tight over ribs, marked ‘ewe’ neck, and narrow at the base of neck
Poor (1)	Sunken rump cavity; pelvis, croup and spine well defined, easily visible ribs, skin sunken either side of backbone, ewe neck, and narrow at the base of neck
Moderate (2)	Rump flat on either side of backbone, croup well defined with slight cavity under the tail, pelvis slightly pointed, ribs just visible, and narrow but firm neck
Good (3)	Rounded hips, no visible ‘gutter’, spine and ribs just covered, crested neck in stallions
Fat (4)	Visible ‘gutter’ along the backbone, pelvis and ribs well covered, and wide and slightly crested neck
Very fat (5)	Deep ‘gutter’, pelvis and ribs buried in fat tissue, back broad and fat, and very wide neck with marked crest

Table 4.1: Rubric used to allocate body condition scores to horses in the TTSF. Adapted from Carroll and Huntington (1988), and Rudman and Keiper (1991).

4.2.1. DATA ANALYSES

Analyses were conducted on the basis of a biological year, which begins 1st August and ends 31st July of the following year. The beginning of the biological year corresponds to the beginning of the foaling season. Demographic data of survival and reproduction were recorded as binary variables: ‘0’ for ‘not sighted’ and ‘1’ for ‘sighted’, or ‘0’ for ‘no foal’ and ‘1’ for ‘presence of foal’.

4.2.1.1. ESTIMATION OF FECUNDITY AND SURVIVAL

Annual foaling rate was calculated by recording number of foals born divided by number of adult females observed in a given year. For the purpose of population analysis, reproductive performance of animal populations is characterised by measuring fecundity rate, which in population ecology studies is defined as the number of female offspring born to each female per year (Caughley and Sinclair 1994; Caswell 2001; Bradshaw and McMahon 2008). In the present study, annual fecundity rates were calculated from the observations of foaling rates to be one-half the foaling rate (Dawson and Hone 2012), and long-term studies measured an equal sex ratio at birth in unmanaged feral horse populations (Keiper and Houpt 1984; Garrott 1991a; Roelle et al. 2010). To test whether there were differences in the number of foals born in the three foaling seasons, the numbers of adult females with and without foals were compared with the Pearson contingency table in the statistical package R, ver.3.0.1 (R, Developmental Core Team, 2012).

The age-specific survival (S_i) and recapture (p) probabilities were estimated with the *Multi-State* model (Lebreton et al. 1992) within the program MARK, ver. 2.1 (White and Burnham 1999). The recapture data within each primary sampling period were pooled (each animal was observed at least once in the primary period). This approach allowed increased precision of estimates (Pollock 1982).

Age based models were parameterised to obtain separate survival estimates for four age cohorts: (1) foal, (2) yearling, (3) sub-adult, (4) adult. It is biologically impossible for horses to grow through more than one age cohort per year hence, the *Multi-State* capture-recapture model allowed only transition to the next age cohort in the following year. This method reduced the estimated number of parameters in the model, so that the parameters were estimated with higher precision (Blomberg and Shine 2001). Not all animals were recaptured on every survey. The *Multi-State* model included capture probability and accounted for the unknown transitions that might have occurred while the animal was not observed (Caswell 2001). All horses were assumed to make the transition to the next age cohort at the same time (August), which corresponded with the beginning of the foaling season.

Survival was modelled as either variant over time or constant over time during the primary sampling sessions, and was modelled as variant over time across the four age cohorts. This assumption was based on the fact that mortality in younger age cohorts is higher than in older age cohorts (Bekoff 1977; Gaillard et al. 2000a). Annual recapture probabilities were modelled as either constant over time or as a monthly fluctuation, and transition (ψ) probabilities were set as constant over time, because transition from one age cohort to the next occurred only once in a year.

The fit of models was estimated by the use of chi-square goodness-of-fit tests, and model selection was conducted by examination of Akaike Information Criterion, or AIC (Lebreton et al. 1992; Wagenmakers and Farrell 2004). Models were first ranked by AIC differences (AIC_c). Relative likelihood of each model was then estimated using AIC_c weight, with higher weight (rank) for better models (Lebreton et al. 1992; Burnham and Anderson 1998). Results of annual age specific survival with SEM and 95% confidence intervals (CI) were taken directly from the MARK 2.1 output (White and Burnham 1999).

The goodness of fit (GOF) of the most general model ($S_{cohort*time}$, $p_{cohort* time}$, ψ_{cohort}) was analysed in order to quantify the amount of over-dispersion (a possible source of lack of fit) in the data. The lack of fit in the obtained data could be a result of structural variation not explained by the data, or correlation in capture histories of animals (Anderson et al. 1994). The bootstrapped GOF test of the highest ranked model was performed by simulating (100 times) capture histories for each individual in the original sample and fitted against the most general model in the model set to the simulated data in MARK. The number of simulations was chosen on the base of observed deviance distribution in a simulated analysis (Cooch and White 2002). The over-dispersion coefficient (c-hat) was obtained in two ways. The first approach ($c\text{-}hat_1$) divided the deviance estimate from the original data set by the mean of the simulated deviances in the bootstrapped analyses. The second approach ($c\text{-}hat_2$) divided the observed c-hat value from the original data by the mean of the simulated c-hat values from the bootstraps. In order to adequately calculate c-hat for the chosen model, both methods were applied (Cooch and White 2002). In general terms, if c-hat equals 1, it indicates that the fit of the model to the data is effectively perfect; if c-hat is less than 3, the model is assumed to be structurally adequate, and when c-hat is greater than 3, the model is considered to have insufficient structure to be used for parameter estimation (Cooch and White 2002).

4.2.1.2. ESTIMATION OF POPULATION GROWTH

Population growth was estimated by a deterministic model constructed for the female component of the population using a Leslie age-structured projection matrix (Leslie 1945). As horses reproduce seasonally, the birth-pulse model parametrisation was applied (Caswell 2001), with a four age cohorts matrix model: foals (≤ 1 year old), yearlings (1>2 years old), sub-adults (2>3 years old), and adults (≥3 years old, **Figure 4.1**). Each cohort was assigned age-specific survival (S_i) and age specific fecundity (F_i), as survival and fecundity were expected to change with the age of horses (Seal and Plotka 1983; Cameron et al. 2001). The fecundity rates for females younger than three years of age were assumed to be zero as the youngest females to produce foals were three years old (see results).

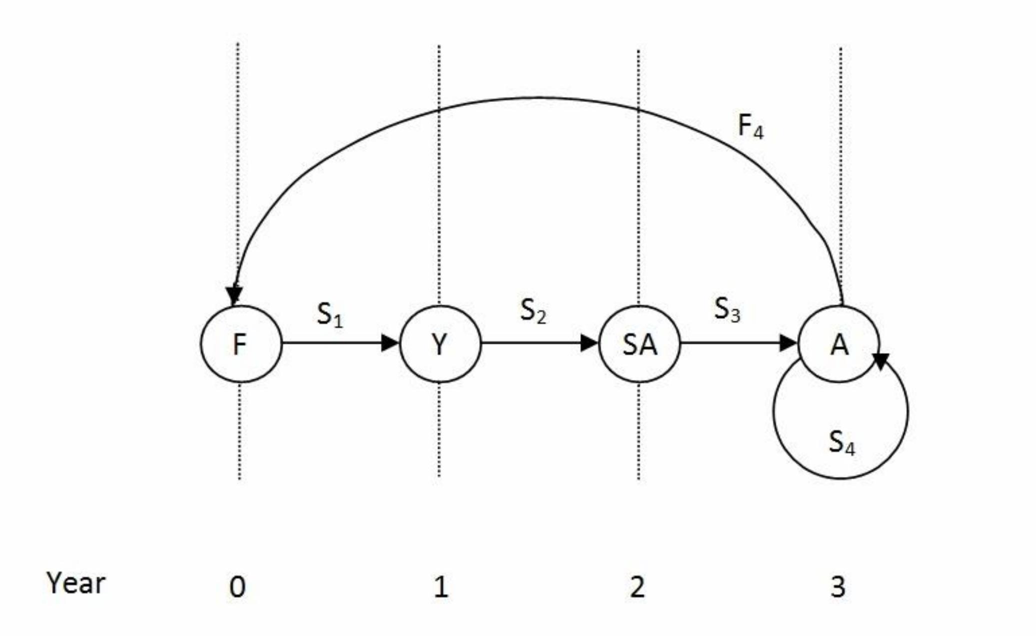

Figure 4.1: Graphic representation of a simplified life cycle of feral horses in the TTSF used for the Leslie matrix model. The age cohorts are represented by circles (F = foals, Y = yearlings, SA = sub-adults, and A = adults; the horizontal arrows between circles represent transition stages from one age to the next; annual survival probabilities: S_1 = foal survival during the first year of life; S_2 = yearling survival between first and second year of life; S_3 = sub-adult survival between second and third year of life; S_4 = adult survival over a third year of age, and F_4 = annual fecundity of adult females. The diagram indicates that only the last age cohort was capable of reproduction (adapted from Gaillard *et al.* 2000).

The annual finite rate (λ) of population increase was determined by estimating age specific fecundity, survivorship and animal abundance coefficients for each age class at time t. The number of individuals in each age class at time $t+1$ was estimated by implicit delineation (Leslie 1945), where F_i were per capita fecundity rates in each age class; S_i was survival probability of an individual in age class t surviving to age class $t+1$; $n_i(t)$ was the number of individuals in each age class at time t, and $n_i(t+1)$ was the number of individuals in each age class at time $t+1$. The four age-stages matrix form ($n_{t+1} = Mn_t$) is presented as ***Eq. 1***:

$$\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{bmatrix} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ S_1 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 \\ 0 & 0 & S_3 & S_4 \end{bmatrix} \begin{bmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{bmatrix}$$ ***Eq. 1***

When the population reaches a stable age distribution, i.e. the ability to maintain the same age allocation over a prolonged time, it will grow exponentially with the intrinsic growth rate (r), being expressed by $r = ln\ (\lambda)$, or equally $\lambda = e^r$ (Caughley 1977; Skalski et al. 2005), where lambda is a multiplier denoting the size of the population one year after the current time (Eberhardt et al. 1982). The exponential growth model for a population increasing over time is described with values of $\lambda > 1.0$. In contrast, a population that is decreasing in size over time will have values of $\lambda < 1.0$, and a stationery population that exhibits no change in size over time will have $\lambda = 1.0$ (Eberhardt 1987).

In order to predict the results of future changes in the population growth rate ($\partial\lambda$) to changes in vital rates of survival and fecundity (∂a_{ij}), the sensitivity analysis (s) was determined using an eigenanalysis of the population projection matrix (Caswell 2001, ***Eq. 2*****)**.

$$s = \left(\frac{\partial\lambda}{\partial a_{ij}}\right) = \left(\frac{\overline{v_\iota}\ w_j}{w,v}\right)$$ ***Eq.2***

where $\overline{v_\iota}$ is the ith element of the reproductive value vector;
w_j the jth element of the stable stage distribution; and
w, v the eigenvectors for age-classified populations.

The finite (λ) and intrinsic (r) growth rate, as well as the results from the sensitivity analysis and expected age distribution values were taken directly from the R ver.3.0.1 (R 2012) output. To test whether the population had a stable age distribution, the comparison of observed and expected number of females in each age cohort was tested with the Pearson X^2 test.

The mean annual BCS for each age and sex cohort was calculated by a conditional logit model with BCS as the (ordered) response and year (2012 and 2013), sex (Ma = male; Fe = female); age class (F = foal; Y = yearling; SB = sub-adult; A = adult), and their interactions as fixed explanatory factors; this model was used to test annual differences in BCS between age and sex cohorts. The model allowed the analysis of ordinal data, which was necessary because BCS is a ‘rank’ categorical variable and the ‘distance’ between adjacent ranks is not meaningful. Analyses were conducted using the ‘ordinal’ package for R, ver.3.0.1 (R 2012). All parameter estimates are presented as mean ± SEM, with a significance level of $P = 0.05$.

4.3. RESULTS

4.3.1. FOALING RATE

Feral horses in the Tuan and Toolara State Forest showed well defined foaling season throughout the study. The majority of foals (n = 153) were born between August and April; two foals were born in June, and two in July. The observed annual foaling rates are presented in **Table 4.2**, but undetected pregnancies and neonatal deaths cannot be discounted, although likely to be small in number. The mean foaling rate for three breeding seasons was 0.46 ± 0.07 SD. Foaling rates increased gradually from 0.40 in 2012 to 0.54 in 2014, however the annual difference between mares with foals and mares without was not significantly different when analysed using the Pearson chi-square test ($\chi = 4.26$, df = 2, $P = 0.119$). The corresponding estimate of mean fecundity was 0.23 ± 0.07 SD.

Foaling season	Adult females (*n*)	Foals (*n*)	Foaling rate (foals : adult females)	Fecundity rate (half foals : adult females)
2012	115	46	0.40	0.20
2013	136	62	0.46	0.23
2014	90	49	0.54	0.27
Total	341	157	-	-
Mean ± SD	114	52	0.46 ± 0.07	0.23 ± 0.07

Table 4.2: Details on foaling season, number of recorded adult females and foals of both gender, and the estimate of foaling and fecundity rates, in the population of feral horses over the study period.

Some adult females were observed repeatedly throughout the study while others were observed variably within any one year or across the study period. Sixty seven mares were observed monthly, producing 104 foals over the three foaling seasons (0.52 foals per female per year) and accounting for 66.2% of all foals detected. Some females (7.5%; *n* = 5) did not give birth during the study period, 38.8% (*n* = 26) produced one foal; 44.8% (*n* = 30) two foals, and 9.0% (*n* = 6) three foals (**Figure 4.2**). Mares rarely gave birth in consecutive years. Two sub-adult females were identified as being pregnant based on increasing abdominal size but foaling was not observed.

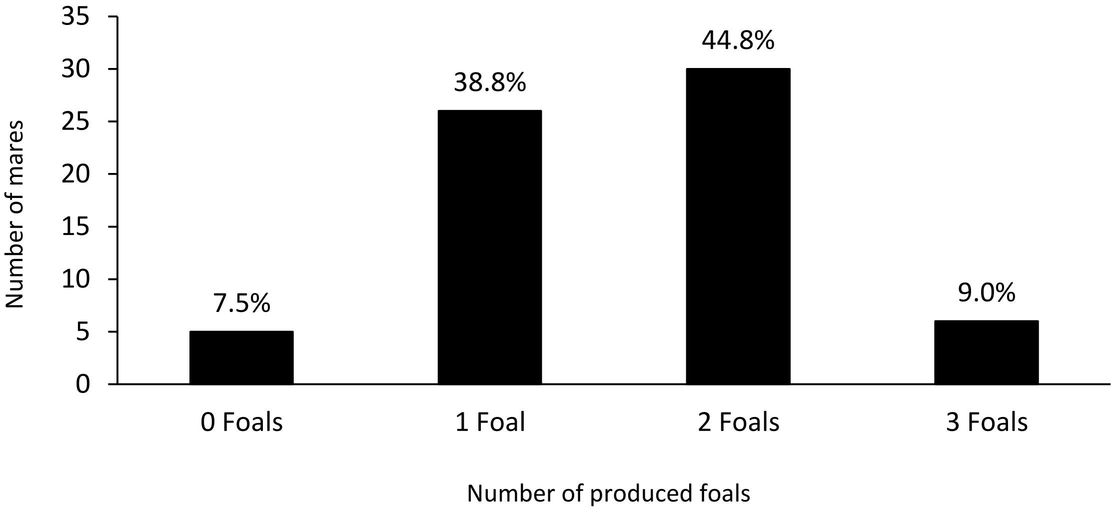

Figure 4.2: Foals born to the 67 mares that were identified each month over the duration of the study. The numbers illustrate how uncommon it was for a mare to foal in consecutive years.

4.3.2. SURVIVAL RATE

Results from the mark-recapture indicated that the model with constant survival and time varying recapture probabilities was supported most strongly (AIC_c w = 1.000) when compared with other models (**Table 4.3**). Calculations of the over-dispersion coefficient, estimated the value of c-hat_1 to be 1.077 and c-hat_2 to be 3.025 respectively, which indicated that the proposed model adequately fitted these data.

Age specific survival models	K	AIC_c	ΔAIC_c	AIC_c w
S_{cohort}, $p_{cohort*\ time}$, ψ_{cohort}	112	7452.534	0.000	1.000
$S_{cohort*time}$, $p_{cohort*\ time}$, ψ_{cohort}	11	376082.783	368630.249	0.000
S_{cohort}, p_{cohort}, ψ_{cohort}	101	376125.070	368672.536	0.000
$S_{cohort*time}$, p_{cohort}, ψ_{cohort}	179	376218.774	368766.239	0.000

Table 4.3: Models used to estimate age specific survival (S), recapture (p) and transition probabilities (ψ). Statistics for best-fit model are presented in descending order of the AIC_c. Subscript "t" gives time parameterisation to recapture parameters; "cohort" indicates age cohort parameterization, and K = number of estimable parameters.

Survival estimates were consistently high across all age cohorts (**Table 4.4**). Uniform survivorship was recorded in foal and yearling (0.95) cohorts and marginally lower in the adult (0.94) cohort. Survival of sub-adults (0.92) was slightly lower than adults but not different statistically as indicated by 95% confidence intervals (**Table 4.4**). These data did not allow for sex specific survival estimates as gender of 51 foals, 10 yearlings, 9 sub-adults, and 12 adults was not established.

Age cohort	S (95%CI)	SEM
Foal (S_1)	0.95 (0.92 – 0.96)	0.01
Yearling (S_2)	0.95 (0.92 – 0.96)	0.01
Sub-adult (S_3)	0.92 (0.88 – 0.94)	0.01
Adult (S_4)	0.94 (0.94 – 0.95)	0.00

Table 4.4: Annual survival (S) rates (95% CI and ± SEM) of horses in the four age cohorts during the study period.

4.3.3. POPULATION GROWTH

The Leslie population projection matrix revealed that the average annual finite rate of population increase (λ) in the TTSF was 1.088, with the corresponding exponential rate of increase (r) equal to 0.037. The comparison of observed and expected number of females in each age cohort indicated that the population was stable in its age distribution (χ^2 = 2.639, df = 3, P = 0.451).

The results of the sensitivity analysis indicated that adult survival had the greatest effect on the finite rate of population increase (**Figure 4.3**). Change in adult survival, (S_4 = 0.710), had approximately seven times more impact on finite population growth than the equivalent change in juvenile survival ($S_{1\text{-}3}$ = 0.111). Fecundity had a lesser impact on population growth than adult survival, but its impact was four times higher (F_4 = 0.457) than that of survival in the first three years of life.

$$s = \begin{bmatrix} 0.000 & 0.000 & 0.000 & \mathrm{F4} \\ \mathrm{S1} & 0.000 & 0.000 & 0.000 \\ 0.000 & \mathrm{S2} & 0.000 & 0.000 \\ 0.000 & 0.000 & \mathrm{S3} & \mathrm{S4} \end{bmatrix} = \begin{bmatrix} 0.000 & 0.000 & 0.000 & 0.457 \\ 0.111 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.111 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.111 & 0.710 \end{bmatrix}$$

Figure 4.3: Demographic sensitivities that defined the feral horse population in the TTSF in 2012-2014. $S_{1\text{-}3}$ – age specific survival of juveniles; S_4 - survival of adults, and F_4 - adult female fecundity.

The estimated population age structure (**Table 3.6**, Chapter 3); age-specific survival (S_i = 0.92 – 0.95; **Table 4.4**); mean fecundity rate (F_i = 0.23; **Table 4.2**); finite rate of change (λ = 1.088), and the estimated population size (n = 1321; **Table 5.7**, Chapter 5) were used to model population growth from 2012 – 2026. Given the constancy of the estimated parameters over the next 15 years, the Leslie matrix model projected that the population would double in size within 9.21 years (**Figure 4.4**).

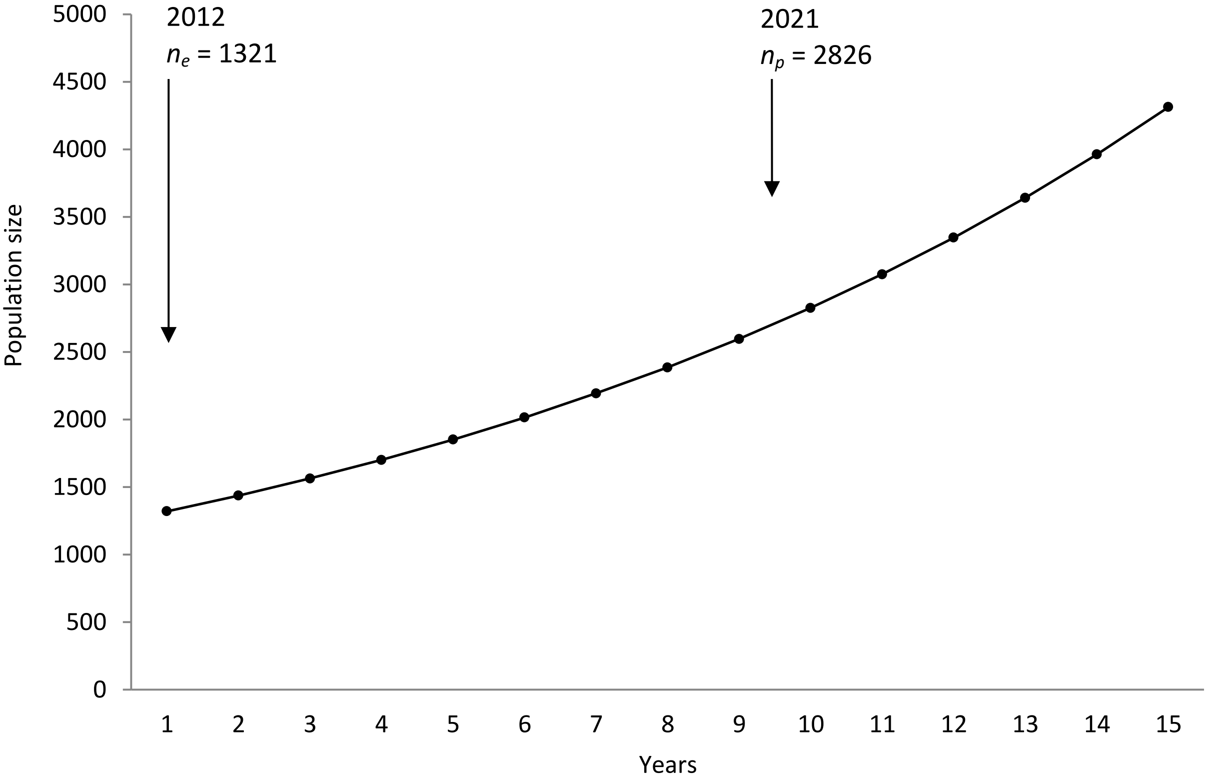

Figure 4.4: Projected population size of feral horses in the TTSF over 15 years using the Leslie age-structured matrix simulation model. n_e – estimated population size in 2012, and n_p –projected population size in 2021.

4.3.4. BODY CONDITION

The number of horses, their age, sex, and annual mean BCS are presented in **Table 4.5**. Body condition scores varied insignificantly between horses in different age cohorts within each year of the study ($\chi^2 = 6.235$, df = 3, P = 0.100). All age cohorts obtained a slightly higher BCS in the second year of the study, but the difference between the two years was not significant ($\chi^2 = 0.024$, df = 1, P = 0.876). An evaluation of the mean annual BCS specifically for adult male and female horses indicated a significant difference between the two in both years ($\chi^2 = 113.11$, df = 1, $P < 0.001$).

Cohort	2012		2013	
	(*n*)	BCS ± SD	(*n*)	BCS ± SD
Foal	(24)	2.38 ± 0.44	(29)	2.48 ± 0.43
Yearling	(17)	2.29 ± 0.49	(27)	2.57 ± 0.47
Sub-adult	(21)	2.67 ± 0.41	(29)	2.60 ± 0.38
Adult Female	(99)	2.08 ± 0.60	(101)	2.18 ± 0.60
Adult Male	(62)	2.84 ± 0.47	(88)	2.98 ± 0.47

Table 4.5: Comparisons of the annual mean (± SD) body condition score (BCS) of four age cohorts and two gender groups of feral horses in the TTSF in 2012 - 2013. *n* – Number of individuals.

Data for cohorts less than 3 years of age was pooled for both sexes, as gender of 12 foals, 7 yearlings, and 10 sub-adults was not established, and the number of assessed horses in these age cohorts was insufficient after elimination of the unknown sexes from the analysis. Because of the differences in energy expenditure and demands of adult female and male horses (Cameron et al. 2001), and an adequate sample size, the adult cohort was analysed separately for each gender.

The body condition score of adult horses varied seasonally, however the trend was not uniform. Adult males maintained higher body condition scores than females throughout the entire study period (**Figure 4.5**). The lowest BCS in males was recorded from autumn to spring 2012 and in females from spring 2012 to summer 2013.

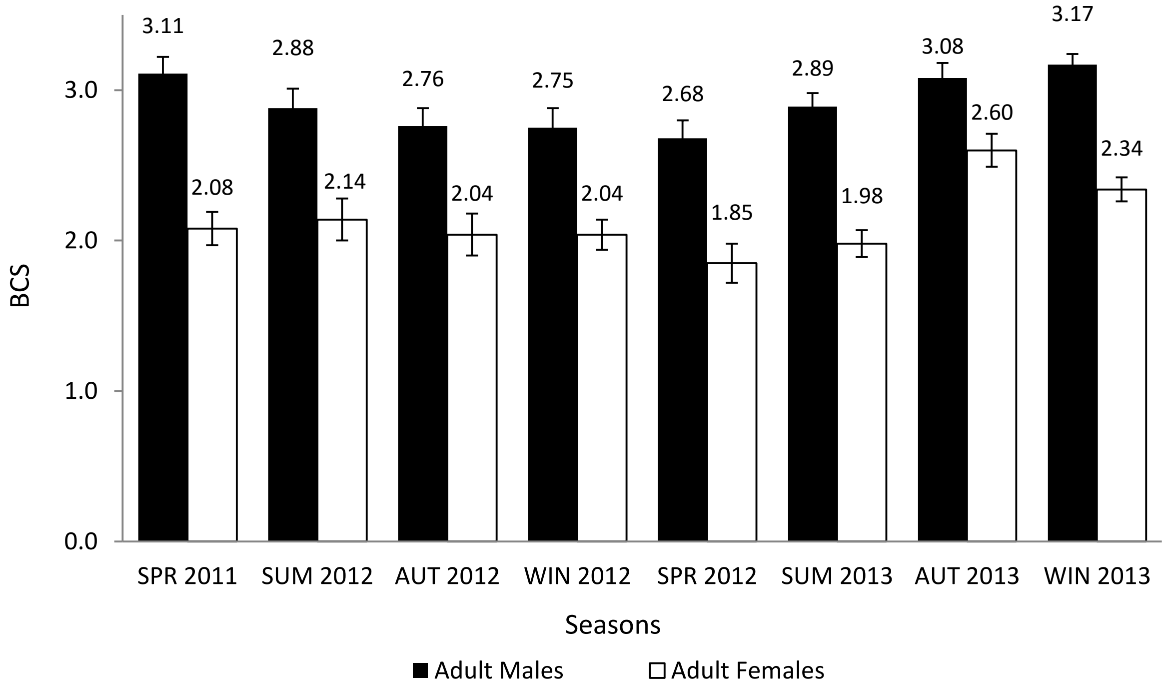

Figure 4.5: The mean (± SEM) seasonal body condition scores (BCS) of adult male and female horses in the TTSF between spring 2011 and winter 2013.

The distribution of BCS of adult male and female horses in 2012 and 2013 is presented in **Figure 4.6**. The majority of adult males (66.1% in 2012; 81.8% in 2013) maintained BCS of ≥ 3.0, and four horses had BCS of 4.0. There were no observed stallions with body condition scores above 4.0. The majority of adult females (58.6% in 2012; 55.5% in 2013) attained moderate body condition scores, but a sizeable number (27.3% in 2012; 23.7% in 2013) had a BCS of less than 2.0. The lowest BCS of 0.5 was recorded in two (2.0%) mares in 2012. In the following year, one of these females died and the other increased her BCS to 1.0.

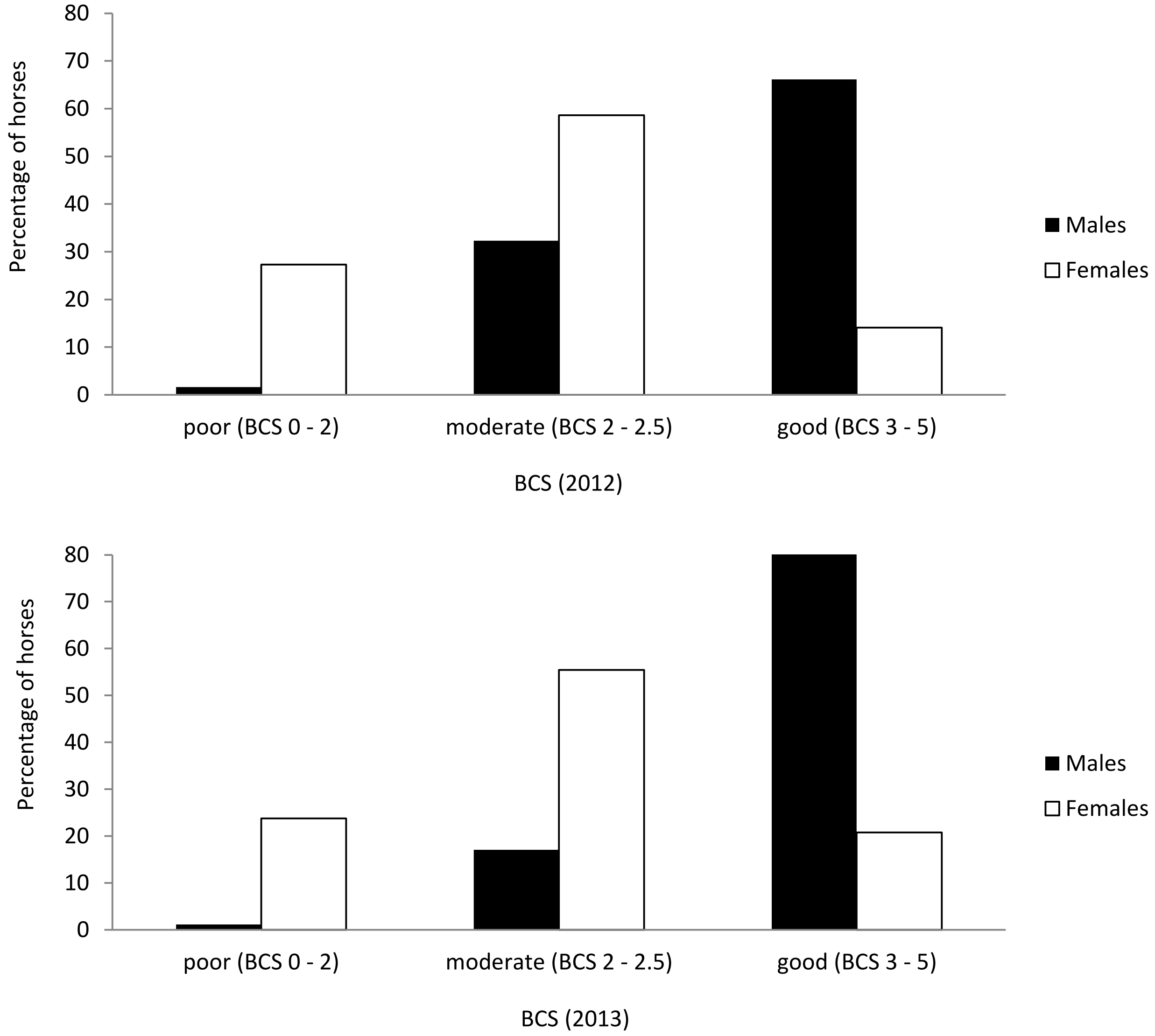

Figure 4.6: Distribution of body condition scores in adult horses over the study period.

4.4. DISCUSSION

The population dynamics of feral horses in the TTSF were consistent with those previously published for large terrestrial herbivores (Gaillard et al. 2000a; Dawson and Hone 2012). The observed mean annual fecundity was low (0.23), adult survivorship was high (0.94), and annual finite population growth rate was 1.09, which was less than the maximum growth rate values (1.18 – 1.25) reported for populations living in favourable conditions in Northern America (Eberhardt et al. 1982; Garrott et al. 1991b); Europe (Duncan 1992; Grange et al. 2009), and Argentina (Scorolli and Lopez Cazorla 2010a).

Reproduction in the TTSF was seasonal and synchronised with the availability of vegetation most likely to maximise offspring survival (Festa-Bianchet 1988; Rosser 1989; Gaillard et al. 2000a). The majority of births occurred between August and April and was similar to that of other southern hemisphere feral horse populations (Berman 1991; Linklater et al. 2004; Scorolli and Lopez Cazorla 2010a).

The age of primiparous mares in the present study was three years. Mares less than three years of age were not observed to foal. This is consistent with the findings of Hall (1972); Feist and McCullough (1975); Boyd (1979); Perkins *et al*. (1979); and Keiper and Houpt (1984). In two studies, in which younger females were observed to be sexually active no foals were born the following year (Welsh 1975; Salter and Hudson 1982a). In the current study, two sub-adult females were visibly pregnant, but on subsequent inspections no dependent foals were observed and therefore suggestive of abortion or neonatal mortality.

The TTSF fecundity was at the lower end of the reported range for northern hemisphere populations (Keiper and Houpt 1984; Berger 1986; Ganskopp and Vavra 1986; Garrott and Taylor 1990; Duncan 1992; Greger and Romney 1999; Goodloe et al. 2000), but comparable to values from the southern hemisphere, where populations were stressed by limited seasonal food supply (Berman 1991; Cameron and Linklater 2000; Walter 2002), or shortage of pasture secondary to high population density (Scorolli and Lopez Cazorla 2010).

There are two possible explanations for the low fecundity in the current study. Firstly, there may have been undetected neonatal mortalities. Accurate estimates of foaling rates require that all new born foals within a population are recorded (Greger and Romney 1999; Linklater et al. 2001). Despite regular sampling, not all horses were observed in each month. It has been shown that post-natal mortality is highest in the first two months of life (Welsh 1975; Boyd 1979; Berger 1986) and therefore monthly surveys may miss foal deaths occurring between surveys.

The second possibility relates to the low BCS of many of the females. Adult females had significantly lower scores than adult males at all times of the year, but particularly during the breeding season. It appears that the high cost of pregnancy and lactation prevented mares from improving their body condition, thus the gender difference in BCS was due to reproductive demands (Rudman and Keiper 1991; Duncan 1992; Cameron *et al*. 2001).

Mares with dependent foals were invariably in poor condition (**Figure 4.7**) and seldom foaled in consecutive years. Low quality or poor availability of forage prior to the onset of the foaling season is known to considerably affect the weight and body condition of mares, which decreases fecundity (Garrott and Taylor 1990; Duncan 1992; Dawson and Hone 2012).

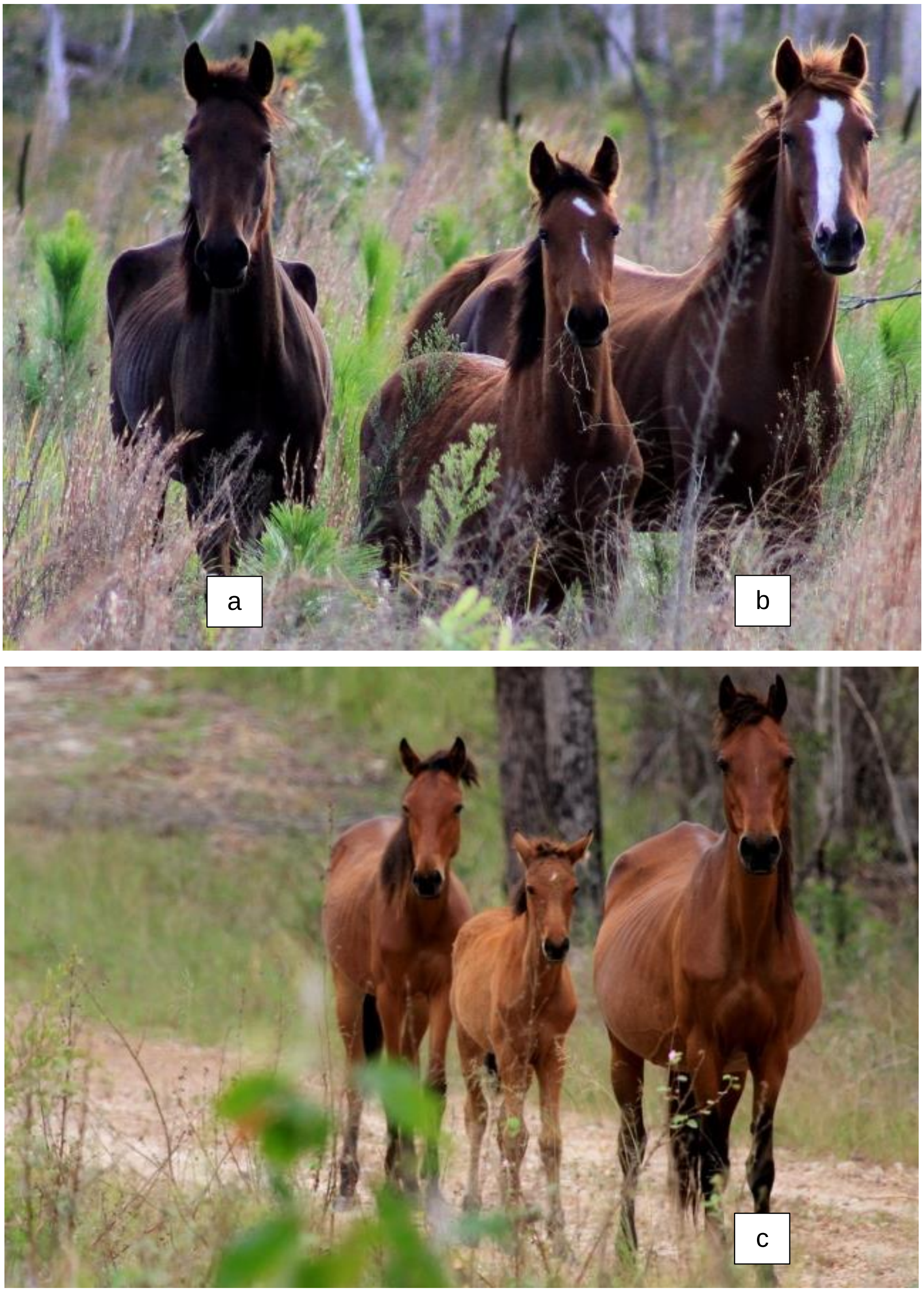

Figure 4.7: Both images clearly demonstrate the low body condition scores noted in many of the mares that were suckling foals. Both the chestnut mare (b) on the right in the top image and the bay mare (c) on the right in the bottom image were allocated body condition scores of 1.0. These mares foaled once during the study period. The brown mare (a) on the left in the top image was allocated body condition score of 0.5 and she did not foal during the study period.

The observed transiency of adult females between harems did not influence foaling rates, but other factors, such as the age of mares, might have contributed to the low foaling rates in the present study (Eberhardt et al. 1982; Linklater et al. 2004; Cameron et al. 2001). Older females are reported to have higher foaling rates and are more likely to foal in consecutive years (Cameron et al. 2001). Additionally, foals born to older mares are more likely to survive because older females put more effort into maintaining a close relationship with their neonatal offspring (Cameron et al. 2001). As the age spread of adult females was not assessed in the present study, the age span of mares was unknown.

Feral horses characteristically show high adult survival with low annual variation (Eberhardt et al. 1982; Duncan 1992; Cameron et al. 2001; Dawson and Hone 2012). Interestingly, annual survivorship of adults and juveniles in the TTSF was towards the high end of reported values (Berger 1986; Ganskopp and Vavra 1986; Turner et al. 1992). The exceptionally high survival rates of foals prior to weaning suggest high levels of maternal care, but at considerable cost to the dams which lost substantial weight throughout pregnancy and lactation. Although the mortality for all age cohorts was low and the population grew over the study period, the low body condition of suckling mares reduced fecundity, which in turn inhibited the rate at which the population grew. A similar relationship was observed in feral horses in Argentina where shortage of forage resulted in females foaling only when the environmental conditions were supportive, which reduced their fecundity but increased foal survival (Scorolli and Lopez Cazorla 2010). The absence of harsh winters, drought and predators in the TTSF may have also influenced foal survival (Berman 1991; Greger and Romney 1999; Crittle and Jackson 2004; Kaczensky et al. 2010)

This study did not test the differences in survival between the sexes as gender of all juvenile horses was not determined. However as the adult sex ratio was not significantly different from parity, it can be concluded that the survivorship of female and male horses was identical. As a result, equal sex ratio and survivorship of mares and stallions might have negatively contributed to the population’s growth rate, as not all stallions contributed to the population’s reproductive success (Linklater 2000b).

Annual average population growth rate in the TTSF increased comparably to other feral horse populations experiencing nutritional limitation or inhabiting limited spaces (Keiper and Houpt 1984; Goodloe et al. 2000; Cameron et al. 2001; Dawson and Hone 2012). The highest rates of population increase have been reported where food was abundant and disease and predation were minimal (Eberhardt et al*.* 1982; Garrott et al. 1991; Duncan 1992; Grange et al. 2009).

The availability of food and its quality are likely to be significant factors in the reduced fecundity, low body condition scores of adult females and low population growth in the TTSF. Forage quality and quantity were not assessed; however, it has been shown that the TTSF soils are poor in nutrients (Young and Dillewaard 1999; Baynes 2004; Dhont 2011). The mono-specific pine vegetation increases soil acidity and alters soil structure by preventing the recruitment of annual grass species, while dense stands of pine trees hinder the germination of grasses (Weber 2003; Dhont 2011). These factors, in conjunction with the grazing pressure imposed by space limitations, and by the slow but constant increase in population density, have created an environment where those members of the population with the greatest energy requirements are disadvantaged, in particular pregnant and lactating mares.

Animal populations that are limited by food availability and/or experience high population densities demonstrate low juvenile survival, followed by reduced fecundity, and in some instances reduced adult survival (Eberhardt 1977; Gaillard et al. 1998). If density-dependent processes existed in the current study, they had a considerable effect on female body condition and fecundity, but did not affect juvenile survival. Perhaps the observed emigration of horses to less densely occupied plantation areas prevented the focal-population from reaching its maximal carrying capacity, therefore density-dependent processes were only manifested by reduced female reproductive performance and not reduced survival. This is in agreement with Escos and Alados (1991), who found that the density of large herbivores had the greatest effect on population fecundity and not on survival of offspring, which was mainly affected by environmental limitations. Similar relationships to that found in the present study were observed in Argentina, where low fecundity of mares and high offspring survival were believed to be a result of the population approaching maximum carrying capacity (Scorolli and Lopez Cazorla 2010).

If the estimated demographic parameters remain constant, the TTSF population is projected to double in size in just over nine years. This would double the average animal density for the entire forest, which is currently estimated to be 1.79 horses/km^2. This in turn could further reduce the population’s vital rates, or stimulate the population to seek new resources and spread to other areas, or both.

Demographic analyses of large herbivores show that population growth rates are highly sensitive to changes in adult survival, moderately sensitive to changes in fecundity, and considerably less sensitive to changes in juvenile survival (Escos et al*.* 1994; Gaillard et al*.* 2000a; Dawson and Hone 2012). In the present study, adult survival was seven-fold higher than juvenile survival and nearly twice as high as the fecundity rate. The current reproductive success of females in the TTSF involves investment in carrying for their young but at the cost of lower fecundity. The cost of pregnancy and lactation prevents mares from foaling every year, which limits population growth. Survival in the non-adult age cohorts was similarly sensitive, which means that changing survival of foals, yearlings or sub-adults would have exactly the same impact on the overall population growth (Gaillard et al. 1998). Similar relationships were reported for three feral horse populations in the Australian Alps (Dawson and Hone 2012), and for various other ungulate species (Nelson and Peek 1982; Escos et al. 1994; Walsh et al. 1995), where authors concluded that population growth rate was most sensitive to adult female survival.

If a proportional change in adult survival has a greater effect on population finite rate of change than the same change in fecundity or juvenile survival, then increased mortality or forced removal of adult females from the population would most influence population control in the TTSF. A decrease in population reproductive rate achieved by targeting female fecundity (e.g. fertility control) would also slow the rate of population increase, but to a much lesser degree. The overall discussion on management strategies based on obtained results will be presented in Chapter 8.

4.5. CONCLUSION

Although the population of feral horses in the TTSF is only increasing slowly, there are reasons to be concerned about the rate of growth. Overpopulation is likely to occur in the near future and will lead to horses moving into unpopulated areas both within and outside the plantation. Thus, effective management emphasis should be on substantial and continuing removal of adult horses, or manipulation of survival and fecundity. The greatest success would be achieved by targeting adult females because reducing the number of males may increase reproductive rate of the population by increasing the stability of harems (Dobbie and Berman 1992). As selective removals will likely alter adult sex ratio and age structure of the population, further modelling should be performed to minimise adverse welfare outcomes. Further monitoring of the TTSF population is needed to account for annual changes in population recruitment. When designing long-term control measures for the TTSF population, accurate estimates of adult survival should be of the highest priority.

Despite remarkable similarities in the population dynamics of the TTSF feral horses and those of the three feral horse populations in the Australian Alps (Dawson and Hone 2012), generalisation about other feral horse populations in Australia should be discouraged. Detailed studies on feral horse populations in different environments are necessary before data obtained from the present study could be regarded as having generic significance.

CHAPTER 5: POPULATION SIZE

5.1. INTRODUCTION

Estimation of terrestrial animal population size (abundance) or the number of animals in a particular area (density) is difficult, especially if census methods are not possible (Bayliss and Yeomans 1989b; Linklater et al. 2001). The difficulty in testing the accuracy of obtained values usually lies in the lack of information about the true population size (Margues et al. 2001). Estimation of abundance can be performed via direct and indirect methods. Direct methods usually include visual counts of animals from aerial surveys (Bear et al. 1989; Lubow and Ransom 2009; Vernes et al. 2009), or from the ground (Plumptre 2000; Blomberg and Shine 2001; Acevedo et al. 2008). Both aerial and ground surveys employ a variety of sampling techniques, such as line transect (Buckland et al. 2001), strip transect (Burnham et al. 1985), or mark-recapture (White and Burnham 1999), while ground counts can additionally include point transects (Buckland et al. 2001). Counts of animals are widely used to estimate density in open habitats, where animals are easily detected (Plumptre 2000; Margues et al. 2001). In coniferous habitats, where it is difficult to visualise animals, thermal imaging is sometimes used (Hemami et al. 2007).

The main advantage of direct methods is that they may provide information on the age and sex structure of the studied population, and if performed shortly after the breeding season, on the number of new offspring (Margues et al. 2001). Their main disadvantage is that they may provide ambiguous information on the population abundance as they are often performed at one point in time, therefore only providing information relevant to the time of the survey (Lancia et al. 1994; Margues et al. 2001). Estimation of population abundance based on direct visual methods in forested habitats is difficult (Hemami et al. 2007), and sometimes not feasible due to low detection rates (Ratcliffe 1987). Direct methods are also more costly and labour-intensive in comparison with indirect methods as they require a wider survey area and an accurate method of animal detection (Buckland et al. 2001; Schott 2004).

Indirect methods of estimating animal abundance are generally more effective in impenetrable environments, such as forests; where animals are difficult to detect due to dense vegetation (Takenoshita and Yamagiwa 2008). These methods are based on counting signs that animals leave behind, such as dung (De Silva 2001; Tsaparis et al. 2009), tracks (Wilson and Delahay 2001; Stephens et al. 2006), and nests (Carroll 1988; Buckland et al. 1993; Morgan 2007). Data collected from these methods provide a longitudinal measure of the activity of animals, and may offer information on seasonal habitat use (Neff 1968; Berman 1991; Forsyth et al. 2007).

The use of dung counts was first published by Bennett et al. (1940). (Bennett et al. 1940)Since then, many studies have provided useful estimates of population abundance of various wildlife species, including deer (Margues et al. 2001), elephants (Barnes 2001), gorilla (Carroll 1988; Fay 1989), koala (Sullivan et al. 2002), and feral horses (Berman 1991; Schott 2004). Estimation of dung density is frequently used as an indicator of population trends between areas and seasons (Neff 1968). Dung counts may also be used to determine the total number of animals in a given area (Buckland et al. 2001; Linklater et al. 2001), given the assumption that animals deposit dung more frequently in areas where they spend most of their time (Bowden et al. 1969; Gill et al. 1975; Kearney and Gilbert 1976). The latter estimate converts dung density to animal density by incorporating the decomposition rates of dung (the mean number of days to complete dung decay), and mean daily defecation rates (Plumptre 2000; Buckland et al. 2001).

The survey method used depends on the ecology of the studied animal and the type of occupied environment. One technique, known as the clearance plot, is based on counting animal dung distributed within chosen sample plots, which have been previously cleared. The clearance plot method is widely used in estimating the abundance of wildlife in mediterranean-type environments (Smart et al. 2004; Acevedo et al. 2008), however, it can be costly and labour intensive because it requires clearing of chosen sample plots (Buckland 1993). Another technique, the strip transect method, requires surveying randomly chosen sample plots of fixed length and width in order to detect animal dung deposited within the sampled area. Similarly, this method can be time consuming because it is necessary to detect all deposited dung in the selected area (Buckland et al. 1993).

The distance sampling technique is an alternative approach to clearance plot and strip transect methods, as it eliminates the assumption that all objects (dung, nests, animals) within the surveyed area are detected. This is because the concept of the detection function *g(y)*, allows for decreasing probability of detecting an object with increasing distance from a transect line (Buckland et al. 1993, 2001). Therefore, the distance sampling method is more cost effective and less time consuming (Buckland et al. 1993; Margues et al. 2001).

There is little information available on feral horse population abundance and density in Australia (Dyring 1990; Dawson et al. 2006). The most recent and detailed figures are available from aerial surveys that employed distance sampling of sighted animals in the Australian Alps region (Walter and Hone 2003) and Carnarvon National Park (Lundie-Jenkins et al. 2006), or mark-recapture in Guy Fawkes National Park (Vernes et al. 2009). A survey conducted in the Alpine National Park used the mark-recapture approach to estimate horse densities at three sites (Dawson and Hone 2012). Another survey performed in the Greenbank Military Area, estimated density and total abundance of horses using mark-recapture and distance sampling of sighted horses (Berman 2008). An estimate of horse density was also attempted in the Guy Fawkes National Park using distance sampling and opportunistic sightings of horses (Schott 2004). Although feral horse dung count has been used to estimate population density (Berman 1991) and changes in relative abundance indices (Berman 2008; Schott 2004), no formal study has applied feral horse dung count to estimate feral horse population abundance in Australia.

The first report on the feral horse population in the TTSF was based on a brief survey in 2001 - 2002, which estimated the population to be 181 animals (Crittle and Jackson 2004). In 2009, a more comprehensive survey applying distance sampling of sighted animals was conducted, and estimated the population size to be 995 (95%CI 583-1691) animals (Berman 2013). Since those surveys, the incidence of horse sightings within the plantation area and vehicle collisions with feral horses had increased (Fraser Coast Workplace Health and Safety Report 2012), suggesting an increase in population numbers and the necessity to undertake an accurate appraisal of population abundance. Population density directly affects the distribution and habitat use of animals in the population. For that reason there is a need to understand how feral horses interact with this particular environment. Information on abundance, density and distribution of feral horses in the TTSF would enable the development of population control management strategies.

AIMS AND OBJECTIVES

The principal aim was to define the range of population spread and highlight areas of low and high horse density. This was achieved by a dung count method incorporated within a strip transect survey. Secondary aims were to estimate population abundance and density of horses using dung counts, dung decay and defaecation rates incorporated into a distance transect survey, and to determine monthly changes in horse abundance using a mark-recapture technique. Data will be compared with previous population distribution maps and to model population changes into the future.

HYPOTHESES

1. The population of feral horses is not evenly distributed across the TTSF;
2. An indirect method based on dung count, dung decay rate and defecation rate of feral horses is a practical tool for assessing density and abundance of horses in the coniferous environment of the TTSF, and
3. A direct method based on mark-recapture (resight) of identified horses permits assessment of population abundance trends in the most densely occupied plantation areas.

5.2. METHODS

5.2.1. SURVEY DESIGN

The survey design is presented in **Figure 5.1**. The first investigation incorporated a vehicle strip transect survey, which aimed to estimate feral horse dung distribution and density on plantation roads. The second investigation used a distance line transect survey to estimate horse dung density within plantation habitats (Buckland et al. 2001). Both surveys involved the total plantation area (TTSF; 756 km^2) and therefore included the previously defined study area (SA; 99 km^2). The third investigation provided an estimate of monthly and bi-monthly horse abundance trends in the SA by incorporating mark-recapture of identified horses over two years using the Pollock Robust Design (Pollock 1982).

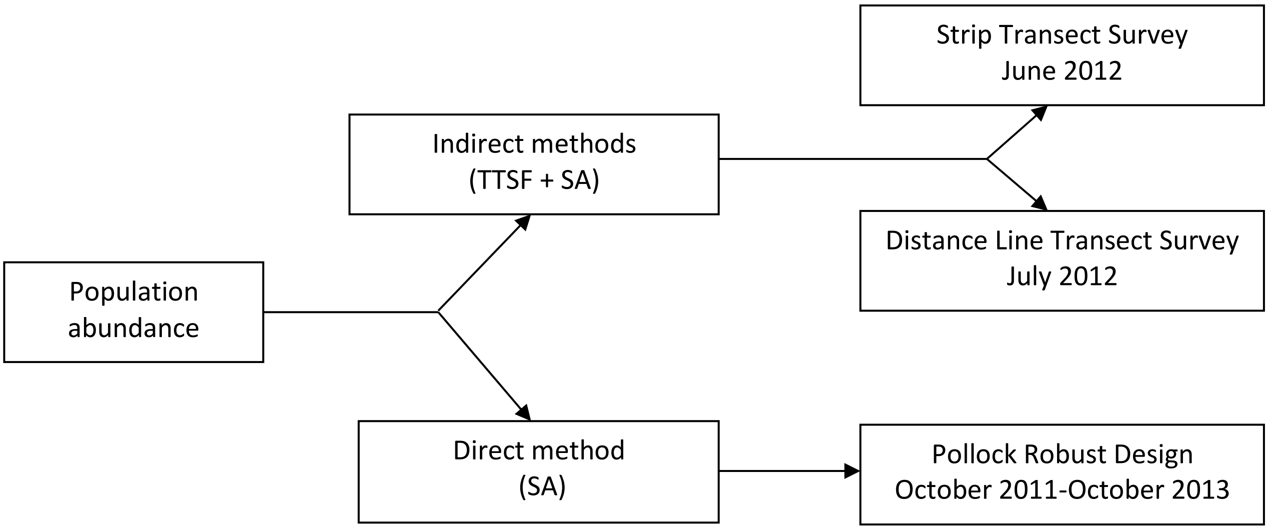

Figure 5.1: Methodology used to estimate the density and abundance of feral horses in the study area (SA) within the Tuan and Toolara State Forest and in the remainder of the forest (TTSF).

5.2.2. GEOGRAPHICAL STRATIFICATION

To ensure an adequate estimate of dung (and horse) density in the TTSF, the plantation was divided into two geographical areas: the SA; and the remainder, which was the majority of the plantation area (TFA) totalling 656.7km^2. These two areas were further subdivided (stratified) into four habitats, representing different growth stages of the pine forest. The area stratification was undertaken to ensure that the sampling was proportionate to animal density, which would increase the accuracy of the overall estimate. This was recognised in the pilot study, which indicated that dung density varied between different habitats. Habitat stratification is described in detail in Chapter 2 but briefly:

1. Harvested pine (HP) - cleared forest often overgrown by annual plant species;
2. Young pine (YP) - pine seedlings up to 3 years old, densely inhabited by annual and perennial grasses;
3. Juvenile pine (JP) - tree canopy between 3 - 7m in height and age between 3 - 10 years, and
4. Mature pine (MP) - with the height of old stands above 7m and the age above 10 years.

5.2.3. VEHICLE STRIP TRANSECT SURVEY

The four day (12th -15th of June 2012) survey used plantation roads and followed a strip transect design (Buckland et al. 1993). Strip transects were established running north-south and east-west with a total length *"L"* of 582 km and width "2w" of 6 meters. The average distance between transects was 4km (Appendices 1). Two surveyors were used. The first surveyor drove the vehicle, while the second counted all horse dung that was detected. Detections of dung outside of the surveyed road strips (beyond "*2w*") were disregarded. The total surveyed area "*A*" was estimated as $A = 2wL$, and density of dung "$\widehat{D}$" was estimated as $\widehat{D} = n/2wL$, where *"n"* was the dung count from a complete strip census (Buckland et al. 1993).

5.2.4. DISTANCE TRANSECT SURVEY

The distance transect survey was performed from 2nd - 12th of July 2012 on 111 randomly distributed transects in four plantation habitats, totalling 44.3 km. The survey was carried out by five surveyors. The sampled area (S) was surveyed along straight transect lines (m) of length (l_i) and sampled the number of dung (n_i) located at perpendicular distance (cm) from the survey transect (Buckland et al. 1993). The total number of dung detected on the line was denoted as $n = \sum_{i=1}^{m} n_i$; the total length of a surveyed transect in a given habitat class was denoted as $l = \sum_{i=1}^{m} l_i$; and the mean transect length was $\overline{l} = l/m$. Dung observed on either side of the transect line was counted in the survey up to a distance (w), and the sampled area was denoted as $a=2wl$. The distance (w) was a maximum distance at which dung was detected from the transect line and varied from habitat's topography and vegetation status.

5.2.4.1. DISTRIBUTION OF TRANSECTS

The location of transect's starting points within each habitat was assigned using a random GPS coordinate point generator function in Geographic Midpoint Calculator (Geo Midpoint, hhttp:/www.geomidpoint.com). The boundary of the Tuan and Toolara State Forest was established by selecting a rectangular region with north- and south-limit latitude coordinates and west- and east-limit longitude coordinates. The generated number of random point coordinates was then transferred to Google Earth Map (Google Incorporaton, California, USA) and into hand-held GPS units (Garmin Oregon 550 Navigator, Garmin International, Kansas, USA). Direction (compass bearing) of each transect was generated using the equation "=RANDBETWEEN (1,360)" in Microsoft Excel (Microsoft Corporation, Redmond, Washington USA; Forsyth 2005). All transects were then transposed onto a map of the TTSF. If a randomly generated transect point appeared outside of the plantation boundary or within the plantation but in an inaccessible location, that point was excluded and a new transect point was drawn from the database. In situations where a transect approached the boundary or encountered a barrier (dense vegetation, streams, swamps, waterholes) the line was then turned 90^0 to the right or left (determined randomly) and continued along a new bearing (Buckland et al. 1993). Transect length averaged 400 metres. A compass was used to determine and maintain transect direction.

5.2.4.2. DETERMINATION OF THE TOTAL TRANSECT LENGTH (SAMPLING INTENSITY)

Dung encounter rate from the pilot study was used as reference to estimate the total transect length required for each geographical area and habitat class in the survey. Total transect length (L) in each strata was determined by: $L = L_0 \times CV(D)^2 / CV_t(D)^2$, where L_0 and CV(D) were the total transect length and coefficient of variation of dung density for each habitat acquired in the pilot study, and $CV_t(D)^2$ was the chosen coefficient of variation in the main survey (Buckland et al. 1993). Because sampling intensity needs to be increased in the areas of lesser dung density (Neff 1968), dung encounter rate in respective habitats was evaluated on a daily basis so that the total required transect length could be determined.

5.2.5. DETERMINATION OF DEFECATION RATES

To determine defecation rates of the feral horse in the TTSF, horses of both sex and all age groups were observed from a distance of 50 to 300 meters with the aid of 10x22 binoculars (Nikon Corporation, Tokyo, Japan) over 30-180 minutes. Observation time was discontinued if the visibility deteriorated or if horses moved so that further observation was not possible. Defecation events were only counted for undisturbed horses. As the estimation of defecation rates of animals may change seasonally due to changes in animal feeding behaviour, diet, metabolism and habitat pasture quality (Rogers 1987); the observations were performed over five consecutive days every month for a period of 12 months.

5.2.6. DETERMINATION OF DUNG DECOMPOSITION RATE

101 dung samples were measured from September 2011 to November 2013 to determine dung decay rate over time. Freshly deposited dung was encountered over five sampling periods from September 2011 to February 2012 (**Table 5.1**). Samples of fresh dung were observed in either an open canopy habitat (HP and YP) where the dung would be more exposed to the prevailing weather, or in a closed habitat (JP and MP) where it would be more protected from direct exposure to sun, wind and rain.

Sampling month	Open canopy habitats	Closed canopy habitats	N dung
Sept 2011	7	1	8
Oct 2011	16	11	27
Dec 2011	12	9	21
Jan 2012	12	9	21
Feb 2012	19	5	24
Total	66	35	101

Table 5.1: Fresh dung encountered in two habitats over five sampling periods and used to determine dung decomposition rates.

Dung was regarded as being fresh if a horse was observed to defecate or if green in colour, moist with shiny surface and with fresh faecal smell, and without any signs of coprophagus insect activity (Hemami and Dolman 2005). The location of fresh dung was initially marked on a 1:50 000 topographical map (Forestry Plantations Queensland 2011) and uploaded on a hand-held GPS. Each sample was marked with a plastic peg and given a unique ID number. Monitoring of dung was carried out monthly from October 2011 to November 2013 until the samples were no longer visible when standing within one metre (this was the distance where the detection of dung declined from the centre line during the line transect surveys). Colour and structure were recorded during each observation as indicators of aging (Loydi and Zalba 2009). The mean time of decay was calculated as the time from defecation to the time the sample disintegrated and was no longer visible.

5.2.7. MARK-RECAPTURE SURVEY

Detection of individually identified horses was undertaken each month from October 2011 to October 2013 over a 4 – 5 day period, giving a total of 23 primary periods. Observations were collected during daylight hours and the observer was either on foot or in a slow moving vehicle. Horses were observed until identification was confirmed, which was based on body colour, presence or absence of body markings, gender, approximate age, and group association (Roelle et al. 2010). During each day of the survey an attempt was made to cover the entire study area to maximise the chance of seeing horses for the first time (“capture”), or in consecutive observations (“re-capture”). The survey path and location of horse groups were recorded using a hand-held GPS. Features recorded for each horse group included group type such as harem/bachelor, and new group/known group. A digital SLR camera with optical 400mm lens (Canon Incorporation, Tokyo, Japan) was used to record visual details of observed horses. Individual features were later cross-referenced between surveys to determine whether a new capture or a re-capture had occurred.

5.2.8. DATA ANALYSIS

5.2.8.1. STRIP TRANSECT

Data were analysed using the kernel density tool in ARCGIS 10.1 (ESRI, Redlands, California, USA). The kernel density tool created a raster (rectangular grid of pixels) with grid cells of 1.7 ha for the whole plantation area. For each grid cell the number of dung was recorded within a selected search distance (7km) and this number was assigned to the value for that grid cell. This method mathematically mapped areas with different probabilities of dung density, which were later presented graphically.

5.2.8.2. LINE TRANSECT

Line transect data were analysed independently in each habitat in each geographical area. Dung encounter data were firstly converted into dung density/km^2 and then into horse density/km^2 in the program DISTANCE 6.0 (Thomas et al. 2010). Three models (half-normal, uniform, and hazard rate), and three adjustable expansions (cosine, simple-polynomial, and hermite-polynomial) were considered for the analysis (Buckland et al. 1993). Histograms were examined for clumping of data at some distances with eventual spikes at zero distance and a distinct “shoulder” near the transect line. Models that showed an unrealistic spike at zero distance were disregarded. The choice of the final model was based on the fit of models, which was estimated by using χ^2goodness-of-fit tests, and on the lowest Akaike Information Criterion (AIC$_c$) (Buckland et al. 1993; Margues et al. 2001). The measure of each model relative to the best model was also calculated as ΔAIC$_c$ = AIC$_c$ – AIC$_{best}$, where AIC$_c$ was the AIC value for any candidate model, and AIC$_{best}$ was the AIC value of the best model. As a rule, $\Delta_i < 2$ suggests substantial evidence for the model, values between 3 and 7 indicate that the model has considerably less support, and values over 10 indicate that the model is very unlikely (Burnham and Anderson 1998). Dung encounter rate and its variance was computed empirically in DISTANCE 6.0 using CV($\widehat{D}$) = $\sqrt{\widehat{var}(\widehat{D})}/\widehat{D}$ as a measure of precision, where CV is coefficient of variation of the estimated dung density ($\widehat{D}$) (Buckland et al. 1993). Separate horse densities were calculated for each habitat in two geographical areas, and these were used to obtain the overall population density estimate. Population abundance was obtained by multiplying the density of horses in a given area by the area size. Confidence limits and standard errors of the estimates were taken directly from the DISTANCE 6.0 output.

5.2.8.3. ESTIMATION OF DUNG DENSITY

Dung density was estimated as:

$$\widehat{D} = \frac{n \cdot \hat{f}(0)}{2L}$$

Where (*n)* was the number of dung detected; (*L)* was the total length of transect line in each habitat, and $\widehat{f}(0)$ was the probability density function of the perpendicular density evaluated at zero distance from the transect line (Buckland et al. 1993). Estimates of dung density were computed for each habitat by pooling transects contained within each habitat class (stratum) in each geographical area (SA and TFA). The distance sampling method incorporated several assumptions in order to calculate an estimate and these assumptions were: all objects were detected on the centre of the transect line; all objects were recorded at their initial location and irrespective of the side of the transect line, and each object was recorded individually, not in clusters (Buckland et al. 1993). An exception was made for stallion piles, which were recorded as clusters, as it was not possible to count the number of defecations per pile. However, the number of stallion piles detected was very small (n=31), and did not influence the overall estimate. Dung density is presented as per square kilometre.

5.2.8.4. ESTIMATION OF HORSE DENSITY

The estimates of dung density were automatically calculated to horse density (D_h) in DISTANCE 6.0 (Thomas et al. 2010) by applying the equation $D_h = D/(DDR \times D_f)$, where DDR was the mean number of days required for dung to decompose and D_f was the mean defecation frequency of feral horses. The estimate of horse density was weighted by the size of each stratum in the SA and TFA sites, respectively, to produce estimate of horse abundance (N). Abundance estimates from SA and TFA were then pooled to produce the estimated population size for the entire plantation. Density and abundance estimates, SEM, CV and 95% confidence intervals (CI) were obtained from the DISTANCE 6.0 output.

5.2.8.5. DEFECATION RATE

Defecation rates were calculated by dividing the total time of observation of individual horses by the number of dung produced. If a group of horses was observed, the total observation time was multiplied by the number of horses in each group. The average dung defecation rate per hour was then adjusted to a 24-hour period (Rogers 1987; Linklater et al. 2001). The calculation was performed using Microsoft Excel® (Microsoft Corporation, Redmond, Washington, USA) and is presented as mean ± SD.

5.2.8.6. DUNG DECOMPOSITION RATE

Survival of dung was defined as the length of time between deposition and decomposition; measurements were collected over a period of two days at monthly intervals. Each of these intervals was constructed to be such that the observed decay was contained within the interval, and the time of decay was taken to occur at the end of the interval. The Cox-survival regression model was used to explore the relationship between the decomposition probabilities (survivorship) of deposited dung over time with ‘time’ being the factor impacting survival (explanatory variable). One-way between groups analysis of variance (ANOVA) was conducted to compare the effect of time of dung measurement (month) on dung decomposition rate, and the T-test was used to compare the influence of canopy cover on dung decomposition rates, with significance level at $P \leq 0.05$. The mean ± SD dung decomposition rate (days) was calculated in Microsoft Excel.

5.2.8.7. MARK-RECAPTURE

The survey was designed to satisfy the conditions of the Pollock Robust Design (Pollock 1982). Statistical analysis of the mark-recapture data were performed using the Closed Robust Design within the program MARK 2.1 (White and Burnham 1999). Time intervals were set to 1 or 2 months, because surveys were conducted on a monthly or bi-monthly basis (primary periods), therefore the estimates of population abundance (N) were for each survey (primary period). Estimates of abundance were calculated separately for harems and bachelors.

Three models were initially fitted to the data, and were: No Movement (NM), Markovian Movement (MM), and Random Movement (RM) (Cooch and White 2002). Parameters for the NM model, a model with no temporary emigration, were estimated under the assumption that observable individuals will always remain observable, and those that are unobservable will remain unobservable over all primary periods. The MM model assumes that the probability of an individual moving between availability states between primary periods is conditional on the state of the individual at time t-1, while the RM model assumes that the probability of moving between availability states between primary periods is independent of the previous state (White and Burnham 1999).

Candidate models were chosen prior to the analysis, which were based on prior knowledge of feral horse detection rates based on observations. All analyses were done in several stages. Abundance was modelled as a variant over time because of varying resighting rates of horses amongst primary periods. Capture (p) and recapture (c) probabilities were set to constant during secondary sampling occasions because of high resighting rates of horses in consecutive survey days but were allowed to vary in time between primary periods because of variable resighting rates between months. Survival (Φ) and movement parameters of immigration (ɣ’) and emigration (ɣ”) were modelled as either constant over time or as a function of time between primary sampling periods. Subscript *time* refers to time dependence of parameters, no subscript means that parameters were constant over time, and K was the number of estimable parameters.

The fit of models was estimated by the X^2 goodness-of-fit test, and model selection was conducted by examination of Akaike Information Criterion (AIC_c) (Lebreton et al. 1992; Wagenmakers and Farrell 2004). Models were first ranked by AIC_c differences. The relative likelihood of each model was then estimated with AIC_c weights (AIC_w), where higher weights suggested better model fit (Lebreton et al. 1992; Burnham and Anderson 1998). Standard errors of the mean and 95% confidence intervals (CI) were taken directly from the MARK 2.1 output.

5.3. RESULTS

5.3.1. DISTRIBUTION OF FERAL HORSE DUNG IN THE TTSF FOREST

A total of 1619 dung were encountered in the 582km strip transect survey. The survey indicated that horse dung was not evenly distributed on roads within the plantation. The highest dung encounter rate (which reflected the highest horse density) was concentrated in the central plantation, which corresponded to the SA. No dung was recorded at the western and eastern extremities of the plantation (**Figure 5.2**).

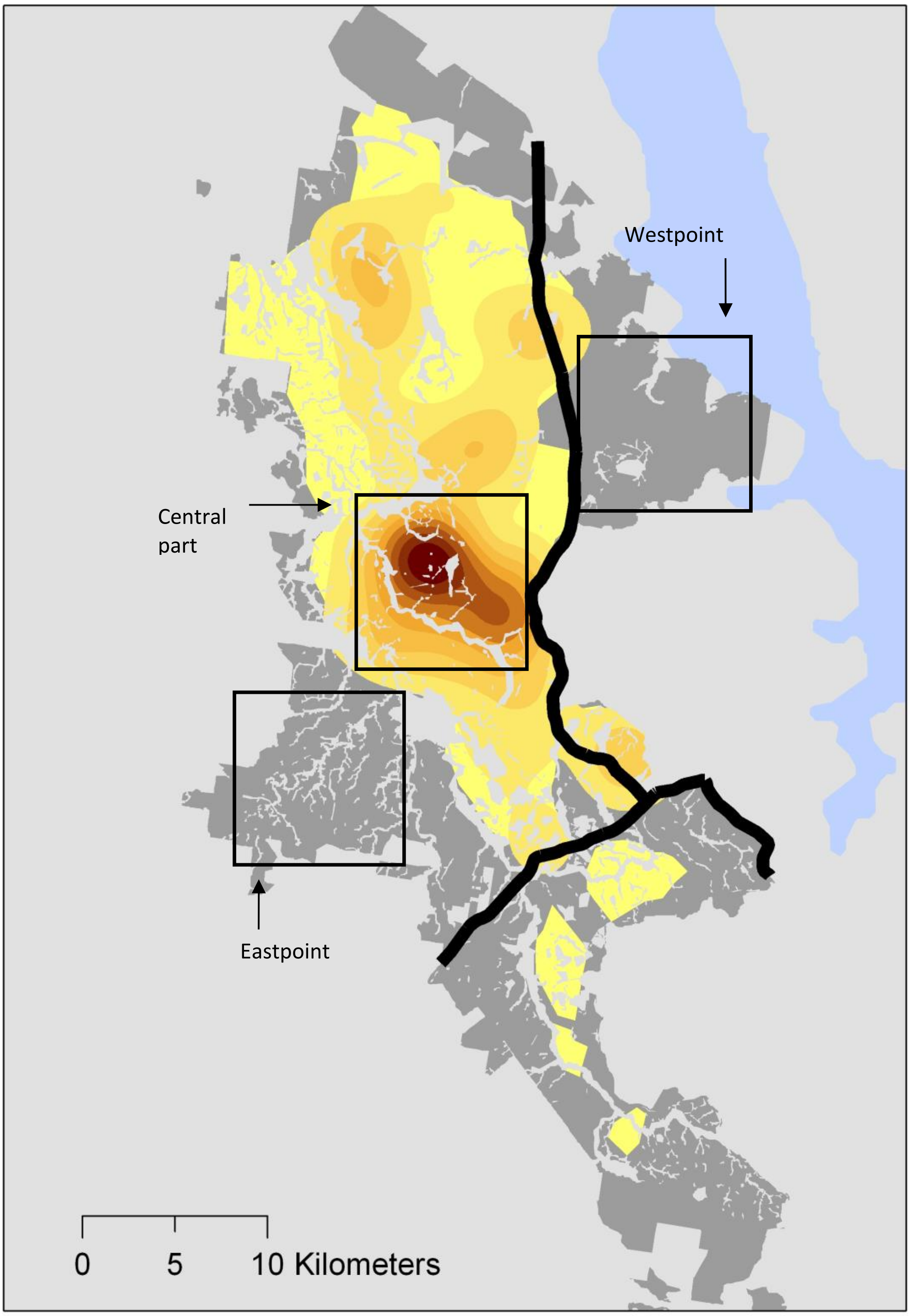

Figure 5.2: Distribution of feral horses based on dung counts recorded in the strip transect survey along forestry roads in June 2012. Black lines – main public roads; dark grey - plantation area with no dung recorded; coloured areas - areas with dung density in ascending order: yellow, 2000 – 4000 dung/km^2; orange, 4000 – 8000 dung/km^2, and dark brown, 8000 - 12000 dung/km^2.

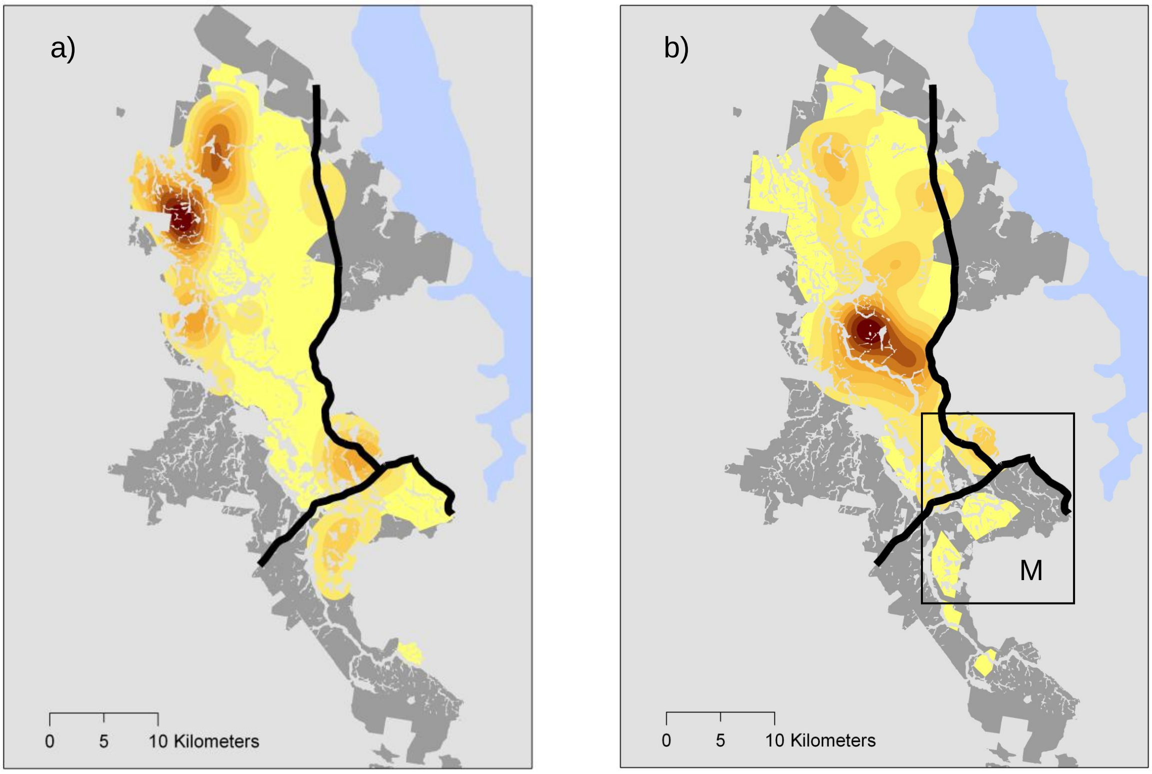

Figure 5.3: These two figures illustrate the change in feral horse population distribution between a) 2009 (Berman 2013), and b) 2012 (current study). Both surveys used analogous methodology based on dung encountered on plantation tracks. Yellow = 2000 – 4000 dung/km^2; orange = 4000 – 8000 dung/km^2; brown = 8000 – 12000 dung/km^2; grey - plantation area; black lines – major public roads, and M – management area where 73 horses were removed from 2009 – 2012.

5.3.2. DEFECATION RATE

Horses (n = 124) were observed for 386.5 hours over 12 months, and 111 defecations were detected. The mean defecation rate per horse per 24 hours was calculated to be 7.97 ± 8.74 (± SD; range 5.69 - 12.24).

5.3.3. DUNG DECOMPOSITION RATE

Distribution of dung decomposition rates is presented in **Figure 5.4**. Mean time of dung decomposition was 443.9 ± 150.7 (Mean ± SD) days and ranged from 121-760 days. The results indicated that there was a significant effect of time of dung measurement (month) on dung decomposition rate for the five months tested [F (4,96) = 3.73, P = 0.007]. Dung measured in the spring months of September (mean 575.9 ± 189.2 SD, n = 8) and October (mean 483.0 ± 87.7 SD, n = 27) decayed at a slower rate than dung measured in the summer months of December (mean 369.0 ± 134.5 SD, n = 21), January (mean 427.0 ± 179.5 SD, n = 21), and February (mean 436.3 ± 148.7 SD, n = 24).

There was a negative correlation between the amount of rainfall recorded in the two weeks following dung deposition and the rate of dung decomposition (r = -0.28, df = 99, P < 0.05) indicating a negative linear relationship between these two variables. The results signify that rainfall shortly after dung deposition increased dung decay rate. A significant difference was also observed in dung decomposition rates within the open (mean 404.3 ± 156.4 SD, n = 66) and closed (mean 518.5 ± 106.3 SD, n = 35) canopy habitats (t = -3.87, df = 99, P = 0.0002), indicating that sheltered habitats, which offered partial protection from the environmental conditions, slowed the process of dung decay.

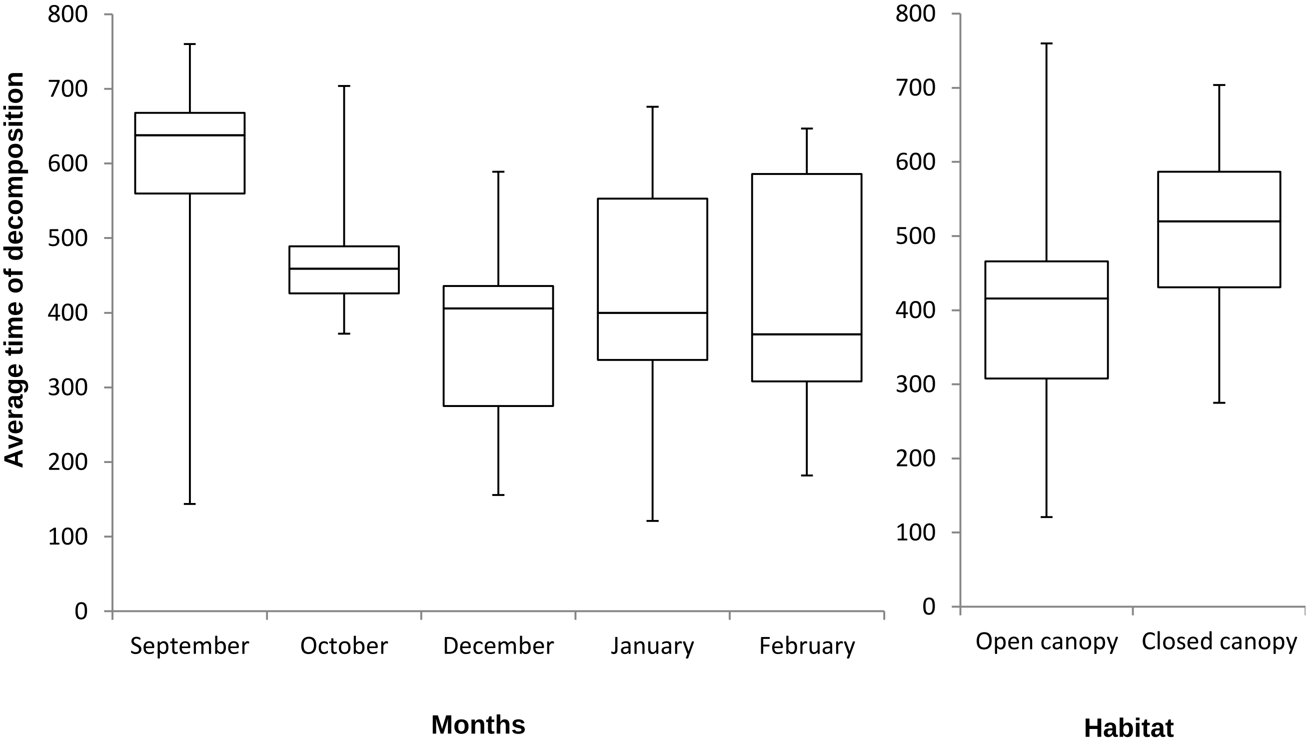

Figure 5.4: The influence of month of collection and habitat type on dung decomposition rate (expressed as median, upper and lower quartiles, minima and maxima).

5.3.4. LINE TRANSECT SURVEY

5.3.4.1. MODEL CHOICE

Amongst the tested detection function models, the half-normal model with cosine adjustment had the best fit to the data, because it had the lowest AIC value (AIC_c = 5417.45), suggesting that it was the best model for explaining the data (**Table 5.2**). The fit of the model was further improved by discarding those dung counts that were measured at the extreme edge of the line transect and could be considered as outliers; these accounted for 5% of the observations (Buckland *et al.* 2003). The hazard rate and uniform models fitted the data poorly and were excluded from the analysis.

Model description	K	AIC_c	ΔAIC_c
Half-Normal Cosine	23	5417.45	0.000
Uniform Cosine	26	5437.85	20.40
Half-Normal Simple Polynomial	20	5456.70	39.25
Half-Normal Hermite Polynomial	8	5530.28	112.83

Table 5.2: Models used to estimate density and abundance of feral horses in the Tuan and Toolara State Forest. Statistics for best-fit models are presented in descending order of the AIC_c. K represents the number of estimable parameters.

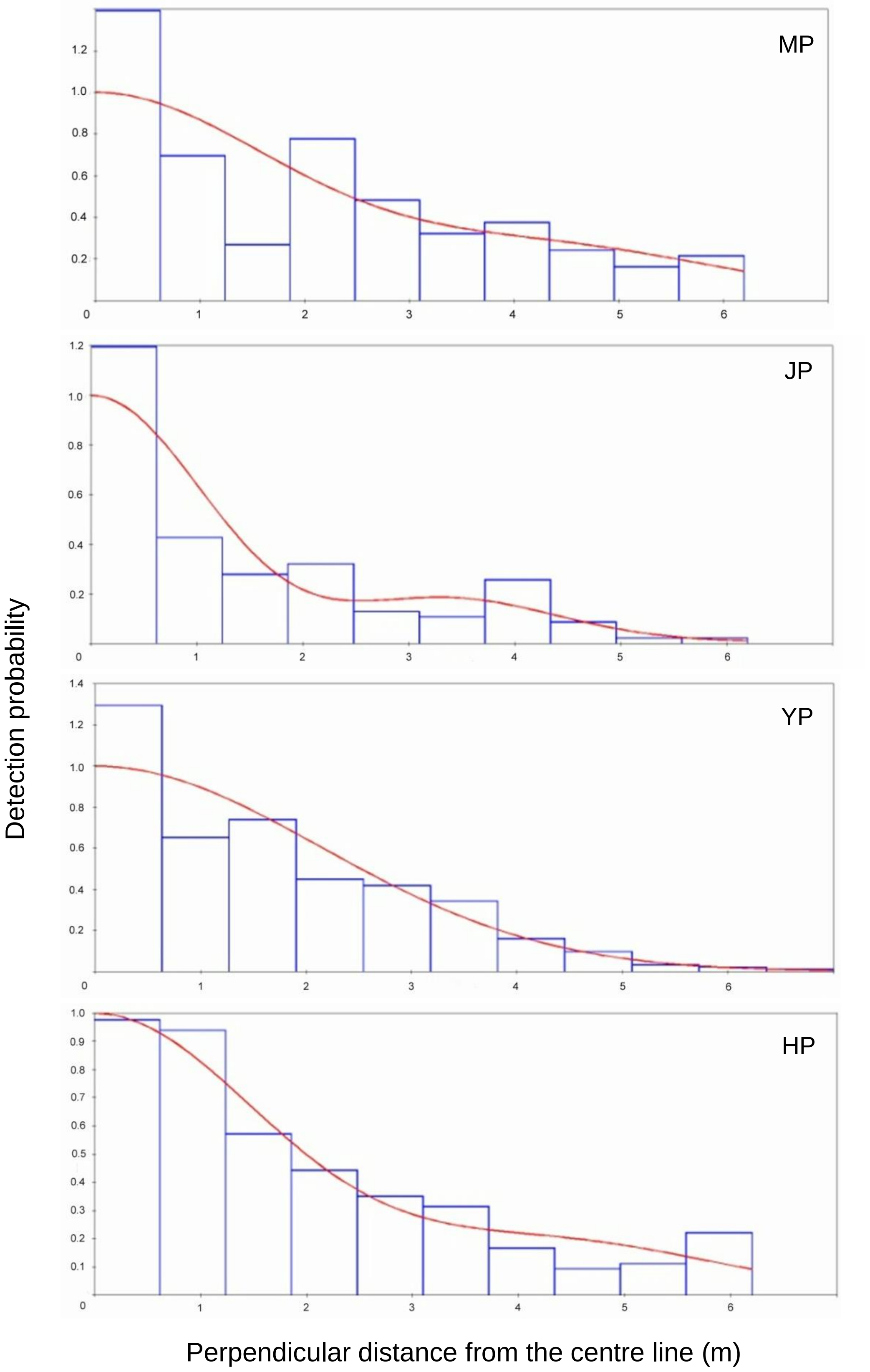

Figure 5.5: Histograms of the half-normal model with cosine adjustment fitted to the dung encounter rate obtained in the line transect survey in four habitats in the TTSF. The sudden drop on the histogram in JP habitat indicates decline in dung detection rate above 1 m from the centre line. MP - mature pine; JP - juvenile pine; YP - young pine, and HP - harvested pine habitats.

5.3.4.2. DENSITY OF DUNG

Dung encounter rate was not uniform between habitats. The highest dung encounter rate was obtained in HP and YP and lowest in JP and MP habitats (**Table 5.3**). Dung density in the four habitats in the two surveyed areas is shown in **Table 5.4**.

Habitat	Area size (km^2)	Number of transects	Total transect length (km)	Number of dung	Dung encounter rate/km
MP	326.72	39	16.68	415	24.88
JP	205.12	35	12.24	327	26.72
YP	195.25	19	7.18	435	60.58
HP	28.80	17	8.17	558	68.30
TOTAL	755.89	110	44.27	1735	39.19

Table 5.3: Dung encounter rate in the four habitats surveyed in June 2012. MP - mature pine; JP - juvenile pine; YP - young pine, and HP - harvested pine habitats.

Area/Habitat	$\hat{D}$	95%CI	SEM	%CV
Study area				
MP	8508	6502-23315	2980	29.50
JP	12313	9023-32488	3632	29.85
YP	11864	7554-18634	2553	21.53
HP	7998	4956-12908	1668	20.86
TF area				
MP	2958	1803-4851	729	24.65
JP	4497	2504-8074	1312	29.18
YP	10079	4814-21097	3486	34.59
HP	12114	7701-19054	2502	20.66

Table 5.4: Estimates of dung density/km^2 ($\hat{D}$) in respective habitats in the SA and TF, with confidence intervals (95%CI), standard errors (SEM), and percentage coefficient of variation (%CV).

5.3.4.3. DENSITY AND ABUNDANCE OF HORSES

The accuracy of population estimates was influenced by habitat type. The variance was high for all habitats but lowest in the open habitat of harvested pine in both the SA and TFA (**Table 5.5**). Abundance estimates were 290 in the SA and 1031 in the TFA, which when averaged provided an estimate of 1321 (95%CI 940 - 1965) horses in the TTSF at an average density of 1.79 (95%CI 1.24 – 2.60) horses/km^2.

Area/Habitat	Habitat size (km^2)	$\widehat{D}$	95%CI for $\widehat{D}$	$\widehat{N}$	95%CI for $\widehat{N}$	%CV
Study area						
MP	41.4	2.40	1.13 - 5.09	100	47 - 211	36.7
JP	28.7	3.48	1.79 – 6.73	100	52 - 194	31.5
YP	22.8	3.35	2.05 – 5.47	76	47 - 125	24.2
HP	6.2	2.26	1.36 – 3.74	14	8 - 23	23.6
Total	99.1	2.92*	1.92 – 4.45	290	191 - 441	20.9
TF area						
MP	285.3	0.84	0.49 – 1.42	238	140 - 407	27.0
JP	176.4	1.27	0.68 – 2.36	224	121 - 416	31.2
YP	172.4	2.84	1.34 – 6.07	491	230 - 1047	36.3
HP	22.6	3.42	2.10 – 5.57	78	48-126	23.4
Total	656.7	1.57*	0.99 – 2.49	1031	650 - 1635	22.5
TOTAL TTSF	755.9	1.79*	1.24 – 2.60	1321	940-1965	18.3

Table 5.5: Estimates of feral horse density/km^2 ($\widehat{D}$) and abundance ($\widehat{N}$) in the SA, TFA, and the entire TTSF, obtained from distance sampling of dung, dung decay rate and defecation rate. *The average horse density estimate was weighted by the size of each habitat and was taken directly from DISTANCE 6.0 output. 95%CI – confidence intervals, and %CV – coefficient of variation.

5.3.5. MARK-RECAPTURE SURVEY

5.3.5.1. MODEL CHOICE

Capture histories were obtained for 121 harems and 114 bachelors. Results of model fit for harem group revealed that the Markovian model, which characterised constant survival and movement parameters, was the best model based on AIC_c weight and was used to calculate all values. It had the lowest AIC (1827.8) and an Akaike weight of ~100%. The remaining models could not be supported (**Table 5.6**). The same model showed the best fit for the bachelor group. Model fit indicated that the best Markovian model, with constant survival and movement parameters yielded the smallest value of AIC_c (1827.8) and an Akaike weight of ~100% in the candidate set. Therefore, it was believed it generated values with greater precision than other models.

Harems

Model ID	Model description	K	AIC_c	ΔAIC_c	AIC_c w
MM	Φ, γ',γ'', p_{time}=c_{time}, N_{time}	44	1827.788	0.000	0.997
NM	Φ, γ'=γ'',p_{time}=c_{time}, N_{time}	44	1840.135	12.346	0.002
NM	Φ_{time}, γ'=γ'',p_{time}=c_{time}, N_{time}	62	1842.248	14.459	0.001
MM	Φ_{time}, γ', γ'',p_{time}=c_{time}, N_{time}	63	1844.534	16.745	0.000
RM	Φ, γ'=γ'',p_{time}=c_{time}, N_{time}	44	1867.465	39.676	0.000
MM	Φ, γ'_{time}, γ''_{time}, p_{time}=c_{time}, N_{time}	79	1868.137	40.349	0.000
RM	Φ_{time}, γ'=γ'',p_{time}=c_{time}, N_{time}	62	1880.444	52.655	0.000
MM	Φ_{time}, γ'_{time}, γ''_{time}, p_{time}=c_{time}, N_{time}	98	1887.678	59.890	0.000

Bachelors

Model ID	Model description	K	AIC_c	ΔAIC_c	AIC_c w
MM	Φ, γ',γ'', p_{time}=c_{time}, N_{time}	36	1556.192	0.000	0.998
NM	Φ_{time}, p_{time}=c_{time}, N_{time}	54	1569.316	13.124	0.001
NM	Φ, p_{time}=c_{time}, N_{time}	37	1575.098	18.905	0.000
MM	Φ, γ'_{time}, γ''_{time}, p_{time}=c_{time}, N_{time}	72	1576.379	20.187	0.000
MM	Φ_{time}, γ', γ'',p_{time}=c_{time}, N_{time}	58	1577.558	21.366	0.000
MM	Φ_{time}, γ'_{time}, γ''_{time}, p_{time}=c_{time}, N_{time}	87	1583.505	27.313	0.000
RM	Φ, γ'=γ'',p_{time}=c_{time}, N_{time}	37	1586.964	30.772	0.000
RM	Φ_{time}, γ'=γ'',p_{time}=c_{time}, N_{time}	52	1589.646	33.454	0.000

Table 5.6: No Movement (NM), Markovian Movement (MM), and Random Movement (RM) models of survival (ϕ), immigration (γ'), emigration (γ''), capture (p), and recapture (c) used to estimate abundance (N) parameters of harems and bachelors in the SA of the Tuan and Toolara State Forest. Statistics for best-fit models are presented in descending order of the AIC_C. Subscript *time* refers to time dependence of parameters; no subscript means that parameters were constant over time, and K - number of estimable parameters.

5.3.5.2. ABUNDANCE ESTIMATES

Harems and bachelors were observed from October 2011 to October 2013. The proportions of new captures and recaptures of harems and bachelors in the SA over a period of 24 months are presented in **Figure 5.6**. As the study progressed, the number of recaptures increased and the number of captures decreased.

The estimates of harem and bachelor abundance with 95% confidence intervals calculated in MARK 2.1 based on the Markovian model are shown in **Figure 5.7**. Harem abundance estimates fluctuated during the study, and ranged from 19 (± 0.89 SEM) to 44 harems (± 10.61 SEM). The precision of the estimates was high as the recapture rates were generally high (0.45 – 0.57). The precision was more variable during the first two months of the study (± 8.29 and 10.61 SEM respectively) because of higher rates of captures compared to recaptures (0.14; **Figure 5.7**), which resulted in a temporary overestimate of harem abundance in December 2011. As the study progressed, a larger proportion of marked harems were resighted. There was a less clear trend in bachelor abundance estimates with precision varying across study periods. Bachelor abundance estimates ranged from 9 (± 0.01 SEM) to 38 (± 8.13 SEM). Estimations were not possible in October and December 2011 because there were no recaptures.

Monthly (or bi-monthly) estimates in mark-recapture in the SA ranged from 19 - 44 harems and 9 – 38 bachelors. Considering the mean harem size of 4.95 (95%CI 4.53 - 5.41) horses; the overall monthly (or bi-monthly) abundance of horses in the SA ranged from 120 - 256.

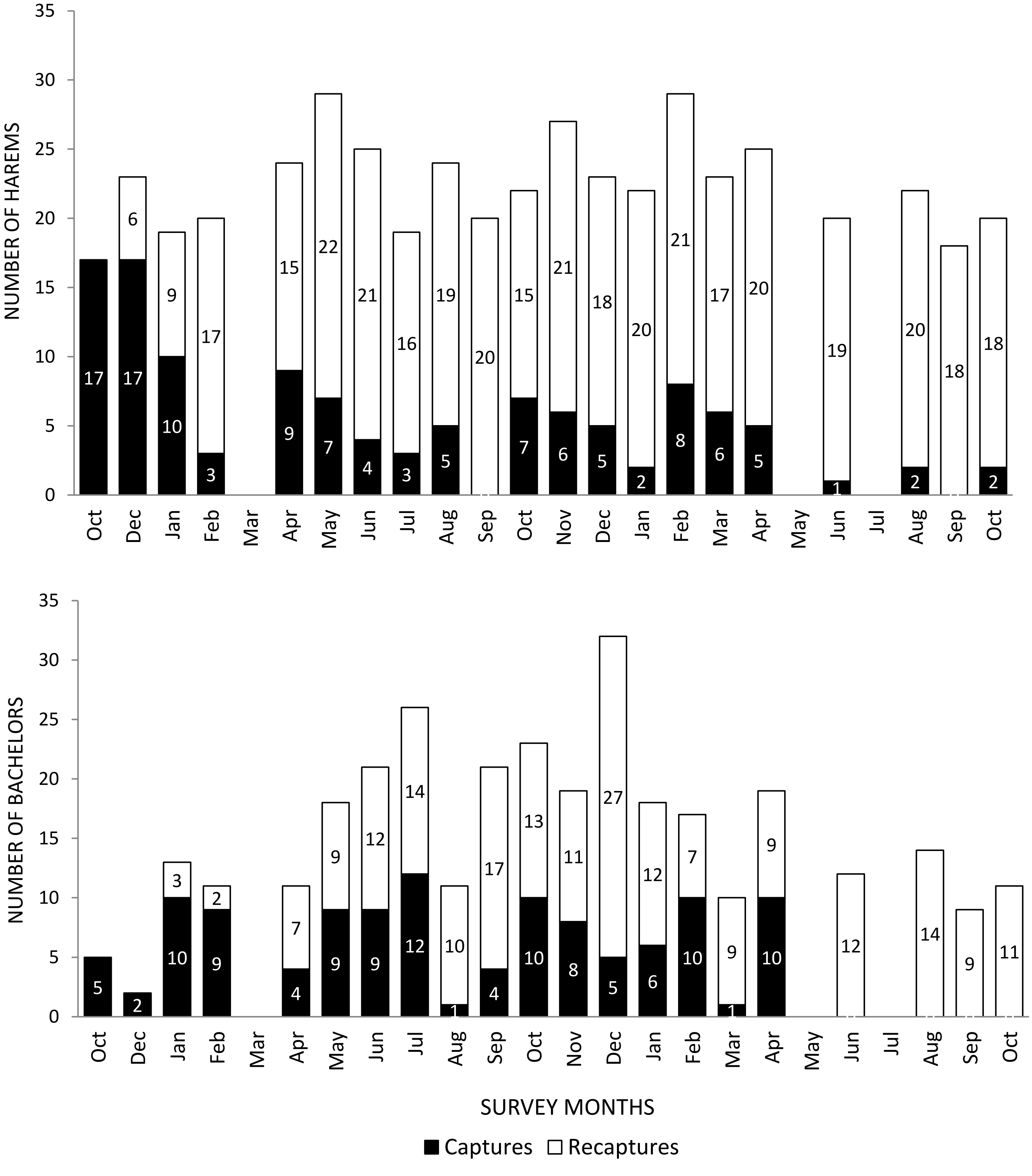

Figure 5.6: The number of captures and recaptures of harems and bachelors, respectively shown as black and white bars, aligned by month over the study period. Months where no survey was undertaken are seen as gaps between bars.

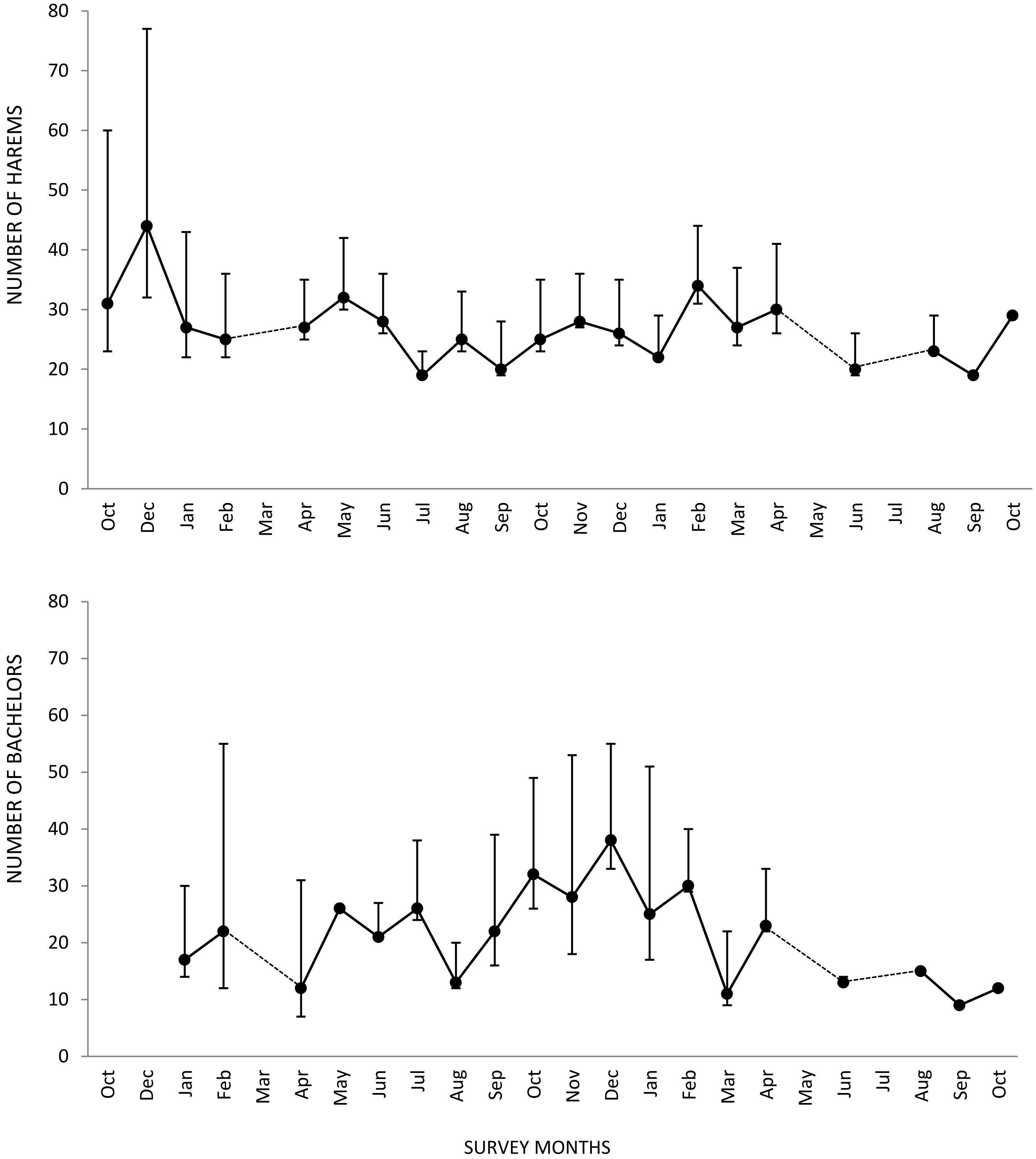

Figure 5.7: Estimates of harem and bachelor abundance with 95%CI obtained from the mark-recapture surveys from October 2011 - October 2013. Dashed lines between observations indicate no estimates were calculated during that time because either no surveys were undertaken or no recaptures occurred.

5.4. DISCUSSION

This study illustrates that distance sampling of feral horse dung together with dung decomposition and defecation rates can estimate feral horse population size with acceptable precision. Distance sampling indicated that the TTSF was occupied by 1321 (95%CI 940-1965) horses, which corresponds to an average density of 1.8 horses/km^2. Given the estimated annual population growth rate of 8.8%, this result was comparable to a population estimate in 2009 of 995 (95%CI 583-1691) horses (Berman 2013). If the 2009 estimate was accurate, the TTSF population has increased from 2009 to 2012 by about 32%, an annual average growth of 10%.

Based on dung density and distribution, horse distribution was not uniform across the TTSF being greatest in the core region, and undetectable in some areas of the plantation. In a previous study of the TTSF horse population distribution in 2009, which also used a strip transect survey of dung on plantation roads, it was estimated that horses occupied an area of at least 522km^2 with the majority of the population concentrated in the north-west of the plantation and near the major roads (Berman 2013). Since 2009, 77 horses have been removed from the forestry area adjacent to the major public roads (management area ‘M’, **Figure 5.3b**), which explains the reduced dung encounter rate in that area in the present study.

Differences in population distribution between 2009 and 2012 surveys reflect habitat selection and availability. In 2009 the highest dung counts corresponded to the distribution of young and juvenile pine trees in that area. Between 2009 and 2012, major harvest and planting operations took place in the central part of the plantation creating new and extensive open habitats, which corresponded to the highest dung counts in the present study. Results previously discussed identified that feral horses in the TTSF have preference for open canopy habitats. Therefore, it is likely that creation of new open areas in the central part of the plantation offered greater grazing opportunities, which consequently, influenced population distribution in 2012.

Dung surveys in 2012 indicated that some areas of the forest were either not occupied or occupied by only a small number of horses. Such areas offer sites into which the population could expand in the future. Environmental disruptions, such as floods and fires, and human disturbances, such as harvesting or planting, regularly affect the forest structure (Gill et al. 1996; Kuiters et al. 1996). Horses adapt by moving between habitats and utilising available resources within their home range (Linklater 2000a). As the plantation management areas are mostly unfenced, and are usually separated by roads or topographical barriers, such as creeks, streams, or patches of dense native vegetation, there would be minimal impediment to the colonisation of these areas, as has been shown to be the case with feral horses elsewhere in Australia (Dawson 2005).

Line transect analysis of encountered dung in the SA gave higher abundance estimates than that of mark-recapture for the same area. It is not possible to determine the accuracy of each technique because actual population size was not known. It is known, however, that direct sighting methods are less precise, because not all animals are detected equally (Seber 1992), especially in heavily vegetated habitats (Bayliss and Yeomans 1989a; Gill et al. 1996; Walter 2002; Stephens et al. 2006; Vernes et al. 2009) where observations are fewer resulting in an underestimation of population parameters (Otis et al. 1978; Crane et al. 1997; Walter 2002; Stephens et al. 2006). Therefore, it is likely that mark-recapture underestimated horse abundance in the SA.

Habitat characteristic had a strong influence on the overall detection rate of horses in the mark-recapture surveys. The dense habitats of JP and MP limited detection of horses beyond 70 metres from the road. Horses occupying these habitats may have moved out of sight to avoid the approaching vehicle. Although a greater proportion of time was allocated to dense habitats in the mark-recapture surveys, it may be that the dense vegetation disproportionally decreased horse sightings thereby negatively affecting abundance estimates.

Identification of individual horses was dependent upon careful scrutiny but in dense habitats individual horses within a group may have been missed. It was not possible to assume that group composition was the same from one study period to the next; this was particularly the case with bachelor groups where membership was very fluid. Poor visibility in mark-recapture surveys may result in misidentification of animals, which in turn will affect the proportion of known to new individuals (Stephens et al. 2006). Higher encounter rates of known (or assumed to be known) individuals underestimate the actual population abundance, while higher encounter rates of new individuals will overestimate the population abundance (Jachmann 1991; Barnes 2001).

Horses were often wary of people and vehicles and would flee when disturbed, which complicated detection. Some individuals were more wary than others and therefore partial disjoining of groups was not uncommonly observed. In open habitats, fleeing horses frequently stopped within visual range and could still be identified, but in dense habitats movement of horses away from the observer resulted in loss of visual contact. Shyness was suggested to be the reason for the lower detection rates of feral horses in the mark-recapture study by Vernes *et al*. (2009). Drive counts of species such as deer in forested habitats were similarly influenced by the flight response elicited by an approaching vehicle (Hemami et al. 2007; Borkowski et al. 2011). This was not such an issue in the open habitats of the TTSF where a wide strip could be surveyed enabling detection of animals at a considerable distance.

According to the mark-recapture surveys, harem abundance in the SA was more uniform across all sampling periods, while bachelor abundance exhibited considerable monthly variation. The increased number of bachelors observed between October 2012 and February 2013 was possibly due to temporary immigration associated with the breeding season with males moving from outlying areas into the more densely populated SA to take advantage of breeding opportunities. Changes in male behaviour during the breeding season have been well documented (Tyler 1972; Berger 1986). This movement was not observed in the 2011/2012 breeding season, probably because the proportion of captured to recaptured bachelors during the early stages of data collection was small.

The variations in harem and bachelor abundance estimates in the SA site could have been also a result of disturbances to available habitat. Forestry management activities, such as harvesting, planting, and prescribed burning, alter habitats, which results in temporary relocation of horses to other sites. Prescribed burning and harvesting of MP habitat in the winter of 2012 resulted in a smaller number of horses detected in the SA, and contributed to the decrease in abundance estimate from June until September. Extensive harvesting in early winter of 2013 resulted in lower detection rates of horses because of relocation to other areas within the plantation. This movement was partially reversed in spring, when some harems and bachelors returned to previously occupied habitats. Human activity is known to influence wild herbivore distribution and density at a landscape scale (Kuiters et al. 1996; Vernes et al. 2009). In particular, iatrogenic changes in distribution and availability of forested habitats have the greatest consequences on habitat use by forest ungulates (Putman 1986; Gill et al. 1996). Aerial (Linklater et al. 2001; Vernes et al. 2009), and ground (Berman 1991; Linklater et al. 2001; Schott 2004) surveys have been also observed to have short term impact on feral horse distribution due to horse movement in response to the observers. In one study, horses moved as far as three kilometres from the observer when disturbed (Berman 1991) and in a transect study, horse movement, and the resultant detectability near observable limits, was such that it was responsible for an overestimation of population abundance (Schott 2004).

The first assumption of the distance sampling method is that all objects located on the centre line are detected, therefore the fit of the model on and near the centre line was most important when analysing the data (Buckland et al. 1993). The half-normal cosine model performed the best on the line, giving detection probabilities equal to 1. Additionally, the chosen model tended to correct for the lack of dung detection near the centre line, and hence appeared to have less bias than uniform and hazard rate estimators, which performed poorly near the line, giving detection probabilities below 1.

By utilising randomly surveyed transects and stratification as suggested by Lancia *et al*. (1994) and Stephens *et al*. (2006), the differences in animal density between habitats within surveyed areas was discernible and provided information on the overall population size with high precision. Surveys performed in heterogeneous habitats require stratification to increase precision of the estimate (Buckland et al. 2001). Recognition of the relationship between sampling intensity and precision in the line transect surveys necessitated increased sampling intensity in the areas of lesser dung density, which improved overall precision (Caughley 1977). Precision of the estimate was highest in the HP habitat, because the encounter rate of dung was greater than in other habitats.

A limitation was however observed in dung encounter rate in the JP habitat. In this habitat, the detection of dung declined dramatically beyond one metre from the centreline. This sharp decline in detection rate was most likely due to dense vegetation obstructing visibility when the observer was standing on or near the centre line. Juvenile habitat was the most difficult to survey, because of the high density of juvenile trees in the pre-thinning management stage, and abundant ground vegetation cover. Dense ground vegetation and accumulation of organic litter have previously been found to obstruct visibility leading to decline in dung detection rates (Buckland et al. 1993; Hedges and Lawson 2006). This was not such an issue in other habitats where a wider strip was surveyed. In order to improve dung detection rates near the centre line, the transect survey was executed in winter months when ground cover was less.

The assumptions accompanying distance sampling (Buckland et al. 1993; Barry and Welsh 2001; Thomas et al. 2010) were fulfilled in the present study. These include that objects must be detected in their original location (dung is immobile), that the perpendicular distance of the object to the centre is accurately measured (distances were measured in cm), and that the object cannot be countered more than once (spacing between transect lines was restricted to distances greater than the maximum visibility from any given transect). It can be assumed that the estimation of population abundance from dung counts will produce less precise estimates due to the variability in defecation rate and dung decomposition rate. These variables have their own variance, which can potentially complicate analysis and calculation of abundance (Barnes 2001). However, this potential disadvantage was balanced by the low variance in the estimate of dung density because of high sampling intensity, which was also found to be the case in other studies (Barnes 2001; Buckland et al. 2001).

Agreement with the assumptions that qualify mark-recapture analyses (White and Burnham 1999) was partially satisfied in the present study. The assumption of equal catchability (equal likelihood of being captured) was violated as horses in closed canopy habitats did not have equal likelihood of being sighted compared with those occupying open habitats. Capture probability of animals has a positive relationship with the variability in vegetation cover and density of animals in a given area (Bailey et al. 2004). This is because greater density of animals makes them easier to be captured (observed) in mark-recapture surveys. This relationship was evident in the present study. More horses and better visibility enabled greater detection of horses in open habitats than in closed habitats (81.2% and 18.8% respectively).

Equal catchability of marked and unmarked horses was improved by calculating the estimates of abundance separately for harems and individual bachelors. The reason for considering harems (and not harem members) as separate units of measure was that detection of one horse from a harem influenced the detection of the remainder of that harem (Walter 2002; Vernes et al. 2009). The majority of harems were stable across the study period, only the minority showed occasional disbanding or acquisition. In contrast, bachelor group size and composition changed frequently between primary and secondary survey periods. As detection of one bachelor did not influence the detection of the remainder of bachelors, it was more appropriate to treat bachelors as separate units of measure as suggested by White and Burnham (1999). Despite the improvement in the estimate calculation, the violation of the assumption of equal likelihood of detecting all horses may have led to negative bias in the abundance estimate in the mark-recapture survey as has been postulated by others (Gill et al. 1996; White and Burnham 1999; Bailey et al. 2004; Walter 2002).

As the mark-recapture method applied a visual appraisal of animals based on unique phenotypes, the method was non-invasive for the studied population (Seber 1992; White and Burnham 1999). Marked horses were correctly identified, as horses were photographed, and detailed phenotypic characteristics were collected for cross referencing between sampling sessions. Mortality rate should not be different between marked and unmarked individuals; marked individuals could not lose their ‘marks’ as phenotype in horses is permanent; and marked animals could mix randomly with unmarked animals, as the marking process did not affect a horse’s natural behaviour (Thomas et al. 2010).

Studies, which estimate the densities of wildlife populations from dung counts, assume that density of dung is a function of defecation rate and dung decomposition rate (Buckland et al. 1993; Linklater et al. 2001; Acevedo et al. 2008). The assumption in the current study was that defecation rates did not change with time of the day, therefore observations conducted during daylight hours were representative of defecation rates over a 24 hour period.

Ungulate defecation has been shown to vary diurnally (Collins and Urness 1981; Irby 1981). However, as nocturnal activity by feral horses has been well established (Berman 1991; Petersen et al. 2012), and since feral horses have tendency to defecate more often while grazing (Rubenstein and Hohmann 1989), it was assumed that defecation rates in the present study were uniform over a 24 hour period.

In general, inappropriately high estimates of defecation rates may underestimate the population size; while lower defecation estimates may overestimate the population size (Linklater et al. 2001). Seasonal variation in pasture availability and quality may have considerable effects on animal diet, digestion and therefore on defecation frequencies (Rogers 1987). Large consumption of fibre may increase gut motility and defecation frequency (Rogers 1987), whereas reduced feed intake decreases defecation frequency (Hale et al. 1962; Rogers 1987). In order to allow for seasonal differences in defecation rates resulting from differences in quality and quantity of forage, defecation rates of horses in the current study were obtained over a period of 12 months.

Evaluation of dung decomposition rate is based on the assumption that the decay rate is constant over time (Wigley and Johnson 1981; Barnes and Jensen 1987; Latham et al. 1996). However, dung decay rate reflects climatic conditions, such as rainfall, air and ground temperature, moisture, evaporation, and air movement (Dickinson et al. 1981; Linklater et al. 2001; Aarons et al. 2004). Decomposition is also influenced by coprophagous insect activity, growing vegetation and scattering by animals (Neff 1968; Latham et al. 1996).

Although fresh dung in the current study was monitored for decomposition rate in different habitats and under natural environmental conditions, a larger proportion of dung (65%) was exposed to direct climatic conditions, which increased the rate of dung decomposition. In contrast, sheltered habitats prevented dung from direct exposure to environmental conditions, making dung less susceptible to decomposition. Monthly, seasonal and between years variations in rainfall are known to have the greatest influence on dung disintegration (Mayle and Peace 1988; Barnes 2001; Hemami and Dolman 2005; Vanleeuwe 2008).

The large variation in the rate of dung decomposition in the present study indicates that the habitat type and time of the year in which dung is deposited influences the rate of decomposition. If a large proportion of dung is obtained from habitats where dung decays at a faster rate, which was the case in the present study, the consequence is an overestimation of the population size (Linklater et al. 2001). The bias could have been reduced by equal sampling of dung from open and closed canopy habitats. However, this exercise would involve moving dung from deposited locations into respective habitats, which would likely affect the integration of its surface and in turn would affect the decay rates. As the aim was to provide the most representative information on dung decay rate in the TTSF, it was difficult to obtain the same number of samples from open and closed canopy habitats. Therefore, it is acknowledged that the rate of dung decay was overly influenced by observations obtained from open habitats resulting in a higher rate of decay than if open and closed habitats had contributed equally to the observations. However, despite topographical and climatic differences between the current study and that of Linklater *et al*. (2001), dung decay rate of feral horses in the TTSF was remarkably similar to that of feral horses in New Zealand.

5.5. CONCLUSION

The purpose of the current study was to provide an appropriate and accurate method for estimating feral horse abundance in a coniferous environment where a census of animals was not possible. The significant finding was that estimates involving dung count, dung decomposition and defecation rates provided population density and abundance figures with acceptable precision and were comparable to an earlier estimate by Berman (2013) using distance sampling of observed horses. Dung count sampling is known to be a convenient, simple and low cost survey method suitable for determining changes in distribution, and abundance of animals. Given that defecation frequency and dung decomposition rate are well defined for feral horses, dung count sampling would appear to be a very effective technique for monitoring changes in population distribution and abundance in habitats where aerial surveys are not feasible.

Because of its susceptibility to error in dense habitats and where human contact occurs, mark-recapture should not be used as the only method to estimate population abundance. However, if performed in the same area over a prolonged period (months or years), it can provide useful data about population fluctuations, reproduction, survival rate, and population growth, which cannot be defined by dung count surveys.

Results showed that feral horses were not evenly distributed across the plantation, in part due to the history of horse introduction into the TTSF, and in part dependent upon habitat preferences. Evidence indicates that the population is growing and that management practices influence habitat availability, which in turn influences population distribution.

CHAPTER 6: HABITAT USE

6.1. INTRODUCTION

Studies of habitat selection by herbivores are predominantly undertaken to provide information on the interaction between animals and plants in a given environment, to assess impact on other animal species or to quantify the number of animals that need to be removed (Crane et al. 1997). This knowledge is valuable for protection or eradication management of plants or animals in a particular environment. Differences in habitat and climate may mean that animal management applicable to one area is not applicable in another (Ganskopp and Vavra 1986).

Data on the impact of large herbivores and feral horses in particular on commercial forests are sparse (Putman 1996). The most studied wild herbivores in managed forest ecosystems are roe deer (Welsh et al. 1990; Gill et al. 1996; Kuiters et al. 1996; Putman 1996; Hemami et al. 2004), muntjac deer (Kuiters et al. 1996; Hemami et al. 2004) and red deer (Welsh et al. 1990; Putman 1996). Wild ungulates achieve higher densities in younger forest stands, cleared forests, and in open habitats, all of which are characterised by sparse canopy cover (Gill et al. 1996; Hemami et al. 2004). It has been postulated that immature coniferous stands are associated with more palatable ground cover than mature stands (Gill et al. 1996; Crane et al. 1997).

Forest management influences habitat selection, which may influence the number and distribution of species, and population size of each species (Hansson 1994; Mathur et al. 2011). Partial thinning of the forest canopy can enhance diversity of undergrowth vegetation stimulating the expansion of microorganisms, insects and wildlife (Kuiters et al. 1996).

Studies of feral horse habitats invariability demonstrate a strong relationship between habitat selection and dietary requirements (Denniston et al. 1982; Berman 1991; Schott 2004). Most feral horse habitat studies have been conducted in semi-arid and arid environments, which are characterized by low pasture diversity and restricted water availability (Denniston et al. 1982; Miller 1983a; Ganskopp and Vavra 1986; Berman 1991), but some studies have looked at mountainous sagebrush and coniferous habitats (Salter and Hudson 1979; Crane et al. 1997), and native eucalyptus forest (Schott 2004). While habitat selection of free-ranging horses has been studied in a European temperate forest ecosystem (Putman 1996), little information is available on patterns of habitat use in exclusively coniferous forests.

Accurate information on vegetation utilisation is fundamental to the understanding of foraging behaviour of wild herbivores (Salter and Hudson 1982b; Gordon 1995; Mueller et al. 2008; Mathur et al. 2011). In areas with few resources, feral horses (Turner et al. 1993; Hampson et al. 2011), Asian elephants (Campos-Arceiz et al. 2008) and Asiatic wild asses (Kaczensky et al. 2008) cover long distances in search for food, or participate in seasonal migrations to increase access to higher quality vegetation. In areas with adequate food and water, feral horses (Hampson et al. 2011) and Przewalski horses (Kaczensky et al. 2008) tend to decrease their home range and daily movement.

Visual observation of wild and feral herbivores is commonly used to characterise population abundance and distribution (Crane et al. 1997; Linklater et al. 2001; Schott 2004). Visualisation of animals is problematic in dense woodland habitats because of reduced detection, which leads to inaccuracies in population size estimations (Schott 2004; Hemami et al. 2007; Vernes et al. 2009). Detection may also be influenced by other topographical features such as hills and gullies (Otis et al. 1978; Crane et al. 1997), which may be partially overcome by building observational platforms (Neff 1968). Timing of surveys may also influence observational data with both seasonal (Linklater et al. 2001) and diurnal effects needing to be considered in certain circumstances (Sasimowski et al. 1990b; Margues et al. 2001). Animals may move in response to the observer (Hulbert and French 2001; Lamoot et al. 2004). These difficulties can be substantially reduced by performing longitudinal observations at different times of the day and across multiple seasons (Chapman et al. 1985; Ganskopp and Vavra 1986; Crane et al. 1997).

The use of indirect methods, such as dung counts, has been widely applied in ecological studies of herbivores in which both abundance and habitat use was assessed (Neff 1968; Putman 1986; Linklater et al. 2001; Hemami et al. 2004). Dung counts are not influenced to the same degree by the difficulties associated with seasonal and diurnal variation in animal visual detection and the technique may also provide information on habitat use, and population distribution and size (Bennett et al. 1940; Putman 1984; Chapman et al. 1985; Lamoot et al. 2004; Acevedo et al. 2008; Mathur et al. 2011). In some herbivore species, faecal shape and size can be used to identify the population sex and age structure, while in other species faecal chemistry permits assessment of animal dietary quality (Bubenik 1982; Sinclair et al. 1982; Coe and Carr 1983; Maccracken and van Ballenberghe 1987; Pegard et al. 2009).

Dung count techniques assume that animals defecate randomly in space and time, therefore defecation will be proportionally correlated to grazing activity (Lamoot et al. 2004; King and Gurnell 2007) and time spent in a given area (Irby 1981). Furthermore, dung density in a given area is assumed to be dependent on the number of animals using the area (Hemami et al. 2004; King and Gurnell 2007). Temporal variation in defecation rate and habitat use may sometimes lead to purposive defecation causing non-random accumulation of faeces (Putman 1984). However, in a study of red, roe, and sika deer, dung counts and direct animal counts were comparable (Ratcliffe 1987) and in studies of snowshore hare (Krebs et al. 1987), Asian elephants (Barnes 2001), and several deer species (Neff 1968; Theuerkauf and Rouys 2008) there was strong correlation between dung density and the use of different habitat types.

Since the development of the Global Positioning System (GPS), spatiotemporal data of animal movement is very precise, can be collected at pre-programmed regular intervals and independently of climatic conditions, and does not involve personnel on the ground to follow studied animals (Hulbert and French 2001; Weimerskirch et al. 2002; Brooks et al. 2008; Kaczenski 2010a). GPS tracking collars meet animal welfare standards and usually do not interfere with natural behaviours of studied animals (Murray and Fuller 2000; Brooks et al. 2008).The accuracy of GPS tracking exceeds that of more traditional methods, such as radiotelemetry and direct observation, and is a very useful tool for mapping vegetation utilisation (Capaccio et al. 1997; Hulbert and French 2001), home range size (Kaczensky et al. 2008; Naidoo et al. 2012; Whyte et al. 2013), seasonal movement (Johnson et al. 2002; Forester et al. 2007; Naidoo et al. 2012) movement between habitats (Brooks et al. 2008; Hampson et al. 2011), and travel speed (Nelson et al. 2004).

Although earlier studies found that increasing vegetation height and forest canopy cover affects GPS performance (Rempel et al. 1995; Dussault et al. 1999; Di Orio et al. 2003), recent technical improvements have significantly enhanced the accuracy of GPS tracking collars (Hansen and Riggs 2006). Recent studies show that GPS technology is a widely used method in habitat evaluation of wild and feral herbivores (Johnson et al. 2002; Sundaresan et al. 2007; Brooks et al. 2008; Kaczensky et al. 2008; Naidoo et al. 2012).

Studies focusing on population ecology of wild herbivores have shown that population density is influenced by the management regimen of the forest industry (Gill et al. 1996; Hemami et al. 2004). However, there have been no previous studies of feral horse habitat use in managed coniferous forests in Australia. The Tuan and Toolara State Forest is a pine plantation with a relatively uniform ecosystem and is therefore very different to the more natural ecosystems typically occupied by feral horses in Australia (Dyring 1990; Berman 1991; English 2001; Walter 2002). It is important to address habitat selection of feral horses in the coniferous forest environment so that appropriate population management recommendations can be developed. Management of feral horses is of a particular interest in forested areas adjacent to major public roads due to an increased risk of vehicles colliding with horses (Crittle and Jackson 2004).

AIMS AND OBJECTIVES

The first aim of this study was to assess habitat preferences of feral horses in the TTSF and to evaluate horse movement and use within and between different forestry habitats by using three methods: direct observations, dung counts and GPS. The study was designed to address the suitability of each method for monitoring population movement trends within the plantation. The second aim was to measure the relationship between horse dung found on forestry roads versus dung found within the habitats traversed by those roads to determine horse presence in these habitats. If determined that the dung count method was reliable, the method could be used on forest roads to assess the distribution of feral horses in the TTSF.

HYPOTHESES

1. Feral horses in the TTSF do not use all habitats proportionate to habitat area showing preference for open habitats and avoidance of closed canopy habitats, and
2. There is a correlation between distribution of horse dung on-road and off-road within forest habitats.

6.2. METHODS

6.2.1. HABITAT CLASSIFICATION

Habitats were classified on the basis of age and approximate tree height, which were indicators of canopy density. Open canopy habitats included harvested pine (HP), which was a cleared forest often overgrown by annual plant species, and young pine (YP), with pine seedlings up to 3 years old. Closed canopy habitats included juvenile pine (JP) with tree canopy from 3 – 7 meters, and mature pine (MP), with mature pine stands above 7 meters and age older than 10 years. Distribution, size and detailed characterisation of each habitat was assessed from the records of Forestry Plantations Queensland and is presented in detail in Chapter 2.

6.2.2. DIRECT OBSERVATION OF HORSES

Horse habitat use was derived from all sightings of individually recognised horses within the habitats of the study area (SA; 99.1 km^2) from September 2011 to August 2013. Horses were observed during the day (0600 – 1800 hours) in 20 surveys; surveys were either performed monthly or every second month and were over a 4 - 5 day period. Each individual horse sighting was considered an independent observation and was assigned to one of the four habitats. Horses were observed with binoculars (Nikon Corporation, Tokyo, Japan; 10 x 22 magnification) from a distance of 50-1000 metres, taking care not to disturb the animal. The location of each sighting was marked on a 1:50 000 topographical map (Forestry Plantations Queensland 2011), and on a hand-held GPS (Garmin Oregon 550 Navigator, Garmin International, Kansas, USA). When horses moved in response to the observer, the initial habitat was documented. This approach eliminated a potential bias towards habitat preferences resulting from movement from one habitat into a different habitat.

6.2.3. DUNG COUNT METHOD

Horse habitat use was assessed for the SA, and the reminder of the plantation areas (TFA; 656.7 km^2), and was estimated from a dung count survey in June and July 2012 (Chapter 5). Dung density was estimated by the distance sampling method (Buckland et al. 2001), which was then used to estimate horse density by incorporating the individual defecation rate (7.97 ± 0.83 SEM defecations per 24 hours), and dung decay rate (444 ± 15 SEM) days. Horse abundance in each habitat and in each area was estimated by multiplying horse density/km^2 by respective habitat size (km^2). Total number of horses was obtained by adding the horse numbers from each habitat for the given area. Abundance estimates were taken from **Table 5.5**.

6.2.4. GPS TRACKING

Seven stallions and one mare, which were members of eight established harems were tracked from August 2013 to July 2014 (Chapter 7). The positional GPS (Sirtrack Ltd, Havelock North, New Zealand) data point (longitude and latitude) collection was two hourly. As forested habitats with dense canopy may sometimes affect GPS location determination (Moen et al. 1996), to increase precision of each data point, only these signals, that were obtained from ≥ 5 satellites were analysed. Each successful data point was imposed on the digitalised forestry topographical map in ARCGIS 10.1 (ESRI, Redlands, California, USA), which contained information on habitat classification and size.

6.2.5. DATA ANALYSES

Analyses of direct horse observations and dung counts were performed in multiple steps. Initially, the chi square test was used to determine the association between horse habitat use and habitat availability. The observed and estimated number of horses (O_i) derived in each habitat in each area from observations and dung counts were compared with the expected number of horses (E_i) in relation to the habitat size by the use of the Pearson chi-square statistic (*Eq. 1*).

$$\chi^2 = \sum_{i=1}^{N} \frac{(O_i - E_i)^2}{E_i} \qquad \textit{Eq. 1}$$

O_i – Observed frequencies
E_i – Expected frequencies
N – Number of pairs of expected and observed outcomes

Habitats that were used disproportionally relative to their distribution were identified by comparing the habitat selection ratio ($\widehat{w}_i$) to habitat availability (A_i) (*Eq. 2*). A habitat selection ratio $\widehat{w}_i$ greater than 1 indicated that the habitat was used at a higher frequency than its availability, while values of $\widehat{w}_i$ less than 1 indicated that the habitat was used at a lower frequency than its availability. Values $\widehat{w}_i$ equal to 1 signified an equivalent usage of the habitat to its availability (Neu et al. 1974; Byers et al. 1984; Manly et al. 2002). The relative probability of habitat selection was further determined by applying the standardized selection ratio index (B_i; *Eq. 3;* Manly et al. 2002).

$$\widehat{w}_i = O_i / A_i \qquad \textit{Eq. 2}$$

$$B_i = \widehat{w}_i / (\textstyle\sum_{i=1}^{1} \widehat{w}_j) \qquad \textit{Eq. 3}$$

To assess if there were seasonal changes in habitat use, the number of detected horses across seasons and habitats was assessed by two-way ANOVA with significance level at $P = 0.05$. For GPS tracking, the number of recorded GPS locations of each harem in each habitat was compared to the area of each habitat in the home range. Home range size was estimated as the 100% minimum convex polygon (MCP) that contained all data points (Moorcroft 2008) in ARCGIS 10.1. Harem membership remained stable during the study.

Because the size and distribution of habitats varied within the home range of each harem, these parameters were analysed by harem. This permitted assessment of habitat preferences of individual harems using *Eq. 2* and *3*. The differences in habitat selection ratio between harems were calculated with the Pearson chi-square contingency table with the significance level of $P = 0.05$. The overall habitat selection ratio was assessed by pooling data from six harems using the equation given below (*Eq. 4;* Manly et al. 2002).

$$\hat{w}_i = \hat{u}_{i+}/(\sum_{j=1}^{N} \hat{\pi}_{ij}\, \hat{u}_{+j}) \qquad \textit{Eq.4}$$

$\hat{w}_i$ - Habitat selection ratio from pooled observations for all harems
$\hat{u}_{i+}$ - Number of GPS locations for each habitat type for each harem
$\hat{u}_{+j}$ -Total number of locations for each harem
$\hat{\pi}_{ij}$ - Estimated proportion of available habitat of *i-th* and *j-th* harems
N – Number of harems

The detectability of horses in each of the habitats within the SA was obtained for 326 horse groups observed from a stationery vehicle over 10 months. Distances between horse groups and the observer were measured for 53, 37, 134, and 102 horse groups detected in MP, JP, YP, and HP habitats respectively. As confers are not deciduous, their canopy is not affected by season and therefore the assumption was made that the influence of canopy density on horse detectability would remain constant throughout the year. The initial location of undisturbed horse groups was marked on the topographic map and recorded with GPS, from which a perpendicular distance in metres to the observer was approximated to ± 10 metres. Differences in sighting distances within and between closed and open habitats were compared with the two tailed T-test.

Pearson's correlation coefficient was used to test the relationship between the dung encounter rate/km on-road and off-road. The relationship was measured on 18 square plots each 3km^2 which were randomly obtained from the TTSF topographical map. For each plot, information was recorded on dung encounter rate/km from on-road and off-road transect surveys. The strength of the relationship was measured with the two tailed T-test.

Data were analysed with Microsoft Excel® (Microsoft Corporation, Redmond, Washington USA) and R script (Calenge 2006) using standard statistical techniques. All results are presented with standard errors of the mean (SEM) and/or 95% confidence intervals (CI). The significance level was measured at $P = 0.05$.

6.3 RESULTS

6.3.1. DIRECT OBSERVATION OF HORSES

Total sightings of feral horses (*n* = 4903) were recorded in the SA over the observation periods. The highest number of horse sightings (*n* = 2468; 50.34%) occurred in YP, followed by HP (*n* = 1510; 30.80%). Closed canopy habitats of MP (*n* = 515; 10.50%) and JP (*n* = 410; 8.36%) were associated with the least number of sightings (**Table 6.1**).

Year	Closed canopy habitats		Open canopy habitats		Total
	MP	JP	YP	HP	
2012	174	199	1342	516	2231
2013	341	211	1126	994	2672
Total (*n*)	515	410	2468	1510	4903
Total (%)	10.50	8.36	50.34	30.80	100.00
	18.86%		81.14%		

Table 6.1: Number of feral horses sighted in the four habitats within the study area from September 2011 – August 2013. MP – mature pine; JP – juvenile pine; YP – young pine, and HP – harvested pine habitats.

6.3.2. DETECTABILITY OF HORSES

The detectability of horses in each of the habitats within the SA is presented graphically in **Figure 6.1**. There was no significant difference (*P* = 0.45) between sighting distances when the two closed habitats were compared to each other (MP mean 70 ± 8.4 m, and JP mean 60 ± 12.6 m). There was no significant difference (*P* = 0.88) between sighting distances when the two open habitats were compared (YP mean 260 ± 20.9 m, and HP mean 260 ± 20.4 m). When pooled data from closed and open habitats were compared, the difference in sighting distance was significant (*P* < 0.0001).

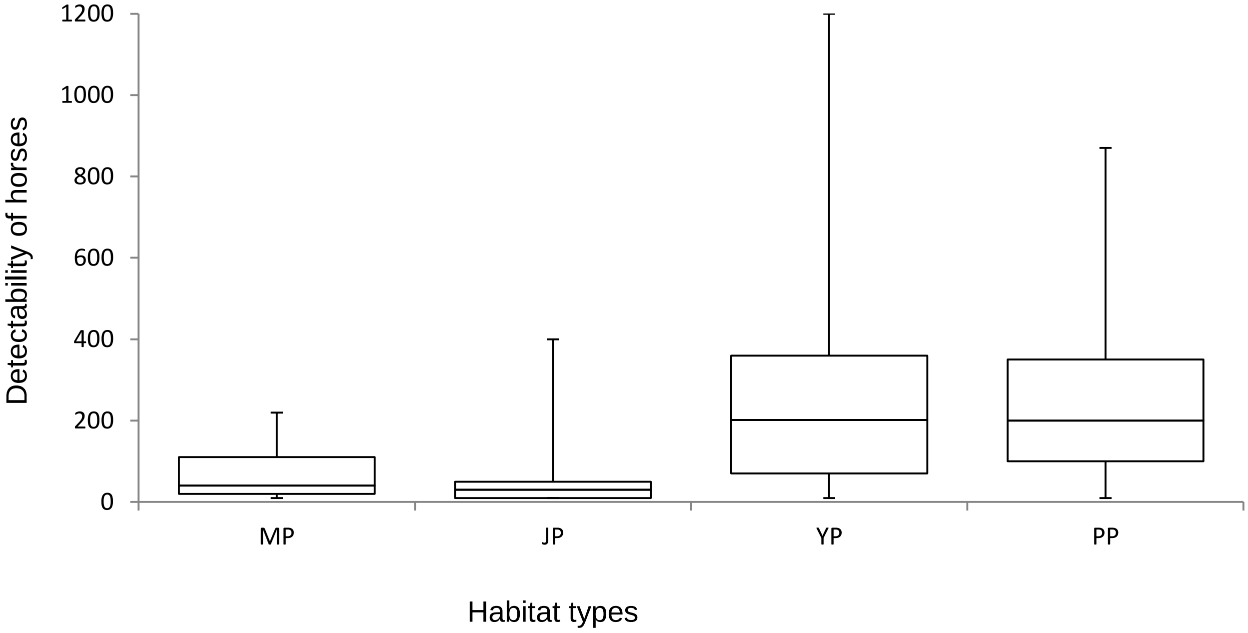

Figure 6.1: Detectability presented as median, upper and lower quartiles, and minimum and maximum range of feral horses in the four habitats within the study area. MP - mature pine; JP - juvenile pine; YP - young pine, and HP - harvested pine.

Analysis demonstrated that the expected and observed habitat use was significantly different ($\chi^2 = 903.0$; df = 3; $P \leq 0.001$), indicating that horses were not distributed proportionally across the available habitats in the study area. YP was the only habitat, which was used in proportion to its distribution (**Figure 6.2**).

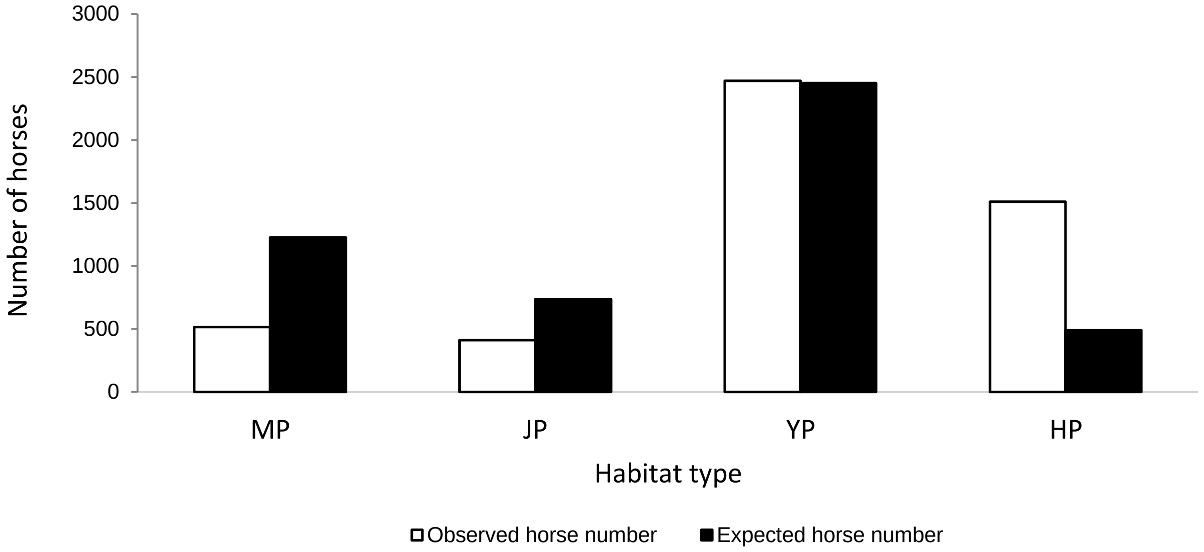

Figure 6.2: Observed and expected habitat use by feral horses relative to habitat availability is presented in white and black bars respectively. Data obtained from direct observations of horses between September 2011 and August 2013 within the study area. X axis – habitat type: MP - mature pine; JP - juvenile pine; YP - young pine; HP - harvested pine, and y axis – total number of observed horses.

The habitat selection index was calculated on pooled data across all seasons, because the number of detected horses in tested habitats did not vary significantly by season ($P = 0.165$). The index revealed that the closed canopy habitats of mature and juvenile pine were less likely to be selected by horses ($B_{MP} = 0.083$; $B_{JP} = 0.110$) than were open canopy habitats (**Table 6.2**). Young pine habitat ($B_{YP} = 0.199$) was twice as likely to be selected compared to juvenile and mature pine. Harvested habitat ($B_{HP} = 0.608$) was three times more likely to be selected than young pine and six times more than closed canopy habitats. The same relationships for given habitats is demonstrated by the $\hat{w}_i$ values.

Habitat type	Habitat availability (SA_i)	Number of sightings (U_i)	Expected habitat use $E_i=\pi_i*\Sigma U_i$	Observed habitat use $O_i=U_i/\Sigma U_i$	Habitat selection ratio $w_i=O_i/A_i$	Habitat selection index $B_i=w_i/\Sigma U_i$	SEM	Low 95% CI	Upper 95% CI
MP	0.25	515	1226	0.105	**0.420**	0.083	0.004	0.412	0.429
JP	0.15	410	735	0.084	**0.557**	0.110	0.004	0.550	0.565
YP	0.50	2468	2452	0.503	**1.007**	0.199	0.007	0.993	1.021
HP	0.10	1510	490	0.308	**3.080**	0.608	0.007	3.067	3.093
Total	1.00	4903	4903	1.000	5.064	1.000			

Table 6.2: Estimation of habitat selection based on direct observations from September 2011 to August 2013 within the SA. The selection ratio (BOLD) $w_i > 1$ indicates that habitats are used at a higher frequency than their availability; where $w_i < 1$ indicates that habitats are used less frequently than their availability, and where $w_i = 1$ indicates that habitats are used proportionate to their availability.

6.3.3. DUNG COUNT METHOD

The overall expected and estimated habitat use by horses in the study area was not significantly different ($\chi^2 = 4.43$; df = 3; $P = 0.219$). Horses were distributed evenly and in proportion to the size of the available habitats (**Figure 6.3a**). However, habitat use was significantly different ($\chi^2 = 149.0$; df = 3; $P < 0.001$) in the TFA area, indicating that horses were not distributed proportionally across all habitats in the remainder of the plantation (**Figure 6.3b**).

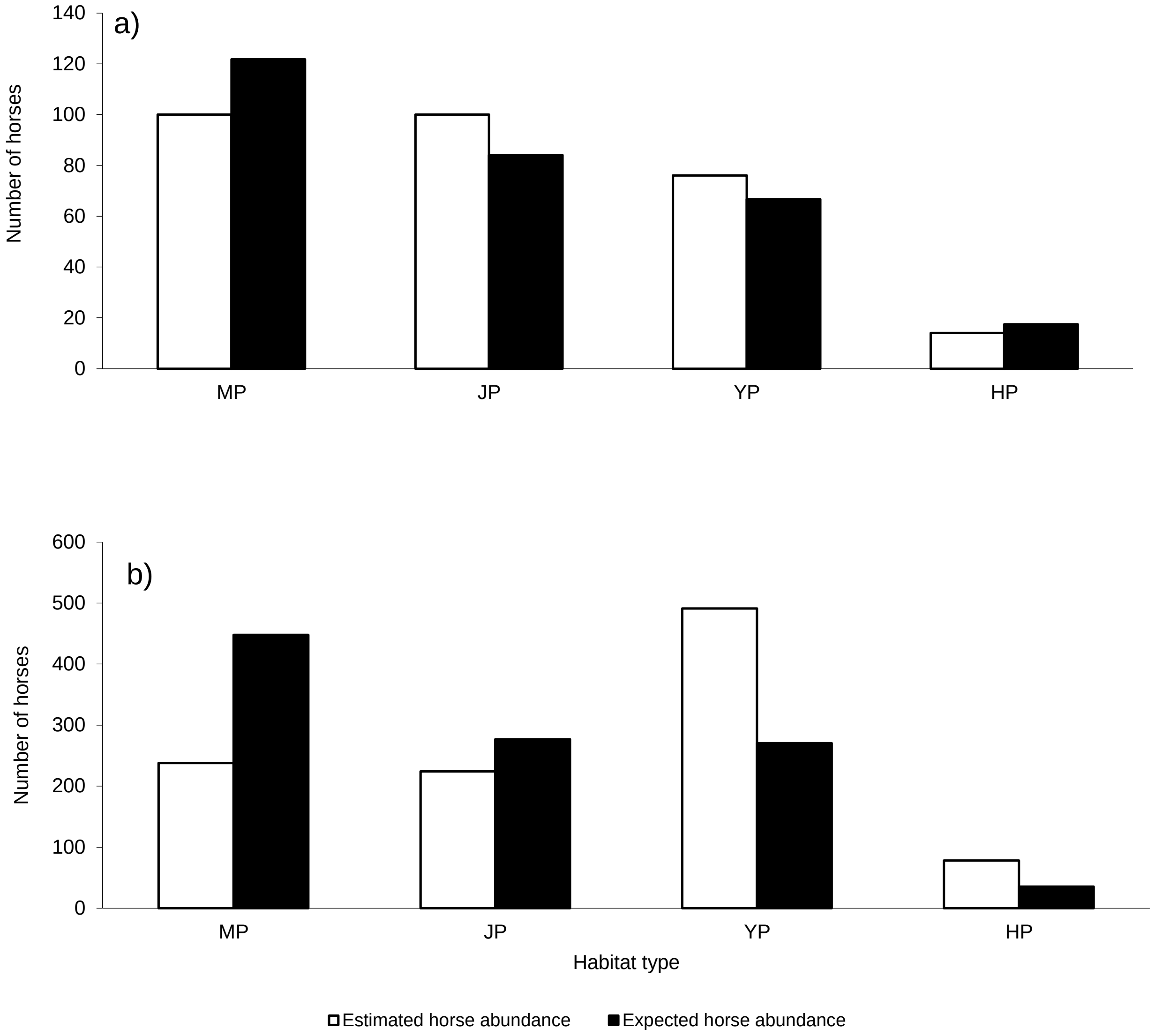

Figure 6.3: Observed and expected habitat use by feral horses relative to habitat availability is presented in white and black bars respectively. Data obtained from dung counts in July 2012 within a) SA and b) TFA. X axis – habitat type: MP - mature pine; JP - juvenile pine; YP - young pine; HP - harvested pine, and y axis – total number of estimated horses.

The habitat selection index calculated in the study area based on dung counts was the highest for juvenile ($B_{JP} = 0.301$) and young pine ($B_{YP} = 0.288$), indicating these habitats were more likely to be selected by horses than mature ($B_{MP} = 0.208$) and harvested pine ($B_{HP} = 0.203$, **Table 6.3**). The habitat selection index calculated for TFA revealed that horses demonstrated strong preferences for open habitats. Harvested ($B_{HP} = 0.373$) and young pine ($B_{YP} = 0.362$) habitats were selected the most, and more than twice as much as juvenile ($B_{JP} = 0.159$) and nearly four times more than mature pine ($B_{MP} = 0.106$) habitats (**Table 6.4**).

Habitat type (SA)	Habitat availability (A_i)	Estimated number of animals (U_i)	Expected habitat use $E_i=\pi_i*\Sigma U_i$	Observed habitat use $O_i=U_i/\Sigma U_i$	Habitat selection ratio $w_i=O_i/A_i$	Standardized selection index $B_i= w_i/\Sigma U_i$	SEM	Low 95% CI	Upper 95% CI
MP	0.42	100	122	0.345	**0.821**	0.208	0.028	0.766	0.876
JP	0.29	100	84	0.345	**1.189**	0.301	0.028	1.134	1.244
YP	0.23	76	67	0.262	**1.139**	0.288	0.026	1.089	1.190
HP	0.06	14	17	0.048	**0.805**	0.203	0.013	0.780	0.829
Total	1.00	290	290	1.000	3.954	1.000			

Table 6.3: Estimation of habitat selection based on dung counts within the SA. The selection ratio (BOLD) $w_i > 1$ indicates that habitats are used at a higher frequency than their availability; where $w_i < 1$ indicates that habitats are used less frequently than their availability, and where $w_i = 1$ indicates that habitats are used proportionate to their availability.

Habitat type (TFA)	Habitat availability (A_i)	Estimated number of animals (U_i)	Expected habitat use $E_i=\pi_i*\Sigma U_i$	Observed habitat use $O_i=U_i/\Sigma U_i$	Habitat selection ratio $w_i=O_i/A_i$	Standardized selection index $B_i= w_i/\Sigma U_i$	SEM	Low 95% CI	Upper 95% CI
MP	0.43	238	443	0.231	**0.537**	0.106	0.013	0.511	0.563
JP	0.27	224	278	0.217	**0.805**	0.159	0.013	0.780	0.830
YP	0.26	491	268	0.476	**1.832**	0.362	0.016	1.801	1.862
HP	0.04	78	41	0.076	**1.891**	0.373	0.008	1.875	1.908
Total	1.00	1031	1031	1.000	5.065	1.000			

Table 6.4: Estimation of habitat selection based on dung counts in the remainder of the plantation (TFA). The selection ratio (BOLD) $w_i > 1$ indicates that habitats are used at a higher frequency than their availability; where $w_i < 1$ indicates that habitats are used less frequently than their availability, and where $w_i = 1$ indicates that habitats are used proportionate to their availability.

6.3.4. GPS TRACKING

Failure of the GPS tracking loggers to transmit data meant that habitat use by two harems could not be assessed. Six harems contributed 11881 location coordinates with a mean of 1980 ± 1174 locations per harem.

The results of the habitat selection index pooled for six harems revealed that the closed canopy habitats of mature and juvenile pine were less likely to be selected by horses ($B_{MP} = 0.087$; $B_{JP} = 0.205$) than open canopy habitats. Harvested pine ($B_{HP} = 0.397$) was twice as likely to be selected as that of juvenile pine and over four times more likely to be selected than mature pine (**Table 6.5**).

Habitat type	Habitat selection ratio (w_i)	Standardized selection index (B_i)	SEM	Low 95% CI	Upper 95% CI
HP	**1.784**	0.397	0.469	1.288	2.253
YP	**1.238**	0.310	0.353	0.885	1.591
JP	**0.864**	0.205	0.241	0.623	1.105
MP	**0.339**	0.087	0.100	0.239	0.439
Total	4.225	1.000			

Table 6.5: Estimation of habitat selection of six harems based on GPS location data. The selection ratio (BOLD) $w_i > 1$ indicates that habitats are used at a higher frequency that their availability; where $w_i < 1$ indicates that habitats are used less frequently than their availability, and where $w_i = 1$ indicates that habitats are used proportionate to their availability.

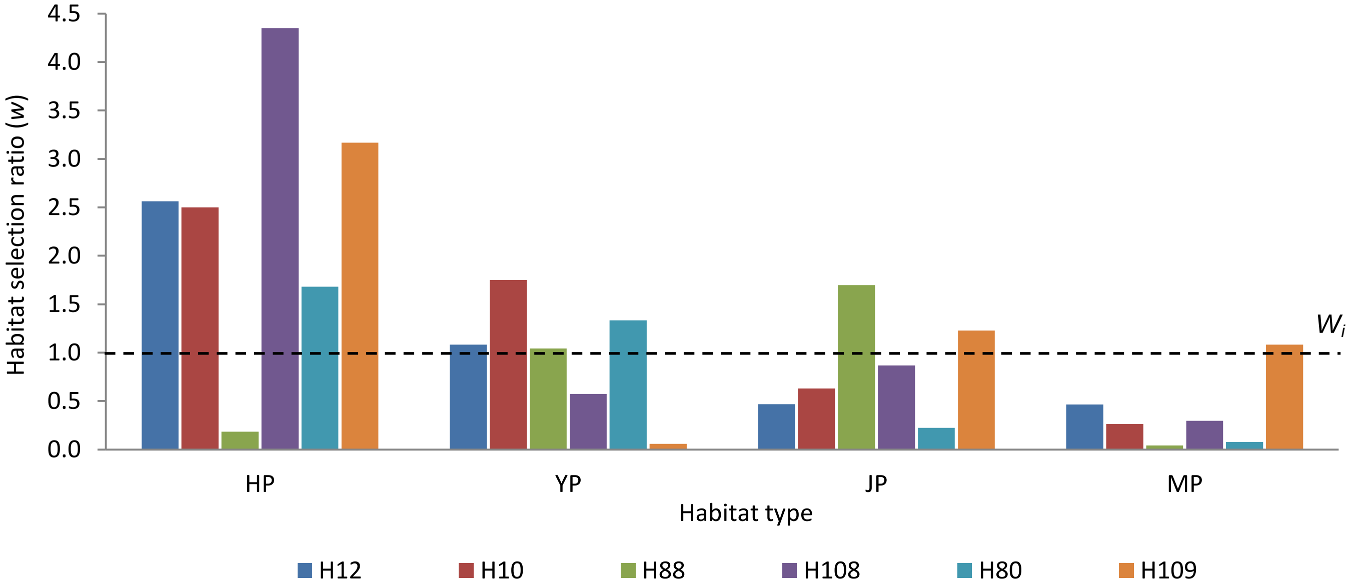

Figure 6.4: GPS location coordinates of six harems in the four habitats within the TTSF. HP – harvested pine; YP – young pine; JP – juvenile pine; MP – mature pine; where the habitat selection ratio $w_i > 1$ indicates that habitats are used at a higher frequency that their availability; where $w_i < 1$ indicates that habitats are used less frequently than their availability, and where $w_i = 1$ indicates that habitats are used proportionate to their availability.

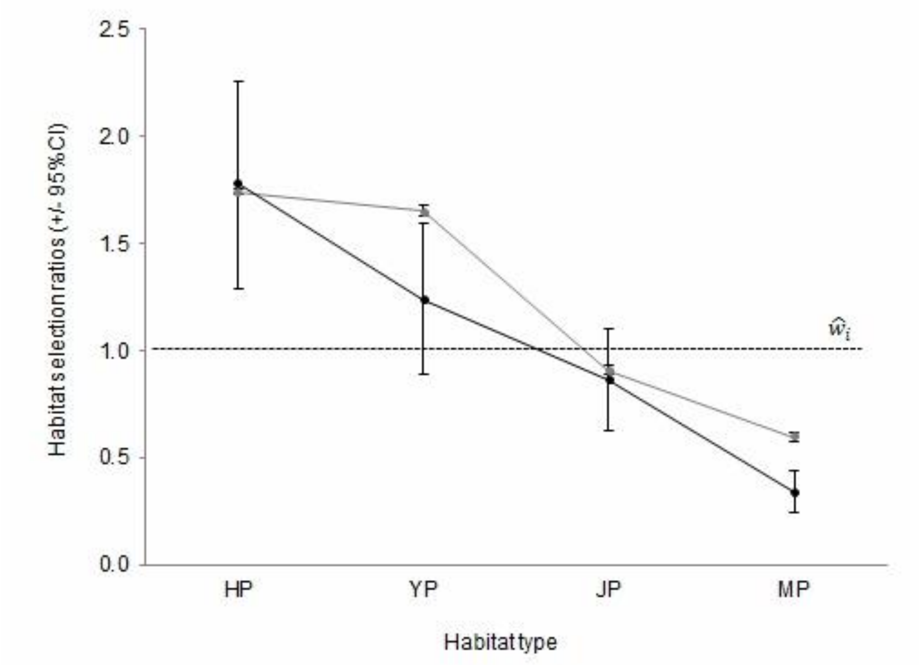

Figure 6.5: Habitat selection ratios with 95%CI from pooled SA and TFA sites from dung counts (grey) and pooled GPS tracking (black) in the four habitats within the TTSF. HP – harvested pine; YP – young pine; JP – juvenile pine; MP – mature pine. Habitat selection ratio $w_i > 1$ indicates that habitats were used at a higher frequency than their availability, and where $w_i < 1$ indicates that habitats were used less frequently than their availability.

6.3.5. DISTRIBUTION OF HORSE DUNG

There was a positive correlation between dung encounter rate off-road within forestry habitats and that encountered on forestry roads ($r = 0.64$, $df = 16$, $P < 0.01$). This indicates that the distribution of dung on forestry roads can be used to determine feral horse preference for particular habitats (**Figure 6.6**).

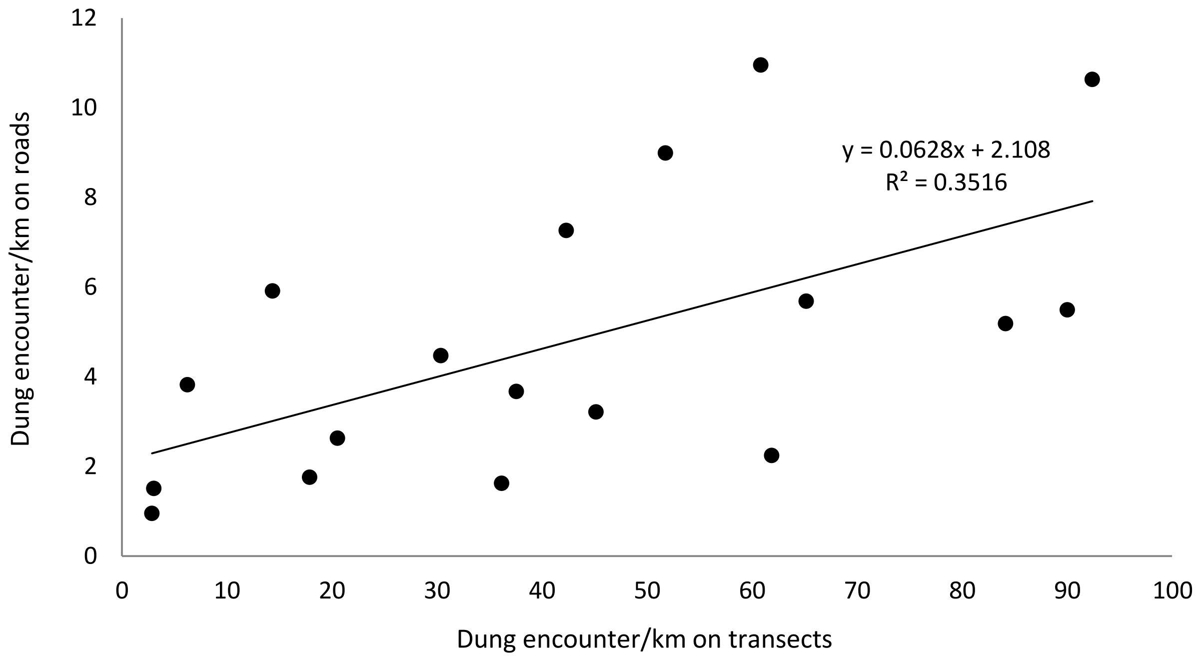

Figure 6.6: The relationship between horse dung off- and on-roads in the Tuan and Toolara State Forest in June and July 2012.

6.4. DISCUSSION

Feral horses in the Tuan and Toolara State Forest showed a preference towards open habitats, and avoidance of closed canopy habitats of juvenile and mature pine. The likely explanation for the preference of open habitats is greater availability of forage although this was not analysed. It has been recognised previously that the composition and density of ground vegetation is influenced by forest maturation (Wang 2008), and this, in turn, impacts on the population dynamics of resident herbivores (Doerr and Sandburg 1986; Putman 1986; Gill et al. 1996). Studies of various Cervidae and mouflon sheep show that these species achieve higher population densities in cleared areas and young forest stands, and decline as the canopy of older stands close (Irwin and Peek 1979; Staines and Welch 1984; Gill et al. 1996; Kuiters et al. 1996). Cleared, open forest habitats stimulate the growth of grasses offering greater grazing opportunities. As the canopy closes, less light penetrates the canopy resulting in a decline in pasture quality and quantity, which in turn leads to decrease in animal numbers (Gill et al. 1996; Hemami et al. 2004).

Open habitats permit greater visibility for grazing animals and therefore reduce the risk of predation and other threats. The majority of horses observed in open environments were located on slopes and open ridges, which maximised their ability to visualise danger. It was very difficult to approach these animals without alerting them. Other studies have also observed that feral horses preferred elevated terrains (Pellegrini 1971; Welsh 1975; Keiper and Berger 1982; Ganskopp and Vavra 1986). Keiper and Berger (1982) speculated that feral horses occupied ridge-tops to minimise harassment by insects, and Ganskopp and Vavra (1986) hypothesized that elevated terrain enhanced the visual detection of danger.

In the current study, ease of detectability in open habitats is likely to have influenced outcomes creating a bias that would find in favour of increased use of open habitats. Unequal detectability in woodland and streamside habitats is a common predicament in observational studies of wild herbivores, resulting in an underestimation of animal detection rates in denser habitats (Otis et al. 1978; Crane et al. 1997). An additional bias may have been introduced by the restriction of observational studies to daylight hours as large herbivore activity has been shown to vary between day and night (Putman 1986; Dyring 1990; Moen et al. 1996; Margues et al. 2001). Open habitats are more used during foraging and closed canopy habitats are more preferred when resting (Cook et al. 1998), hiding from predators (Turner 1979), or relieving from environmental conditions (Parker 1988; Wood 1988).

Putman (1986) evaluated horse habitat preferences in a coniferous-only habitat in the UK, and showed that horses occupied open areas more extensively during daylight hours and in milder weather but moved into woodlands overnight and during the winter; the suggestion being that closed habitats provided better protection from changing weather conditions. The lack of night-time observations may therefore misrepresent the true habitat preference; particularly as nocturnal activity by feral horses has been well documented (Putman 1986; Berman 1991; Petersen et al. 2012). If horses in the TTSF used closed canopy habitats overnight, this behaviour would have gone undetected in the current study.

Diurnal observations performed by Crane et al. (1997) revealed that feral horses used the same foraging areas the following day. This is consisted with observations in the current study. Such observations, however, do not exclude the possibility of habitat changes occurring overnight with horses migrating from open to closed habitats. Forest ungulates are known to prefer open habitats located in close vicinity to cover (Keay and Peek 1980; Takatsuki 1989; Hansson 1994). The TTSF is sectioned into numerous small compartments, where closed and open habitats are often in close proximity and horses can move easily between them (**Figure 6.7**). Open habitats are often interspersed with long strips of native vegetation, which offer shelter to the horses during hot days but could also provide overnight shelter.

Figure 6.7: Dense habitats of juvenile pine and native woodland, located beside open habitats of young and harvested pine, provide feral horses with shelter and protection.

Distribution of dung permits longitudinal assessment of animal occupancy in a given habitat (Neff 1968). This is because higher densities of dung are expected in habitats of higher and longer animal activity (Hemami et al. 2004). For this reason, dung counts can be used to provide useful and more realistic estimates of habitat use of large herbivores when compared with the results obtained from visual detection of animals (Margues et al. 2001).

The dung count surveys, however, showed greater preference of horses for open habitats in the TFA compared to the SA. The difference in habitat use between these sites may be due to differences in horse density. The SA had a much higher density (2.92 horses/km^2) than the rest of the forest (1.79 horses/km^2), possibly offering fewer grazing alternatives for the horses. The lower density of horses elsewhere in the plantation would appear to offer greater grazing opportunities because of the greater availability of ground vegetation (Kuiters et al. 1996). Horses are known for their selective feeding behaviour and avoidance of less digestible components of the available forage (Berman 1991; Duncan 1992). This behaviour could therefore result in a larger spacing of animals in less densely occupied forest areas and increased foraging options in open areas.

Differences in habitat use between the SA and TFA may have been due to differences in habitat distribution. Both contained open habitats of similar total area but the open habitats of the SA were essentially two in number whereas those of the TFA were more diffusely dispersed. The large, coalesced open habitats of the SA meant that closed habitats were very peripheral in location whereas the closed habitats of the TFA were near to the open habitats. The geography of the two areas may therefore have influenced habitat selection and preference.

The use of GPS meant that data collection was not affected by season, time of the day or weather (Brooks et al. 2008). Moreover, it permitted constant monitoring of animals in dense woodland environments, which was unattainable by direct observations. Although restricted to six harems, GPS tracking provided extensive data on habitat use within the home ranges of the six harems and demonstrated significant horse preferences towards open habitats, in particular to harvested pine. These results were consistent with those obtained from the dung count method for the TFA.

Differences in habitat use between individual harems were likely the result of differences in habitat distribution and size in their respective home ranges and not solely a reflection of habitat preferences. Harems have been shown to be philopatric in the TTSF; therefore it appears that horses were making the best use of resources within habitats contained within their respective home range, rather than searching for resources beyond their home range. However, this behaviour could be the result of there being sufficient foraging options within the open habitats of their home ranges as five of six harems preferentially used open habitats. Strong philopatry of wild and feral horses and utilisation of available habitats within home ranges has been reported previously (Tyler 1972; Gates 1979; Linklater 1998; Kaczensky et al*.* 2008). The harem that showed almost equal use of open and closed canopy habitats was small, consisting of one stallion, one mare, and her offspring. Perhaps the lower energy requirements of this small group meant that their energy needs were met by all of the habitats within their home range.

Dung disappearance rates showed that fresh dung indicated horse activity within the previous several weeks and, in certain circumstances, old dung could persist in plantation areas for up to two years. The positive relationship between the distribution of horse dung on plantation roads and within plantation habitats means that road dung surveys can be used to assess population distribution thorough the TTSF. Moreover, the presence of fresh dung in plantation areas, which were previously clear from dung may indicate colonisation of new areas, while lack of fresh dung can be used as a measure of the effectiveness of population management within specific areas of the plantation.

6.5. CONCLUSIONS

This is the first study to measure habitat use by feral horses in a coniferous forest in Australia. Not all habitats in the Tuan and Toolara State Forest were used equally and there was a strong preference for open habitats of young and harvested pine. This imbalance of habitat use imposes varying grazing pressures and influences carrying capacity of the available habitats. This pattern of use means that horses tend to move into newly created (harvested) open areas located within or adjacent to their home range.

Dung counts were shown to be a useful method for determining longitudinal habitat occupancy of horses. Although less costly and less time consuming, opportunistic visualisation method has limited use in closed canopy habitats due to reduced animal detection rates. GPS data collection is the most reliable method to investigate seasonal variations in habitat use and would enable predictive modelling of forestry harvesting regimens for the purposes of feral horse population management. Cost of the GPS collars and the logistics and costs involved in their application precludes their routine use in the determination of management strategies at this time (Zabek et al. 2014).

CHAPTER 7: HOME RANGE

7.1 INTRODUCTION

Home range size and movement are governed by the spatial needs of animals, and are indicators of how animals interact with their environment (Johnson et al. 2002; Kaczensky et al. 2008; Whyte et al. 2013). Home range is defined as area animals are entirely familiar with and where normal activities occur such as searching for food, water and shelter, caring for offspring, and breeding (Burt 1943; Berger 1986; Springer 2003). Often, home range is defined as the smallest area associated with a 95% probability of finding the animal (Fieberg and Kochanny 2005). Locations, which are temporarily occupied as a result of immigration, emigration, or infrequent excursions, are not usually considered to be a part of home range (Moorcroft 2008).

Home range utilisation may vary in intensity. Core use areas are regions in which animals concentrate the majority of their activities, and are usually correlated with utilisation of resources (Moorcroft 2008). Differences in home range size and utilisation intensity can be due to different gender behaviours (Anderson et al. 2005; Harless et al. 2010; Whyte et al. 2013), seasonal activity (Bauer et al. 1994; Anderson et al. 2005; Ryan et al. 2006), and diurnal and nocturnal living (Harless et al. 2010).

Historically, wildlife movement was tracked (sampled) using previously identified (and usually marked) individuals (Welsh 1973; Ganskopp and Vavra 1986; Linklater 2000a). Historically, many feral horse population studies have used direct observation to estimate home range size (**Table 7.1**). Radio telemetry revolutionised the study of animal movement, allowing routine assessment of animal location by attaching very high frequency (VHF) transmitters (Moorcroft 2008; Kaczenski 2010a). Since the development of Global Positioning System (GPS) technology the collection of spatiotemporal data related to animal movement and location can be obtained in a systematic manner independent of terrain, climatic conditions and time of day (Brooks et al. 2008; Moorcroft 2008). The use of GPS telemetry can provide invaluable data without disrupting natural behaviours (Hulbert and French 2001; Johnson et al. 2002; Brooks et al. 2008; Blackie 2010).

Mean number of locations (range)	Study length (months)	Home range (km^2)	Habitat type	Estimation method	Location	Source
290-1357	4 - 29	152 - 826	AS+SD	100% MCP	Gobi B, Mongolia	Kaczensky et al. 2008
648-1570	13-22	4449 - 6835	AS+SD	100% MCP	Gobi B, Mongolia	Kaczensky et al. 2008
90-145	32	0.96 - 17.7	MG+SH	95% MCP	Kaimanawa Ranges, NZ	Linklater 1998
20.4 (10-56)	17.7	5.4 – 25.2	AS+AG	100% MCP	Oregon USA	Ganskopp & Vavra 1986
45-131	30.4	73.0 – 303.0	AS+AG	100% MCP	Wyoming USA	Miller 1983
23.3 (13-33)	10.3	2.6 – 14.4	CF+DF	NP	Western Alberta, CAN	Salter & Hudson 1982
NP*	24	2.50 – 3.28	MG	100% MCP	Exmoor UK	Gates 1979
NP	36	0.8 – 10.2	MG+W	NP	New Forest UK	Tyler 1972
NP	5 years	20.0 – 25.0	MGS+W	NP	Shackleford Island, USA	Rubenstein 1981
NP	7	3.0 – 32.0	AS+AG	NP	Pryor Mountain, USA	Feist and McCullough 1976
NP	36	< 7.0	MGS	NP	Sable Island USA	Welsh 1973

Table 7.1: Published studies on home range size of wild and feral equids using data obtained by GPS and direct observation. * sample size not provided, but observations were performed weekly for 3 days over 2 years; NP – sample size not provided by the source; habitat classification: AS - arid steppe; SD – semi-desert and desert; CF - coniferous forest; MG - mesic grassland; SH - shrub heath; AG - arid grassland; DF - deciduous forest; W – woodland, and MGS - maritime grassland and shrub-land.

The minimum convex polygon (MCP) is a widely employed method to estimate the ‘absolute home range size’ of animals (Getz et al. 2007; Moorcroft 2008; Nilsen et al. 2008; Harless et al. 2010). It provides an estimate of the home range area by joining the outermost points of a distribution in the form of a polygon such that no internal angle is greater than 180^o (Hayne 1949; Harless et al. 2010). The method however; does not allow precise assessment of geographical distribution within the area measured, so it does not accurately represent where animals spend time within their home range (Taulman and Seaman 2000; Burgman and Fox 2003; Ryan et al. 2006; Nilsen et al. 2008).

The local convex hull (LoCoH) method permits a more comprehensive analysis of spatial use by defining the outer boundary of home range, and simultaneously identifying the density of space used (Getz and Wilmers 2004; Getz et al. 2007). It also allows the construction of a convex hull polygon, which is associated with each data point and its nearest neighbouring points ‘k’. Convex hull polygons are progressively merged from smallest to largest, until a chosen percentage of data points are included (Getz and Wilmers 2004). The constructed areas are represented by isopleths, which define regions with different probabilities of animal use (Getz et al. 2007). The delimited boundaries exclude areas unused by animals (holes within the home range), which can be a result of habitat avoidance, and areas arising from the movement of animals influenced by hard boundaries, such as fences, roads, and rivers, and irregular environmental structures such as rock formations or changes in habitat structure (Getz et al. 2007).

AIMS AND OBJECTIVES

While it has been demonstrated that feral horses adjust their home range size and movements to available resources (Tyler 1972; Linklater 1998; Hampson et al. 2011), it is unclear how a coniferous habitat influences the spatial use of the environment by feral horses. This study was designed to determine the extent and spatial use of the home range of feral horses in the TTSF using a LoCoH method and two sampling techniques: visual localisation of horses and GPS tracking. Information on home range size and core use areas will be used to model horse removals from forest areas bordering public roads.

HYPOTHESES

1. Home ranges of observed and GPS-tracked harems are small and overlapping, and
2. Feral horses do not utilise their entire home range with equal intensity, with certain areas (core areas) being utilised more intensively than other areas.

7.2. METHODS

7.2.1. VISUAL LOCALISATION OF HAREMS

Locations of all known harems (n = 72) were identified monthly between September 2011 and March 2014 using mark-recapture surveys, line transect surveys, and opportunistic sightings while performing other research activities in the TTSF. Harems were located visually, with and without aids (Nikon Action, Nikon Corporation, Tokyo, Japan,10 x 22 magnification binoculars). Each daily sighting was considered an independent observation. Sighting locations were marked on 1:50 000 topographical maps (Forestry Plantations Queensland 2011) and on a hand-held GPS (Garmin Oregon 550 Navigator, Garmin International, Kansas, USA). The input file contained date, harem identification number, habitat type, and longitude and latitude. When horses moved in response to the observer, the initial location prior to moving was documented.

7.2.2. HAREMS TRACKED BY GPS

Between August and November 2013, one female and seven adult male horses, who were members of known, established harems, were immobilised with medetomidine hydrochloride (Bova Compounding, New South Wales, Australia), and toletamine-zolazepam (Zoletil; Virbac, Queensland, Australia; Zabek et al. 2014). These horses were fitted out with a GPS collar (Sirtrack Ltd, Havelock North, New Zealand), which was equipped with a Pinnacle Iridium Satellite System (Iridium Incorporation, Virginia, USA). Collars were equipped with an automatic release mechanism, a built-in VHF antenna, and were powered with 3A lithium batteries, simultaneously powering GPS and VHF transmitters. Collars were placed around the cranial aspect of the neck immediately caudal to the ears and mandibular rami, and were snugly fitted to allow a 3cm gap between the collar and the skin. Collars weighed 900g being approximately 0.23% of horse body weight based on animal body weight of 400kg and were in the accepted body to collar weight ratio (Brooks et al. 2008). The GPS data logger was scheduled to transmit a signal to satellites at two hourly intervals and data were subsequently available for downloading at 48 hourly intervals. As dense canopy habitats may sometimes affect GPS location determination (Moen *et al*. 1996), only data obtained from ≥ 5 satellites were included in the analysis. Location data were superimposed on a digitised forestry topographical map (FPQ Fraser Coast Map 2011) in ARCGIS 10.1 (ESRI, Redlands, California, USA), which contained information on habitat classification and size. Downloaded data included: date, time, latitude, longitude, altitude, speed (km/h), heading, number of satellites, and horizontal dilution of precision (HDOP).

7.2.3. DATA ANALYSES

Home range size was defined as an area that horses were known to use during the study period and was estimated by the LoCoH method for two sampling techniques. The LoCoH technique allowed a construction of the convex polygon hull, which was associated with each data point (latitude and longitude) and its k-1 nearest points (k-LoCoH), (Getz and Wilmers 2004; Getz et al. 2007). Convex hulls were successively merged from smallest to largest into respective isopleths, representing high and low animal density (Getz and Wilmers 2004). Home ranges (100% LoCoH) were calculated by setting the number of k-nearest points to the value of the square root of the number of all data points (Getz and Wilmers 2004). The chosen k-value was then evaluated against different isopleths for the best fit to the portion of previously covered area.

Quantitative assessment of the space use and site fidelity (core use area) was determined by measuring the largest amount of time animals spent in a given location (Worton 1987; Harless et al. 2010). Plots of the utilisation distribution of fixes indicated that the biggest change in slope of the line occurred between the 70 and 80% isopleths. The core area was therefore defined as the area enclosed by the 70% isopleth (Horsup 1994).

Longitude and latitude data were collected in decimal degrees and re-projected to Universal Transverse Mercator (UTM) in ARCGIS 10.1 (ESRI, Redlands, California, USA). All statistical analyses were performed in the software R (R, Developmental Core Team 2012) with the '*LoCoH adehabitat'* package. Home range size and core use areas estimates (m^2) were taken directly from the software output and converted into square kilometres.

To determine the number of data points required to approach an asymptote of home range, each visually located harem's cumulative home range area was plotted against the number of data points for individual harems, which were located at least once a month and not less than 40 times. This was the approximate sample size obtained by direct observations at which home-range size did not increase in the population of Kaimanawa feral horses in New Zealand (Linklater 1998). Therefore, harems (n = 59 of 72) located less frequently were excluded from home range analyses.

The overlap of home ranges of all harems was quantified using the index proposed by Horsup (1994), and Baker (2001), which was expressed as follows: [(the percentage of the home range of harem X that overlaps the home range of harem Y) + (the percentage of the home range of harem Y that overlaps the home range of harem X)]/2.

To investigate the relationships between sampling frequency (number of obtained location coordinates) on home range size, home range size and core use areas, and harem size on home range size, the Pearson correlation test was used. For all tests the significance level was set to $P < 0.05$. Results are presented as mean ± SD and range.

7.3. RESULTS

7.3.1. TRACKING LENGTH

The duration of observations and number of visual localisations of 13 harems located at least 40 times is presented in **Table 7.2**. The frequency of observed harems varied because of harem movement relative to the study area where the surveys were conducted and habitat type. On average, harems were observed over 24.74 ± 3.59 (range 21 - 29) months, giving 50.25 ± 14.82 (range 40 - 83) locations, at 2.0 ± 0.59 (range 1 - 9) locations per survey.

Harem ID	Start date	End date	Observation period (months)	N Locations	Mean ± (SD) locations per month
H1	Sep 2011	Mar 2014	29	60	2.1 (1.3)
H5	Oct 2011	Mar 2014	28	46	1.6 (1.1)
H7*	Oct 2011	Sep 2013	21	66	3.1 (1.9)
H9	Oct 2011	Mar 2014	28	42	1.5 (1.3)
H15*	Oct 2011	Oct 2013	23	58	2.5 (1.5)
H29	Dec 2011	Mar 2014	27	43	1.6 (1.8)
H45	Dec 2011	Mar 2014	27	49	1.8 (1.6)
H46	Jan 2012	Mar 2014	26	52	2.0 (1.7)
H47	Jan 2012	Mar 2014	26	48	1.8 (1.4)
H52	Jan 2012	Mar 2014	26	83	3.2 (2.5)
H54	Jan 2012	Mar 2014	26	70	2.7 (1.9)
H71	Apr 2012	Mar 2014	23	55	2.4 (1.9)
H75	May 2012	Mar 2014	22	40	1.8 (1.6)
Mean (SD)			24.74 (3.59)	50.25 (14.82)	2.00 (0.59)

Table 7.2: Harem identification, and start, end, and length of data collection, and number of locations of 13 harems observed more than once monthly from September 2011 to March 2014. * harems that disbanded before the end of the study.

GPS tracking provided data of variable duration, ranging from five days to 10 months (**Table 7.3**). Differences in tracking length were due to failure of the GPS tracking loggers to transmit data, which meant that home range size for two harems (H1 and H106) could not be assessed. For the remaining six harems, tracking length was too short to allow seasonal assessment of the spatial use of home range. After the exclusion of H1 and H106 from GPS analysis, the mean tracking period of six harems was 178 ± 211 days, with an average of 1980 ± 1174 GPS locations per harem.

Harem ID	Start date	End date	Tracking period (days)	N GPS fixes
H12	17/08/13	12/06/14	299	3413
H10	17/08/13	10/06/14	297	3286
H88	13/10/13	11/03/14	149	1730
H108	16/11/13	01/06/14	197	1972
H80	16/11/13	21/01/14	67	771
H109	17/11/13	17/01/14	62	711
Mean (SD)			178 (211)	1980 (1174)

Table 7.3: Harem identification, and start, end, and length of data collection, and number of obtained data points of six harems tracked by GPS from August 2013 to June 2014.

7.3.2. HOME RANGE SIZE ESTIMATE

Home range size of individual harems from direct observations are presented in **Table 7.4** and from GPS tracking in **Table 7.5**. Home range sizes estimated by the LoCoH method from direct observations ranged from 1.30 - 14.18 km^2, and averaged at 6.71 ± 3.30 km^2. Home ranges of the GPS tracked harems differed significantly in size from home ranges constructed using location coordinates from direct observations ($P = 0.003$) and averaged 16.9 ± 9.11 km^2 (range 8.43 – 33.36 km^2). Harems used one distinct core area, averaging 2.21 ± 1.11 km^2 (range 0.38 - 4.12km^2) for observed harems, and 2.78 ± 0.64 km^2 (range 1.27 to 3.46 km^2) for GPS tracked harems.

Harem ID	Mean harem size	Home range size (km^2)	Core area (km^2)
H1	9.5	7.08	2.45
H5	6.3	11.18	2.25
H7	5.3	4.93	1.17
H9	4.9	8.44	3.36
H15	4.0	1.65	0.68
H29	5.0	1.30	0.38
H45	7.4	9.16	4.12
H46	7.0	14.18	2.85
H47	5.6	9.24	4.04
H52	10.0	7.22	2.11
H54	5.2	5.15	2.18
H71	5.6	4.82	1.45
H75	4.5	5.68	1.05
Mean	6.18	6.71	2.21
(SD)	(1.71)	(3.30)	(1.11)

Table 7.4: Harem identification, and size, home range size, and size of core use area of 13 harems observed more than once monthly from September 2011 to March 2014.

Harem ID	Mean harem size	Home range size (km^2)	Core area (km^2)
H12	4	8.44	2.29
H10	4	17.43	3.18
H88	4	16.56	1.63
H108	3	33.36	3.46
H80	8.8	8.43	1.94
H109	4.5	17.16	1.27
Mean	4.72	16.90	2.78
(SD)	(1.88)	(9.11)	(0.64)

Table 7.5: Harem identification, and size, home range size, and size of core use area of six harems tracked by GPS from August 2013 to June 2014.

The home ranges of visually located harems were under-sampled. This is shown by the lack of asymptotes in the cumulative home range areas of individual harems, with the exception of harem H15 (**Figure 7.1**). This indicates that 12 harems were not located often enough to provide representative home range size estimates.

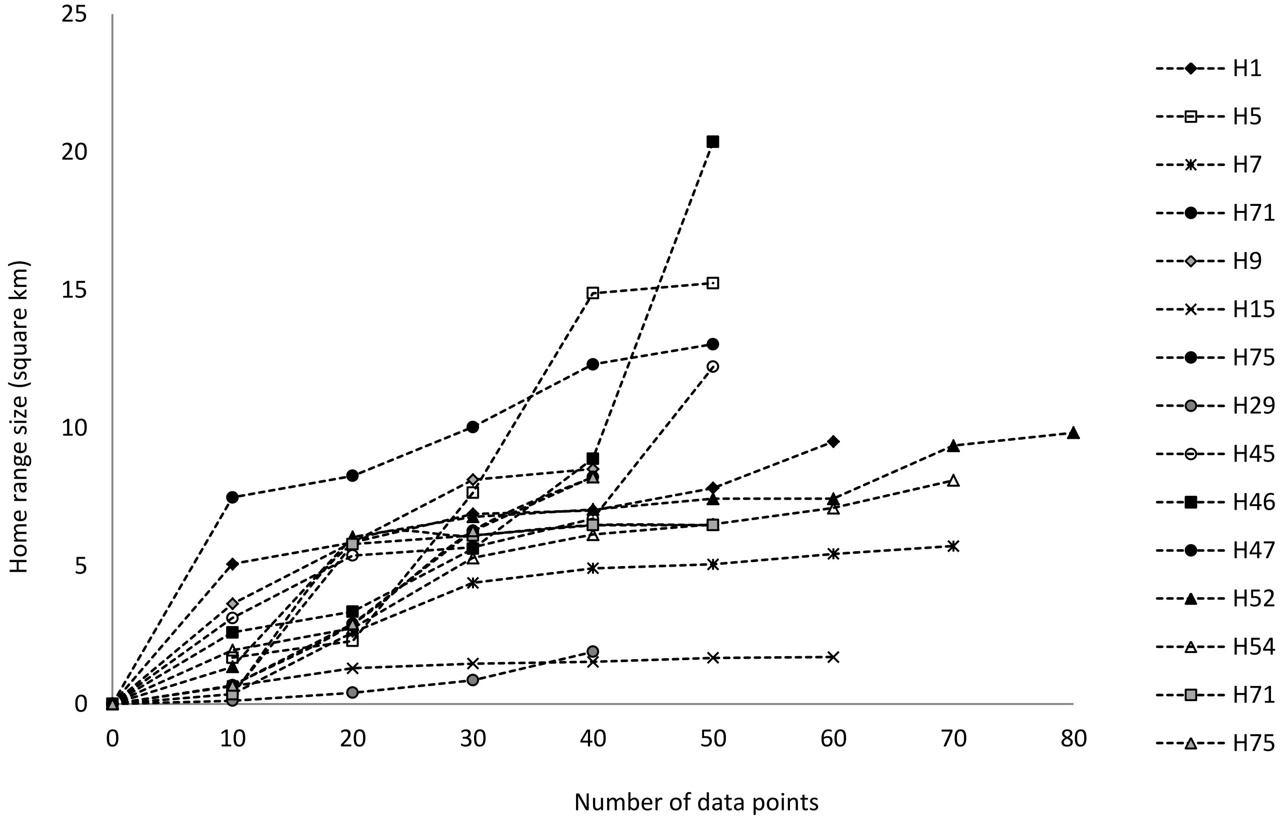

Figure 7.1: The effect of sample size on home range size estimate of 13 harems obtained by visual observation. Sample sizes ranged from 40 points for harem H75 to 83 points for harem H52.

The patterns of overlap of the individual LoCoH-calculated home ranges of the harems directly observed and tracked by the GPS are shown in **Table 7.6**. Home range of each harem overlapped with 1 - 10 home ranges of other harems and the overlap ranged from 5 - 80%.

	H1	H5	H7	H9	H15	H29	H45	H46	H47	H52	H54	H71	H75	H10	H12	H109	H80	H88
H5	5%	-																
H7	0	60%	-															
H9	0	40%	45%	-														
H15	0	45%	60%	30%	-													
H29	0	0	0	0	0	-												
H45	40%	5%	0	0	0	0	-											
H46	0	35%	40%	70%	35%	0	0	-										
H47	40%	5%	0	0	0	0	20%	10%	-									
H52	0	0	0	0	0	70%	0	0	10%	-								
H54	0	0	0	0	0	60%	0	0	45%	50%	-							
H71	5%	0	0	0	0	20%	0	0	30%	70%	60%	-						
H75	0	50%	40%	25%	55%	30%	0	45%	0	0	0	0	-					
H10	0	0	0	0	0	0	5%	0	0	0	0	0	0	-				
H12	0	0	0	0	0	0	0	0	0	0	0	0	0	50%	-			
H109	0	0	0	0	0	0	10%	0	0	0	0	0	0	10%	0	-		
H80	0	35%	60%	55%	45%	0	0	55%	0	0	0	0	60%	0	0	0	-	
H88	30%	25%	55%	40%	60%	0	10%	80%	40%	0	0	0	40%	0	0	0	55%	-
H108	0	0	0	0	0	0	5%	0	0	0	0	0	0	15%	0	50%	0	0

Table 7.6: Percentage overlap (%) of individual home ranges of 13 observed and six GPS tracked harems as a measure of fidelity to home range.

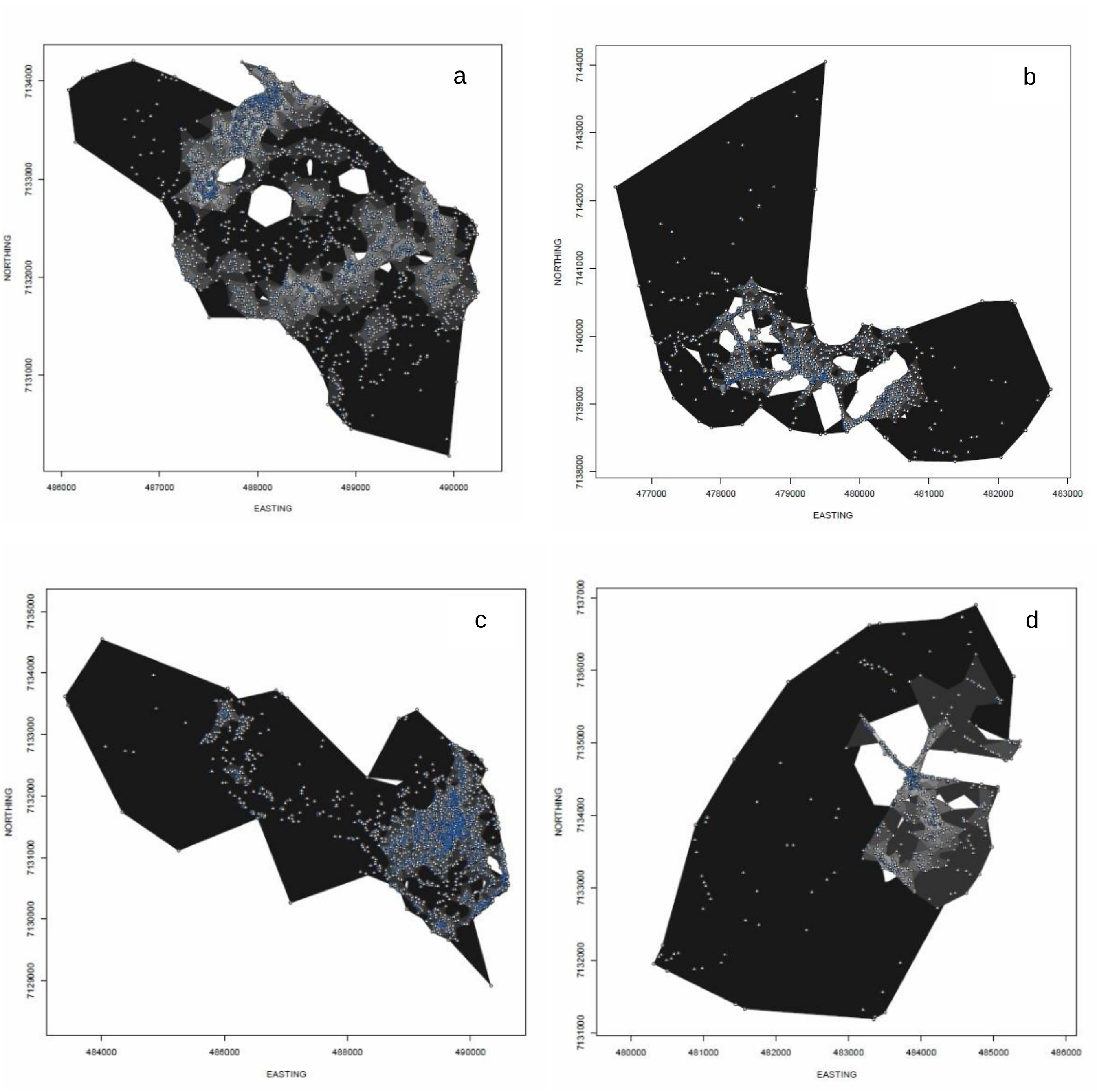

Figure 7.2: Examples of home range size and shape estimated by the LoCoH method of four harems tracked with GPS: a – 3413 points, b – 1730 points, c – 3286 points, and d – 711 points. Blue points – harem localisations; grey areas – areas with high data point density (core areas), and white areas within home ranges – areas (habitats) avoided by harems.

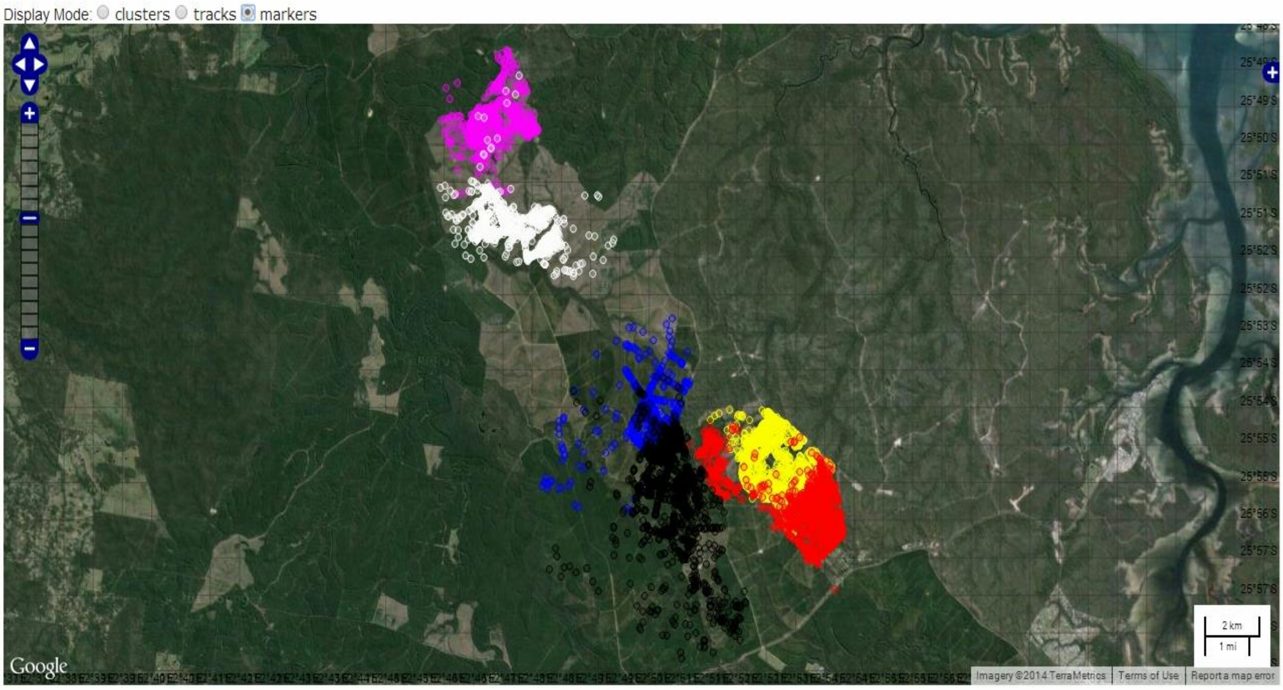

Figure 7.3: Graphical representation of home range overlap of six harems tracked by GPS in the TTSF. Large concentrations of points indicate high density data collection, which correspond to highly used plantation areas. Light green areas – open canopy habitats; dark green areas – closed canopy habitats; pink – H80; white – H88; blue – H109; black – H108; yellow – H10, and red – H12.

There was an insignificant negative correlation between harem size and LoCoH home range size for all harems tested (r = -0.32, *P* = 0.18), which indicates that larger harems did not have larger home ranges. A significant correlation, however, was found between home range size and the size of the core area (r = 0.46, *P* = 0.04), which demonstrates that harems with larger home ranges also had larger core areas. There was no correlation between the number of obtained location coordinates for each harem and home range size (r = 0.52, *P* = 0.52).

7.4. DISCUSSION

Two factors influence the reliability of home range estimates: the duration of data collection and the frequency of unbiased identification of the same individuals (Swihart and Slade 1985; Harless et al. 2010). Home range size is underestimated when the volume of data collected is low (Linklater 1998; Ostro et al. 1999). In the current study, home range size estimates based on visual observations were significantly smaller (average of 50 observations over 25 months) than those for harems tracked by GPS (average of 1980 data points). The GPS based estimates can be considered to be without bias because a large number of locations were obtained with great frequency (Fieberg and Kochanny 2005).

A number of studies involving the estimation of home range size from direct observations have used feral horse populations accustomed to human contact (Gates 1979; Rubenstein 1981; Linklater 2000a), or in very open environments where humans and horses established visual contact at substantial distances (Miller 1983b; Berger 1986; Ganskopp and Vavra 1986). Additionally, some studied populations inhabited smaller and fenced areas (Gates 1979) or islands (Welsh 1973; Rubenstein 1981). Home range size investigation by means of visual localisation in the present study was limited due to the dense coniferous vegetation. Horses were significantly more difficult to visualise in closed canopy habitats of juvenile and mature pine. The timid nature of the horses often resulted in flight towards closed habitats, further complicating group identification. There is consensus amongst researchers that studying large herbivores in forested habitats present difficulties (Hemami et al. 2004). This is because animal numbers are generally lower in closed habitats, and they are more difficult to see (Putman 1996; Margues et al. 2001).

Results from the GPS tracking supported the hypothesis that home ranges of harems in the TTSF were moderate in size and were comparable to those of feral horses in mesic grassland in New Zealand: 1 - 17.7 km^2 (Linklater 1998), and arid grassland in Northern America: 6.7 – 25.1 km^2 (Berger 1986); 5.4 – 25.2 km^2 (Ganskopp and Vavra 1986). Studied home ranges were smaller than those observed for feral horses in arid environment in northern America: 73 – 303 km^2 (Miller 1983b), and for Przewalski horses (152 – 826 km^2) and Asiatic wild asses (4449 – 6835 km^2) in arid steppes in Mongolia (Kaczensky et al. 2008) but larger than those recorded for feral horses in European mesic grasslands: 0.8 – 10.2 km^2 (Tyler 1972); 2.5 – 3.3 km^2 (Gates 1979) and isolated Atlantic islands: < 7.0 km^2 (Welsh 1973).

Topography, habitat availability and climatic conditions influence the size and shape of home ranges of feral horses and other herbivores (Tyler 1972; Gates 1979; Linklater 1998; Oehler et al. 2003; Anderson et al. 2005; Hampson et al. 2011). Evidence suggests that large herbivore home range sizes are smaller where important resources are abundant. If the forage availability within the home range does not meet nutritional and energetic requirements of the resident population, its home range size needs to be increased (Anderson et al. 2005). For example, feral horses in New Zealand demonstrated seasonal shifts in the use of their annual home range by moving to higher altitudes in spring and summer and lower altitudes in autumn and winter. These shifts appeared to be related to horses avoiding subzero temperatures (Linklater 1998). Topography and habitat type were also the main determinants of home range size of New Forest horses in the UK (Tyler 1972). When there was close proximity between grazing areas, shelter and water, home range was smaller than that of horses that were required to travel longer distances between resources (Tyler 1972). Similarly, the size of the home range of feral horses in Australia was smaller when water was more accessible (Hampson et al. 2011).

In the TTSF, creeks and streams were evenly distributed across the entire plantation; therefore access to water did not appear to be an important determinate of home range size. The strong preference of horses towards open habitats in the TTSF suggests that habitat type and distribution were the likely predictors of resource use and the size and shape of home ranges. The reason that harems ranged over a larger area than that limited to open canopy habitats (Chapter 6) could have been that open habitats did not entirely meet a harem’s nutrient requirements, or that forested areas offered additional benefits to the horses (i.e. increased protection from predators and reduced thermal stress), which was previously demonstrated in mountain sheep (Oehler et al. 2003) and in elk (Anderson et al. 2005).

In a previous study, increasing harem size was correlated with increasing home range size and postulated to be the result of greater resource demands required by a greater number of horses (Linklater 1998). However, this was not observed in the TTSF population but for reasons that remain unclear. Interestingly, Ryan et al. (2006) found that African buffalo home range size was not correlated with herd size. Moreover, buffalo herds did not decrease in size or break into smaller groups in response to increased resource pressure. It would appear that the home range size of large herbivores is governed by various factors in addition to the higher resource demands of larger groups.

Results showed that home ranges of harems overlapped; findings also reported by others (Tyler 1972; Berger 1986; Linklater 2000a). Exclusive home ranges have only been observed in populations where movement was restricted by topographical barriers (Rubenstein 1981) and fences (Gates 1979). Home ranges of observed and GPS tracked harems in the present study overlapped with 1 – 10 other harems and the overlap was up to 80% in some cases. It has been demonstrated that herbivores, which occupy sparsely distributed, unpredictable or low-quality pastures, do not tend to favour territorial defence as this process is energetically costly (Linklater 2000b; Moorcroft 2008). The home ranges of the TTSF harems were distinguished by core area that was more frequently occupied than the remainder of the home range; this observation is consistent with established evidence (Gates 1979; Putman 1986; Linklater 2000a). The increased competition for pasture that results from sharing a home range and core use areas amongst animals of the same species, particularly in group-living species, can be outweighed by the potential to increase reproductive success (Kaufmann 1974; Jarman and Southwell 1986; Horsup 1994), and reduce predation risk (Jarman 1974).

The spatial use of available landscape within the home range was quantitatively assessed for GPS tracked harems only. The observed long-term plasticity in areas being preferentially utilised and avoided by the horses obtained by direct observations and dung counts suggest that feral horses in the TTSF adapt to changes in habitat availability. It was also very apparent that TTSF feral horses also adjust movement within their home range to human forestry management. Similar observations were made by Tyler (1972), who found that New Forest horses relied on food resources provided by woodland clearing, which often supported a large number of animals. A change in availability of forage and their impact on habitat preference of resident herbivores in managed forested ecosystems has also been observed for sika deer and roe deer (Gill et al. 1996; Kuiters et al. 1996).

Placement of GPS collars was attempted on horses in a number of visually observed harems in the current study. Collar placement involved remote immobilisation of horses (Zabek et al. 2014). In one harem (H1), the collar detached from the horse and in another (H9) it stopped transmitting data five days after deployment. Placement was attempted with harems H46 and H47, but it was not possible to get within shooting distance. Successful collar placement occurred on a horse in harem H15, but an injury sustained during immobilisation necessitated euthanasia the following day. It was therefore not possible to make a comparison between home range sizes based on direct observation and GPS tracking.

7.5. CONCLUSION

Understanding spatial needs of feral horses in the Tuan and Toolara State Forest is important in planning management strategies for population control. Harems in the TTSF occupy home ranges and core areas involving substantial overlap. The study established that home ranges were moderate in size, horse movements within home ranges were predictable, and there was a preference for open habitats; such findings will significantly influence management strategies in the future. This would be of particular importance when facilitating physical removal of horses (e.g. placement of traps) or planning tree harvest operations, particularly near the major public roads.

CHAPTER 8: GENERAL DISCUSSION

8.1. SIGNIFICANT OUTCOMES AND MANAGEMENT RECOMMENDATIONS

This study had its origin in the need to obtain detailed information about the demographics of feral horses located in the Tuan and Toolara State Forest. It is the first ever study where the population dynamics of feral horses has been determined in an extensive coniferous pine plantation and subsequently used to establish management control strategies.

Variation in use of the spatial landscape by invasive animals such as feral horses may substantially influence population management (Arthur et al. 2002; Whyte et al. 2013). Knowing how animals move across the landscape in response to habitat availability may help predict how a population will respond to control strategies.

It had been proposed that trapping and re-location of TTSF feral horses from plantation areas located near the major roads would reduce the risk of vehicle collisions (Crittle and Jackson 2004; Berman 2013). The proposal recommended that horse-free zones be established parallel and on either side of busy roads and in other specified areas where horses were likely to cross roads (Berman 2013). These liberated areas would provide a buffer zone and it would take time for horses to re-occupy them. It was assumed that feral horses in the TTSF had limited home ranges to which they were loyal, and within which their movements were predictable (Berman 2013). Experience gained from horse removal in the Barakula State Forest indicated that horses were slow to recolonise new areas if entire harems were removed because adjoining groups of horses apparently preferred to remain in familiar areas (Crittle and Jackson 2004). Similar management strategies kept the Finke Gorge National Park free of feral horses for almost 20 years (Bryan 2001).

For horse removal to be an effective management tool, it is obvious that the distribution and abundance of horses must be ascertained with home range size and habitat use being of particular importance. Trapping, as a removal tool, will be most effective in those areas where horse numbers are high but can also be used to target those horse groups whose home ranges have been identified to include major roads.

Results show that harems in the TTSF occupy moderately sized home ranges with small, but distinctive core use areas that predominantly consist of open canopy habitats. These findings suggest that if buffer zones bordering busy roads were maintained as closed habitats, it is likely that feral horse numbers would be low or non-existent in these zones. Strong preference of horses for open habitats, particularly harvested pine, suggests that harvested areas located in or near buffer zones would require more intense management (higher capture rate) and continued monitoring to maintain these areas horse-free. In particular, bachelor groups are likely to be an issue in such areas because their home ranges appear less well defined and are therefore likely to move into unoccupied open habitats where feed is ready available.

Counting dung on plantation roads provided very useful information on population distribution across the TTSF. Additionally, the distribution of dung on plantation roads was positively correlated with the distribution of dung in adjoining forest habitats, which suggests that road dung surveys can be used to monitor colonisation of buffer zone and to assess population spread into new plantation areas. In particular, an annual surveillance of dung would provide oversight as to whether buffer zones continued to remain horse-free. However, dung surveillance on roads is limited in its usefulness as it cannot be used to assess population abundance trends, which requires distance sampling of dung.

Management of horses along the major public roads, involving the capture and removal of 77 horses, has been successful since its implementation in 2009, with the risk of collisions being reduced by 68% (Berman 2013). However, as the population grows, there will be a need to remove a greater number of horses (Lundie-Jenkins et al. 2006).

Currently, there are an estimated 1321 horses in the TTSF, at a density of 1.8 horses per km^2, and annual population growth is 8.8%. In 2009, the population was estimated to be 955 horses (Berman 2013). If this estimate was accurate, the TTSF population has increased from 2009 to 2012 by about 32%, an annual average growth of 10%. Although the published accuracy of the 2009 survey was less than that of the present study, the estimated average annual population increase was remarkably similar for both studies, and comparable to published values for unmanaged populations that have been studied over a number of years (Keiper and Houpt 1984; Cameron et al. 2001; Dawson and Hone 2012). Therefore, to maintain the population at its current size considering the rate of increase requires the removal of 120 horses per year. As shown by others (Lundie-Jenkins et al. 2006), management strategies such as local buffer zones bordering roads will not be effective as stand-alone programs but must be incorporated into forest-wide programs that are inclusive of the considerable mobility of feral horses

Although the TTSF feral horse population is dispersed across the forest, it is most abundant in the central region. This has important management implications. Removal of horses from the periphery of the central region will have little influence on the population dynamics in the central region because of the delay involved in horses moving into the depopulated area. This means that resource pressure will be maintained in the central region slowing the rate of population growth, which in turn reduces the number of animals that need to be removed (Walter 2002). However, when the population reaches the carrying capacity threshold, it may substantially impact on the environment by destroying water sources, damaging native vegetation (Caughley 1976; Dyring 1990) and possibly young pine stands (**Figure 8.1**; Crittle and Jackson 2004). This may also have welfare implications because of food and water shortages.

Figure 8.1: Feral horse-induced soil erosion and damage to the banks of water holes located in the study area.

By 2021, based on current rate of population growth, horse density per km^2 across the entire forestry will be 3.58, which will severely test the carrying capacity of the TTSF. As the population increases, horses will move to minimally occupied or unoccupied areas, including areas outside the TTSF, as has been shown to be the case in the Australian Alps (Dawson 2005). The area of particular concern would be the border of the TTSF with the Great Sandy National Park, which is unfenced and provides no barrier to expansion of horses into the national park (**Figure 8.2**).

Although fencing is not generally compatible with forestry operations (Crittle and Jackson 2004), there may be some places where fences could be built to restrict horse movement without interfering with forestry activities. Feral horses are highly mobile and other studies have identified well defined movement corridors between habitats (Dyring 1990; Schott 2004). Targeted fencing in the TTSF may prevent horses moving into areas that have been depopulated by horse removal programs (**Figure 8.2**). Although fencing may prevent horses from crossing major roads thereby reducing the risk of collisions, it cannot be the only strategy used to control the growing and expanding population.

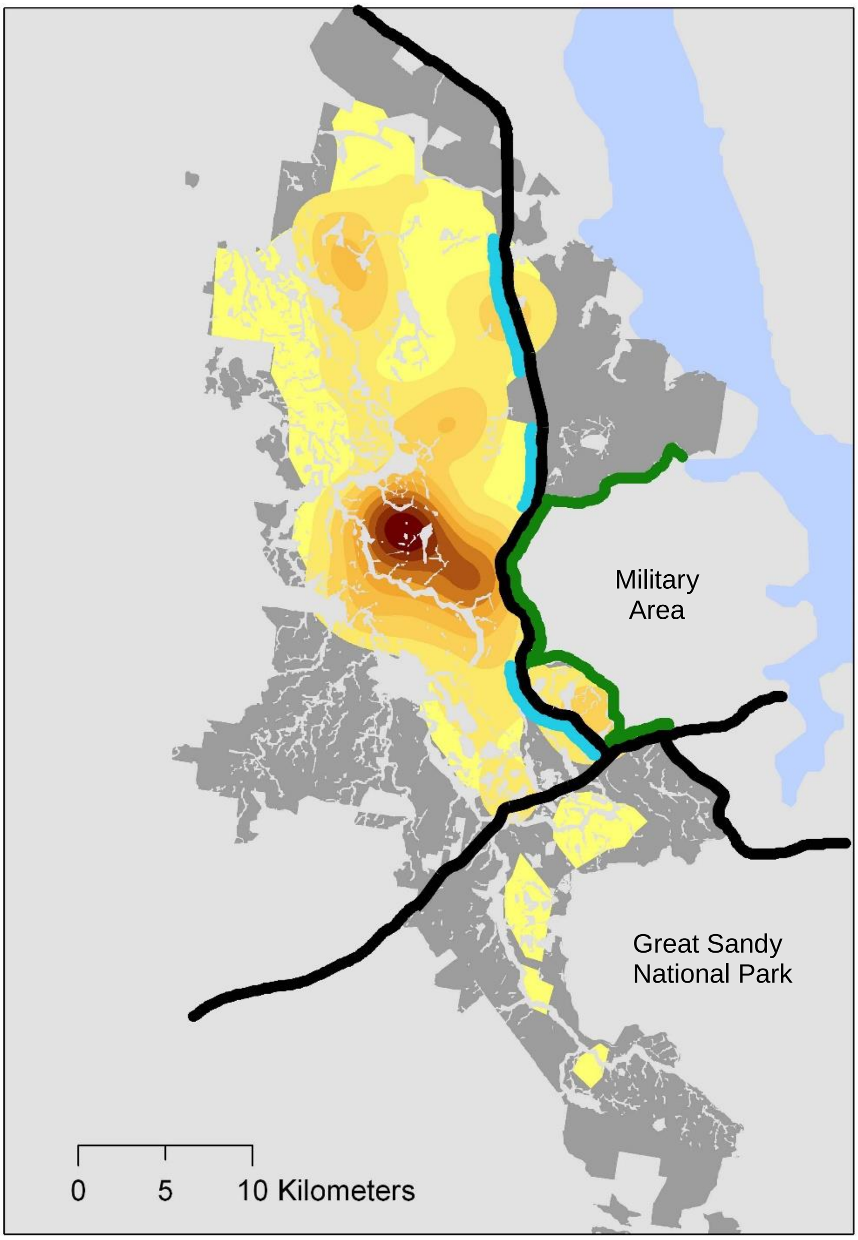

Figure 8.2: Location of proposed fence (blue lines) to discourage horses from crossing major roads (black lines) and recolonising eastern areas of the plantation once all horses have been removed from these areas. Green lines – fenced off Military Area.

Management practices can limit feral horse population size by controlling fertility or by culling. A view commonly held by animal welfare groups is that fertility control is the logical and humane solution to the problem of feral horses in Australia (Chapple 2005; Nimmo and Miller 2007; Dinn 2012). However, many studies have confirmed that fertility control is only feasible in small, contained and accessible populations, where every individual horse can be identified (Kirkpatrick and Turner 1991; Kirkpatrick 1995; Cameron et al. 2001; Turner et al. 2001; Killian et al. 2008).

The administration of most immunocontraceptives requires close contact with the targeted animal and therefore the animal must be mustered and captured (Stafford et al. 2001; Gray et al. 2010). Alternatively, animals can be treated by remote delivery of the agent by dart or pellet (Kirkpatrick et al. 1990; Willis et al. 1994), but failure of delivery has been reported (Stafford et al. 2001). Current contraceptives require multiple doses to achieve, at best, fertility control for 2-3 years, which limits their usefulness because of cost and the logistics involved (Liu et al. 1989; Fraker et al. 2002; Hernandez et al. 2006; Turner et al. 2007; Killian et al. 2008; Gray et al. 2010).

Based on the estimated population of 1321 horses, age distribution (adult component equal to 68%), and equal sex ratio of adults, there should be about 450 breeding females in the TTSF. Considering that a relatively high proportion (60-80%) of females in the population must be treated to significantly influence population reproductive rates (Turner and Kirkpatrick 1991); there would be a need to target between 270 - 360 females. Locating, identifying, capturing, treating and re-treating this number of horses would be very challenging logistically and very expensive.

It is also essential to note that the current study demonstrated that adult survival was a far more important contributor to population growth than was fecundity (fertility). The current reproductive success of females in the TTSF involves high investment in caring for their young but at the cost of lower fecundity. The high cost of pregnancy and lactation prevents mares from foaling every year, which limits population growth. Therefore management emphasis should be on influencing adult survival and not fecundity. The greatest success would be achieved by targeting adult females because reducing the number of males may increase reproductive rate of the population by increasing the stability of harems (Dobbie and Berman 1992). Management based on fertility control of females should be of secondary importance, with removal of juveniles being of lowest importance.

8.2. CONCERNS

Direct observation of horses to determine population abundance and habitat use had its disadvantages. Extensive areas of heavily vegetated habitats in association with forest management meant that there was a low rate of horse detection in some parts of the study area. This created a bias and resulted in the underestimation of various demographic parameters. Although study design attempted to correct the bias by increasing sampling rates in the closed (dense) habitats, this appears to have only been partially successful and therefore in future studies involving dense habitats alternative techniques should be considered such as the use of a combination of mark-recapture and line transect techniques. Thermal imaging should also be considered as it has been shown to provide considerably greater detection of animals in densely forested habitats when compared with traditional sighting techniques (Naugle et al. 1996; Gill et al. 1997; Haroldson et al. 2003).

The problem with estimates obtained using applied techniques to determine population abundance is that the accuracy of those estimates cannot be ascertained if the actual size of the population is unknown. Dung counts have been shown by others to overestimate population abundance when compared with results obtained by mark-recapture (Linklater et al. 2001). Determination of dung decay rate in the current study was found to be influenced by environmental conditions. Since a larger proportion of dung was exposed to direct climatic conditions; the rate of dung decay increased. Dung decay rate would be best calculated using equal sampling of dung from open and closed canopy habitats. It is likely that the TTSF population size has been slightly exaggerated using dung counts.

The process by which harems were recruited into the home range size estimate created a bias towards harems that were observed with greater frequency. Harems that were less frequently observed may have had larger home range size, but this was not established.

Placement of GPS collars was attempted on horses that were members of visually observed harems in order to compare home range sizes calculated from direct observation with those determined by GPS tracking. However, this comparison was unfortunately thwarted because of contingencies encountered with GPS collar placement, which included collar failure, collar damage after placement, and not being able to place collars on the most appropriate animals (Zabek et al. 2014). These issues meant that although useful data were obtained, it was not paired data and therefore comparisons were not possible.

Information on the demographic and population dynamic of the TTSF feral horses was collected over a period of two and one half years. The effect of time on population dynamics of long-living large herbivores such as feral horses is likely to be considerable. Monitoring over several years should account for fluctuations (Gaillard et al. 2000a). It is however possible that the present study may not have been of sufficient duration to observe time-related fluctuations that have been observed in similar but longer studies (Berger 1986; Kaseda et al. 1995; Goodloe et al. 2000; Scorolli and Lopez Cazorla 2010a).

8.3. CONCLUSION AND FUTURE RESEARCH

The focus of the initial management strategy was to prevent collisions between horses and vehicles on the major public roads that traverse the TTSF (Crittle and Jackson 2004). This has been partially successful following the removal of 77 horses from forest areas adjacent to the major public roads over the period 2009 – 2014 (Berman 2013). This program should be continued and expanded to incorporate the removal of entire harems and be supported by strategies to prevent re-colonisation of horse-free areas.

Effective management strategies in other plantation areas must address feral horse population growth. This can be achieved through ongoing monitoring of demographic trends of fecundity and survival. Management strategy should also involve substantial and continuing removal of adult female horses, or manipulation of survival and fecundity to control population growth. As selective removals will likely alter adult sex ratio and age structure of the population, further modelling should be performed to minimise adverse welfare outcomes.

If fertility control is to be one of the future management strategies, it would be most effective to initially reduce the current population by other means before using such a strategy. Financial expense and the logistical difficulties of applying fertility control measures need to be further evaluated to identify the cost-benefit relationship.

Changes in distribution of horses can be detected by monitoring dung counts on forest roads. Since detection of horses was significantly less in closed habitats, this influenced the abundance and habitat use results. Thus, evaluation of these parameters can be more accurately performed by the application of distance sampling of dung. Monitoring body condition scores of horses, particularly of the adult females, will alert management to feed shortages associated with increasing population pressure, which has the potential to cause adverse publicity around welfare (Walter 2002; Scorolli 2012).

The current study has identified the need to define the relationship between horses and their effect on the TTSF environment. Wild fires are a major management issue in the TTSF and the feral horse population may have a role in reducing the fuel load by their grazing habits. The optimal population size for this potential benefit has not been determined. Again, the damage caused by horses to the remaining natural environment in the TTSF, but also to the introduced pine environment, has not been established. Do horses significantly damage young pine or, by grazing competing vegetation, do they enhance the growth of young pine? Information relevant to these questions needs to be gathered over a number of years and between seasons.

8.4. KEY FINDINGS AND RECOMMENDATIONS ARISING FROM THE STUDY

1. Changes in distribution of horses can be detected by monitoring dung counts on forest roads.
2. Accurate evaluation of population abundance can be achieved through distance sampling of dung.
3. Further monitoring of the TTSF population is necessary to account for annual changes in population growth.
4. Monitoring body condition scores of horses, particularly of the adult females, will alert management to feed shortages associated with increasing population pressure, which has the potential to cause adverse publicity around welfare.
5. Effective management strategies should involve substantial and continuing removal of adult female horses, or manipulation of survival and fecundity to control population growth. As selective removals will likely alter the adult sex ratio and age structure of the population, ongoing assessment is necessary to minimise adverse welfare outcomes.
6. When designing long-term control measures for the TTSF population, obtaining ongoing accurate estimates of adult survival should be of the highest priority.
7. If fertility control is to be one of the future management strategies, it would be most effective to initially reduce the current population by other means before using such a strategy. Financial expense and the logistical difficulties of applying fertility control measures need to be further evaluated to identify the cost-benefit relationship.
8. Strategic use of fencing to reduce horse movement across the public roads.

9. Maintenance of narrow strip of closed canopy habitat bordering main roads to take advantage of the preference for open habitats thereby reducing the likelihood of horse-vehicle collisions
10. Continuing removal of horses from the forested areas located near the public roads together with recording the number of horse-vehicle collisions, to assess the success of the removal program.

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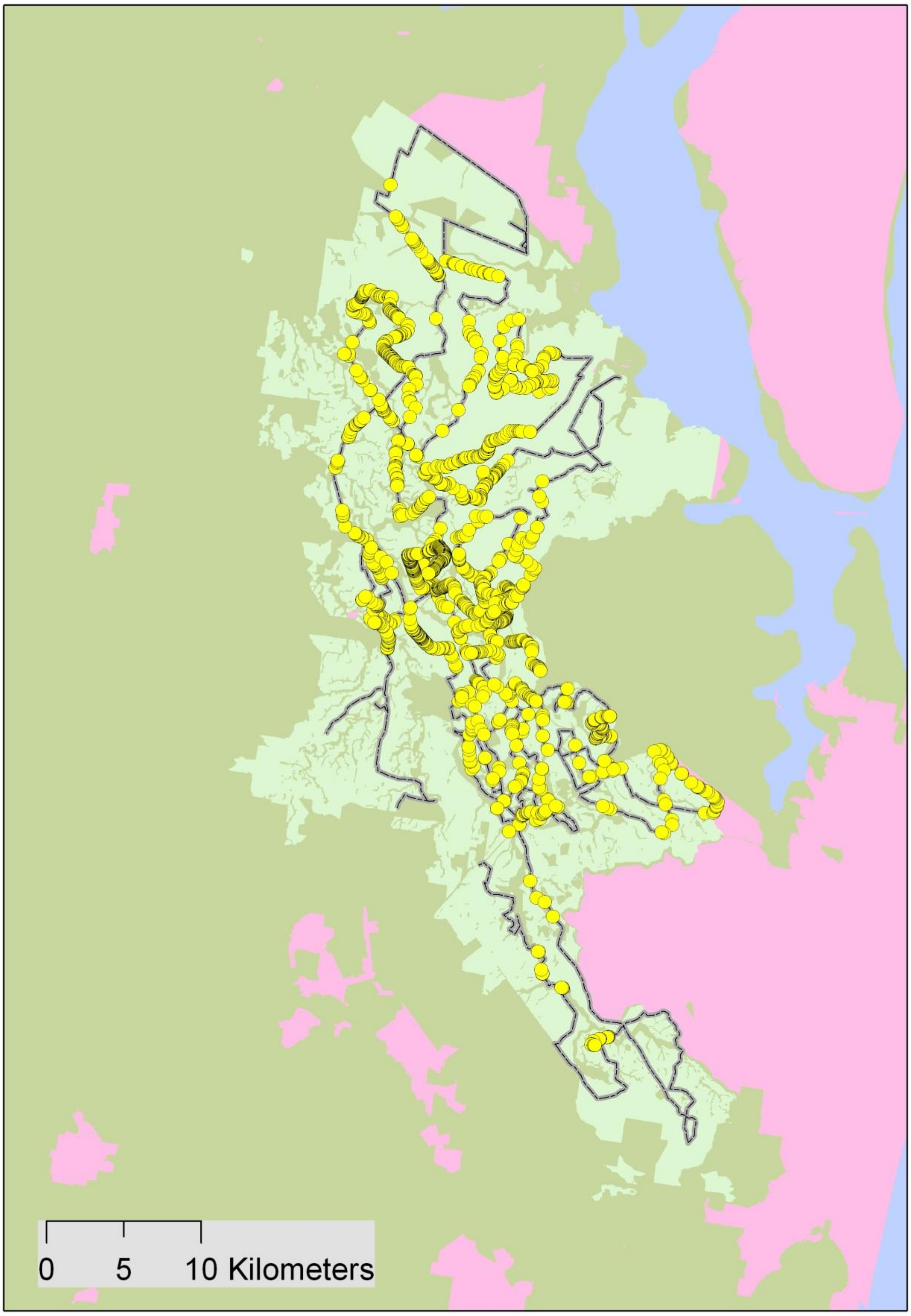
APPENDICES



Appendices 1: Strip transect survey performed on plantation roads in June 2012. Light green area – TTSF plantation; grey lines – area surveyed by a vehicle, and yellow points – dung recorded in the strip transect survey.

PUBLICATIONS INCLUDED IN THE THESIS:

ASSESSING THE EFFICACY OF MEDETOMIDINE AND TILETAMINE-ZOLAZEPAM FOR REMOTE IMMOBILISATION OF FERAL HORSES (*EQUUS CABALLUS*).

Magdalena A. Zabek [a], *John Wright* [a], *David Berman* [b], *Jordan O. Hampton* [c], *Christina W. Collins* [a]

[a]University of Queensland, School of Veterinary Science, Gatton, QLD 4343, Australia;
[b]Queensland Murray-Darling Committee, Toowoomba, QLD 4350, Australia;
[c]Ecotone Wildlife Veterinary Services, Canberra, ACT 2601, Australia;

Abstract

The study of any wild animal's home range requires the collection of spatiotemporal data, obtained independently of climatic conditions or time of day. This can be achieved by the attachment of Global Position System (GPS) data loggers, which, in large species, is best achieved by remote immobilisation. Feral horses (*Equus caballus*) usually occupy remote areas of Australia, however a considerable population increase has been observed in a close proximity to metropolitan areas of the Australian east coast, creating increasing conflict with human interests. The aim of this study was to investigate the efficacy of remote chemical immobilisation of feral horses with medetomidine combined with tiletamine-zolazepam to facilitate placement of satellite GPS collars. Nine feral horses were darted from the ground with 60 mg of medetomidine and 1500 mg of tiletamine-zolazepam. The effects of medetomidine were reversed with 50-100 mg of atipamezole 30-40 minutes post induction (IV/IM). Physiological variables monitored during anaesthesia were heart rate, respiratory rate, temperature and oxygen haemoglobin saturation (S_pO_2). All horses were successfully immobilised with between one and three darts (*n* = 9). The mean dose of medetomidine was 0.15 ± 0.01 mg kg^{-1} (SEM) and tiletamine-zolazepam was 3.61 ± 0.16 mg kg^{-1}. Mean time from darting to lateral recumbency was 13 ± 2.7 min, and mean recumbency time was 54 ± 13 min. Vital signs for all anaesthetised animals remained within normal range during anaesthesia, with the exception of one animal displaying a transient drop in S_pO_2. No mortalities were encountered. The combination of medetomidine and tiletamine-zolazepam provided adequate anaesthesia in feral horses in the field for application of GPS collars. Although a limited number of horses were immobilised, this study shows that medetomidine and tiletamine-zolazepam provides effective short-term anaesthesia for feral horses, providing a practical and field-accessible capture technique. This method could also be applied to other management actions requiring safe and humane capture of feral horses.

Additional keywords: feral horse, remote immobilisation, medetomidine, tiletamine-zolazepam, atipamezole.

Introduction

To safely and humanely place GPS collars on wildlife, reliable capture methods are essential (Geschke and Chilvers 2009). In the case of feral horses, a reliable method of remote immobilisation is necessary to facilitate safe and humane capture and subsequent handling of the subject animal (Kaczenski 2010). For field anaesthesia to be effective, it should be fast, smooth, reversible, and pose minimal safety risks to the target animal and personnel involved in the anaesthetic regimen (Walzer et al. 2006). Remote immobilisation of wild equids in the field is often perceived to be difficult (e.g. Walzer and Kaczensky 2004) despite a large number of demonstarted techniques for wild herbivore species with similar body size (e.g. Jalanka and Roeken 1990; Tyler et al. 1990; McMahon and Bradshaw 2008; Boardman et al. 2014).

The most commonly used agent to remotely immobilise non-domesticated equids is the potent opioid, etorphine hydrochloride (Matthews 1993; Walzer et al. 2006; Hampson et al. 2010; Rosu et al. 2012). Despite its high potency and availability of an antagonist that enables rapid and complete reversal, etorphine is restricted for use in many countries, including Australia, and difficult to import (Woolnough et al. 2012; Australian Government, Department of Health and Aging, 2013).

Investigations of alternatives to etorphine have led to use of combinations of α-2 adrenergic agonists (xylazine, detomidine, romifidine, medetomidine) with cyclohexamines (ketamine, tiletamine; Barasona et al. 2013; Matthews et al. 1995; Walzer et al. 2006; Rosu et al. 2012). In particular, the potent α-2 adrenergic agonist medetomidine, in combination with the cyclohexamine ketamine, has demonstrated reliable and reversible remote immobilisation of a diverse range of ungulate species, including forest reindeer

(*Rangifer tarandus fennicus*; Jalanka 1989), ibex (*Capra ibex*; Jalanka and Roeken 1990), Przewalski's horse (*Equus ferus przewalskii*; Matthews et al. 1995), donkeys (*Equus asinus*; Woolnough et al. 2012) and dromedary camels (*Camelus dromedarius*; Boardman et al. 2014). The anaesthetic effects of medetomidine can be reversed, or antagonised, by the α-2 adrenergic antagonist atipamezole, with the effects of cyclohexamines dissipating over time (Woolnough et al. 2012).

Medetomidine is an α-2 antagonist with significant sedative and analgesic properties which provides muscle relaxation and allows smooth induction and recovery from anaesthesia (Muir and Hubbell 2009). Ketamine and the closely related tiletamine, cause dissociative anaesthesia characterised by catalepsy, amnesia, and analgesia (Muir et al. 2000; Muir and Hubbell 2009). Zolazepam is a benzodiazepine-like drug with sedative and muscle relaxation effects (Muir et al. 2000). Tiletamine is commercially available combined with zolazepam (Zoletil® (Virbac, Milperra, NSW) or Telazol® (Zoetis, Kalamazoo, MI)), a benzodiazepine-like tranquiliser (Muir et al. 2000). The advantage of the medetomidine and tiletamine-zolazepam combination is that it acts synergistically, with lower required doses, offers broad anaesthesia safety margins, well-preserved cardiovascular function and muscle relaxation (Jalanka and Roeken 1990). However, these effects, sometimes result in prolonged recovery and there is no readily available antagonist, or reversal agent (Matthews et al. 1991; Muir et al. 2000). The solubility of the concentrated ketamine preparations is insufficient to allow dosing darts with a capacity restricted to 3mL. In contrast, the advantage of using the tiletamine-zolazepam combination over ketamine is its superior solubility, permitting very high drug concentrations in minimal volumes (Matthews and Myers 1993), which in turn permits usage of darts of smaller capacity (such as the Pneu-dart tracker dart (Pneu-Dart, Williamsport, PA) with a capacity of 3.0 mL used in the present study). In addition, the combination improves the reliability of sedative properties of either drug alone (tiletamine or zolazepam) without adding extensively to further vital organ depression (Booth and McDonald 1988).

The combination of medetomidine and tiletamine-zolazepam has not previously been tested in remote immobilisation of feral horses in field conditions. Therefore, the purpose of this research was to investigate the efficacy of medetomidine in combination with tiletamine-zolazepam as a case study for remote immobilisation of nine feral horses for the placement of GPS collars. Anaesthetic and physiologic data was collected in order to evaluate efficiency and safety of this drug combination, to provide rapid and smooth induction by remote intramuscular injection, and to be easily reversible, which will provide an effective form of anaesthetic for shorter field procedures performed on feral horses.

Materials and methods

Study area

This study was conducted in the Tuan and Toolara State Forest (TTSF), located on South-East Queensland in Australia (25^o53’S and 152^o50’E) between August and November 2013). The mean temperatures during the study were in a range of 20.4 - 27.0°C (Bureau of Meteorology 2013, available at http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=136&p_display_type=dailyDataFile&p_startYear=2013&p_c=-328943740&p_stn_num=40555, accessed 12 December 2013). High environmental temperatures need to be considered when performing general anaesthesia in the field, with regard to potential hyperthermia of immobilised animals (Geschke and Chilvers 2009; Berger et al. 2010; Woolnough et al. 2012).

Animals

Horses involved in this study were members of established breeding groups (n = 9), which were a part of a larger observational study. Individual horses were selected randomly and included mature males (n = 7) and females (n = 2). Selected horses were healthy in appearance with an estimated body weight based on visual appraisal of 400-500 kg. Selected females were not obviously pregnant and were without dependent foals.

Immobilisation procedure

All horses in the study were immobilised with medetomidine hydrochloride (Bova Compounding, Caringbah, NSW, Australia), and toletamine-zolazepam (Zoletil; Virbac, Milperra, NSW, Australia), which is a soluble powder consisting of equal parts of tiletamine and zolazepam. All horses received the same drug dosage which was approximated for 450 kg animal. Medetomidine (60 mg, at concentration of 40mg/mL) was mixed with 750 mg of tiletamine powder, 750 mg of zolazepam powder, and 0.5 mL of saline. Following several attempts to solubilise the tiletamine-zolazepam powder using only medetomidine, it was ascertained that 0.5 mL of sterile saline facilitated the solubilisation process, as well as providing a balanced dart volume. Remote injection of the anaesthetic agents was facilitated by 3 mL C-type explosive-powered metal darts equipped with VHF transmitters (Pneu-Dart, Williamsport, PA, USA) which enabled location of the darted animals in dense forested vegetation using a Yagi antenna (Sirtrack, Havelock North, New Zealand). This requirement limited the available dart volume to 3 mL because of the commercial availability of tracking darts. Darts were fitted with 3.8 cm wire twin-barbed needles (Pneu-Dart) and were delivered using an x-calibre® CO_2 powered dart gun (Pneu-Dart, Pennsylvania, USA). Because transmitters added considerable weight to the dart, the shooting range to non-habituated to human presence horses was reduced to 40 m. Remote immobilisation was performed by a professional shooter and supervised by a veterinarian.

All animals were approached on foot and were darted while standing or grazing and the chosen darting site was the lateral shoulder, neck or rump and the intended injection route was intramuscular (i.m.). Distance travelled by each horse was measured by a GPS (Garmin Oregon 550, Garmin International, Olathe, KA, USA) and reported distances are from the last successful dart. Immobilisation was deemed to be achieved when the darted animal was observed to be in lateral recumbency (as per Walzer et al. 2006). Once immobilised, horses were quietly approached from behind and sometimes repositioned to avoid rocks and vegetation, or to reduce visceral pressure on the diaphragm secondary to head- down-hill positioning. Animals were blindfolded with a blanket to reduce visual stimulation and to diminish potential injury to their eyes.

Anaesthetic monitoring of physiological parameters was performed immediately after lateral recumbency was achieved and then every 15 min until the animal was standing. Heart rate was recorded by auscultation; respiratory rate by counting chest excursions; pulse strength by digital pressure of the facial artery and body temperature by a thermometer placed in the rectum. Mucous membrane colour, capillary refill time, palpebral reflex response and anal tone were also evaluated. Haemoglobin saturation (S_pO_2) was measured by a battery powered c-clamp pulse oximeter (Edan, San Diego, CA, USA), placed on the tongue. Oxygen supplementation via nasal insufflations at 10 L min^{-1} was administered when S_pO_2 fell below 90%. Oxygen was delivered from a portable high pressure cylinder (BOC Australia, Sydney) fitted with a regulator flow meter and connected to the horse by 3 m of 14 mm internal diameter plastic tubing.

Body weight was calculated while the animal was anaesthetised and in lateral recumbency using the formula of Carroll and Huntington (1988):

$$\text{Weight (kg)} = \frac{girth^2 x\ length}{Y}$$

The perpendicular distance from the dorsal midline immediately caudal to the withers and the ventral midline was doubled to provide the girth measurement. The distance from point of hip to point of shoulder was measured as being representative of body length (Milner and Hewitt 1969), and the divisor 'Y' equalled to 11900 (Carroll and Huntington 1988). This calculation allowed approximation of drug administered per kg of horse. Age was approximated by dental examination (as per Baker and Easley 1999).

Time to lateral recumbency was measured as the time from first dart placement to the time the horse became recumbent (as per Woolough et al. 2012). In horses darted multiple times, some darts bounced off or embedded in superficial tissues. In horses darted with more than one dart, time to lateral recumbency was measured from the successful delivery of the last dart to lateral recumbency. Drug absorption from these ineffective darts was assumed to be zero (as per Woolough et al. 2012) and they were not included for calculation of final drug dosage. Total recumbency time was measured from initial recumbency to standing in minutes.

Immobilisation was reversed with an initial dose of 50mg of atipamezole (Illium Atipamezole, Troy Laboratories, Glendenning, NSW, Australia; 5mg/mL, i.v. and/or i.m.) 30 - 40 minutes post induction. If the recovery was prolonged, then an additional dose of atipamezole equal to 25mg, i.v., was given 25 and 60 minutes after the initial dose. Recovery time was measured in minutes as the time from first administration of atipamezole to the time the horse stood and remained standing.

Further observations were performed from a safe distance to ensure recovery was complete, which was expressed as sufficient muscular strength and coordination of movements to remain standing (Clark-Price 2013). Within 24 - 48 hours of recovery, all horses were reassessed to see if they were of normal demeanour and that they had returned to their harems. All handling procedures were approved by the University of Queensland Animal Ethics Committee (approval no SVS/215/11/F.P Qld). Results are presented as mean ± SEM and range.

Results

Immobilisation

Drug doses, animal details, induction, anaesthesia and recovery data for all horses are presented in **Table 1**. Tabulated drug doses were calculated retrospectively after estimation of body weight post darting. Five horses (Animals 1 - 5) became laterally recumbent after administration of one dart, three horses (Animals 6, 7, and 8) required two darts to become recumbent and one horse (Animal 9) required three darts to achieve lateral recumbency. The mean dose for medetomidine for all nine animals was 0.15 ± 0.01 mg kg^{-1} and for tiletamine-zolazepam was 3.61 ± 0.16 mg kg^{-1}. In all horses, a stilted gait was observed within 2 - 3 min of darting, followed by progressive ataxia and lateral recumbency within 13 ± 3 min. Distances travelled by horses after a successful dart varied from 60 to 813 m, and averaged 194 ± 80 m.

ID	Sex	Age (years)	Body weight (kg)	Medetomidine (mg kg^{-1})	Tiletamine-Zolazepam (mg kg^{-1})	Atipamezole (mg kg^{-1})	No. of darts	Time to LR (min)	LR time (min)	Recovery time (min)
1	F	6	434	0.15	3.44	0.23	1	6	139	115
2	F	15	320	0.20	4.69	0.15	1	5	46	19
3	M	11	474	0.13	3.16	0.10	1	10	28	5
4	M	5	430	0.14	3.49	0.12	1	28	26	7
5	M	7	414	0.14	3.60	0.18	1	9	62	37
6	M	6	481	0.17	3.12	0.10	2	25	18	5
7	M	6	432	0.15	3.47	0.12	2	15	46	18
8	M	4	387	0.16	3.88	0.13	2	8	29	2
9	M	5	446	0.14	3.63	0.22	3	14	92	70
Mean ± s.e.m.		7.2 ± 1.2	424.2 ± 16.1	0.15 ± 0.01	3.61 ± 0.16	0.15 ± 0.02	2.0 ± 0.2	13.3 ± 2.7	54.0 ± 13.0	30.9 ± 12.7

Table 1. Summary data detailing animal characteristics, drug dosages based on calculated horse weight, number of delivered darts; and anaesthetic time effects in nine feral horses remotely immobilised with medetomidine and tiletamine-zolazepam in the Tuan and Toolara State Forest; LR – lateral recumbency; s.e.m. – standard error of the mean.

Anaesthesia

On average, all horses were laterally recumbent for 54 ± 13 min. All measured variables were within normal ranges for the duration of the anaesthesia in all horses (**Table 2**) with the exception of one horse (Animal 1) displaying a transient drop in haemoglobin saturation.

Parameter	Mean ± SEM	Range
HR (b.p.m.)	42.9 ± 1.4	35 - 48
RR (min^{-1})	19.5 ± 1.6	14 - 30
Temp (^{O}C)	38.4 ± 0.2	38.2 - 38.7
S_pO_2 (%)	86.7 ± 2.2	79 - 94
CRT (s)	2.3 ± 0.2	2 - 3

Table 2. Parameters measured in feral horses (n = 9) remotely immobilised with medetomidine and tiletamine-zolazepam in the Tuan and Toolara State Forest. Data are the mean ± HR, heart rate; RR, respiratory rate; S_pO_2, haemoglobin saturation; CRT, capillary refill time

Recovery

Following the administration of atipamezole at a mean of 37 ± 2 min post induction, all horses stood within 31 ± 13 min. In one horse, where 75% of the calculated dose of atipamezole was given i.m. and 25% i.v., totalling 100 mg, the recovery was prolonged and lasted 115 min. In the second horse, where 25 mg atipamezole was given i.v. and 25 mg i.m., the recovery was rapid and lasted 5 min. Subsequently, the remaining seven horses received 50 mg i.v. atipamezole. For six horses, the average recovery length was 9.3 ± 3.2 min. One horse experienced a longer recovery; therefore, it additionally received 25 mg, i.v., atipamezole 25 minutes after the initial dose and recovered in 37 min. One horse did not recover from the initial dose, so subsequently it was given 25mg, i.v. atipamezole at 25 min and then again at 60 min after the initial dose, totalling100 mg. The recovery length of this horse was 70 min.

Most horses (*n* = 7; 77.8%) had a smooth recovery, which started with head-lifting and progressed to sternal recumbency, followed by less than three attempts to stand. Two (22.2%) horses had shorter recoveries characterised by three attempts to stand before standing. Despite remaining standing, all horses appeared moderately sedated, and, if not stimulated, moved very little for the next 3 - 4 h. If stimulated to move, horses were ataxic, but the full control of body movements returned after 2 h standing.

Eight individuals eventually returned to their harems. One horse re-joined his harem on the same day, five horses the following day; and two horses remained by themselves for more than 2 days before re-joining their harems. One horse was euthanised within 16 h of recovery because of an injury sustained during anaesthetic induction. The post-mortem examination revealed that while the horse fell to the ground, its body weight had driven the dart into the chest cavity causing a pneumothorax and lung collapse.

Discussion

The combination of medetomidine and tiletamine-zolazepam produced adequate short-term immobilisation of all feral horses in field conditions. This is the first known study, to have used this drug combination to remotely immobilise free ranging horses. A single 3-mL dart was sufficient to produce immobilisation in 55.6% horses, with consistently short times to lateral recumbency. Depth of anaesthesia in these horses was variable but anaesthesia was generally short, and all measured physiological parameters were within normal ranges (Coumbe 2001). The recoveries varied in time, but were smooth and resulted in no visible injuries to immobilised horses. Similarly, 44.4% of horses that required more than one dart to become recumbent exhibited short times to lateral recumbency after the administration of the final dart. The stability of lateral recumbency in these horses was more variable as were the average recovery times. The overall recumbency time produced by this combination was longer than for many similar studies (e.g. Woolnough et al. 2012; Boardman et al. 2014).

In four horses, which were not immobilised with one dart, the initial dart bounced off or embedded in the target tissue subcutaneously. As a result, two horses in which the dart bounced off, showed a lack of response to the initial drug dosage, and in the other two instances, responses to the drugs were muted despite at least one of the subsequent darts embedding in the targeted animal's tissues. This procedure agitated the horses, and caused them to move, potentially bypassing the sedative effect. It is possible to conclude from these observations that where the dart did not initially lodge, or embed in the subcutaneous tissue, it may not have impacted with adequate force to inject a sufficient volume of drug to cause immobilisation, or the drug was subcutaneous and, therefore, had a slower effect (Rosu et al. 2012). Residual drug present in darts that bounced off the animals was observed but was not measured in the current study. Individual variation of anaesthetic responses varies between animals of the same species, and differences in age, gender, body condition, physiological state of the animals at the time of drug delivery may potentially affect drug absorption rates (Geschke and Chilvers 2009; Roelle and Ransom 2009).

Despite the differences in body size between the individual horses, it was not possible to constitute and deliver individual drug doses under the field conditions in which the study was conducted. The use of standardised total drug doses, rather than tailored individual doses, is reflected in the variability in drug dosages seen in **Table 1**. Measurement of body weight after immobilisation in the first four horses indicated that the drug combination dose selected was more appropriate for male horses with a more uniform body weight of around 450 kg, hence the preponderance of males in the present study.

In the present study, all animals were darted while standing or grazing, but numerous factors potentially influenced dart performance. For example, thick ground vegetation made it easier for the shooter to approach the horses, but the vegetation impeded progress of the dart. Observations made by the shooter revealed that wind speed affected dart trajectory which deviated from the target in two instances. Sudden movement of two horses also resulted in darts not embedding in the target tissue correctly.

The dose of medetomidine used in the current study was higher than the dose used in a previous study on use in Przewalski's horses (0.07-0.10 mg kg^{-1}; Matthews et al. 1995), and slightly higher than that used to immobilise feral donkeys (0.14 mg kg^{-1}; Woolnough et al. 2012). Other studies have shown that comparable doses of medetomidine to those used in the current study have been administered to large ungulates previously without lethal side effects (Tyler et al. 1990; Haulena et al. 2000; Woolnough et al. 2012; Boardman et al. 2014).

Heart and respiratory rates were within normal ranges, but S_pO_2 values showed that haemoglobin saturation decreased with anaesthesia and was of sufficient concern in one horse (11.1%) to warrant the administration of oxygen by nasal insufflation. If nasal oxygen is not available in the field then anaesthetic duration should be minimised by administering atipamezole as soon as possible to reverse medetomidine. The risk of early atipamazole use, however, could lead to residual effects of tiletamine and zolazepam, such as prolonged ataxia and distress to the animal (Muir et al. 2000). Greater dosing accuracy of medetomidine and tiletamine-zolazepam is also likely to reduce unwanted effects of anaesthesia, such as decreased haemoglobin oxygen saturation (Muir and Hubbell 2009).

Sedative and anaesthetic agents depress thermoregulatory function and both hypo-and hyperthermia can be of significance depending upon the ambient temperature and the duration of anaesthesia in the field (Delvaux et al. 1999). The metabolic effects associated with the escape response in wild animals may significantly raise the core and therefore rectal temperature of captured animals (Woolnough et al. 2012). Despite moderately high ambient humidity and temperature during the period over which the darting study occurred, the rectal temperature of immobilised horses remained within the published normal range (Coumbe 2001).

The use of reversal agents is desirable in feral and wild animal field anaesthesia, as it diminishes the risks associated with anaesthetic procedures (Walzer et al. 2006). In wild animal capture studies involving α-2 adrenergic sedatives, atipamezole has been successfully employed to accelerate animal recovery and reduce the costs of anaesthesia monitoring (Matthews et al. 1995; Ramseyer et al. 1998; Hubbell and Muir 2006). However, timing of atipamezole administration is important irrespective of whether an α-2-antagonist is the only drug administered or if it is combined with other sedatives or anaesthetics. In field anaesthesia, atipamezole administered subcutaneously (s.c.) and i.v. at doses of 0.17-0.23 mg kg^{-1} 30 minutes after remote delivery of medetomidine and ketamine did not result in complete reversal and was associated with variable recovery times in Przewalski's horses, which was believed to be due to persisting effects of ketamine (Matthews et al. 1995). Larger doses of atipamezole administered 15 minutes after medetomidine and ketamine, significantly shortened recovery time but did not eliminate residual effects of ketamine in feral donkeys (Woolnough et al. 2012).

There is no readily available antagonist for tiletamine-zolazepam (Muir and Hubbell 2009). Administration of atipamezole in this study was deliberately delayed to a mean (± s.e.m.) 37 ± 4 min post induction to ensure that when the effect of medetomidine was neutralised, the residual effects of tiletamine-zolazepam were reduced. Earlier administration of atipamezole would have meant that the level of α -agonist reversal would have been influenced by the persistent of the tiletamine-zolazepam sedation and arousal would have been diminished. As a result, rapid and smooth recoveries and return to standing was obtained in 77.8% horses. The approach was similar to that of Woolnough et al. (2012), where α-2 adrenergic antagonist administration to 30 - 40 min post induction, avoiding residual ketamine effects and enhancing the smoothness of recoveries.

The anaesthetic time of wild equids should be reduced to a minimum (Walzer et al. 2006; Woolnough et al. 2012) but our study reported an extended mean time in lateral recumbency of 54 ± 13 min. For example, the first horse received 75% of the calculated dose of atipamezole by i.m. injection. Time to standing in this horse was slow (115 min), which could have been influenced by the route of administration. Subsequent horses were given 50% (*n* = 1) or 100% (*n* = 7) of the calculated atipamezole dose i.v., which considerably shortened their recumbency and recovery times (**Table 1**). When atipamezole was administered intravenously, the recovery was considerably more rapid, was associated with a moderate degree of ataxia, and in general involved a lower dosage. Extended recovery time of the last horse could have been a result of a larger dose of anaesthetic agents received by three consecutive darts. The amount of drug injected from darts which dislodged and/or bounced off was unknown and was assumed to be nil when calculating dose rates, however some absorption could have occurred. To reduce recumbency times, further research could investigate the combination of the shorter-acting but less soluble ketamine with medetomidine (as per Mathews et al. 1995) in contexts that permit larger dart sizes (helicopter darting, trapped animals). Investigation of adding the enzyme hyaluronidase (as per Cattet and Obbard 2010) may also be warranted to reduce induction times.

Legislative requirements surrounding the use of the potent opiate etorphine are prohibitive in Australia (Australian Government, Department of Health and Aging, 2013). The occupational hazards posed by etorphine make it very difficult to acquire licenses to use the drug for operational immobilisation programs (Woolnough et al. 2012). Less potent opiates, such as butorphanol, are often added to the medetomidine–ketamine combination (e.g. Miller et al. 2009; Boardman et al. 2014). However, opiates are Schedule 8 drugs in Australia (Australian Government Department of Health and Aging 2013), reducing their accessibility for field techniques (see Woolnough et al. 2012). In addition, the high cost of butorphanol, and its antagonist, naltrexone, render such regimes relatively expensive when compared with methods not including an opiate. For these reasons, an opiate was not included in the immobilisation regime in the current study. In contrast, the use of medetomidine and tiletamine-zolazepam offers an accessible and practical option for operational control programs of feral animals in the field.

Conclusion

The combination of 60 mg of metedomidine and 1500 mg of tiletamine-zolazepam allowed safe, partially reversible and cost effective remote immobilisation of nine feral horses in their natural environment of the TTSF. This approach was practical for the study operators as it only involved the use of three drug preparations and did not require the use of restricted substances. The ability to safely immobilise feral horses for the attachment of telemetry equipment or collection of health and physiological data is important for the understanding of the biology of the species. The practicality of capture techniques is an important consideration for managers to facilitate live removal or euthanasia of feral horses during management operations where lethal methods are not acceptable (Chapple 2005; Nimmo and Miller 2007). The ability to capture feral horses in the TTSF and similar land tenures by chemical immobilisation will advance current non-lethal management options which are primarily based on mustering and trapping (Berman 2013). This technique will be of particular importance in the forestry areas located near major public roads, where mustering of animals may increase risk of collisions with vehicles. Future research should be aimed at optimising dose rates and delivery mechanisms for medetomidine and tiletamine-zolazepam, comparing with medetomidine-ketamine, and providing additional information on the safety, efficacy, and physiological responses of horses immobilised with this drug combination.

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POPULATION DYNAMICS OF FERAL HORSES IN THE TUAN AND TOOLARA STATE FOREST (2011 – 2014).

By Magdalena A. Zabek, Christina W. Collins, Dave M. Berman, Simon Blomberg, and John Wright

Report prepared for FPQ Plantations
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INTRODUCTION

This report discusses the results of a study conducted from September 2011 to April 2014. The study had its origins in the need to define the demographics of the feral horse (*Equus ferus caballus*) population in the Tuan and Toolara State Forest (TTSF). As the population of feral horses in the TTSF has grown, the number of horse-vehicle accidents has risen and the impact of increasing horse numbers on the forest environment and management practices has not been fully elucidated. There has been a steady and consistent growth in horse numbers and if this trend continues the consequences will significantly impact on animal welfare and forestry practices.

Australian literature reveals very little about the origin of feral horses in the TTSF and surrounding region. First reports of unclaimed horses by local residents occurred in the 1990s (cited by Dobbie *et al.* 1993), however anecdotal evidence suggests that feral horses have been present in TTSF and surrounding areas since the early 1940s; being liberated as a result of mechanisation of the forest industry (Crittle and Jackson 2004). Since that time, additional deliberate releases of unwanted domestic horses have apparently occurred (Forestry Plantation Queensland personnel, pers. comm.). The absence of population control measures by management until recently, in association with wild dog eradication programs in 2003, have increased the survival of younger horses and accelerated population growth (Crittle and Jackson 2004).

Feral horses have been recognised as a problem in the TTSF over the last decade (Crittle and Jackson 2004). In 2002 a brief survey was undertaken by the Department of Primary Industries and Fisheries (DPI&F), which roughly estimated the population to be 181 animals (Crittle and Jackson 2004). In 2009, a more comprehensive survey was undertaken, which was carried out over an area of 430 km^2. The survey applied a distance sampling technique based on observed animals and estimated the population size for the surveyed area to be 995 horses (95% CI 583 to 1691), with an average density/km^2 of 1.9 horses (Berman 2013).

Both surveys identified feral horses as a serious distraction for motorists, and identified the potential for serious horse-vehicle accidents. The lack of fencing along public roads meant that horses became desensitised to road traffic and crossed roads singly or in groups, resulting in near-collisions and collisions with vehicles, horse deaths and vehicle damage (Crittle and Jackson 2004; Berman 2013; pers. obs.).

The risk of logging vehicles colliding with feral horses within the plantation was assessed as high and collisions with motorists on the major public roads as very high (Crittle and Jackson 2004). To reduce the danger of animal-vehicle collisions, risk minimisation protocols were implemented, which included installation of warning signs along the major public roads running through the forest, and removal of horses from the forested areas bordering public roads. At the time of writing, this management plan has resulted in the capture and removal of 77 feral horses (Berman 2013).

Although control by removal is currently effective, increasing horse numbers will reduce the efficacy of this control measure (Berman 2013). The increasing number of horses within the plantation and particularly near major public roads demanded that a comprehensive risk assessment be urgently undertaken. Multiple aspects of feral horse ecology need to be identified to facilitate long-term management of the population (Walter 2002). Knowledge of TTSF population distribution and abundance would assist in targeting areas where control measures are likely to be of greatest benefit. Estimation of population birth rate, age specific survival and annual population growth rate would assist in making decision on the number of animals to be removed and the age cohort to target to achieve the best outcome (Lande 1988). For management to consider using suppression of fertility to control population size, it is vital to first determine the social stability of the population and its reproductive performance.

SITE LOCATION

The Tuan and Toolara State Forest forms a contiguous coniferous plantation owned by Forestry Plantation Queensland (FPQ). The plantation stretches from the coastal lowlands of the Great Sandy Straight, to the Great Dividing Range, covering an area of approximately 1000 km^2 (**Figure 1**). The plantation is located east of Gympie, south of Maryborough, and west of Rainbow Beach. Two main roads divide the plantation; the Maryborough-Cooloola road divides the forest into western and eastern sections, and Tin Can Bay Road divides the forest into northern and southern sections.

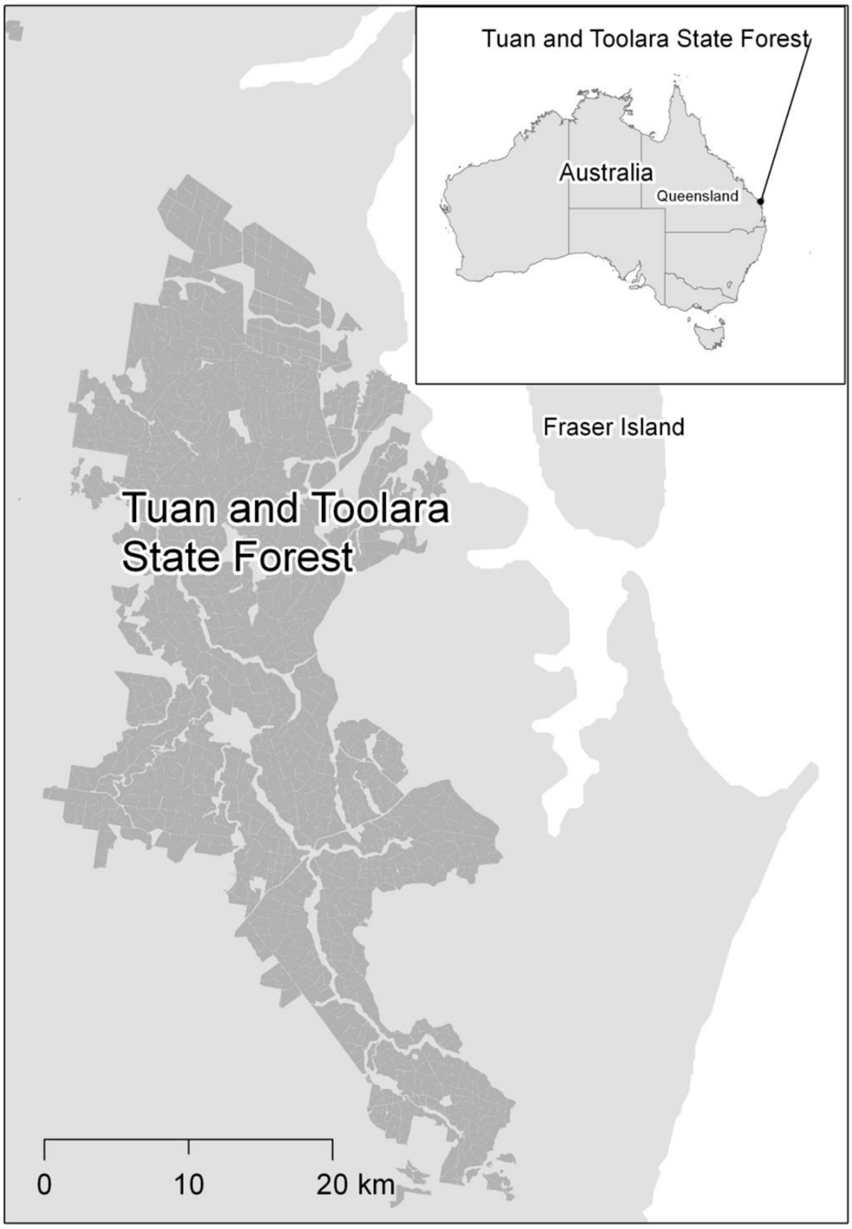

Figure 1: The location of the Tuan and Toolara State Forest in southeast Queensland.

Detailed description of methodology used to quantify feral horse population demographics in the TTSF is presented elsewhere (Zabek 2015). All data were collected in the study area (SA, 99.1 km^2), which included logging areas of Ulirraba, Sugarloaf, Missings and part of Hakea (**Figure 2**). This area was chosen as the main research site because of its central location within the plantation, it contained comparable proportions of open and closed canopy habitats to that found in the entire TTSF, and no horses were scheduled to be removed from the site during the study.

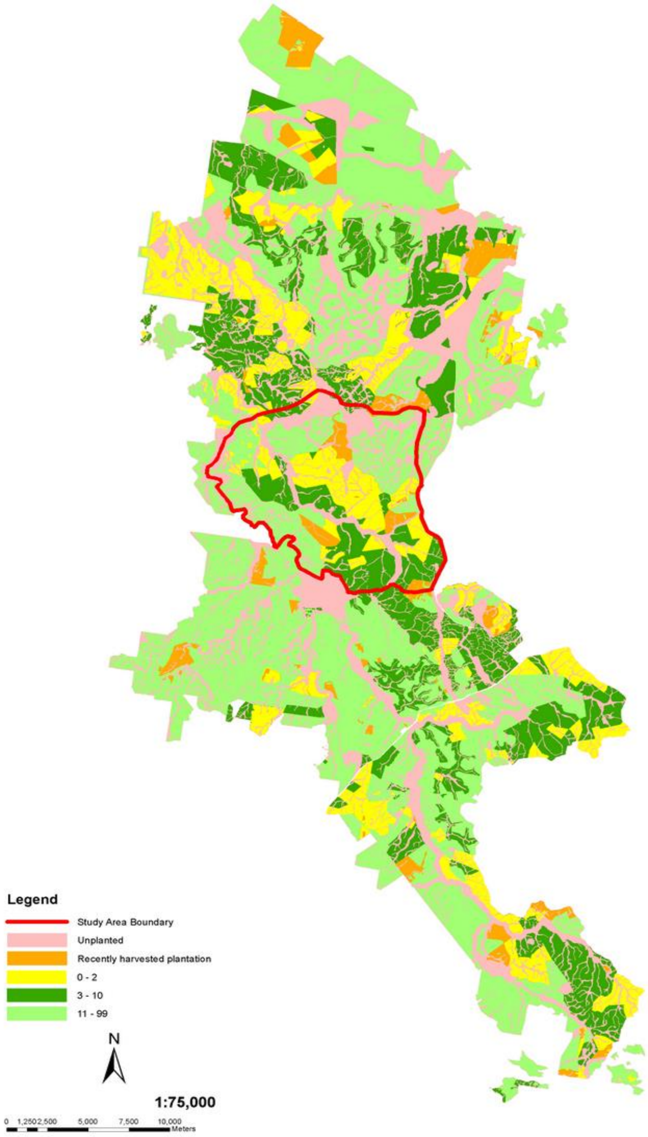

Figure 2: Habitat distribution in the study area and in the entire TTSF in 2012: red line – study area boundary; orange - harvested pine; yellow - young pine; dark green - juvenile pine; light green - mature pine, and pink - native bushland.

An estimate of feral horse population size in the entire TTSF (756 km^2) was inclusive of the plantation-controlled habitats (mature pine, juvenile pine, young pine, and harvested pine) but excluded native bushland. The estimate was calculated from two geographical areas: the SA; and the reminder, which was the majority of the plantation area (TFA) totalling 656.7km^2. These two areas were further subdivided (stratified) into four habitats, representing different growth stages of the pine forest.

POPULATION DISTRIBUTION

Population density directly affects the distribution and habitat use of animals in the population. Since the incidence of horse sightings within the plantation and vehicle collisions with feral horses on the major public roads had increased (Fraser Coast Health and Safety Report 2012), the obvious conclusion was that the population had increased in size. There was also a need to establish what effects the increasing numbers were having on the TTSF environment, both native and managed. Information on distribution, abundance, density, and habitat use of feral horses in the TTSF would enable the development of population control management strategies.

Assessment of the population distribution based on a strip transects survey using horse dung on forest tracks was conducted in 2009 (Berman 2013) and was repeated in the current study. The population distribution map from 2009 indicated the highest dung encounter rate (which reflected the highest density of horses) was in the north-west part of the plantation and in the area neighbouring the Maryborough-Cooloola and Tin Can Bay roads (management area M). No dung was recorded at the western and eastern extremities of the plantation in the 2009 study (**Figure 3a**). In 2012, the highest dung encounter rate on forest tracks was observed in the central part of plantation. Again, no dung was detected at the western and eastern extremities of the plantation. Since 2009, 77 horses have been removed from the forestry area adjacent to the major public roads (management area M), which explains the reduced dung encounter rate in that area in the present study (**Figure 3b**).

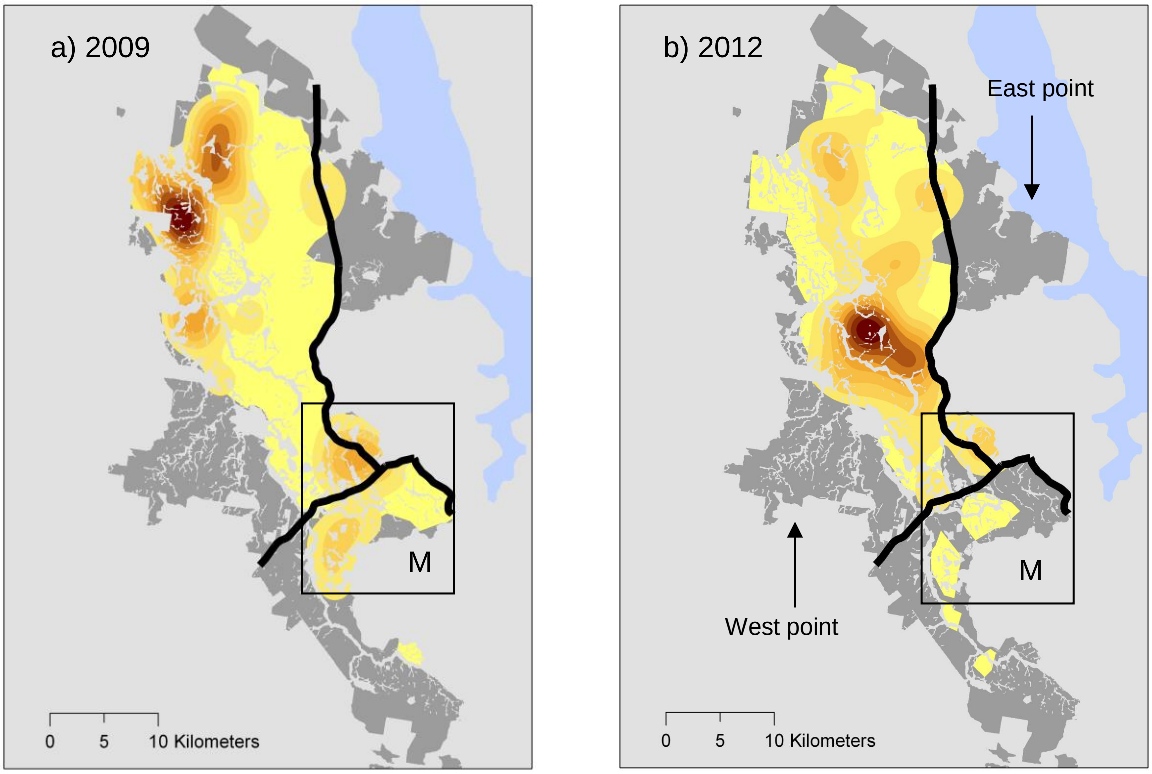

Figure 3: Feral horse distribution in the TTSF **a)** 2009 (Berman 2013), and **b)** 2012. Both surveys used analogous methodology based on dung encountered on plantation roads and tracks. Yellow = 2000 – 4000 dung/km^2; orange = 4000 – 8000 dung/km^2; brown = 8000 – 12000 dung/km^2; grey - plantation area; black lines – major public roads, and M – management area where 77 horses were removed between 2009 – 2014.

Differences in population distribution between the 2009 and 2012 surveys reflect habitat selection and availability. In 2009, the highest dung counts corresponded to the distribution of young and juvenile pine trees in that area. Between 2009 and 2012, major harvesting and planting operations took place in the central part of the plantation, creating new and extensive open habitats, which corresponded to the highest dung counts in 2012. The results of the two studies show that feral horses in the TTSF prefer open canopy habitats. Therefore, it is likely that creation of new open areas in the central part of the plantation offered greater grazing opportunities, which consequently, influenced population distribution in 2012.

Dung surveys in 2012 indicated that some areas of the forest were either not occupied or occupied by only a small number of horses. Such areas offer sites into which the population could expand in the future. As the plantation management areas are mostly unfenced, and are usually separated by roads or topographical barriers, such as creeks, streams, or patches of dense native vegetation, there would be minimal impediment to the colonisation of these areas, as has been shown to be the case with feral horses elsewhere in Australia (Dawson 2005).

POPULATION DENSITY AND ABUNDANCE

Abundance and density of horses were estimated by distance line transect survey of dung counts, dung disappearance rate in 444 (± 150.7 SD) days, and individual defecation rates of 7.97 (± 8.74 SD) over 24 hours. The analysis indicated that the TTSF was occupied by 1321 horses (95%CI 940 - 1965), which gives a density of 1.8 horses/km^2.

Density of horses was not uniform across the surveyed areas (**Table 1**). The overall highest density (2.9 horses/km^2) was estimated in the central part of the plantation, which corresponded to Sugarloaf, Ulirraba and Missings logging areas. Dung surveys indicated that some areas of the forest were not occupied (North Dempster, Taurus, Bungawatta, Red Ridge, and Tinana; 125km^2) or occupied by fewer horses (Malaleuca, Boonooroo, Como and Round). As previously discussed, these unoccupied or lightly occupied areas offer potential sites for expansion of the population in the future.

Area/Habitat Description	Area Size (km^2)	Density Estimate ($horses/km^2$)	Abundance Estimate	%CV
SA				
Mature pine	41.4	2.40	100	36.7
Juvenile pine	28.7	3.48	100	31.5
Young pine	22.8	3.35	76	24.2
Harvested pine	6.2	2.26	14	23.6
Total SA	**99.1**	**2.92***	**290**	**20.9**
TFA				
Mature pine	285.3	0.84	238	27.0
Juvenile pine	176.4	1.27	224	31.2
Young pine	172.4	2.84	491	36.3
Harvested pine	22.6	3.42	78	23.4
Total TFA	**656.7**	**1.57***	**1031**	**22.5**
TOTAL TTSF	**755.9**	**1.79***	**1321**	**18.3**

Table 1: Estimates of feral horse density/km^2 and abundance in the SA, TFA, and the entire TTSF, obtained from distance sampling of dung, dung decay rate and defecation rate. *The average horse density estimate was weighted by the size of each habitat and was taken directly from DISTANCE 6.0 output. %CV – coefficient of variation

HOME RANGE AND HABITAT PREFERENCES

Topography, habitat availability and climatic conditions influence the size and shape of home ranges of feral horses (Gates 1979; Linklater 1998). The mean home range size of harems in the TTSF was 16.9 ± 9.11 km^2 SD. All harems were loyal to their home ranges; harem members occupied one core area more than other parts of their range, and home ranges highly overlapped (**Figure 4**).

Habitat use quantified by visual detection of horses, dung counts, and Global Positioning System (GPS) tracking, identified horse preference for the open habitats of young pine forest and harvested areas, and avoidance of the closed canopy habitats of juvenile and mature pine. The observed long-term plasticity in areas being preferentially utilised and avoided by the horses suggest that feral horses in the TTSF adapt to changes in habitat availability and tend to move into newly created (harvested) open areas located within or adjacent to their home range. It was also very apparent that TTSF feral horses also adjust movement within their home range to human forestry management.

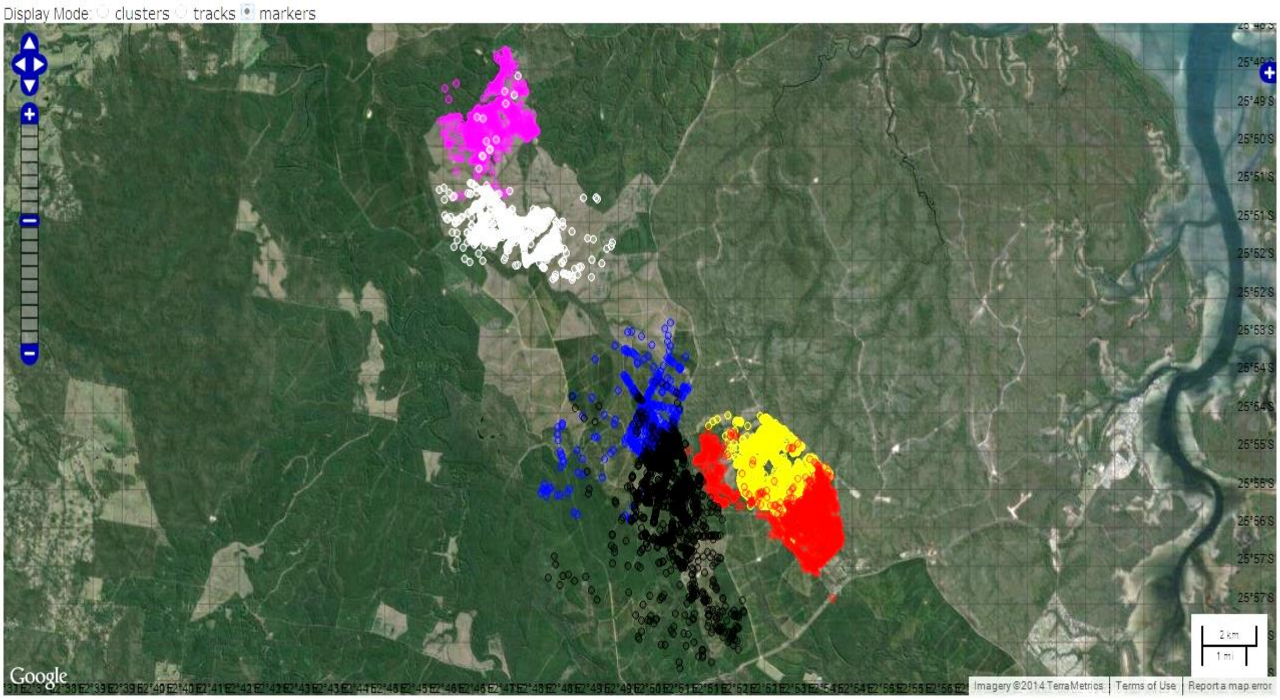

Figure 4: Graphical representation of home range overlap of six harems tracked by GPS in the TTSF. Large concentrations of points indicate high density data collection, which correspond to highly used plantation areas. Light green areas – open canopy habitats; dark green areas – closed canopy habitats.

POPULATION DEMOGRAPHY

The TTSF population did not show significant annual variation in demographics, which is consistent with measurements in other unmanaged feral horse populations in Australia and abroad. The social structure was characterised by well-defined breeding groups (harems), which involved the majority of the population. The average harem size was estimated as 4.95 (95%CI 4.53-5.41), and usually consisted of 1 stallion, 2-3 adult females, and 2 immature offspring (≤ 3 years of age, **Figure 5**). Males not associated with harems consisted of adult (≥ 3 years old) and sub-adult (2 years old) individuals, either forming groups of 2 – 6 or living by themselves. The age distribution of the TTSF feral horse population was stable across the entire study period, with adult horses constituting the largest group (68%). The sex ratio of adult female to male horses was nearly equal (0.99:1.00), which indicates identical survivorship of adult female and male horses.

Figure 5: Typical size and composition of harems in the TTSF consisting of one stallion, two adult females, and two juveniles.

POPULATION DYNAMICS

Feral horse population dynamics have been studied in a range of environments in many parts of the world (Garrott *et al.* 1991; Goodloe *et al.* 2000; Linklater *et al.* 2004; Scorolli and Lopez 2010), but very little is known about feral horse population dynamics in Australia, particularly in regard to reproductive performance (fecundity), mortality and the rate of population growth. Variability in population dynamics is due to different limiting factors operating at different locations. Predation can considerably affect foal survival, food limitation reduces survival of juveniles and limits the ability of females to reproduce, and human management reduces population size by culling or by employing fertility control measures to reduce birth rates.

The population dynamics of feral horses in the TTSF were comparable to those obtained for other feral horse populations where the environment imposed nutritional limitations (Berman 1991; Cameron *et al.* 2000; Dawson and Hone 2012). The mean foaling rate was 46% and adult females were observed to foal on average every second year. The overall nutritional status of the population expressed as body condition score (BCS; 0 - 5) was 2.55 ± 0.51 SD with adult females having poorer scores than other age and gender groups. Survival estimates were consistently high (92 – 95%) across all age groups. The average annual rate of population increase for the three years of the study was 9%, which was lower than the maximum reported for populations living in the most favourable conditions (**Figure 6**). Elasticity analysis demonstrated that the TTSF population growth rate was almost seven times more sensitive to changes in adult survival compared with juvenile survival, and almost twice more sensitive than changes in fecundity (fertility).

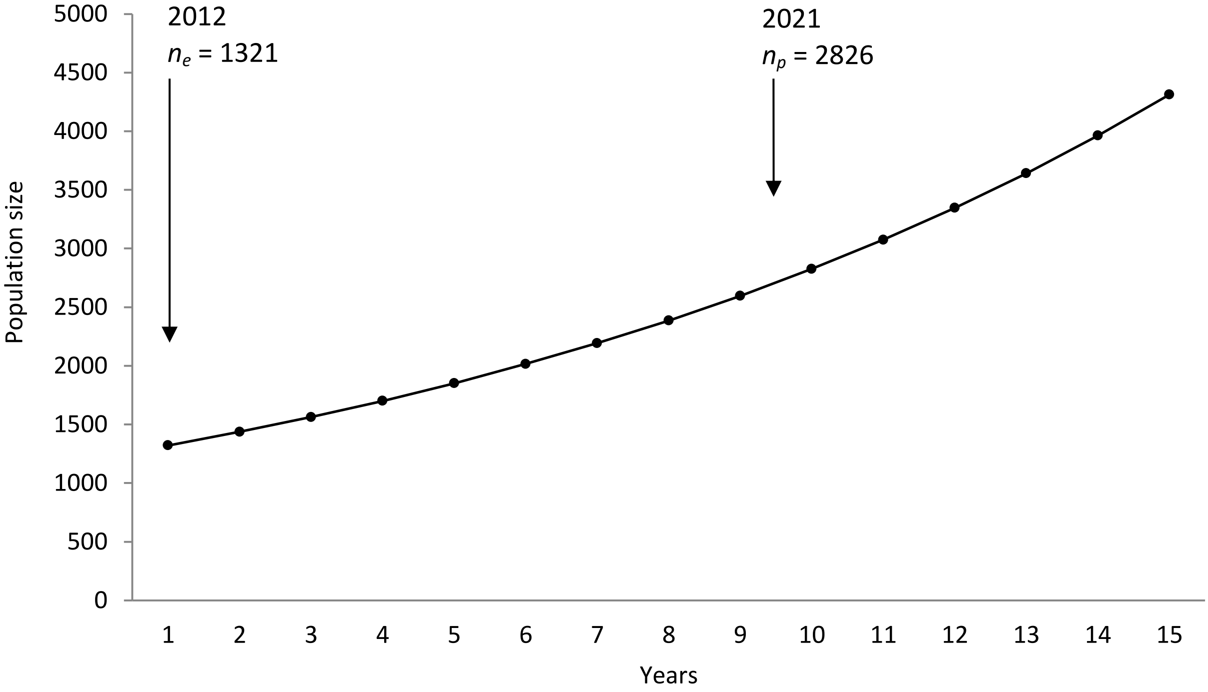

Figure 6: Projected population size of feral horses in the TTSF over 15 years using the Leslie age-structured matrix simulation model. n_e – estimated population size in 2012, and n_p –projected population size in 2021.

GENERAL DISCUSSION

It had been proposed that trapping and re-location of TTSF feral horses from plantation areas located near the major roads would reduce the risk of vehicle collisions (Crittle and Jackson 2004; Berman 2013). One proposal recommended that horse-free zones be established parallel to and on either side of busy roads and in other specified areas where horses were likely to cross roads (Berman 2013). These liberated areas would provide a buffer zone and it would take time for horses to re-occupy them. It was assumed that feral horses in the TTSF had limited home ranges to which they were loyal, and within which their movements were predictable (Berman 2013). Experience gained from horse removal in the Barakula State Forest indicated that horses were slow to recolonise new areas if entire harems were removed because adjoining groups of horses apparently respected home range boundaries (Crittle and Jackson 2004). Similar management strategies kept the Finke Gorge National Park free of feral horses for almost 20 years (Bryan 2001).

For horse removal to be an effective management tool in the TTSF, it is obvious that the distribution and abundance of horses must be ascertained with home range size and habitat use being of particular importance. Trapping, as a removal tool, would be most effective in those areas where horse numbers are high but could also be used to target those horse groups whose home ranges have been identified to include major roads.

Results from the current study show that harems in the TTSF occupy moderately sized home ranges with small, but distinctive core use areas that predominantly consist of open canopy habitats. These findings suggest that if buffer zones bordering busy roads were maintained as closed habitats, it is likely that feral horse numbers would be low or non-existent in these zones. Strong preference of horses for open habitats, particularly harvested pine, suggests that harvested areas located in or near buffer zones would require more intensive management (higher capture rates) and continued monitoring to maintain these areas horse-free. In particular, bachelor groups are likely to be an issue in such areas because their home ranges appear less well defined and are therefore likely to move into unoccupied open habitats where feed is ready available.

Counting dung on plantation roads provided very useful information on population distribution across the TTSF. Additionally, the distribution of dung on plantation roads was positively correlated with the distribution of dung in adjoining forest habitats, which suggests that road dung surveys can be used to monitor colonisation of buffer zones and to assess population spread into new plantation areas. In particular, an annual surveillance of dung would provide oversight as to whether buffer zones continued to remain horse-free. However, dung surveillance on roads is limited in its usefulness as it cannot be used to assess population abundance trends, which requires distance sampling of dung.

Management of horses along the major public roads, involving the capture and removal of 77 horses, has been successful since its implementation in 2009, with the risk of collisions being reduced by 68% (Berman 2013). However, as the population grows, there will be a need to remove a greater number of horses.

Currently, there are an estimated 1321 horses in the TTSF, at a density of 1.8 horses per km^2, and the annual population growth is 9%. In 2009, the population was estimated to be 955 horses (Berman 2013). If this estimate was accurate, the TTSF population has increased from 2009 to 2012 by about 32%, an annual average growth of 10%. Therefore, to maintain the population at its current size, considering the rate of increase, requires the removal of 120 horses per year. As shown by others (Lundie-Jenkins *et al*. 2006), management strategies such as local buffer zones bordering roads, will not be effective as stand-alone programs but must be incorporated into forest-wide programs that take into account the considerable mobility of feral horses.

Although the TTSF feral horse population is dispersed across the forest, it is most abundant in the central region. This has important management implications. Removal of horses from the periphery of the central region will have little influence on the population dynamics in the central region because of the delay involved in horses moving into the depopulated area. This means that resource pressure will be maintained in the central region slowing the rate of population growth, which in turn reduces the number of animals that need to be removed (Walter 2002; Scorolli 2012). However, when the population reaches the carrying capacity threshold, it may substantially impact on the environment by destroying water sources, damaging native vegetation (Caughley 1976; Schott 2004) and possibly young pine stands (**Figure 6**; Crittle and Jackson 2004). This may also have welfare implications because of food and water shortages.

Figure 6: Feral horse-induced soil erosion and damage to the banks of water holes located in the study area.

Although the population of feral horses in the TTSF is increasing slightly slower than predicted, there are reasons to be concerned about the rate of growth. Overpopulation is likely to occur in the near future as a consequence of its increasing size. By 2021, based on current rate of population growth, horse density per km^2 across the entire forestry will be 3.6, which will severely test the carrying capacity of the TTSF. This will cause horses to move to unpopulated areas both within and outside the plantation and increase the risk of motor vehicle collisions. The area of particular concern would be the border of the TTSF with the Great Sandy National Park, which is unfenced and provides no barrier to expansion of horses into the national park.

Although fencing is not generally compatible with forestry operations (Crittle and Jackson 2004), there may be some places where fences could be built to restrict horse movement across major public roads without interfering with forestry activities. Feral horses are highly mobile and past studies have identified well defined movement corridors between habitats (Dyring 1990; Schott 2004). Targeted fencing in the TTSF may prevent horses moving into areas that have been depopulated by horse removal programs (**Figure 7**). Although fencing may prevent horses from crossing major roads thereby reducing the risk of collisions, it cannot be the only strategy used to control the growing and expanding population.

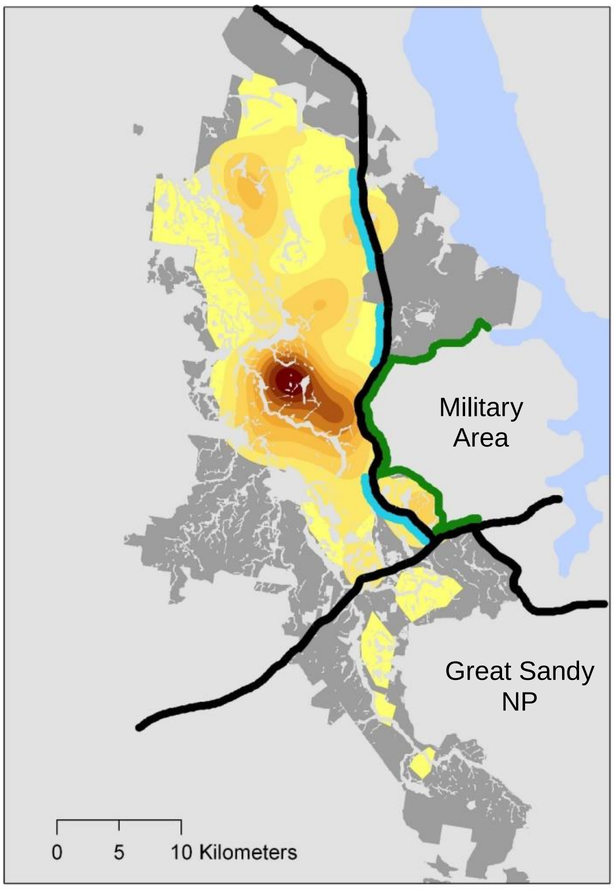

Figure 7: Location of proposed fence (blue lines) to discourage horses from crossing major roads (black lines) and recolonising eastern areas of the plantation once all horses have been removed from these areas. Green lines – fenced off Military Area.

Management practices can limit feral horse population size by controlling fertility or by culling. A view commonly held by animal welfare groups is that fertility control is the logical and humane solution to the problem of feral horses in Australia (Chapple 2005; Nimmo and Miller 2007; Dinn 2012). However, many studies have confirmed that fertility control is only feasible in small, contained and accessible populations, where every individual horse can be identified (Kirkpatrick and Turner 1991; Cameron *et al*. 2001; Killian *et al.* 2008).

Based on the estimated population of 1321 horses, age distribution (adult component equal to 68%), and equal sex ratio of adults, there should be about 450 breeding females in the TTSF. Considering that a relatively high proportion (60 - 80%) of females in the population must be treated to significantly influence population reproductive rates (Turner and Kirkpatrick 1991); there would be a need to target between 270 - 360 females. Locating, identifying, capturing, treating and re-treating this number of horses would be very challenging logistically and very expensive.

It is also essential to note that the current study demonstrated that adult survival was a far more important contributor to population growth than was fecundity (fertility). The high cost of pregnancy and lactation prevents mares from foaling every year, which limits population growth. Therefore management emphasis should be on influencing adult survival and not fertility. The greatest success would be achieved by targeting adult females because reducing the number of males may increase the reproductive rate of the population by increasing the stability of harems (Dobbie and Berman 1992). Management based on fertility control of females should be of secondary importance, with removal of juveniles being of lowest importance.

CONCLUSIONS

The focus of the initial management strategy was to prevent collisions between horses and vehicles on the major public roads that traverse the TTSF (Crittle and Jackson 2004). This has been partially successful following the removal of 77 horses from forest areas adjacent to the major public roads over the period 2009 – 2014 (Berman 2013). Qualitative assessment of the effectiveness of the imposed management should be measured by monitoring records from the Department of Transport and Main Roads involving vehicle accidents caused by horses. Continued successful management based on horse removal will only be achieved if the information obtained from the current study is incorporated into management plans.

KEY FINDINGS AND RECOMMENDATIONS ARISING FROM THE STUDY

1. Changes in distribution of horses can be detected by monitoring dung counts on forest roads.
2. Accurate evaluation of population abundance can be achieved through distance sampling of dung.
3. Further monitoring of the TTSF population is necessary to account for annual changes in population recruitment.
4. Monitoring body condition scores of horses, particularly of the adult females, will alert management to feed shortages associated with increasing population. pressure, which has the potential to cause adverse publicity around welfare.
5. Effective management strategies should involve substantial and continuing removal of adult female horses, or manipulation of survival and fecundity to control population growth. As selective removals will likely alter adult sex ratio and age structure of the population, ongoing assessment is necessary to minimise adverse welfare outcomes.
6. When designing long-term control measures for the TTSF population, obtaining ongoing accurate estimates of adult survival should be of the highest priority.
7. If fertility control is to be one of the future management strategies, it would be most effective to initially reduce the current population by other means before using such a strategy. Financial expense and the logistical difficulties of applying fertility control measures need to be further evaluated to identify the cost-benefit relationship.
8. Strategic use of fencing to reduce horse movement across the public roads.
9. Maintenance of narrow strip of closed canopy habitat bordering main roads to take advantage of the preference for open habitats thereby reducing the likelihood of horse-vehicle collisions.
10. Continuing removal of horses from the forested areas located near the public roads together with recording the number of horse-vehicle collisions, to assess the success of the removal program.

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