Feral Horse Ecology in the Rocky Mountain Foothills of Alberta, Canada.

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By

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ABSTRACT

Boyce, P. Feral horse ecology in the Rocky Mountain Foothills of Alberta, Canada. Ph.D., Department of Biology, University of Saskatchewan, Saskatoon, Canada. September, 2022.

Feral horses have been present in western Canada since the early 1720s, though little is known about fundamental components of their ecology. In the foothills of the Rocky Mountains in Alberta, Canada, increasing socio-political conflict regarding feral horse management, their role, and their impacts in the Foothills ecosystem highlights a growing need for nuanced management approaches predicated on robust ecological information. My objective was to assess several key aspects of feral horse ecology within the largest known population of horses in western Canada, located west of the township of Sundre, Alberta. In Chapter 1, I provide a general introduction to the history and ecology of feral horses in western Canada and North America, to the study area, and to the key questions motivating the research. In Chapter 2, I begin by reviewing the causes and consequences of a lack of robust ecological information for many feral horse populations, and feral wildlife generally, and found that both political and biological asymmetries in feral populations can favor the persistence and expansion of populations of feral species relative to native species. Ideological opposition to the necessary study of feral populations as wildlife also has important implications for increasingly contested population management of feral species.

In Chapter 3 I assessed key spatial and social characteristics of the population within the Sundre equine management zone (EMZ) using a combination of GPS telemetry and camera-trap data. Social characteristics such as band size and sex-ratio were consistent with earlier work and with feral horse populations generally. Home-ranges overlapped considerably between individual bands with sizes ranging from 47.6 to 93.0 km^2. These were larger than those that were identified by Salter in 1978 within an area now encompassed in the Sundre EMZ, though were similar to those identified by Girard in nearby Bragg Creek, Alberta with the difference likely representing differences in methodology. Movement and detection rates of horses were greater in summer, and horses showed reduced diel activity in the middle of the day in summer, compared to winter. The number of foals detected, and the mean number of foals within each band was highest from June to August and composed less than 15% of the total individuals detected each year. Identification of individuals based on natural markings was possible, though the influence of non-independent movement and social grouping was evident, and problematic for capture-recapture analyses.

In Chapter 4, I assessed density and total abundance of the population of horses in the Sundre equine management zone using space-to-event (STE) density models. Feral horse density was 0.602/km^2, 0.606/km^2 and 0.522/km^2 respectively, from 2017 – 2019. Total abundance estimates were similar to minimum aerial count data with confidence intervals from estimates overlapping aerial counts in all years except 2017, suggesting the population declined by approximately 14% from 2018 to 2019. These results are similar to recent trends detected in minimum aerial counts that show a decline in counts of approximately 22% (2019 – 2021) and contrast with expectations based on increasing minimum counts in the Sundre population in recent decades, and populations of many other free-ranging feral horse populations. Reasons for the decline are likely to be multi-factorial and are difficult to determine based on the current data alone. I discuss potential causes and the implications these have for future management.

In Chapter 5, I assessed habitat selection of feral horses with respect to several key landscape and vegetation characteristics of interest using GPS telemetry data, and compared summer occupancy of feral horses, cattle, and elk using camera-trap data. Variation was high among tracked individuals in selection for vegetation type, and counter to expectations, horses avoided native rangeland in summer, compared to greater selection of forestry cutblocks in all but one individual. This was also supported by higher summer horse occupancy probability with increasing areal coverage of cutblocks. This contrasted to cattle occupancy which declined strongly with increasing cutblock coverage. Cattle occupancy was also negatively influenced by terrain, though positively influenced by the presence of linear features and lower distance to roads. These results have important implications for the spatio-temporal partitioning of cattle and horses over summer and suggest that horses may avoid areas with high overlap with cattle.

In Chapter 6, I summarize the findings from each chapter, and discuss their wider management implications.

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Chapter 1 General Introduction

Ecological context and history of horses

Caballine horses evolved on the North American plains and were abundant components of a diverse Pleistocene megafauna (Haynes, 2009). Wild horses are presumed to have gone extinct on the North American continent approximately 6000 – 13000 years ago during widespread megafaunal extinctions and associated habitat shifts (Grayson, 2006; Murchie et al., 2021). However, prior to their extinction, horses expanded westward into Eurasia, and were domesticated approximately 5500 years ago in what is now Khazakstan (Outram et al., 2009). Following domestication, horses became an integral part of human society including in agriculture, warfare, and as direct sources of food (Robinson, 1999), and accompanied much of human expansion throughout the planet. This led to the reintroduction of horses as domesticates to the North American continent during exploration and colonization (McKnight, 1959; Scasta, 2019). European expansion, agriculture and ranching, and trading between Europeans and Indigenous peoples within the continent led to the widespread establishment of feral horse (*Equus ferus caballus*) populations, which often grew quickly, particularly in regions where predator populations were extinct or heavily persecuted, or where land was managed for large mammalian grazers (e.g., cattle [McKnight, 1959]). Contemporary feral horse populations in North America are therefore representative of a legacy of natural evolutionary processes, human expansion, and ecosystem modification. This complex history coupled with our close relationship with horses (Robinson, 1999; Salter, 1978) drives considerable debate and speculation regarding feral horse legitimacy, and their ecological roles, in modern ecosystems (Kincaid, 2008; Scasta et al., 2018).

Feral horses were present in western Canada from as early as the 1720s following trading among Europeans and Indigenous peoples after the reintroduction of the horse to the United States (McKnight, 1959; Salter, 1978). Logging, mining, and oil and gas exploration became prevalent in the Canadian west following settler expansion westward in the 18th and 19th centuries, with horses being the primary mode of physical labor and transport until the development and adoption of machinery (Kincaid, 2015). In addition, open-range cattle ranching was widespread on both native and cleared rangeland in the Rocky Mountain Foothills and interior plateaus across much of western Canada (Kincaid, 2008; Thistle, 2015). The associated horse husbandry culture that dominated early ranching practices led to the use of native grasslands as free-ranging winter grazing for domestic horses (Salter, 1978); a practice which continues today in some locations (Leverkus et al., 2018). Domestic horse use was therefore pervasive in western Canada, and feral populations are presumed to have formed through a series of deliberate releases or through husbandry practices (Kincaid, 2015; McKnight, 1959; Thistle, 2008). In the study area for research reported here, in Alberta, Canada, feral horse populations subsequently grew to form the largest population of feral horses in Canada (Kincaid, 2015), and have since been periodically controlled by roundups and culling (Salter, 1978). However, despite the population control efforts over the intervening years since their establishment, the population with the study area, referred to herein as the Sundre Equine Management Zone (EMZ), remains the largest population in Canada today (Kincaid, 2015).

Feral horses in the Sundre EMZ share many characteristics of feral horse populations throughout North America, with some important distinctions. As with many other non-island feral horse populations, understanding of feral horse ecology in western Canada is poor (Girard, 2012), particularly considering the depth and breadth of research regarding native species with which they interact (Boyce & McLoughlin, 2021). Similar again to most other North American populations, socio-political conflict regarding feral horses is predominantly related to competition with native (e.g., elk [*Cervus* elaphus]) and domestic (e.g., cattle) grazers, their impact on the landscape (Beever & Brussard, 2000; Beever & Herrick, 2006), and the methodologies employed to monitor, justify, and subsequently carry-out population control (Boyce et al., 2021). However, feral horses in western Canada generally, and the Sundre EMZ specifically, also inhabit ecosystems considerably different from other, better-studied feral horse populations in arid and semi-arid systems. For example, winters are particularly long and can be harsh, with snow potentially present for more than half of the year (Hebblewhite, 2006; Salter, 1978). Feral horses in western Canada also share the landscape with relatively robust predator populations that are absent in many other areas coincident with feral horse populations in North America (Boyce & McLoughlin, 2021; Ransom et al., 2016). The role of each of these factors can be considerable in large mammal population dynamics and behaviour (Garrott et al., 2008), including those of feral horses (Andreasen et al., 2021; Berger, 1983; Engebretsen et al., 2021; Garrott & Taylor, 1990; Lundgren et al., 2021), and highlight a need for research specific to western Canadian populations.

Management context

The socio-political context of management in the Sundre region is similar to that of many feral horse populations in that it is consistently controversial and hampered by imprecise and outdated policy (Boyce et al., 2021; Scasta et al., 2018). The rangeland management department of Alberta Environment and Parks, has a mandate through the Stray Animals Act (Province of Alberta, 2000), to manage the feral horse population in order to meet vague criteria such as the "ecological integrity of the rangeland and population" (Province of Alberta, 2000). Increases in annual minimum counts of feral horses in the Sundre EMZ in recent decades have caused concern among rangeland ecologists and managers, with overgrazing of native rangeland and competition with other grazers a primary concern (Girard et al., 2013; Kaufmann et al., 2013). However, in contrast to the resources available to research and manage native populations, such as those typical in wildlife or fish and game departments (e.g., capacity for robust long-term population monitoring and modelling, resource-use evaluation, understanding of population demographics etc.; for full review see Chapter 2), decisions about the need for culling or removal have historically been based on advice obtained from a feral horse advisory committee (FHAC) composed of ranchers, fish and game representatives, rangeland managers, and feral horse advocates (Alberta Environment and Parks, 2021; Strategic Relations Inc., 2013). This is typically coupled with raw minimum count data and assessed in reference to rangeland carrying capacity estimates (e.g., combined cattle and horse grazing; Alberta Environment and Parks, 2021). The lack of more robust, science-based management of the population has been widely criticized and continues to be a source of controversy (Rieger, 2018) and even litigation (Court of Queen's Bench of Alberta, 2019). Indeed, the Stray Animals Act, though limited in precise management language, stipulates a requirement for science-based decision making for feral horse management. Thus, the lack of comprehensive and ecologically based information regarding the feral horse population remains critical gap for feral horse managers.

Habitat changes in the Sundre region have also generated interest as a potential influence on feral horse population size and range. In recent decades there has been a large decrease in forest cover throughout the foothills (Schneider, 2002). The increase in clearcut logging and the associated generation of anthropogenic grasslands represents a potential increase in available forage for horses, particularly as horses can capitalize on abundant low-quality forage compared to ruminant grazers (Janis, 1976; Schoenecker et al., 2016). Previous research in other study areas had suggested that clear cuts may be important habitat for horses, particularly during winter (Girard et al., 2013), with the implication that ongoing forestry could result in the spatial expansion and growth of feral horse populations throughout the Alberta foothills. Thus, understanding the relationship between industrial modification and feral horse habitat use and distribution will be critical for long-term management.

Choice of Study Area

Feral horses exist throughout the Alberta Foothills, from as far south as Sheep River to north of the Brazeau River (Figure 3.1; Alberta Environment and Parks, 2021). Populations of horses are grouped by management boundaries, termed Equine Management Zones (EMZ), each of which is monitored separately (Alberta Environment and Parks, 2021). The highest density of horses is located west of the township of Sundre, AB, in the Sundre EMZ. While management implications and research findings of this project apply to Alberta feral horse populations throughout their range in similar ecosystems, spatial bounding of this project followed discussion with Alberta Environment and Parks (AEP) and focused on horses in the Sundre EMZ where data gaps are presumed to be most critical.

Available data

Little scientific data exist regarding feral horse populations in the Alberta Foothills. Within the Sundre EMZ itself, there had been only one ecologically based study of the feral horses undertaken in 1978 (Salter, 1978). Salter’s wide-ranging 1978 study focused on estimating niche overlap and other dietary analyses through fecal pellet counts, assessing habitat use, and describing social and spatial characteristics of the population through observation (Salter, 1978). Another study within the south-central Alberta Foothills had been conducted on a relatively small population (~130 animals) near the township of Bragg Creek, AB, in 2012 (Girard, 2012). This study examined resource use of four horses using GPS collars and pellet counts, establishing movement patterns seasonal habitat selection characteristics in a similar landscape to that of the Sundre area (Girard et al., 2013a; Girard et al., 2013). These two projects constituted the extent of published ecological research regarding the feral horse populations in the Alberta Foothills, with Salter’s work the only such specifically relating to the Sundre population. Non-ecological research and management critiques regarding the feral horses in the Sundre zone, and the wider Alberta foothills were also present (Kincaid, 2008, 2015; Notzke, 2010, 2013), highlighting the controversial nature of feral horse management in Alberta, and reiterating the need for sound science-based management (Nimmo & Miller, 2007).

Research motivation

The purpose of my research was to improve our understanding of feral horse ecology in the Alberta Foothills, with a focus on the population present in the Sundre EMZ, and with reference to several key aspects. In Chapter 2, I review the fundamental limitations in our approach to feral horse ecology, and the consequences this has had, and continues to have, for both management and ecological understanding of feral horses. In Chapter 3, I assess key demographic, movement, and spatial characteristics of the horse population in the Sundre EMZ. In Chapter 4, I assess the abundance and density of the population in the Sundre EMZ and compare estimates with minimum count data to assess the relative trends in population size. In Chapter 5, I assess habitat use and summer occupancy of feral horses in the Sundre EMZ, with reference to key habitats such as native rangeland, forestry cutblocks, and abiotic landscape features. The research described in these chapters aimed not only to answer key gaps in our ecological understanding of the population, but also to inform and facilitate the development of more robust, science-based management. In Chapter 6, I summarize key findings from each chapter. In Appendix A, I review the current understandings and critical knowledge gaps regarding predator-prey interactions involving horses. In Appendix B, I present an essay investigating the role of ideology and conservation philosophy as a form of subjectivity and bias in contemporary ecology and conservation, particularly as they pertain to feral horses.

Notes on terminology

Discourse regarding the influence of the term “feral” in feral horse research and management is well-established (Bhattacharyya et al., 2011) and is not addressed in detail in this thesis (though see Appendix B). Feral, free-ranging, and free-roaming are terms used synonymously herein to describe populations of free-living feral horses that are unmanaged in the wild. Unless explicitly described as otherwise, Sundre and the Sundre equine management zone refer to the region where the population of feral horses studied herein is located (i.e., as opposed to the township of Sundre, AB).

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Chapter 2 Causes and consequences of lags in basic and applied research into feral wildlife ecology: the case for feral horses.

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Abstract

The biomass of feral wildlife is eclipsing that of native wildlife in many parts of the world. Consequently, feral species are playing an increasingly important role in ecological community dynamics. Artificially selected life-history traits of wild but once domesticated species can elicit population dynamics that differ substantially from that of native species. Yet, we continue to lag in our understanding of the ecology and evolution of feral species with direct consequences to resource management and biodiversity conservation. In part, this is because basic and applied research into the ecology of feral wildlife is fraught with social and political challenges unique to science. Feral populations of companion animals or livestock, especially, can evoke strong emotional reactions among advocacy groups, particularly around issues of animal welfare and management policy. Managers tasked with controlling feral populations are often bound by social license, including legislative restrictions, incomparable to that of other wildlife, and harassment or litigation of researchers and managers is not uncommon. Further, research and management of feral species is often delegated to agricultural instead of wildlife government agencies with clear differences in mandate, staff education, and training. Using examples primarily from feral horses in North America, we show how scientists conducting research independent of the management process can find themselves placed between managers, advocates, and opponents of feral species, implicitly tasked with satisfying multiple and often contradictory interests of stakeholders, sometimes with direct and litigious interference. These barriers are exacerbated by inter-disciplinary tendencies to dismiss the importance of basic and applied ecological research into feral species, despite its relevance to sound decision-making. Feral species therefore possess politically and biologically facilitated asymmetries that favor persistence, growth, and expansion relative to native wildlife, while the timely study of these characteristics in nature continues to suffer from ideological opposition.

Introduction

Feral species are those of domesticated ancestry that now live in a free-ranging or "wild" state without direct human control (Bonacic et al. 2019). The domestication process typically involves artificial selection for traits that confer some benefit in the context of animal husbandry (e.g., increased reproductive potential, larger body size [Grange et al. 2009]), while also generating a familiarity and bond between the species and humans [Robinson 1999]). These two factors can produce significant management challenges for feral populations relative to native wildlife. Altered life-history traits may accelerate population growth and expansion (Clutton-Brock 2004) while the close cultural relationship with species invokes heightened public attention around management plans and actions (Scasta 2019). Consequently, politically and biologically facilitated asymmetries favour persistence, growth, and expansion of feral versus native wildlife with growing importance to biodiversity conservation.

Feral species including horses (*Equus ferus caballus*), cattle (*Bos taurus*), pigs and wild boar (*Sus scrofa*), camels (*Camelus dromedarius*), burros (*Equus asinus*), goats (*Capra hircus*), cats (*Felis catus*), and dogs (*Canis lupus familiaris*), have had significant impacts on ecosystems around the world, particularly in sensitive environments, or in areas where native wildlife is poorly adapted to contend with competition or predation generated by feral species (Gering et al. 2019). Feral cats, for example, are efficient predators of naïve native prey and have had significant impacts on native birds, mammals, and reptiles in Australia (Murphy et al. 2019) and New Zealand (Veitch 2001). Feral ungulates such as camels and horses have grown to large population sizes in the Australian outback (Saalfeld & Edwards 2010), as have burros and horses in the Western United States (Scasta et al. 2018), where they compete with native wildlife and can degrade habitat (Edwards et al. 2010, Davies et al. 2014, Hall et al. 2018). All these species attract close scrutiny of population management, due in large part to our close relationship with their domestic conspecifics and public opposition to management practices.

Controversy and politicization around management of feral species is well known, yet socio-political ideologies also extend into academia and research (see Appendix B for further discussion). Relative contributions and investment into basic research regarding feral wildlife ecology are notably lagging compared to management-driven research and publication, centred typically around population control, or quantification of negative economic or ecological impacts

(Gering et al. 2019). This creates gaps in our understanding of basic ecological factors governing dynamics of feral populations, e.g., the increasing role of feral species in community and ecosystem dynamics (e.g., McLoughlin et al. 2016, Boyce and McLoughlin 2021). But also little understanding of the evolutionary ecology and adaptive evolution of feral species (e.g., Regan et al. 2019), including topics such as lags in natural selection in reversing traits of artificial selection. As a result we are left with only limited tools for management that are often founded in agricultural or rangeland management research and policy (e.g., livestock management) for species that function as wildlife in natural systems.

Ecological processes involving feral species are undoubtedly as complex as those of native species. As naturally reproducing, free-roaming animals interacting with native predators and prey, feral species are likely to generate and/or be impacted by processes such as apparent and direct competition (Holt & Bonsall 2017). Histories of artificial selection in feral species when present in natural environments may result in different outcomes than those expected from native species, however (Gering et al. 2019). Altered life-history traits such as increased reproduction for example, may exacerbate apparent competition in predator-prey systems by nature of exaggerated population oscillations (Grange et al. 2009, Boyce and McLoughlin 2021), or through advantages inherent in feral species' natural biology (Forsyth et al. 2019). High fecundity, adaptive behaviour, rapid expansion, and recurrent introductions typical among feral species means direct competition with native wildlife is of wide-ranging concern, while the nature of spread in some species such as feral pigs means eradication is no longer a realistic option (Aschim & Brook 2019). Thus, while simplistic management rubrics employed by departments tasked with feral species management often require only basic information (e.g., minimum counts), effective conservation strategies will require far more nuanced and detailed understanding of feral wildlife ecology in natural systems.

In North America, feral horses typify the interplay between artificially altered characteristics that depart from our understanding of native species and the compounding human dimensions common among some feral species. These factors facilitate a decoupling of feral populations from natural and artificial regulation, while institutional and academic approaches to feral wildlife have lagged in attempting to accurately understand these characteristics. Here, I discuss feral horses in North America as a case study for relating the challenges of conducting basic ecological research on feral species. Horses serve as an ideal model for our discussion as feral populations are widespread and human emotional attachment drives public scrutiny of their welfare across the globe (e.g., Argentina [Scorolli, 2018], Australia [Nimmo & Miller, 2007], and Namibia [Greyling, 2005]). We note that these experiences are not merely limited to feral horses and that they may exemplify expectations for wildlife researchers operating in increasingly exposed and contested landscapes. We further discuss how ideological resistance to investment in research into feral wildlife ecology stands in contrast to ecological and socio-political realities, which clearly indicates that feral wildlife require research investment parallel to that of native species.

The political history of feral horses in North America

Caballine horses evolved in North America, although they went extinct from the continent approximately 6000 – 13,000 years ago (Weinstock *et al.* 2005; Grayson 2006; Haynes 2009; Murchie et al., 2021).. During colonisation and European exploration of the continent in the late fifteenth and early sixteenth centuries, domesticated caballine horses (*Equus ferus caballus*) from Eurasia were reintroduced and subsequently established large, free-roaming populations (Berger 1986; Nuñez et al. 2016). Populations are now widespread in both Canada and the United States (U.S.). In Canada, feral horses occur on the mainland in British Columbia (B.C.), Alberta, Saskatchewan, and Yukon; and on the islands of Sable Island, Nova Scotia, and the French Islands of St Pierre and Miquelon off the coast of Newfoundland. In the U.S., populations are distributed throughout the majority of western states, various national forests across the country, and also occur on some barrier islands of the eastern seaboard (e.g., Shackleford Banks, Assateague Island). Total known populations in Canada likely number less than 5,000 while estimates of the total U.S. population number greater than 180,000 horses (Notzke 2016; BLM 2019).

During the early 1800s, the feral horse population was estimated to number between 2-5 million in the U.S. (McKnight 1959), although numbers were reduced significantly with bounty programs during the First World War and trapping for personal use or for meat (Flores 2008). These practices ceased in the U.S. after passage of the Wild Free-roaming Horses and Burro Act (WFRHBA), 1971, that gave legal protections to feral horses and burros on public land administered by the U.S. Department of the Interior’s Bureau of Land Management (BLM) and the U.S. Department of Agriculture’s Forest Service (USFS; Congress 1971). Advocacy for the protection of feral horses occurred in Canada at a similar time, which focused primarily on the Sable Island horse population. Historically managed in connection to the Canada *Shipping Act*, Sable Island horses came under federal protection following public pressure, with a specific Sable Island amendment to the Act made to prevent any interference with the horses (Canada *Shipping Act* 2001). In the western Canadian provinces, populations established from a number of sources throughout the 1800s; while Indigenous Peoples in Alberta and British Columbia (B.C.) possessed horses from around the mid-1700s (Salter & Hudson 1978). Populations in western Canada were similarly heavily reduced in the 1900s (Notzke 2013; Thistle 2015), with recent population estimates for monitored populations of ~1700 in Alberta (Alberta Environment and Parks 2019); <100 in Saskatchewan (Government of Saskatchewan 2009) and Yukon (Jung et al. 2015); and 700 in B.C. (Hamilton 2010), with explicit legal protections in place for only specific populations (e.g., the wild ponies of the Bronson Forest; Government of Saskatchewan, 2009).

Debate around the legitimacy of the place of feral horses on public landscapes and their subsequent management can fuel antagonism between animal rights groups, land users, stakeholders, and Indigenous peoples (Nimmo & Miller 2007; Bhattacharyya *et al.* 2011; Collin 2017). Horse advocates often view horses as a legitimate wildlife species that have a fundamental right to live freely on the landscape (Rikoon 2006; Notzke 2013). Conversely, conservationists, commercial land users (e.g., ranchers, foresters), and government resource managers typically view horses as an invasive species that causes significant economic and environmental damage (Beever & Brussard 2000; Levin *et al.* 2002; Beever & Herrick 2006; Freedman *et al.* 2011; Davies *et al.* 2014; Baur *et al.* 2017; Hall *et al.* 2018; Norris 2019). This distinction alone can often result in a breakdown among stakeholders (Strategic Relations Inc. 2013), and the complex mix of differing value systems surrounding horses creates highly politicized management scenarios that can suffer from a lack of scientific evidence; a factor common in debates regarding management of other non-native species (e.g., feral cats, Jeschke *et al.* 2014).

Management of feral horses (or any species) is difficult without basic parameters such as population size and age- and sex-structured rates of survival and reproduction, or information on distribution and behaviour (Kirkpatrick *et al.* 1993; Kirkpatrick & Frank 2005).

Without this information, discussions between advocates, opponents, and managers of horses can break down into speculation about growth rates, impacts, and foraging habits, with little peer-reviewed evidence to qualify competing claims (Kincaid 2015). Solutions aiming for compromise in the management of feral horses can lead to policies that would be bizarre for any other species of wildlife. Perhaps the best example is the need for life-long holding pens for captured feral horses in the U.S. (Garrott & Oli 2013), which not only absorbs much of the government budget for horse management (Garrott & Oli 2013; Scasta *et al.* 2018) but restricts animals' free agency in the wild, promoting additional ethical debate over horse welfare (Reed 2008). Thus, current policy and lagging research investment regarding feral horses (and feral species in general) constrains discourse around their varied roles in ecosystems, and predisposes conservation objectives involving feral horses to conflict that wildlife managers are seldom specifically trained to handle.

Species designations and data-deficient management

Feral horse populations offer opportunities to understand equid behaviour, reproductive strategies and population dynamics, along with resource use and social organisation applicable to both native and non-native grazer populations (Moehlman 1998; Linklater 2000; McLoughlin *et al.* 2016). Institutional structures regarding the place of feral species in ecosystems, however, has led to a systemic paucity of information regarding horse ecology. Feral ungulates are typically managed and research conducted within the bounds of agricultural resource management (e.g., Department of Rangeland Management; Bureau of Land Management), with a conceptual focus relating to livestock units and management of commercially grazed areas. Although relevant regarding production agriculture, training and research expertise within agriculturally-driven bureaucracies may cultivate a tendency to disregard the importance of ecological research regarding feral species. This stands in contrast to wildlife management departments where scientists with academic training and expertise in ecology fields, and regular ecological research inform management of native species. For example, in Alberta, Canada, objectives outlined in policy documents governing feral horse management (i.e., the Alberta *Stray Animals Act*) are effectively absent; and a draft feral horse management strategy remains under review by an advisory committee initiated in 2013 (Alberta Environment and Parks 2019). Thus, while management lacks defined goals for feral horses in this region, for sympatric populations of elk (*Cervus canadensis*), grizzly bears (*Ursus arctos*), or wolves (*Canis* *lupus*) management plans are well-defined and research efforts are extensive with large-scale, long-term collaborative projects assessing population dynamics, interspecific interactions, and resource use among many other ecological questions (Gunson 1992, Webb 2009, Berg et al. 2015, Foothills Research Institute 2019).

Prioritization of research investment in native species is expected given ideologies around ecosystem integrity and how species are designated within policy structure (e.g., feral, invasive, wildlife, game). However, this prioritization poorly reflects ecological reality where ecosystems are increasingly dominated by introduced species (Lundgren et al. 2018). Despite feral species' potential significance to management of native species, questions regarding the complexity of species interactions and management complications arising from ecosystem processes are yet to be investigated. In some cases, conflict resolution may explicitly establish the need for commitment to research to deescalate management challenges (Strategic Relations Inc. 2013). Nonetheless, ecologically based studies are seldom funded unless they provide immediate management utility. For example, Salter (1978) and Girard (2012) represent the only two studies investigating feral horse ecology conducted over the past four decades in Alberta, Canada, and in the absence of ecologically relevant information, managers are left to make decisions regarding feral horses using only population count data and simple metrics related to commercial grazing capacity. Such policies and management practice that characterize feral species as stray livestock is also a common inflammatory point for their advocates (Notzke 2013). Thus, the paucity of data regarding feral wildlife ecology and the simplistic management metrics that result, at once fail to recognize the complexity of feral species as naturalized wildlife interacting within native systems, while also being notably unreceptive to the dynamic nature of socio-political context in related conservation dilemmas (Bennett et al. 2017).

Litigation trends: defining management approaches to feral horses

Traditional approaches to population management of feral horses included unrestricted shooting or hunting, bounty programs, and government culling programs (McKnight 1959; Notzke 2013; Thistle 2015). These approaches have generally fallen out of favour with local land-users and Indigenous Peoples (Thistle 2008; Bhattacharyya & Larson 2014), although in some areas roundups for slaughter remain a contentious control method (Kincaid 2015). Management of horse populations has recently come under heightened public scrutiny due to the easier dissemination of imagery and information regarding management practices through mass communication and social media. Legal challenges to management are largely facilitated by outdated and ambiguous policy that requires managers to control populations with limited tools (Scasta et al. 2018), while departmental mandates may not accommodate the appropriate research investment required for the complex nature of feral horse population management. Without independent and accurate information that quantifies ecological characteristics of feral horses in given landscapes, socio-political factors are left to determine management outcomes, and research associated with vague management objectives can be subject to the same legal opposition.

For example, legal appeals to horse management are common in the U.S. where most management plans for federally-managed horses are challenged. These legal challenges can occur from both sides: litigation is brought against the Bureau of Land Management (BLM) for attempts to decrease herd numbers; and conversely for not decreasing herd numbers (for a summary see Scasta *et al.* 2018). The WFRHBA mandates the BLM and the U.S. Forest Service to manage horse and burro populations to "maintain a thriving natural ecological balance" on the landscape but at the "minimum feasible level". The meanings of these phrases are ambiguous, and the federal government has been sued by plaintiffs arguing that removal of horses, or implementing contraception practices, violates management at a "minimum feasible level". Other plaintiffs argue that not removing horses in areas where their population is above the federally-imposed maximum appropriate management level (AML) violates maintaining a "thriving natural ecological balance" (Scasta *et al.* 2018). Court decisions have come down on both sides of the issue; thus, the BLM lacks clear directives on how to manage horses and burros (Scasta *et al.* 2018). Furthermore, available management options are continuing to decline within legislation. For example, language detailing euthanasia or slaughter of excess elderly individuals or those that could not be adopted was originally present in the WFRHBA (US Congress 1971); however, federal government spending and appropriation bills over the last three decades have included language prohibiting destruction of any healthy animals (Brulliard 2018). In comparison, such management barriers are seldom applied to native ungulates, considered to be overpopulated (e.g., game species).

Legal challenges to feral horse population management in Canada are also increasing. For example, immunocontraception is a physiologically proven tool to limit reproductive output in many species and offers an alternative to lethal control (Kirkpatrick 1995; Kirkpatrick *et al.* 2009; Duncan *et al.* 2013). Its efficacy as a management tool in local contexts needs to be assessed, however, as particular landscapes (i.e., relatively inaccessible landscapes) can limit the ability to administer the vaccine effectively (Hobbs & Hinds 2018). Following commencement of a 2014 pilot project to assess the contextual efficacy in Alberta, Canada, a court action and a separate complaint to the Canadian Veterinary Association were brought against the supervising veterinarian, alleging that administration of the contraceptive was unethical, and that the veterinarian's license should be revoked (see the following for reviews on the efficacy and ethics of immunocontraception: Turner & Kirkpatrick 1991; Willis *et al.* 1994; Turner *et al.* 1996; Muller *et al.* 1997; Nettles 1997; Turner & Kirkpatrick 2002; M.L. *et al.* 2007; Kirkpatrick *et al.* 2009; Naz & Saver 2016). In 2019, a second court action was brought against the Alberta government, alleging mismanagement of the horse population, specifically that management actions were developed without appropriate scientific information (Court of the Queen's Bench of Alberta 2019). Therefore, both the lack of scientific information needed for implementing management techniques along with the research aimed at filling such knowledge gaps have been legally challenged.

The inadvertent nature of feral species in natural landscapes and their indeterminate classification has typically led to policy that relegates their management to bureaucratic departments tasked with agriculture and animal production management, rather than those tasked with managing wildlife. In some cases, feral populations and their management can fall under the jurisdiction of departments as distinct from wildlife management as the Canada Coast Guard, as was the case for Sable Island feral horses from the 1960s to 2013, with any proposed research governed by language in the Canada *Shipping Act* (Canada *Shipping Act* 2001). This approach and the subsequent policies regarding feral wildlife, although often vague, do provide sufficient legal support to challenge management in the absence of appropriate ecological information (i.e., ideological management – see Appendix B), and therefore any applied research that attempts to combine management objectives prior to establishing this ecological information. In this legal landscape, and as public scrutiny around management in general increases, simplistic management tools for feral species and the limited monitoring that informs them (e.g., minimum population counts) are unlikely to be sufficient to achieve nor justify management objectives (Yanco et al. 2019). This is particularly relevant when feral populations interact with native species, for which overwhelming consensus among academics and managers dictates an essential need for detailed ecological information to inform management policy and practice. Positive biodiversity conservation outcomes will therefore require a systematic investment into feral wildlife ecology research.

Consequences of inflexible ideologies

Elevated attention and opposition to intervention has long been present regarding management strategies surrounding charismatic species (Simberloff 2003; Sharp *et al.* 2011; Douglas & Veríssimo 2013; Knight 2013). This might be expected for species such as feral horses given the publicity and emotional attachment to horses (Scasta 2019), although similar experiences are found in feral pigs (Sharp *et al.* 2011), feral cats (Farnworth *et al.* 2010; Farnworth *et al.* 2011; Rouco *et al.* 2017), grey squirrels (Dunn *et al.* 2018) and many other species. Direct intervention, such as lethal management of species, intuitively elicits heightened attention and opposition (Sharp *et al.* 2011); however, with increasing instances of human wildlife conflict, and a greater emphasis on science-based management policy (i.e., research required for management decisions) (Young *et al.* 2002, Artelle et al. 2018), it should be expected that research in wildlife or conflict-prone species will experience similar opposition (Treves 2005; Messmer 2009; Dickman 2010; Brook et al. 2015).

Wildlife management is faced with shifting public views about the rights and freedoms of animals, regardless of economic, environmental, or nativism arguments (Franklin & White 2001; Perry & Perry 2008; Wallach et al. 2020). Compounding this shift, recent surveys highlight how trust in scientific institutions and scientists, and government departments continues to erode (3M 2019). Ignoring the social complexities of management has long been understood as an unfortunate barrier to achieving conservation outcomes (Treves *et al.* 2006; Bennett *et al.* 2017); however, evidence in North America with feral horses highlight that research on these species is also often perceived to be analogous to government-management programs (e.g., research is a work-around to otherwise stalled management, or research is aimed at maximising lethal control). For example, feral horse advocates filed an appeal and petition to stay against a recent BLM associated research project in Wyoming, stating formally that “one may question if these ‘research projects’ are intentionally designed as inappropriate population control methods by death and cruelty”, in addition to personal attacks being levied against individual researchers on social media [J Hennig, pers comm]. In Alberta, Canada, research equipment has been subject to intentional damage and researchers themselves subject to harassment, based on apparent assumptions about research links to plans for population control [P Boyce, pers comm]. These reactions are not surprising in highly scrutinised environments where research outcomes are truncated to a management application. In such cases, however, important knowledge gaps are likely to remain and research to address them will continue to be prone to social opposition if answers to critical questions about feral wildlife ecology are not sought.

Absence of expert investigation into the ecology of feral wildlife is an important, but perhaps less appreciated, consequence of the politicized environment around feral species. Management directives that value feral wildlife research only through its application are also implicit in academic culture and practice. Substantial gaps exist in our understanding of feral wildlife ecology for example, and how these species interact with native species as functional ecosystem members. Purely investigative frameworks within non-management contexts are limited to closed systems in which feral species happen to provide research opportunities where native surrogates are absent (e.g., island populations). For example, since 2013, the Sable Island horse population has been managed as naturalized wildlife as part of Sable Island National Park Reserve, and the role of science in understanding the ecological role played by the horse, including its consequences to native biodiversity, has facilitated research (Parks Canada 2019). These systems are atypical of most ecosystems where feral species are established however, which possess complex interactions among multiple species and diverse landscapes, meaning eco-evolutionary processes will involve many direct and indirect interactions. Opportunities to investigate these ecological processes are overlooked despite our unparalleled knowledge of feral species by nature of their domestic history. These opportunities likely remain ignored for two main reasons. The first is a fundamental bias of the basic ecological research community against species perceived as “unnatural” or “impure” because of extensive artificial selection in their evolutionary history. The second is a lack of available funding for basic research compared to often redundant investigation into impact assessment, or control methods of feral wildlife.

The value of basic ecological research on feral species

Feral species have been used as bioindicators (Cai & Calisi, 2016), as models for showing how density-dependence can mediate functional responses (van Beest et al. 2016), and to better understand predator-prey dynamics (McGregor et al. 2020). Nevertheless, basic ecological questions regarding feral wildlife, and how they relate to fundamental theories within the discipline of ecology are seldom investigated for their own merit. Despite the ubiquitous and persistent distribution of feral species throughout nature, and their certain place in current and future ecosystems alongside native species (Lundgren et al. 2018), conservation philosophy and the perceived relevance of feral wildlife ecology, limits opportunities to accurately investigate species that directly impact conservation objectives. Although basic research may lag in feral wildlife ecology, our deep cultural relationship and animal husbandry with feral species, provides the technical and theoretical support to rapidly exploit eco-evolutionary research opportunities.

Feral species often have different biological traits due to artificial selection. Artificial selection has created expectedly maladaptive traits in many species when present in natural environments, such as the investment in reproduction over survival seen in feral horses (Grange et al. 2009). Yet, this same close association and animal husbandry means feral species provide ideal and immediate models with which to study evolutionary processes (Gering et al. 2015, 2019). Extensive genomic mapping in horses, for example, can facilitate investigations into selective processes in free-ranging populations (Regan et al. 2019), and antagonisms between artificially and naturally selected traits can elucidate temporal scales of evolutionary processes (Clutton-Brock 1981; Pan et al. 2018). Thus, feral species provide unique opportunities to investigate fitness trade-offs in natural systems where domestication has considerably altered adaptive capacities, fundamentally restructuring ecosystem dynamics (Gering et al. 2019). Such research has clear utility in managing invasive capacity of feral animals, yet also has an unappreciated role in basic evolutionary research (Henriksen et al. 2018).

Biodiversity conservation in many ecosystems lacks understanding of the contextual biological and ecological characteristics of feral species, and the interactions between feral and native competitors and predators. Specific mechanisms of these interactions, manifest in the remarkable biological asymmetries generated through artificial selection, undoubtedly challenge our current theoretical framing of natural population dynamics and behavioural ecology. These unique opportunities to better understand foundational ecological theories, presented in species where basic life-history characteristics (e.g., survival and reproduction) have been manipulated over thousands of generations, are lost to the prevailing paradigms governing feral species research and management.

Management priorities and approaches regarding charismatic species are complex, influenced by socio-political factors far more so than scientific investigation (Mech 2001). Policy structure and disciplinary practice regarding native wildlife management should, and generally does, require investment in understanding ecological characteristics of populations prior to attempting their management. The inclination to invest in feral species research only if it provides a direct management outcome limits growth in feral wildlife ecology literature and creates an academic culture reluctant to investigate these fundamental aspects of biology in feral species. Little reasoning is required to appreciate the management limitations this creates, both social and practical, particularly where native species research investment provides such stark contrast. Deeper consideration should also illustrate the opportunities feral wildlife provide to basic research and eco-evolutionary questions; opportunities that native species in many cases cannot match.

Conclusion

Feral horses and their management attract significant controversy around the world. This controversy and the antagonism it generates plagues management, and research regarding feral horses is often conflated with management objectives. Institutional philosophy and research ideologies regarding feral species generally, provide few avenues to mitigate this antagonism, while at the same time, fail to address significant knowledge gaps relevant to both conservation and basic ecology. Research ideology which remains inflexible to the relevance of feral wildlife ecology, risks continuing to place researchers and managers in positions unlikely to resolve the increasingly common public reactions to these knowledge gaps. Our reliance on detailed ecological information to inform native species management stands in contrast to that for feral species, and both conservation doctrine, and the socio-political context of feral species clearly indicates this imbalance needs to be addressed. Successful management and research programs that have made such adjustments in their ideology regarding feral species place in the environment have provided significant insight across multiple ecological fields. While management dominates debate around feral species’ place in nature, many opportunities to investigate eco-evolutionary dynamics remain unexploited in feral wildlife ecology. The unique cultural history and artificial selection of feral species, and our in-depth knowledge of their biology provide opportunities that native species cannot. In order to effect meaningful conservation objectives and to capitalize on our knowledge of feral species in eco-evolutionary contexts, research around basic and applied feral wildlife ecology needs to be prioritized for its own merit. Insights resulting from such research will not only improve management outcomes but provide valuable information regarding evolutionary and ecological processes in the Anthropocene.

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Chapter 3 Social and Spatial Characteristics of Alberta Feral Horses in the Sundre Foothills

Abstract

Feral horses in the Sundre Equine Management Zone have not been studied since 1978 and little is currently known about population characteristics. Understandings of key demographic, spatial, and social characteristics improve our understanding of feral horse ecology and can provide critical information for science-based decision making. Using a combination of GPS telemetry collars and trail cameras I described spatial, social, and demographic characteristics of the feral horse population in the Sundre EMZ and compared these with the limited available studies undertaken in semi-forested Foothills ecosystems, and feral horse populations generally. Home range size ranged from 47.6 to 93.0 km^2, showed no relationship to band size, and overlapped considerably between adjacent bands. Mean band size was 4.92 among individually identified bands and adult sex-ratios were similar to those identified in 1978 at 0.86 males to females in identified bands, showing a significant negative relationship with band size ($R = -0.55$; $p<0.00001$). Movement and detection rates of horses were greater in summer, and horses showed reduced diel activity in the middle of the day in summer, compared to winter. The number of foals detected, and the mean number of foals within each band peaked from June to August and composed less than 15% of the total individuals detected each year. Identification of individuals based on natural markings was possible, though the influence of non-independent movement and social grouping was evident, and problematic for capture-recapture analyses. Results here show that horses in the Sundre EMZ display social and demographic characteristics consistent with most non-island populations of feral horses, despite considerable spatial and seasonal variation in habitat.

Introduction

The population of feral horses in the Sundre equine management zone (EMZ) is the largest in Canada (Kincaid, 2015), and inhabits a heavily modified landscape along with several native ungulate species including elk (*Cervus elaphus*), moose (*Alces alces*), and deer (*Odocoileus spp.*), and several large predators (wolves [*Canis lupus*]; cougars [*Puma concolor*]; and grizzly bears [*Ursus arctos*]; Appendix A). The feral horse population originated from releases and escapes of horses throughout the region’s occupation by humans (McKnight, 1959; Irving, 2001;

Salter, 1978). Activities relating to open-range ranching, forestry, and oil and gas exploration and extraction during the 18th and 19th centuries led to horses in large numbers in the foothills throughout western Canada in general, and the population within the Sundre EMZ has since remained despite sporadic attempts to remove them (Alberta Environment and Parks, 2021; Thistle, 2008). Ecological study of the population has been limited, however, due to a number of factors (Chapter 2), with much inference on the population being derived from two studies in the ecosystem: a) work in the Sundre area dating to the late 1970s (Salter & Hudson, 1979, 1980, 1982); and b) similar work conducted more recently in Bragg Creek, AB (Girard et al., 2013a, 2013b). The province of Alberta has also conducted annual aerial surveys of the population tracking trends based on minimum counts, and in 2021, by means of distance sampling (Alberta Environment and Parks, 2021). Combined, these data represent the totality of available ecological information on feral horse populations in Alberta.

Reliable and current data regarding characteristics of the Sundre feral horse population are becoming increasingly necessary to navigate a complex socio-political landscape common to feral horse management (Boyce et al., 2021; Scasta et al., 2018). While the population in Sundre has grown in the four decades since it was last characterized, much is speculated about potential causes, including: 1) whether industrial modification of the Foothills region (colloquial name for the eastern sloping foothills of the Rocky Mountain in which the Sundre EMZ is located) has played a role through increasing resource availability, and 2) if such growth is a shared characteristic of feral horses globally (Grange et al., 2009; Regan et al., 2020). Ongoing modification of the Foothills landscape means changes in resource availability and habitat structure occur frequently. Such disturbances are well-known drivers of change in ecological communities throughout western Canada (Brown et al., 2007; Latham et al., 2011, 2013; Pinard et al., 2012; Serrouya et al., 2015; Wittmer et al., 2007), and the intensity of disturbance in the region's recent history reinforces the need for contemporary population research regarding feral horses within these ecological communities. While horses often inhabit lands of low value to humans, or areas that are heavily modified such as the Sundre EMZ (Schoenecker et al., 2016), the Foothills landscape is also unique among many feral horse populations as a northern semi-forested, semi-mountainous temperate ecosystem replete with predators (Boyce & McLoughlin, 2021). This contrasts with the typically arid or semi-arid ecosystems where many large populations are studied in North America (Andreasen & Longland, 2014; Beever & Herrick, 2006; Berger, 1986; Hennig, 2021; Nimmo & Miller, 2007; Ransom et al., 2016), and leads to interesting questions about population characteristics and the influence of these environmental and ecological community factors among the diversity of feral horse populations worldwide.

A suite of factors unique to populations in western Canada create important ecological distinctions from many other better-studied populations where data are available. For example, the high latitude of the Sundre EMZ leads to long and harsh winters, factors known to influence survival, feeding ecology and behavior of populations of free-roaming horses (Berger, 1983a; Ransom et al., 2016). Additionally, predation is known to influence characteristics such as group size (Creel et al., 2014), sex-ratios (Berger, 1983b; Grange et al., 2015), movement and feeding ecology (DeCesare et al., 2014; Gower et al., 2008; Ripple & Beschta, 2004; Sinclair & Arcese, 1995) in free-roaming equids and ungulates generally. The effect of predators is difficult to study in most feral horse populations, as predators are heavily persecuted, extirpated or extinct (Lundgren, Ramp, Middleton, et al., 2021). By contrast, in the Sundre EMZ, grizzly and black bears (*Ursus americanus*), wolves, and cougars are present in robust and in some cases increasing numbers (Stenhouse et al., 2020). There is increasing evidence of predator specialization on, and selection for, horses in areas where they are abundant relative to other prey species (Andreasen et al., 2021; Engebretsen et al., 2021). These factors, in conjunction with demonstrated predation on feral horses in the Sundre population and declining native prey species (Berg et al., 2015; Knopff, 2010; Webb, 2009), runs counter to early interpretations about the population lacking natural predators (Berger, 1986; Salter, 1978), with important implications for much about the ecology of the population.

In a study in 1978, Salter described a population of 206 horses within a ~200 km^2 study area west of Sundre, AB, now encompassed within the Sundre EMZ (~2200 km^2; Figure 2.1). Salter's results showed, among many other aspects of the population, that social organization conformed to those of other feral horse studies, with stallions and harems of mares forming stable reproductive units of similar size and sex-ratio identified elsewhere, bachelor males congregating in more ephemeral groups, and stable, year-round, reproductive groups exhibiting relatively small home ranges (Boyd et al., 2016; Salter & Hudson, 1978, 1982). Importantly, Salter's primary work was undertaken on a small scale compared to the contemporary distribution and population size of horses in the Sundre EMZ (Alberta Environment and Parks, 2021), was based largely on direct observations, and was conducted prior to substantial landscape change in the Foothills ecosystems in the form of widespread clearcut logging. Clearcut logging is hypothesized to be a source of increased forage for horses in this system, as graminoids and forbs replace tree species in areas where cutting occurs, potentially facilitating expansion and population growth of horses, which are bulk roughage feeders (Girard et al., 2013; Irving, 2001; Salter & Hudson, 1980). If horses are responding numerically to the habitat change caused by clearcut logging, it could have density-dependent demographic and spatial ecology consequences, in turn meaning that Salter's 1978 examination of social characteristics may no longer accurately describe the population (Grange et al., 2009; Manning et al., 2015; Regan et al., 2020; van Beest et al., 2016).

While feral horse social organization is consistent among studied populations (i.e., female-defense polygyny) (Boyd et al., 2016; Klingel, 1975), social, demographic, and spatial characteristics within this pattern of organization vary greatly (Ransom et al. 2016). Home range size for example, has been found to be closely linked to resource availability and quality (Girard et al., 2013; Schoenecker et al., 2016), but also band size (Linklater et al., 2000). Band size has been correlated with lower male:female sex-ratios in many populations (Berger, 1986), which can have consequences for reproduction and long-term population stability (Regan et al., 2020). Moreover, if horses are subject to increasing predation levels as horse relative abundance increases (Andreasen et al., 2021; Engebretsen et al., 2021), this may also have impacted some social characteristics. Predation on equids can be heavily sex- and age-biased (Berger, 1983b), and may influence social behaviours such as group size as a predator defense (Creel et al., 2014; Elgar, 1989). Social and demographic patterns in equids are therefore complex, and many of these components of the population are unknown in Sundre, with researchers and managers continuing to draw much inference from Salter's early work.

One other study has more recently described spatial characteristics of horses in the Foothills region of Alberta. Girard (2013) described the home range and habitat use of four mares from different feral horse bands fitted with GPS collars in an area approximately 120 km south of the Sundre EMZ in Bragg Creek, AB. This area is comparable to the Sundre area in regard to modification and potential increases in available resources as described above. Analyses from GPS collar data in this study suggested several differences in population characteristics compared with Salter's 1978 work. For example, home ranges described by Girard were much larger than those described by Salter, with some suggestion that horse abundance was greatest in conifer cut blocks and grasslands (see Chapter 5 for more detailed discussion of resource selection and occurrence herein), though population characteristics of horses in this contemporary context were not studied. Interestingly, Girard (2013) also found that horses use of clearcut areas was highest in winter, and that this behavior might relate to harsh climatic conditions in winter, and a greater need for thermoregulation. Activity of free-roaming equids has been associated with ambient temperature in studies including feral horses (e.g., Souris et al., 2007), and the large seasonal shift in climatic conditions in Sundre may influence activity. Indeed, Salter found that horses spend more time feeding in winter, supporting the hypothesis for thermoregulation during the cold winter months. Yet, forage availability is also significantly lower in winter, and greater relative activity may reflect increased time required to acquire sufficient resources (A. Berger et al., 1999; King et al., 2016; Salter & Hudson, 1979). Activity patterns in feral equids have also recently been shown to be influenced by predation risk, which lead to a reshaping of burro feeding ecology and reduced nocturnal activity where cougar predation was high (Lundgren, Ramp, Middleton, et al., 2021), suggesting that other feral equid populations subject to predation may similarly adjust diel activity patterns relative to predation risk (Cunningham et al., 2019; Lima & Bednekoff, 1999).

The components of the social and spatial ecology of feral horses in the Sundre population have not been studied since Salter et al.'s early work, and much remains unknown about these characteristics compared with feral horse populations globally. Baseline understanding and long-term monitoring of the population's characteristics are also critical to management. With recent characterization of the population lacking, this chapter describes several key social and spatial characteristics of the Sundre population. In particular, I present demographic characteristics, activity, and home range data from both GPS- radio telemetry data and trail-camera data.

Methods

Study site

The Sundre equine management zone is located in the Alberta Foothills, northwest of Calgary, AB (Figure. 3.1), and is one of six equine management zones in the province (Alberta Environment and Parks, 2021). The area is a heavily used mix of forest, rangeland and meadows, scrub, and wetland ecosystems, with two major rivers – the Clearwater in the north, and the Red Deer in the south – bounding the zone. The Sundre EMZ contains the greatest number of horses within the Foothills, with the other five zones extending to the northern and southern limits of feral horse range in the Foothills (Alberta Environment and Parks, 2021).

Topography in the Sundre EMZ ranges from flat and rolling in the eastern regions to sharp mountainous relief as the area approaches the Rocky Mountains in the west. Elevation ranges from 1027 metres to 3040 metres above sea level (Alberta Environment and Parks, 2017) within the Sundre EMZ (inclusive of a 5km buffer). Forested areas are composed of mixes of Pine (*Pinus spp.*), Fir (*Abies* and *Psuedostuga sp.*), Spruce (*Picea sp.*), and Tamarack (*Larix sp.*), with some Poplar (*Populus sp.*), and Birch (*Betula sp.*) dominant forests interspersed. Non-forested areas are composed of a mix of closed and open shrub (willow [*Salix spp.*], alder [*Aluns spp.*], bog birch [*Betula pumila*]), herbaceous forbs (non-graminoid dominant) and grasses/sedges (graminoid dominant), with bryophytes and lichens making up a small portion of the study area (Alberta Vegetation Inventory, (2016). Vegetation and potential habitat in the study area is a patchwork of forest fragments, with disturbed areas including industrial (e.g., oil and gas wells) and recreational sites (e.g., camping and recreational staging areas) and their associated roads and trails, tame and rough pasture, regenerating shrublands, and extensive historic and current clear-cut logging. Much of the area is thus fragmented and areas containing the botanical species described above should be considered as such. Old growth forest in the area remains under forestry lease (see Chapter 5), and many of the areas that are currently classified as forest or non-forested land have previously been modified (Alberta Biodiversity Monitoring Institute, 2018; see Chapter 5).

The large mammal community in the area is composed of several ungulate species, and a suite of large predators. Ungulates include moose, mule deer (*O. hemionus*), whitetailed deer (*O. virginianus*), elk, feral horses (*Equus ferus caballus*), and domestic cattle that use open range during spring and summer months, while predators include grizzly bears, black bears, cougars, and wolves. Small mammalian species such as coyote (*Canis latrans*), lynx (*Lynx canadensis*), bobcats (*Felis rufus*), and mustelids are also present (Knopff et al., 2010). Additionally, a small number of woodland bison (*Bison bison*) have recently been reintroduced in a nearby area at the western extent of the study area, in the Panther valley.

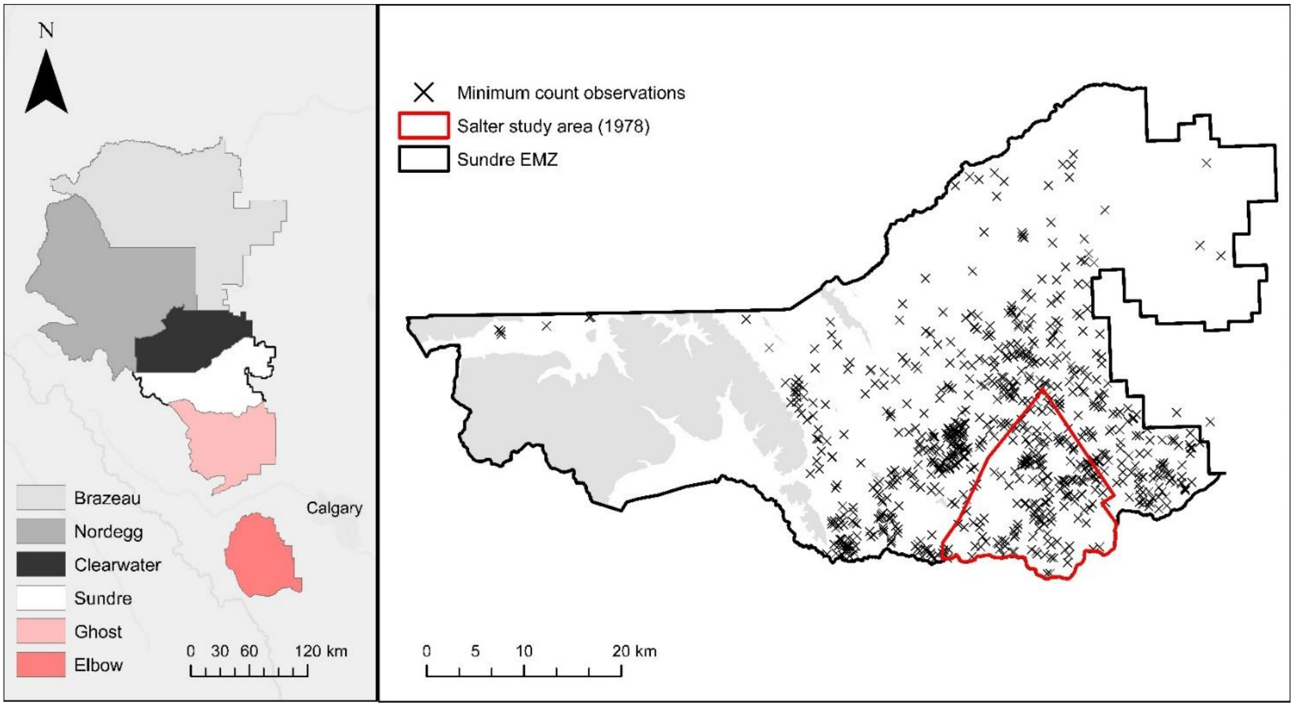

Figure 3.1. Equine management zones located to the west of Calgary city, Alberta. 2016 minimum aerial count horse observations and Salter's 1978 study are shown in the righthand panel. Salter's study area is approximate and was estimated based on aerial coverage and available maps in Salter (1978). Shaded area in the right panel depicts terrain higher than 2000m (Alberta Environment and Parks, 2017).

Trail camera deployment

During an initial pilot study in 2017, a grid of 30 pilot cameras (StealthCam© PX14) (Stealth Cam, 2022) was established to assess the feasibility of identifying horses via natural markings, and to provide potential utility in estimating density following Pettigrew (2017). Cameras were redeployed progressively over fall/winter 2018, to spring 2019, with an additional 100 cameras (BlazeVideo©; model A252 wildlife camera) (Blaze Video Canada, 2022). Using a geographic information system (GIS), cameras were deployed based on four-kilometer grid cells, established over the extent of feral horse distribution identified from aerial minimum counts within the Sundre EMZ, based on observations from 2016 - 2021 (e.g., Figure 3.1). This study design and deployment strategy was undertaken both for feasibility, and to maximize the success of collecting demographic data. Cameras were adjusted minimally (≤500m) from the initial grid locations where needed, based on access and suitability of terrain (Pettigrew, 2017) and to meet general assumptions of future spatial-capture-recapture (SCR) analysis (Fisher et al., 2021; Royle et al., 2013). Cameras were attached to nearby trees (>20cm in diameter), tree stumps, or other appropriate natural features with all cameras attached at approximately waist height, or, where necessary, at a height that approximated waist height relative to animal movement (i.e., in areas with variable topography). This height was chosen following pilot work to maximize the likelihood of capturing an entire large-bodied mammal such as a horse, and importantly, to capture both their feet and facial markings which are used in individual identification procedures (Lubow & Ransom, 2009). Cameras were checked and SD cards and batteries were replaced at approximately 6-monthly intervals with all cameras fitted with 32 GB Sandisk© SD cards, and eight new Energizer© (alkaline) AA batteries.

Given the extent of recreational and industrial roads and trails in the study area, in addition to game trails, some locations assigned in initial grid design were immediately adjacent to, or, on trails or roads. Where present, cameras were placed off, though oriented towards trails to maximize detection of animals if present in the area. Effect sizes of camera placement and baiting at camera sites have been demonstrated to be orders of magnitude lower than effect sizes of habitat heterogeneity on animal movement and selection, suggesting maximizing detection probability at a site should be a priority (Stewart et al., 2019). Moreover, analyses used to estimate abundance have also proven robust to reasonable violations of assumptions of random camera placement (Ausband et al., 2022; Moeller et al., 2018) (See Chapter 4 for more in-depth discussion).

GPS collar deployment, movement and home range analysis

To assess home range size and estimate resource selection functions (Chapter 5), 5 GPS collars were deployed on female horses in winter 2018/19 following the protocol described in Stover and Caulkett (2021) (University of Saskatchewan AUP – 20170117; AEP HCL: RDNS 003 2018; AEP TFAs: 182578, 185269). Collars were a combination of brands: Lotek Iridium Track M 2D series (2 units; 12 hourly fixes; Lotek Wireless Inc., Newmarket, Ontario, Canada) and Vectronic SURVEY 2D Iridium (3 units; SURVEY model; 3-hourly fixes; Vectronic Aerospace GmbH, Berline, Germany) brands and models.

Mean daily movement rates were calculated from individual trajectories of animals monitored via GPS collars, with distances between locations summed at the day (24 hour) scale for each trajectory. As animal movement is spatially autocorrelated, home ranges were calculated using autocorrelated kernel density estimates (AKDE), with both 95% and 50% (core) utilization density calculated for each individual (Silva et al., 2021). Biological seasons were defined using k-means clustering of GPS telemetry data (Zeller et al., 2019), and through comparison of these clusters with Girard's (2013) description of key phenological events in the Foothills, such as spring green up, fall/winter snow fall, and maximum herbage production in the summer months (Girard, 2013).

Image classification and demographic analysis

Field data collected using camera traps deployed across the Sundre EMZ was dense and classification was intensive. Further descriptions are provided in subsequent chapters, though, a summary relevant to Chapter 3 is produced here.

Initial data classification and management work in 2017/2018 was undertaken using a beta version of WildPhotoTrap, a Microsoft Access (Microsoft Corporation, Redmond, WA, United States) based trail camera management system (Kenney, 2017). Due to compatibility issues, all data management and classification work was migrated to, and subsequently completed using TimeLapse2 Image Analysis software (Greenberg et al., 2019) in 2018/2019. Images were classified to species level with two separate approaches: manually, with the assistance of undergraduate students from the University of Saskatchewan (~ 250k images) and using Microsoft's Megadetector and Megaclassifier algorithms (~ 750k images; [Berry et al., 2019]; Microsoft Corporation, Redmond, WA, United States). Horses and all other large mammals (i.e., ungulates and predator species) were then aged (adult, subadult, or juvenile) and sexed (male or female) where possible, with further detailed classification for horses specifically. All classification and identification beyond species level was undertaken by the author.

Initial pilot work identified the short temporal interplay between harems and bachelor groups (i.e., longer intervals consistently grouped bachelor males following harems, into the harems themselves). Subsequently, detection events (episodes) were separated via a two-minute interval (i.e., intervals longer than two minutes between events were classified as separate [not independent]). For horses only, light images were used to identify bands for later capture-recapture analyses where possible, and to assess characteristics of "known" bands for which a group ID was assigned. Night images were not used in individual identification.

Band size, and sex and age structure

Group size, band size, and sex ratios and age structure were calculated using three subsets of data: all identified events inclusive of sightings of individual animals (i.e., group size); events excluding bachelor males and solo animals (i.e., harems only); and events containing only identified bands (i.e., bands with >1 confirmed sighting). This multi-part analysis was undertaken to assess the influence of several factors: imperfect detection of known stable social groups (i.e., detections of portions of a harem) (Emmet et al., 2021); incomplete assignation of sex in the full dataset (i.e., unknown adults in a harem/group), and the influence of pseudo-replication in detections of unidentifiable individuals (Naing et al., 2015; Oliveira-Santos et al., 2008). For the former two datasets, mean band size, and sex ratio and age structure were calculated across all detections, whereas for the latter dataset these were calculated from a single detection of maximum band size across all sightings for each individual band (i.e., a single detection per band incorporating the greatest number of individuals detected of that band [Salter, 1978]).

As a sexually monomorphic species (Neuhaus & Ruckstuhl, 2002), horses can be difficult to sex when genitalia or nursing offspring are not visible, particularly at a distance, in dark or blurry images, and with imperfect (partial) images common in trail camera studies (for comparison with sexually dimorphic species in this study, see Figure C1, Appendix C). The inherent social structure of feral horses can compensate in some cases (i.e., solo males typically defending harems of females), however, horse sexes were assigned conservatively at the classification stage and all classification was undertaken by the author, eliminating potential bias among classifiers. During analyses, sex ratio calculations were compared with two separate approaches based on understanding of feral horse social structure. The ratio of adult males to adult females (Berger, 1983b, 1986) was calculated for those cases where all individuals in a detection could be sexed; and separately, by treating unknown adults in harems as females, if band stallions and at a least one female could be sexed. Mixed- sex groups and pairings that are not harems are rare despite some examples (Linklater et al., 2000), and this second case presumably captures harems where the probability that unknown adults are males, is relatively low.

As noted above, a key component of the study was to identify individual horses using their natural markings for capture-recapture analyses. These identifications were limited to daytime images, and for horses for which there were clear identifiers (coloration, markings, scars). The majority of horses in the Sundre EMZ are bay in color, with few or ambiguous markings, making identification of many individuals difficult. However, identification of bands via incorporating the composition of the social group as an identifier increased the ability to resight bands and the individuals within them given the high social fidelity of horses (Boyd et al., 2016) (i.e., no detection of the individual, but detection of the band they belong to). Thus, while only a segment of the horses detected were “marked”, these confirmed re-sightings provide a greater degree of confidence in analyses and results should be interpreted as such (i.e., results from identified bands represent resighting, whereas “all detections” include some degree of pseudo-replication for unmarked animals). Where relevant, comparisons between those horses able to be identified and resighted (i.e., for which there are repeat sightings) are made to all detections.

Activity

Several aspects of activity at camera locations were assessed. To assess when detections of horses were greatest, detections per 100 trap nights, often used as a metric of relative abundance (O’Brien, 2011; O’Brien et al., 2003), were calculated and compared at the monthly scale to all species. Mean and median return intervals of all horses and of known bands at each camera location were calculated by measuring the time difference between consecutive events. Intervals were calculated once per pairwise detection (i.e., all intervals are temporally separated) for all horses (treated as unmarked) representing the interval between any two horse detections, and for known bands (i.e., the time interval for a specific individual/band to return to a site), with intervals grouped by season and year. Return intervals were not calculated for independent events as non-independence was explicitly assumed (e.g., Hickey & Sollmann, [2018]). Event time (continuous detections of single bands/individuals – length spent at a site) was also compared at the camera scale.

Diel activity patterns were assessed using the *activity* package in R, across the two biological seasons as defined above. Kernel density functions and 95 % confidence intervals were fit to time data and plotted, with weighted functions used to correct for greater detection radii at cameras during the day compared to night images (Rowcliffe et al., 2014). All data manipulation and analysis was undertaken in R (R Core Team, 2022), and ArcMAP (ESRI, 2011).

Results

Camera deployment and detections

There was a high attrition rate of cameras in the study due predominantly to theft but also industrial activity (e.g., logging). Over the three calendar years cameras were deployed, and 154 sites (total deployments including re-deployments), 26 cameras or SD cards were stolen or tampered with, including flipping or damaging of cameras, theft of SD cards, or outright theft of cameras via severing of trees or attachment straps. Four cameras were lost to clear-cut logging, one to animal damage (bear; survey incomplete – camera serviceable), and one to tree-fall (camera serviceable). Approximately 79% of the total grid remained intact following three years of deployment.

Approximately 1 million raw images were captured over a period of 3.5 years from the Sundre EMZ. Following the removal of corrupted images, and general data cleaning, a total of 847,744 images were classified. Outside of empty images, the greatest number of raw images were those of cattle, followed by horses, and ATV/vehicles. The greatest number of events (episodes) were those of ATV/vehicles, which were approximately double the next closest classification (Table 3.1). Capture rate (captures per 100 days) for horses varied throughout the calendar year, with the greatest proportion detected in July and across the summer months (Figure 3.2).

Table 3.1. Total images, events, and proportion of camera sites for species detected by trail cameras. Higher order (canid, felid), and empty images not displayed for brevity.

Species	Total images	Total events	Proportion of sites
cattle	61366	4269	0.51
horse	60234	5103	0.72
ATV/Vehicle	31505	11095	0.61
deer	28109	4982	0.94
moose	4466	645	0.53
elk	3816	319	0.26
human	1859	457	0.51
mystery	1563	802	0.72
wolf	759	215	0.35
coyote	716	259	0.34
bird	565	147	0.26
black bear	467	123	0.29
fox	461	225	0.20
snowshoe hare	352	116	0.15
grizzly bear	255	86	0.26
cougar	169	54	0.15
dog	84	46	0.17
bear	77	28	0.15
lynx	72	24	0.11
bobcat	71	27	0.09

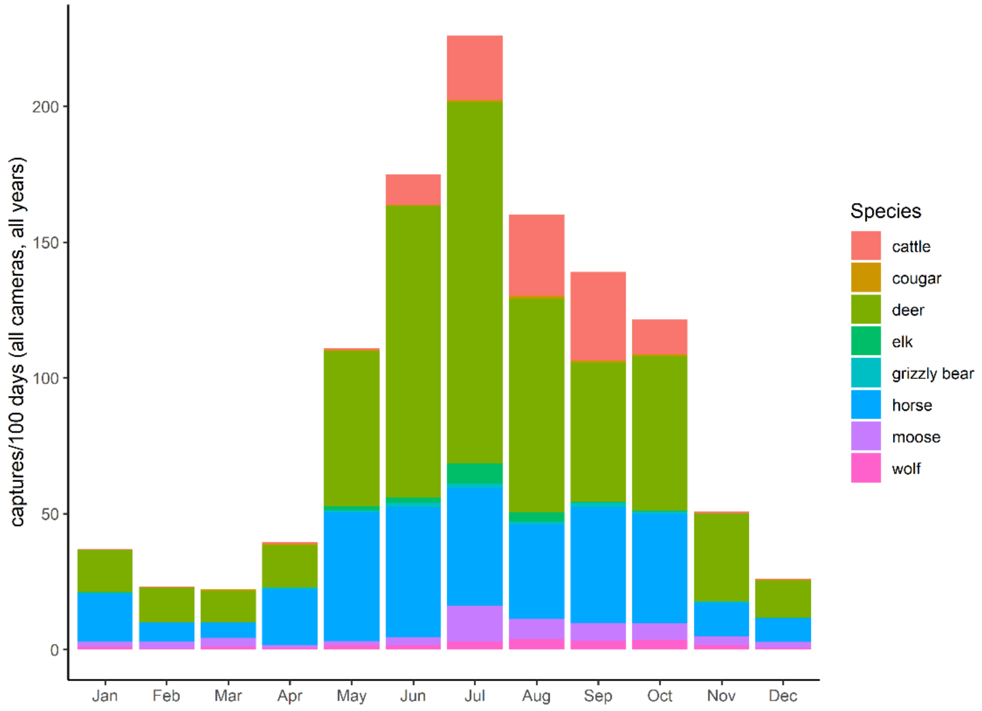

Figure 3.2. Capture rates of species per 100 trap days at the month scale. Bars represent proportions of total yearly captures with data pooled across years and camera locations.

Preliminary classification and analysis showed a clear influence of four particular sites on horses' and other species' behavior. These were sites located adjacent to mineral licks (see activity section below). Event length, group/band size, and group fluidity (in the case of horses) all increased significantly at these sites, as did species interactions. Analyses of group size and sex ratio in this chapter excluded these sites to avoid potential bias from concentrated animal movement.

Band size, and sex and age structure

Group size and Band size

The number of horses detected during events ranged from 1 to 19, with a mean group size across all detections of 2.88 (inclusive of individuals), and for groups of two or more horses of any sex (i.e., excluding individuals) of 3.41. See Appendix C for group sizes of all species.

The most robust measure of mean band size (i.e., harem size; all sexes assigned) was calculated from a single observation of maximum band size of individually identified bands (Salter, 1979; Berger 1986). Mean band size here was 4.92 (sd: 2.7), with a mean of 2.6 females per harem. Mean band size across all detections (at least one male and one female detected) was 3.47, with an average of 1.9 females per harem (Table 3.2). Band size was also compared using the arbitrary, though often used, independence threshold between detections of 30 minutes (O'Brien et al., 2003) (Figure 3.3). Bachelor males were predominantly detected as individuals with frequency of larger bachelor groups declining to a single detection of a group of 9 (Figure 3.4).

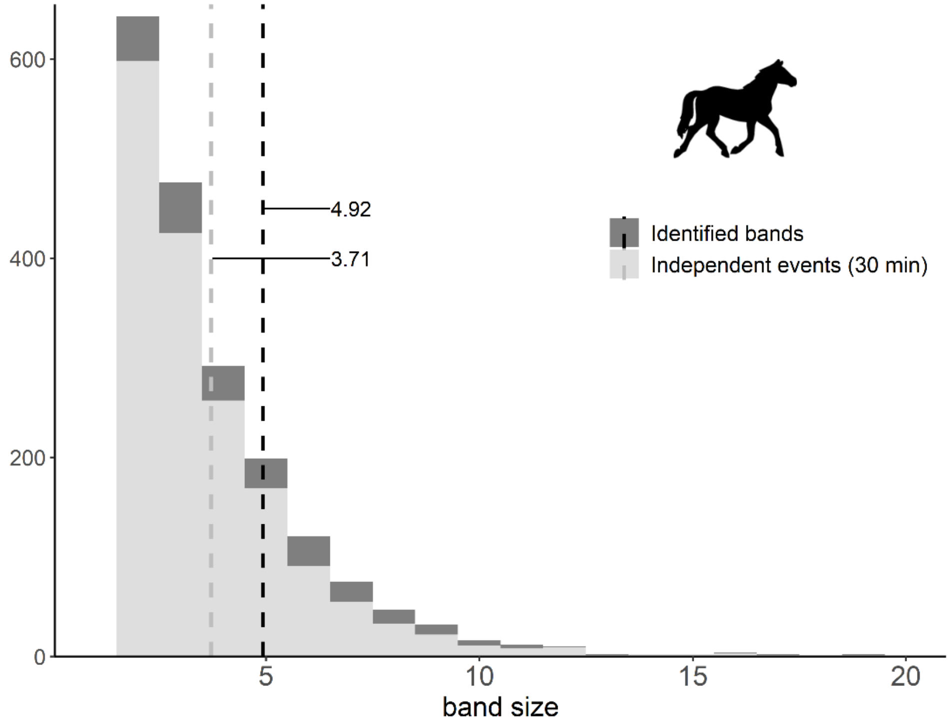

Figure 3.3. Distribution of band sizes calculated from single observations of maximum band size of identified bands, and across all "independent" detections. Independence of 30 minutes is often arbitrarily used for analyses of unmarked and marked animals.

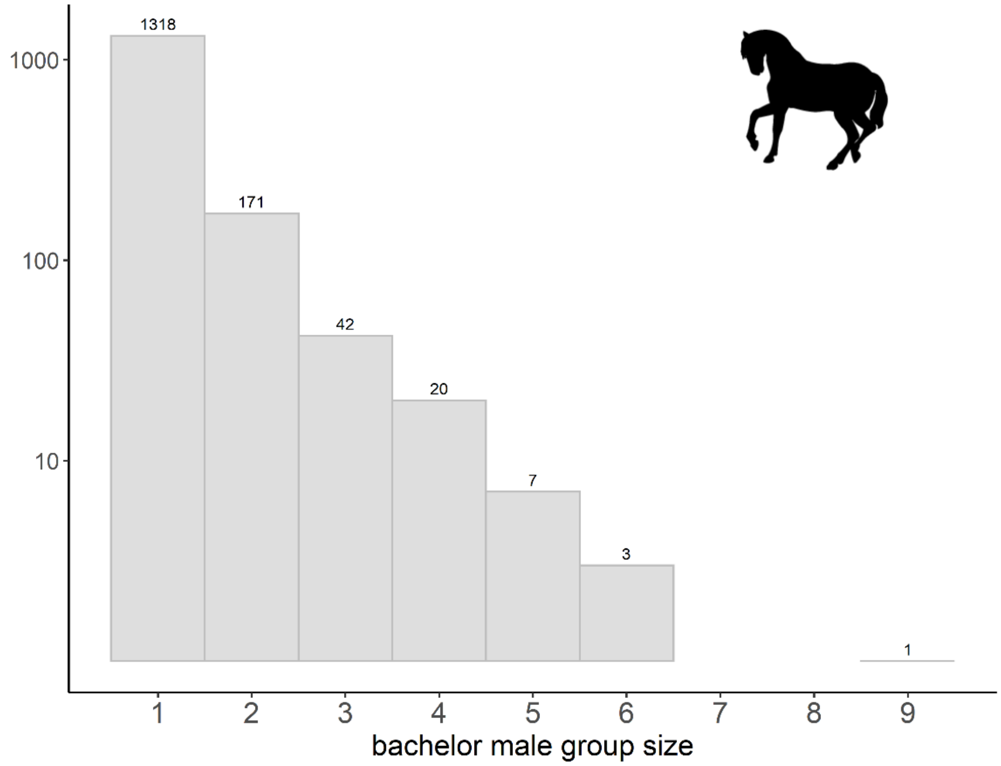

Figure 3.4. Distribution of bachelor herds of different sizes in the Sundre EMZ.

There was a positive relationship between total number of events detected at a site, and the number of individually identifiable bands (mean = 4.9 bands/camera; R = 0.66, *p* = <0.0001, Kendall correlation), with 259 bands and 150 bachelor male (or bachelor bands) individually identified across 84 cameras (including at mineral licks). Interestingly, there was a clear influence on the number of detections of any individual band, and the variation in band size when approaching the mean derived from known bands (Figure 3.5), and a mean of 3.5 detections were needed to observe the maximum band size for individually identified bands (range = 1 - 64). This difference in band size between detections of individually identified bands, came from changes in the number of the adult age class detected in consecutive events (Figure C3; Appendix C), though short temporal intervals and subsequent resighting suggest these changes reflected adults not visible at a given detection, rather than actual changes in band composition.

Table 3.2. Demographic characteristics and return intervals for bands in the Sundre EMZ[a].

Data group	Band size (sd)	Sex-ratio		Proportion of foals	Number of females/band[b]		Return interval			
							summer		winter	
		m:f	(m:[f+u])		F	F + U	mean	med	mean	med
Identified Bands (249)	4.92 (2.8)	0.86	0.80	0.136	2.6	3.5	5.34[c]	1.4[c]	10.6[c]	46.1[d]
All detections (2124)	3.47 (1.82)	0.91	0.88	0.093	1.9	2.5	1.97[c]	136.7[d]	4.3[c]	89.3[d]
Independent events (30 min) (1676)	3.71 (2.31)	0.98	0.98	0.053	1.2	2.3	—			

[a] Categories do not include bachelor male groups except in sex-ratio where ratio is 1

[b] Females per band calculated for bands containing at least one known female and one male (i.e., harems).

[C] units in days

[D] units in minutes

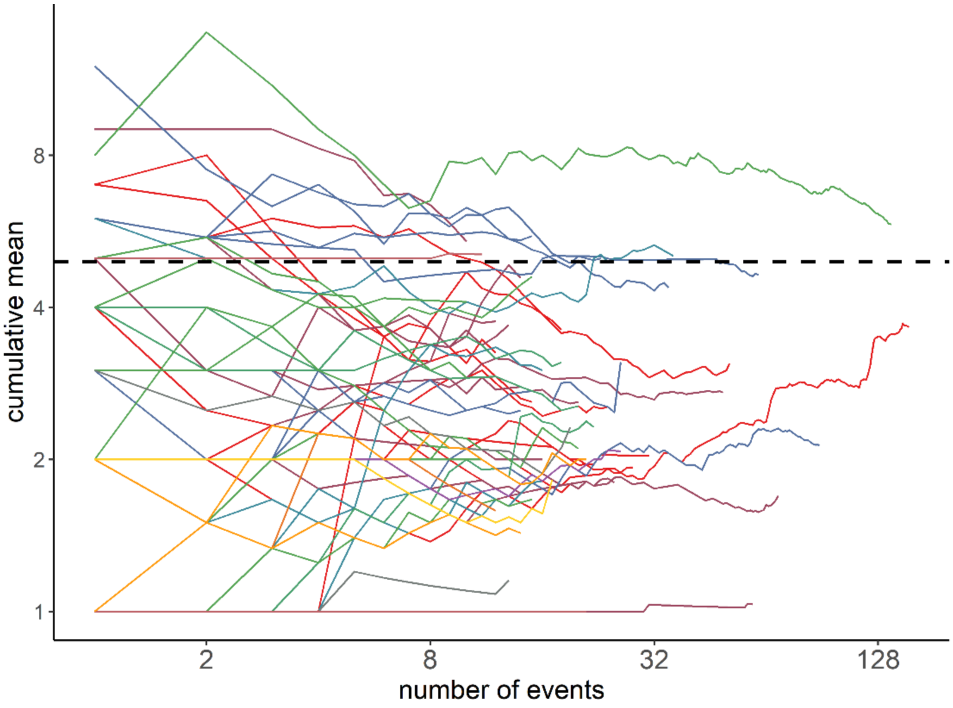

Figure 3.5. Size of bands as number of detections increase showing the influence of single imperfect detections. Each line represents a different identified band with data pooled across all cameras. Bands detected a least 10 times or more are shown, and the black dotted line is mean band size calculated from individually identified bands.

Sex ratio and bachelor males

Adult sex ratios (male:female) across all detections varied. As the study did not census the whole population, and given that a significant proportion of horses detected were not able to be sexed (Figure C1, Appendix C), inference about population-level sex ratios based on these data should be treated with caution. Several values are provided that express sex-ratios based on how data are grouped, though data from individually identified bands that were resighted is more robust.

The mean adult sex ratio (male:female) from all detections was 0.91. The mean adult sex ratio in individually identified bands was 0.86 calculated from a single observation of each band's maximum band size (i.e., the greatest likelihood all individuals are detected). A significant negative relationship was seen between sex-ratio and band size across all detections meaning the ratio of adult males to females declined as band size increased (Figure 3.6). Multi-male bands were also detected with five observations of individually identified bands containing three males, though none were resighted with three males remaining. However, individually identified multi-male bands containing two adult males were resighted from 2 to 5 times with both males present.

Given that female-defense polygyny is consistent among feral horse social systems globally (Boyd et al., 2016; Klingel, 1975), sex ratios were also calculated assuming unknown sexes in a band were female if at least one male and one female were identified (i.e., assuming this therefore constitutes a band that is *unlikely* to contain multiple males: see above). The adult sex ratio for individually identified bands in this case was 0.80 (n 288), and 0.88 (n 1649) across all detections. This calculation would expectedly drop the male to female sex-ratio, however, the values are similar to those calculated only from events where all sexes could be assigned, suggesting the influence of unidentified (i.e., unsexed) males in sex ratio calculations is low. Male-only events made up approximately 30% of all events on average across all sites, however, there was a negative relationship between the number of male-only events and total number of events at a site ($R = -0.25$, $p = 0.0042$; Kendall correlation; Appendix C) indicating that relative detection rates were not due to greater relative activity of bachelor males.

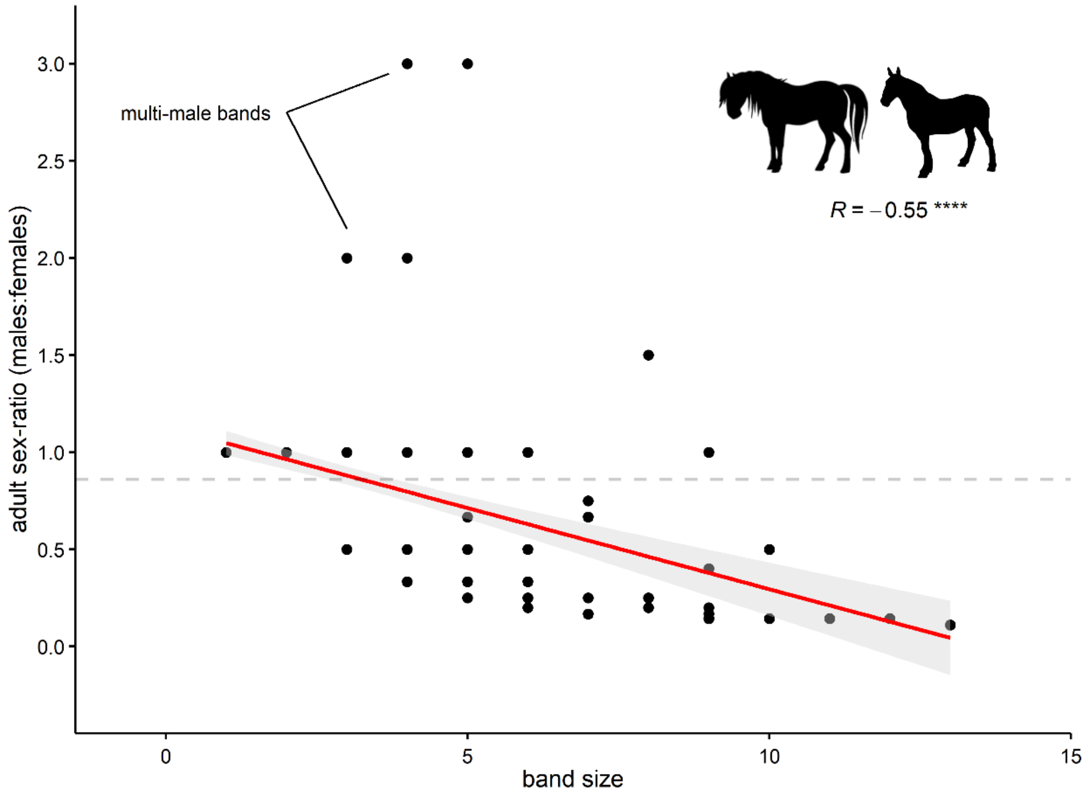

Figure 3.6. Ratio of adult males to adult females from identified bands where all individuals could be sexed. Red line and grey ribbon is Kendall correlation and confidence intervals, respectively. Some multi-male bands are indicated at top left, and strength and significance (p<0.00001) indicated top right.

Foals

Detections of foals followed similar patterns of those identified in other feral horse populations in the northern hemisphere. The greatest number of foals were detected from June through August, and the mean number of foals per band showed a peak across the same months (Figure 3.7). Based on single observations of an individually identified bands' maximum size, foals generally made up less than, or approximately, 15% of all animals identified each year (Figure 3.8), with proportions decreasing slightly over the years surveyed.

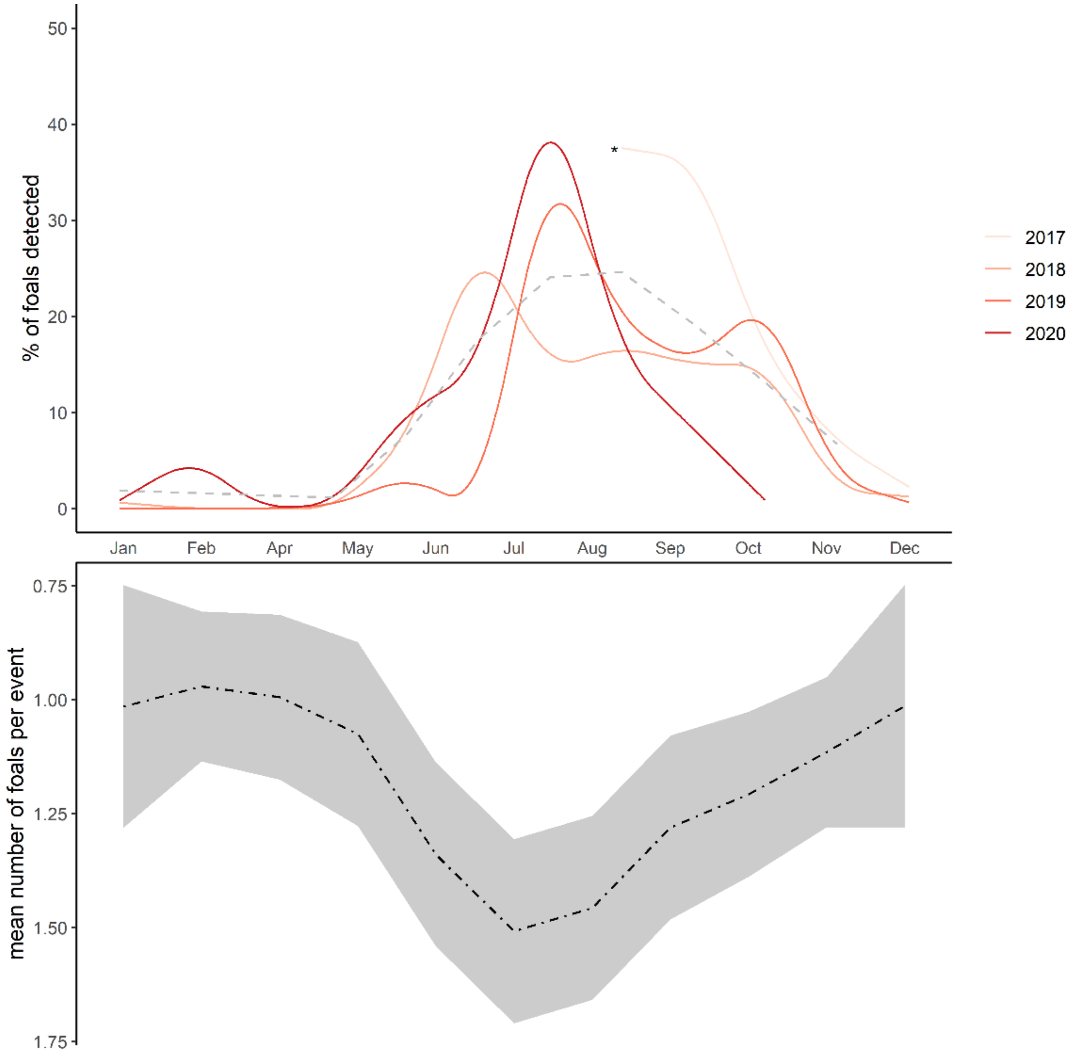

Figure 3.7. Percentage of foals detected by month for each survey year and mean number of foals per band in the Sundre EMZ throughout the year. Dotted lines represent smoothed (loess) functions across years and grey ribbon represents confidence intervals.

In harems containing foals, the number of foals ranged from 1 to 6, with a mean of 1.36. There was no significant relationship (R = - 0.035, *p* = *0*.38) between the number of foals in a band, and the number of subadults, though subadults were detected less frequently (figure 3.8), ranging from 0 to 4 among bands containing foals. While bigger bands tended to have more foals than smaller bands, the proportion of foals in a band declined with increasing band size, and with increasing adult sex-ratio (R= - 0.53, *p*=<0.001; appendix C).

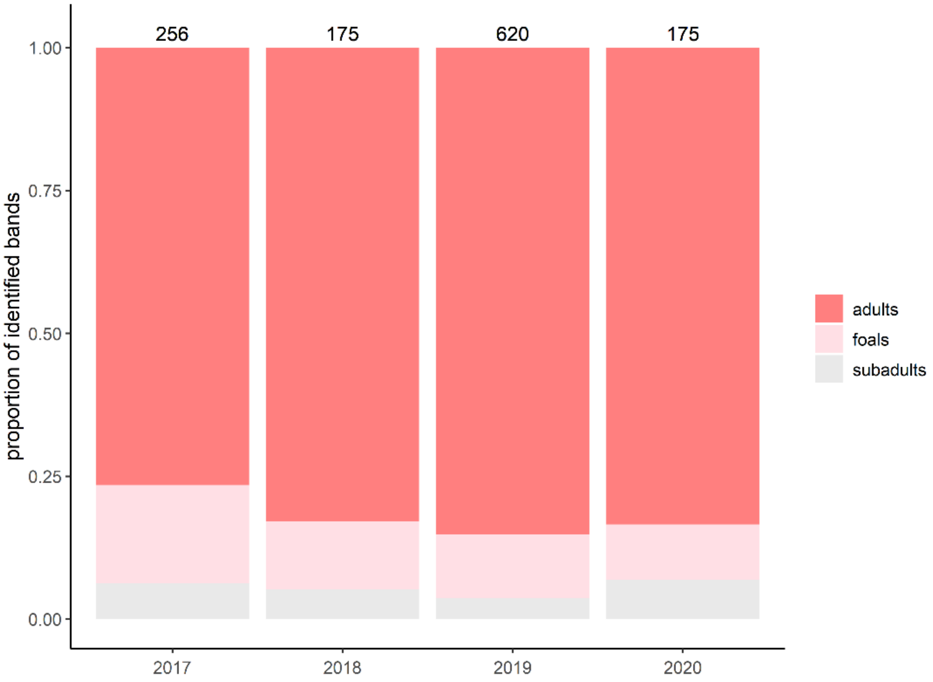

Figure 3.8. Proportion of different age classes from identified bands by year. The proportion of foals in each year was 0.17 (se=0.023; n=256), 0.12 (se=0.024; n=175), 0.11 (se=0.013; n=620), and 0.10 (se=0.23; n=175) for the years 2017 to 2020 inclusive.

Home range and activity patterns.

Home ranges varied between bands monitored with GPS collars with a mean of 63.7 km^2 for 95% AKDE, and a mean of 15.4 km^2 for core utilization distribution (50% core home range; table 3.3). For adjacent bands, both full and core home ranges overlapped (Figure 3.9). K-means clustering of daily animal movement identified two clear biological seasons, and clusters were defined from May 15th to October 31st, and November 1st to May 14th by comparing these dates with Girard's (2013) key phenological events in a similar ecosystem. Mean monthly elevation did not show any consistent pattern across monitored bands, nor when calculated across seasons. Mean daily movement distances were lower in winter months compared to summer however (Table 3.3; Figure 3.10), and activity patterns at camera stations showed a similar difference between summer and winter, with truncated activity in winter months (Figure 3.11). In summer, activity in the middle of the day was lower than that during winter months with partially non-overlapping confidence intervals (e.g., between 10:00h and 18:00h), and showed an inverse pattern of maximum and mean hourly temperatures during summer months (Figure 3.14 in discussion).

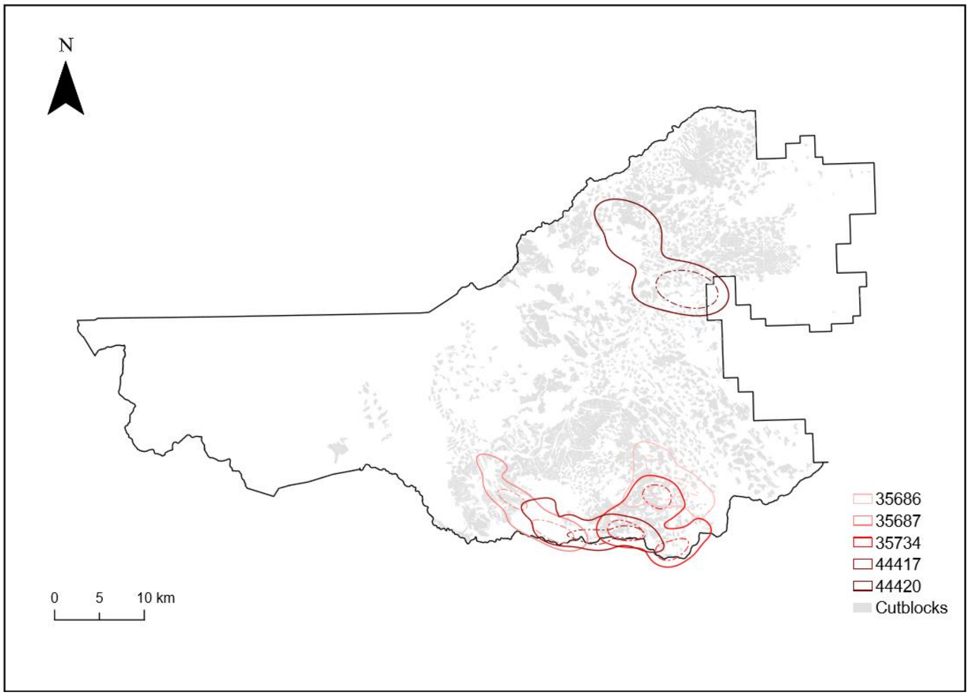

Figure 3.9. Home range estimates for the 5 mares fitted with GPS collars. Solid lines represent 95% kernel density estimates, dotted lines are 50% (core) kernel density estimates.

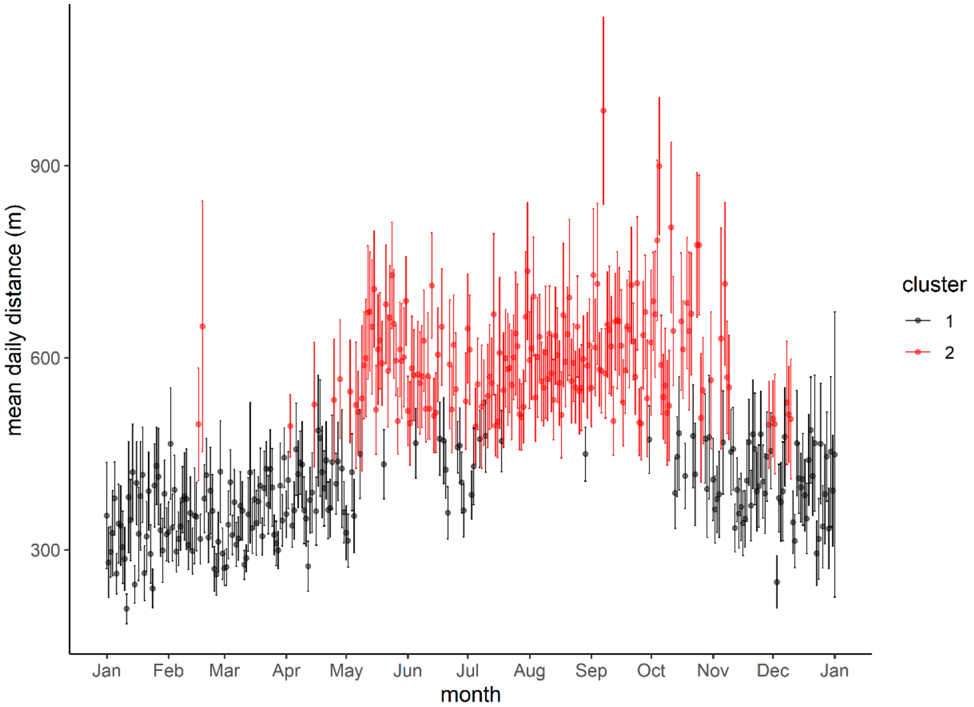

Figure 3.10. Mean daily distance moved of 5 mares in the Sundre EMZ. Data pooled across horses.

Table 3.3. Home range size, mean daily movement and elevation of 5 mares fitted with GPS collars in the Sundre EMZ. Data are pooled by season for movement and elevation.

ID	**Home range – AKDE (km^2)**		**Band size**	**Daily movement (m)**		**Elevation (m.a.s.l.)**[a]	
	95%	**50% (core)**		**summer**	**winter**	**summer**	**winter**
35686	50.09	12.63	9	500.06	329.31	1407.13	1349.00
35687	47.60	11.50	11	411.89	306.59	1498.8	1582.41
35734	74.09	19.69	5	620.42	429.47	1425.58	1398.93
44417	53.39	10.78	12	968.55	676.01	1435.56	1434.64
44420	93.57	22.31	13	1305.35	740.10	1283.48	1240.97

[a] metres above sea level.

Time intervals between horse visits at camera sites varied greatly, and varied between bachelor males and harems (Figure 3.12). The main pattern observed was a lower return rate to a site in winter compared with summer for both known bands, and for horse-horse pairwise detection. Mean values were heavily influenced in both cases by outliers while median values showed this consistent pattern (Table 3.2)

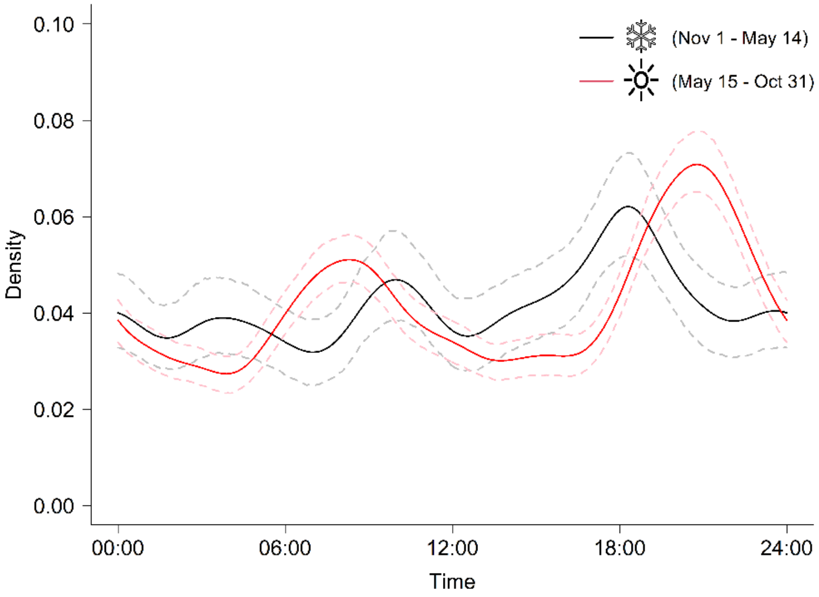

Figure 3.11. Kernel density estimates of hourly proportional activity of horses across biologically defined seasons. Density estimates were calculated from weighted values from both night and day images, with data pooled across all cameras. Dotted lines are confidence intervals.

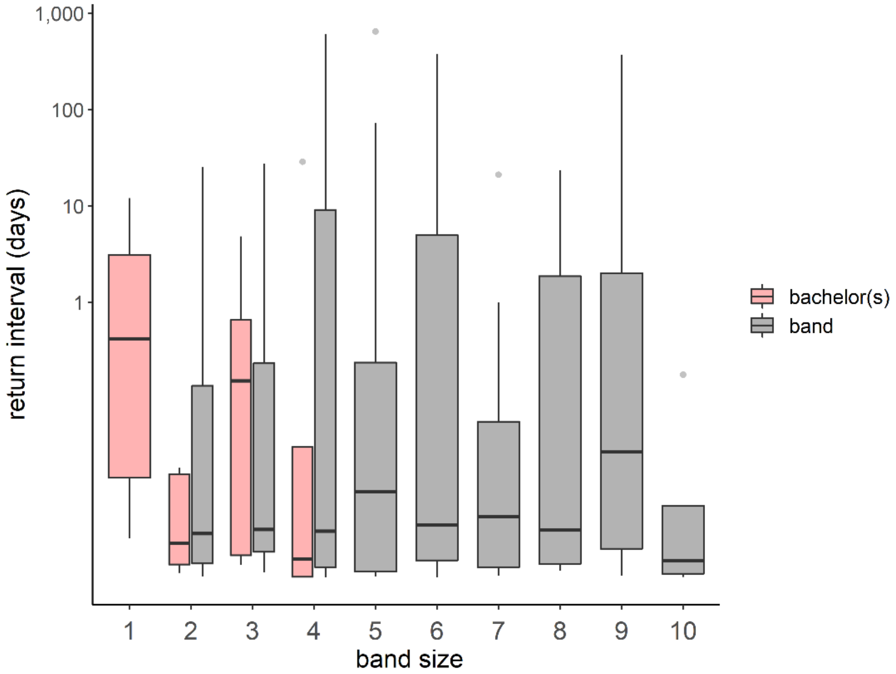

Figure 3.12. Return intervals of different individually identified harems and bachelors of different band sizes from data pooled across cameras. Band sizes are maximum band sizes known for identified bands.

Finally, elk, horses, and cattle were the three species that spent the longest time at a camera site following detection, and event lengths for these species were noticeably longer than other species (for all species see Figure C4, Appendix C; horses shown here for brevity). The majority (>80%) of events containing horses were less than 2 minutes long, though, there were some differences observed in median event length between mineral licks sites and others. Horses spent longer at sites classified as mineral licks (Figure 3.14), and when these sites were grouped together, there was no significant difference in median event length between these two species (p=0.6, Wilcoxon test). However, cattle were seldom detected at these mineral licks (Figure C4, Appendix C), and when considering sites exclusive of mineral licks, event length was significantly lower for horses (p<0.001). Such characteristics were also observed in other ungulates (Appendix C).

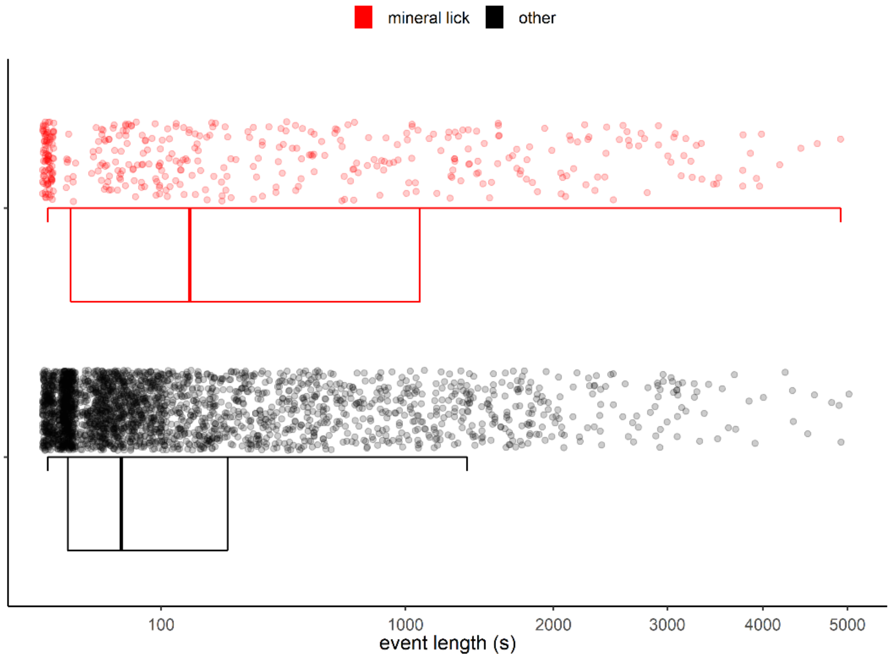

Figure 3.13. Event length following detection of horses at sites characterised as mineral licks and others.

Discussion

Social Characteristics

Horses in the Sundre EMZ exhibited social characteristics consistent with research among other horse populations globally (Boyd et al., 2016). Mean group size for harems was 4.92, which is consistent with sizes calculated from other populations of free-roaming horses in North America (Berger, 1986). While Salter noted a higher mean group size of 7.7 for the population in Sundre in 1982, modal and range values were similar to other populations, which are also similar to values in this study. Salter's calculation was also based on 18 observations, two of which were group sizes greater than 13 (Salter, 1978). Berger (1986) discussed band size in the context of equids subject to predation, suggesting larger band sizes as means of predator defense, while the ability to better access snow-covered resources has also been suggested as a benefit of larger band sizes, as well as greater thermoregulation capacity through grouping behaviour (Boyd et al., 2016; Boyd, 1980; Salter & Hudson, 1979; Welsh, 1975). All of these factors are present in the Sundre area, yet mean band size in this study was not notably different from studies at lower latitudes or those without predators. Rather, studies with noticeably larger mean band sizes tend to be associated with smaller or strongly female-biased island populations (e.g., Assateague Island, R. Keiper & Houpt, [1984]; R. R. Keiper & Sambraus, [1986]), and may be the result of greater relative proportions of females within restricted geographical context and female-defense polygyny.

Adult sex-ratios among bands (0.86) were also similar to those identified in other populations (Berger, 1983b), and similar to Salter's study in 1978 (0.84). The mean number of 2.6 (females only) – 3.5 (females and unknown sexes in harems; see methods) mares in harems is consistent with many other non-island studies, as is the slightly female-biased sex ratio. The negative relationship with band size and sex-ratio (figure 2.7) conforms to both the expectations within feral horse female-defense polygyny, and to observations in most other North American feral horse populations (Berger, 1986). If the predators in Sundre were disproportionately impacting one sex over another, sex-ratios might be expected to shift towards the less vulnerable sex, as seen in some native equid populations (Berger, 1983b). However, the sex-ratio within the Sundre population is similar to that which Salter identified over four decades ago, suggesting that predation is not impacting sex-ratios at the population level, (Andreasen et al., 2021; Engebretsen et al., 2021; Knopff, 2010), though predation impacts are hard to assess without long term data on predator diets and feral horse populations. Though the majority of bands identified were composed of a single stallion, several multi-male bands were also observed. Multi-male bands have been identified in many feral horse and free-roaming equid populations in general (Boyd et al., 2016), with some cases identified as predominantly immature males remaining with natal bands (Keiper, 1986; Berger, 1986) while others having stable associations/alliances of adult males (Linklater et al., 2000). Repeat observations in this study suggest at least temporary stability of some of these associations, and aging based on camera photos suggests these are not only immature males. Though relatedness between the stallions is unknown in this study, bands in the area are known to consist of more than one related adult male (brothers, or sons; pers. comm L. Raymaakers), and observations in this study by the author suggest related (based on natural markings and coloration) males stay within close spatial proximity (i.e., temporal and spatial overlap of unique coloration at single camera locations) following dispersal from natal bands and the acquisition of females, however, the particular function of these associations in terms of reproductive success are still debated and results are inconsistent across studies (Boyd et al., 2016).

Foals typically make up 8-15% of a population of feral horses (Ransom et al., 2016), and similar proportions were observed in this study (Figure 3.8). The proportion of foals in identified bands declined each year throughout the study, matching recent declines in foal survival detected by local observers of bands, and declines in the population in general observed through aerial minimum counts (Alberta Environment and Parks, 2021). Long term or alternative data are not available to assess the cause of this apparent decline, or the reliability of the estimates, however the signal detected in both foals and the population in general is interesting (see Chapter 4 for more detail). There was noticeable peak in the number of foals detected and the mean number of foals per band over the summer months (Figure 3.7). The shape of this peak matches that seen in other feral horse populations in the northern hemisphere, although is delayed compared to populations at lower latitudes (Ransom et al., 2016). This delay is unsurprising, given the severity and length of northern winters. For example, snow and associated low temperatures can remain in the study area through April, and foal survival is anecdotally low when foals are born early in the year. Thus, the majority of births may be delayed to avoid greatest winter mortality at higher latitudes, with populations at low latitudes exhibiting reduced seasonality (e.g., feral ass, (Santiapillai et al., 1999), or southern hemisphere equids such as plains zebra foaling predominantly during the wet season (October - March) (Klingel, 1965; Linklater et al., 2004; Smuts, 1976). Gestation is long in equids, meaning foals can be born throughout the year (Figure 3.7). Interestingly, this later and longer peak foal season might differ from that of many of the native ungulates in the area (e.g., elk early May to early July) (J. E. Berg, 2019), potentially providing more widely dispersed and consistent prey biomass to predators (Boyce & McLoughlin, 2021; Engebretsen et al., 2021), particularly as lower risk (Knopff, 2010) neonates of other species become relatively rare later in the year.

Spatial Characteristics

Home-range sizes were similar to those of bands studied in nearby Bragg Creek, Alberta (e.g., 12.4 – 90.0 km^2 [Girard et al.,2013]; Table 3.3), though were larger than those identified in the Sundre area (≤15 km^2) by Salter (1978). As identified by Girard et al. (2013) this difference in home-range size could be due to potential differences in resource availability or habitat, though Girard’s sampling intensity and methodology differed considerably to the Salter study. The relative similarity in home-range size estimates in this study with those of Girard in a similar environment, using similar methods (e.g., GPS collar locations), suggests home range estimates here and in Girard are representative of true home-ranges, and that differences between these studies and that of Salter are a methodological artefact. Importantly, home-range sizes here are likely to be different compared to locations where horses are studied in open, non-forested landscapes. Forest patches or wider expanses of forest where predation risk can be higher (Knopff, 2010; Latham et al., 2011), and where relative resource availability is low (Girard, 2012) may lead to larger relative home-ranges if horses avoid many areas of the predominantly forested landscape.

In contrast to Girard's findings, home ranges overlapped considerably geographically (Figure 3.9), despite some initial collaring locations being in separate watersheds. Such overlap is seen in other feral horse populations (Girard, 2012; Schoenecker et al., 2016), and as a species exhibiting female- rather than resource-defense polygyny, such spatial overlap is expected. Additionally, though GPS locations were almost entirely within the boundaries of the two major rivers defining the northern and southern extent of the Sundre EMZ (the Clearwater and the Red Deer rivers, respectively), one horse band evidently crossed the Red Deer river at times, with several locations across three different calendar years obtained south of the river. All of these southern locations were obtained in winter months (as defined above), which may suggest that such crossings are limited to times when the river is partially frozen or low prior to spring melt and rainfall floods (Cordes et al., 1997). More generally however, this observation suggests that these major geological features are not necessarily barriers to movement in this ecosystem.

Home range size is closely tied to abundance of resources in equids, and the Sundre area is notable in a number of factors in this regard. Water is not thought to be a limiting resource in this ecosystem, as snow cover and abundant rivers, tributaries, ponds and muskeg cover much of the study area ensuring ready access (Girard, 2012; Salter, 1978). Forage is also relatively abundant compared to many arid ecosystems, meaning relationships between home range size, and band size that relate to resource availability suggested in other populations (Linklater et al., 2000) may not be strong in this ecosystem. Indeed, though this study represents a small sample, home range size and return interval did not increase with band size (Table 3.3), supporting the notion that horses are not limited by resources in the Foothills ecosystem. The presence of particular minerals at lick sites in comparison may be limiting locally (see below and Appendix C), though this requires further investigation (Carbyn, 1975; Hall et al., 2018; Jokinen et al., 2014).

Activity

Horses were most active in the early hours and late evening, in both winter and summer. Relative activity density dropped considerably during dark hours of both seasons (i.e., truncated in winter), consistent with studies showing greatest activity bouts occur at crepuscular hours (King et al., 2016). Activity in the hottest portion of the day in summer was lowest and may reflect increased exposure in open habitats while grazing in the summer months, where temperatures are high (Girard et al., 2013a, 2013b). This is supported by greater relative activity in the middle of the day in winter, which may reflect activity linked to increasing exposure to the sun in winter months (A. Berger et al., 1999; Girard et al., 2013), or driven by a greater need to forage for limited and low-quality feed (A. Berger et al., 1999). The Sundre EMZ is at relatively high latitude, with strong seasonal variation in both temperature and forage availability. For example, temperatures in winter can drop below -30°C, with the vast majority of the study area covered in deep snow (see panel C3 in Appendix C for images), while maximum hourly temperatures in summer can rise above 30°C at midday and late afternoon (Figure 3.14). Ambient temperature is known to influence daily activity in free-roaming equids (Souris et al., 2007), and patterns observed in this system suggest a similar influence.

Median return rates to a site and mean daily movement patterns showed clear differences seasonally, supporting the notion that horses are spending more time feeding than travelling in winter months. For example, daily movement rates (Figure 3.10; Table 3.3), and median return rates (Table 3.2) were lower in winter than summer. These data are congruent in suggesting that horses aren’t moving as much, or as far from a given location during winter. Forage often needs to be accessed by pawing through snow in winter (pers. obs.; Appendix C) and feeding bouts at locations where forage has been accessed may need to be longer compared to summer months when resources are widespread, nutritionally dense, and abundant (Girard, 2012). Salter (1978) for example, observed greater relative time spent feeding in winter, consistent with other studies which often describe a greater metabolic need for forage intake in cold months when forage availability and quality is low, and thermoregulation needs are high (A. Berger et al., 1999; Kaseda, 1983; McBride et al., 1985).

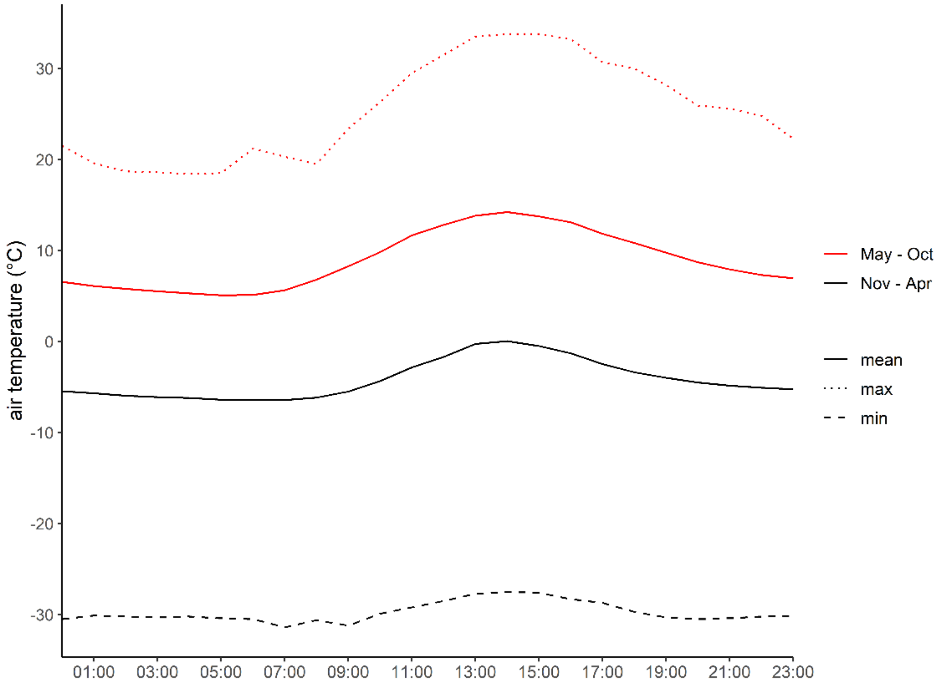

Figure 3.14. Hourly temperature changes over summer and winter months. Max high temperature is shown for summer, and minimum low temperatures shown for winter for conciseness. Data pooled across 2017-2018 from Alberta Climate Information Service (https://acis.alberta.ca/acis/), for the Coalcamp weather station.

Equid distribution and movement are also dependent on the availability of water (King et al., 2016), particularly in summer. While water is not thought to be a limiting resource in this ecosystem for horses (Girard et al., 2013; Salter & Hudson, 1978), water is less available in summer compared with widespread snow cover in winter and horses may need to travel further between feeding or resting bouts to access water. Greater movement in summer may also be due to summer months being dominated by industrial and recreational activities in the Sundre EMZ. Hunting (September-November), ATVs, campers and trail riders, and free-range cattle grazing are all factors in summer that are not present in winter and may result in greater disturbance and subsequent movement patterns of horses during the summer months (Cromsigt et al., 2018; Doherty et al., 2021; Leblond et al., 2013; McInnis & Vavra, 1987; Salter & Hudson, 1980). For example, horses and cattle are widely considered to be in conflict when it comes to grazing assemblages, including in this system (Cromsigt et al., 2018; Ganskopp & Vavra, 1987; McInnis & Vavra, 1987; Salter & Hudson, 1980). An influx of herds of large grazers in spring and during the summer months may result in a need to increase movement to reduce competition for forage or localized resources such as water or mineral licks (Hall et al., 2018). However, the detection of many instances of cattle and feral horses grazing together in this study (Appendix C), does not suggest behavioral antagonism results in exclusion of either species from foraging resources as identified in other studies. Additionally, as cattle are typically supplemented with artificial mineral licks in native range, conflict localized at natural mineral licks may be low between these two species, supported by the evidence that cattle were almost never detected at natural mineral lick sites in summer.

Interactions with other species and interspecific dominance hierarchies based on body mass (see Appendix C for examples), may play a role in this system, where limiting resources are present (Hall et al., 2018; Lundgren, Ramp, Wu, et al., 2021). Interestingly, I often observed bands of horses congregate in large numbers around mineral licks with many other ungulate species, clearly digging in and ingesting soil in both winter and summer and these sites were where horses spent the longest amount of time following detection (Figure 3.13). Wild ungulates are often attracted to mineral licks throughout Canada (Ayotte et al., 2008; Carbyn, 1975; Jokinen et al., 2014; Tobler et al., 2009). Staying time at these mineral licks may reflect a limiting resource present in local minerology, though further investigation of these characteristics is required.

Detection of a social species

The role of imperfect detection in calculating social aspects of feral horses in this study was evident, as band size of known bands changed with subsequent detections, though this was clearly the result of non-detections within a social group, rather than changes to the social group *per se* (Figure 3.5 and Figure C3, Appendix C). Imperfect detection is a fundamental issue with camera traps surveys and many different analyses and approaches have been developed to account for imperfect detection at the population level (Amundson et al., 2014; Chandler et al., 2014; Chandler & Royle, 2013; Clement et al., 2017; Kery & Royle, 2008; Rowcliffe et al., 2008; Steenweg et al., 2017; Yamaura et al., 2016; Yamaura & Royle, 2017). Yet at the band scale, it was clear that multiple detections were needed to capture the diversity and structure of many different bands. This could of course be ameliorated in part with a study designed to assess social group specifically (i.e., multiple cameras at baited sites), or with longer-term data on individuals within social groups. However, as the social unit is fundamental to much about free-roaming equid ecology, and given harems are defended and maintained (i.e., if an individual from a known band is detected, but other members are not, there remains a high probability the other members are in immediate area) these imperfect detections could play a significant role in the outcome and inference derived from studies using camera traps, particularly where animals possess few natural markings to assist in group identification, or, individual detection histories are used to assess population size (Emmet et al., 2021; Hickey & Sollmann, 2018).

Band size calculations here were notably lower (Figure 3.3) when it was assumed no animals were marked (e.g., identifiable individuals of a band were assumed to be alone, if alone) and adopted the often used 30-minute interval of independence used to avoid pseudo-replication (O'Brien, 2011; O'Brien et al., 2003). Taking this approach, many individuals or pairs that are members of larger bands would be treated as bands themselves. Similarly, though animals are likely to be within the area, low movement rates, and short-return intervals (see activity) may combine for spurious results when these social and behavioral aspects are not accounted for. Further complicating these calculations, social dispersal is an important component of equid social systems (Boyd et al., 2016; Linklater & Cameron, 2009; Marjamaki et al., 2013), and thus, changes to band size and composition may or may not be real, between detection events.

This uncertainty also raises interesting questions regarding capture-recapture studies at the individual level. Typical capture-recapture studies collecting detection histories of individuals for example, rely on the independence of individual movement, which is violated in many social species (Hickey & Sollmann, 2018), and may require auxiliary population estimates or monitoring techniques to produce reliable population estimates (López-Bao et al., 2018). However, sociality could serve as a means to improve detection rates as a function of detecting any band member (e.g., cluster SCR in Emmet et al., [2021]) particularly if social fidelity is typically high among populations, as it is in feral horses and often across years for individual groups (Boyd et al., 2016; Linklater, 2000). Feral horses may offer a unique and accessible model species to further develop these approaches (Boyce et al., 2021), which are evidently needed for the diversity of social species globally. Field methods might validate the social fidelity metrics at the band scale for example within populations, facilitating greater use of bands as detection units when probability of social dispersal is known. The wide distribution and often known group composition of many populations compared to wild species could present meaningful opportunities to further advance developing methods (Boyce et al., 2021).

Conclusion

Accurate information regarding basic population characteristics is critical for our understanding of species' ecology and for robust management, yet, such information has been lacking for feral horses in the Sundre EMZ. Results here showed that feral horses in the Sundre EMZ exhibit social and spatial characteristics generally consistent with those identified in other populations. Band size, sex- and age-structure were similar to those identified in other free-roaming populations, outside of island ecosystems. Foals were most prevalent from June through September, though could be born at any time throughout the year. Home range size was larger than that identified by Salter in 1978 using direct observation in a subset of the same geographical region, but similar to that identified in nearby Bragg Creek (Girard, 2013). Overlapping home ranges and a lack of relationship between band size and home range size also indicated that horses are unlikely to be resource limited at the home range scale. Activity patterns were largely crepuscular, with truncated diel patterns in winter months, and appear to reflect ambient temperature. Movement rates were highest in summer, while return rates to a site showed no clear pattern across band size, though were lower in summer. Horses, elk and cattle were the species that remained the longest at a site following detection, yet this seemed to be influenced heavily by the presence of mineral licks for horses. Interestingly, detection characteristics of horses suggested the use of both natural markings and band composition will be critical to accurate capture-recapture analyses of horses, and reiterate that, as seen in other social species, detection histories at the band (e.g., social unit) scale are important in social species where independence of movement among individuals is violated.

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Chapter 4 Estimating feral horse abundance and density in a semi-forested foothills ecosystem using camera-traps.

Abstract

Estimating abundance is a primary goal of ecology and critical to management of populations. Yet, acquiring accurate estimates can be a daunting task, particularly in large and wide-ranging species. Camera-trap technology and analytical techniques have proliferated in recent years, allowing researchers to apply both traditional and novel density estimation techniques to a wide range of both common and cryptic species. Such techniques are particularly valuable where additional population information is lacking; a common issue in feral horse research. I estimated density and abundance of the feral horse population in the Sundre equine management zone using a camera-trap grid and space-to-event (STE) density models, and compared estimates with recent minimum count data from aerial surveys. I also described relative detection rate across the study area to assess the distribution of horses as a function of capture rate. Detection rates were highest in the south-east of the management zone, and aligned closely with detections based on minimum aerial counts, and original data from 1978. Feral horse density was 0.602/km^2, 0.606/km^2 and 0.522/km^2 respectively, from 2017 – 2019. Total abundance estimates were similar to minimum aerial counts with confidence intervals from estimates overlapping aerial counts in all years except 2017, and suggest the population declined by approximately 14% from 2018 to 2019. This decline was also detected in aerial minimum counts from 2019 to 2021 (~22%) and stands in contrast to expectations based on increasing minimum counts in recent decades, and on most other free-ranging feral horse populations. Reasons for the recent decline are difficult to assess from this information alone, however, emigration to adjacent management zones, mass mortatlity events, and management actions were not factors present over the course of the study. Potential additional reasons for the decline are discussed, including the influence of predators.

Introduction

Acquiring accurate estimates of the number of free-ranging animals in open landscapes is a difficult task. Yet estimating population size is one of the fundamental objectives of field ecology, and robust estimates of population size are critical for understanding many aspects of species' ecology and their management (O'Brien, 2011; Rowcliffe et al., 2008; Steenweg et al., 2017). Population estimates are particularly sought after for species that are iconic, that have a strong management context, or are controversial (Steenweg et al., 2017). Feral horses fall into this latter category frequently and estimates of population size are often a key point of contention between feral horse advocates, their opponents, and managers tasked with population control (Boyce et al., 2021; Scasta et al., 2018).

Methods used to estimate population size and density are diverse and depend heavily on the availability of robust alternative estimates to reference (Loonam et al., 2021). In Alberta, Canada, data regarding population sizes of feral horses throughout six equine management zones (EMZs; see Chapter 3) is sourced from aerial minimum counts undertaken by the rangeland management department (Alberta Environment and Parks, 2021). Minimum counts indicate that feral horse populations in the Alberta Foothills region have increased over the last decade (Figure 4.1), and this expansion could be due to a number of factors, including: habitat modification (Girard et al., 2013); a potentially high intrinsic growth rate inherent to feral species (Grange et al., 2009); and a lack of natural predators exerting effective top-down control (Berger, 1983b, 1986; Salter, 1978). In the most recent (2021) aerial survey of the Sundre EMZ, minimum count data suggests the population has recently decreased, with counts approximately 22% lower than the previous survey (2019). Interpreting the historic growth and now decline in the Sundre population is difficult, as methodologies between survey years (e.g., flight paths and survey effort) were variable until 2017 (Alberta Environment and Parks, 2021). Aerial techniques via direct observation in forested and semi-forested habitats can also be inaccurate, particularly where mark-recapture techniques, or thermal imaging are not employed (Fleming & Tracey, 2008; Lubow & Ransom, 2016; Ransom, 2012). Hence alternative estimates of abundance are needed to assess the reliability of the changes observed in the Sundre population.

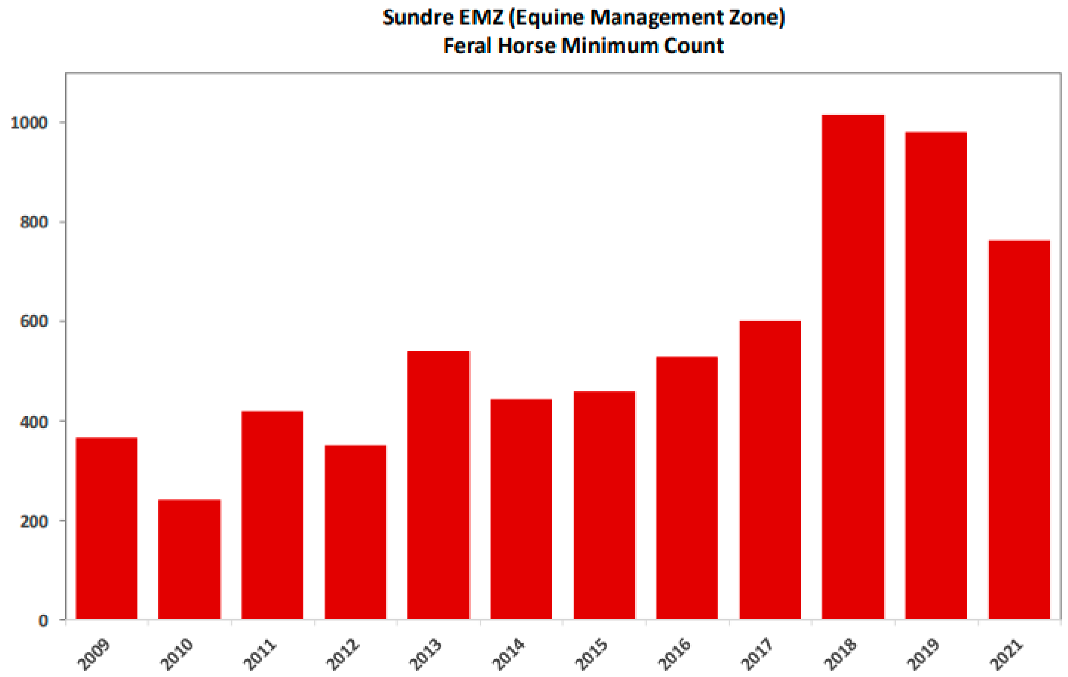

Figure 4.1. Total minimum count data for the Sundre Equine Management Zone. Note that a survey was not flown in 2020 due to the Covid-19 pandemic. Adapted from Alberta Environment and Parks, (2021); https://open.alberta.ca/publications/feral-horse-minimum-count-map

Aside from management utility, several factors in the Sundre EMZ make investigating feral horse abundance valuable from an ecological perspective, as density can influence many aspects of population ecology and behavior of species (Coulson et al., 2000; Forrester & Steele, 2004; Tschanz et al., 2007; van Beest et al., 2016). In feral horses, density has been shown to strongly influence a suite of factors including reproduction and survival (Grange et al., 2009; Laforge et al., 2016; Regan et al., 2020), and social dispersal when density is high (Marjamaki et al., 2013), while a lack of density-dependent effects in some populations may be the cause of high rates of increase (Garrott et al., 1991). High density in large herbivores generally can impact resource selection and home range size at small scales as intraspecific competition increases (Richard et al., 2014; van Beest et al., 2016), while the negative influence of density at population and evolutionary scales underpins much of our understanding of large mammal population dynamics (Eberhardt, 1977; Gaillard et al., 1998).

Relative abundance of interacting species can also be a critical component in community dynamics. Prey-switching and selection for horses by predators as horse relative abundance increases, has been identified in studies where horses exist with declining native prey species (Andreasen et al., 2021; Andreasen & Longland, 2014; Engebretsen et al., 2021). This matches patterns observed in native ungulates where populations fluctuate (DeCesare et al., 2010; Serrouya et al., 2015; Wittmer et al., 2013). Recent increases in the horse population in Sundre, in concert with declining elk (*Cervus elaphus*) populations (Berg et al., 2016; Hebblewhite et al., 2006, 2018), present an interesting potential parallel to these studies. Cougars (*Felis concolor*), wolves (*Canis lupus*), and grizzly bears (*Ursus arctos*) are predators of elk in this system (J. E. Berg, 2019; Griffin et al., 2011), with cougars and wolves also documented as predators of horses (Knopff, 2010; Webb, 2009), suggesting relative increases in horse biomass may be important for these predators as seen elsewhere. Much of the concern about feral horse populations comes from the potential for horses to compete directly with other large grazers (Schoenecker et al., 2016). Potential for competition and niche overlap between cattle, horses, and elk has been identified in the Foothills ecosystem previously (Girard et al., 2013a, 2013b; Salter & Hudson, 1979, 1980), particularly where species overlap temporally and in high-density areas (Salter, 1978). Attaining accurate estimates of horse abundance will help managers to assess the potential for conflict between these species and better estimate risks to rangeland health.

Estimating abundance

The diversity of abundance estimators has increased with the growth of camera trapping in ecological research (O’Brien, 2011; O’Connell et al., 2011). Traditional point-count (Royle & Nichols, 2003), time-to-event (survival) (Moeller et al., 2018), and capture-recapture techniques using animal markings (Karanth, 1995) have been applied to camera trap data to estimate abundance and density, along with the development of several new methods related specifically to data collected using cameras (e.g., time-lapse or staying time [Nakashima et al., 2018]). Assumptions in some of these approaches can be hard to meet however (Moeller et al., 2018), particularly where robust alternative estimates are not available for validation. Capture-recapture techniques are limited to species where natural markings can be used to distinguish individuals from one another at different locations, or, require invasive capture and tagging of individuals prior to studies beginning (Rowcliffe et al., 2008). Many estimators also assume animals move independently, which is inaccurate for socially or spatially clumped species including horses (Hickey & Sollmann, 2018). For estimators that utilize the inherent movement rate of animals to model detection (Random Encounter; Time-To-Event), estimates can be sensitive to minor differences in the precision of movement parameters used (Moeller et al., 2018), while models requiring specific sample densities relative to animal movement (Chandler & Royle, 2013) can be logistically challenging to implement and maintain at large scales (Loonam et al., 2021). Simple indices derived from captures per-unit-time, while offering a straightforward and intuitive metric of relative abundance, are also controversial given detection rate and abundance are not always correlated (Jennelle et al., 2002; Sollmann et al., 2013). Thus, camera trapping approaches to estimate density require careful consideration based on prior knowledge of the species and the landscape and initial study design (Foster & Harmsen, 2012).

Recently, space-to-event (STE) estimators (Moeller et al., 2018) have been shown to produce accurate abundance estimates comparable with more intensive sampling techniques such as genetic sampling, random encounter models, and spatial capture-recapture (Ausband et al., 2022; Loonam et al., 2021). STE estimators address the limitations of rate-based methods in several ways, providing a means to assess abundance when additional population information is not available. Estimates are based off survival model principles which evaluate the time (or space in the case of space-to-event) taken for an event (detection) to occur. Models have been shown to produce reliable abundance estimates of both social and individual living species including elk (Moeller et al., 2018), cougars (Loonam et al., 2021), and recently wolves (Ausband et al., 2022). This estimator could prove useful in feral horse camera studies as well, as in many populations, including in the Sundre EMZ, individuals are difficult to distinguish despite having natural markings. Moreover, strong social clustering and non-independent detection (and non-detection; Chapter 3) may mean adaptations to traditional capture-recapture techniques are required (Emmet et al., 2021; Hickey & Sollmann, 2018).

In this study, I estimated the density and abundance of feral horses in the Sundre EMZ using camera traps and space-to-event models, and compared abundance estimates with annual aerial minimum counts. I also estimated relative abundance across the Sundre EMZ as a function of detection rate per unit time (i.e., a detection rate index), to assess variation in the distribution of horses across the study area. While controversial as an absolute measure of abundance or density (Sollmann et al., 2013), detection rate is known to increase with abundance (Rovero & Marshall, 2009), and relative abundance indices can provide useful information about the distribution of animals (Rowcliffe et al., 2008, 2013). In this chapter I discuss potential reasons for the changes observed in the Sundre population compared with many of free-ranging feral horse populations, and the implications this has for our understanding of feral horse populations generally.

Methods

Field methods

A full description of camera deployment is available in Chapter 3, however a summary relevant to Chapter 4 is provided here.

I deployed a total of 120 cameras across the Sundre EMZ, from 2017/18 to 2019/20. StealthCam© (model PX14) and BlazeVideo© (model A252) (Blaze Video Canada, 2022; Stealth Cam, 2022) brand cameras were deployed at four kilometer grid cells across a total grid area of 1800 km^2 based on the known distribution of feral horses from minimum count observations from 2001-2016. Camera locations were adjusted for access or terrain reasons (e.g., not deployed on rock crags or in ravines) where necessary (Pettigrew, 2017). Where grid locations were adjacent to or near trails, cameras were oriented towards animal movement though hidden from trails to maximize probability of detection if an animal is in the area (Stewart et al., 2019). Thus, the assumption of random placement of cameras was violated to some extent, though not unreasonably (Ausband et al., 2022) and detection rates were not artificially altered as animals were neither lured to, nor deterred from cameras at these sites (Carbone et al., 2002; Rowcliffe et al., 2008, 2013).

Images were classified in Timelapse2 Image Classification Software, using manual classification and Microsoft Megadetector image recognition algorithms (Beery et al., 2019; Microsoft Corporation, Redmond, WA, United States) with horses counted and classified as described in Chapter 3 and Appendix C.

Detection rate mapping

To provide a basic description of relative abundance as a function of detection rate (see caveats above) across the Sundre EMZ, heat maps of detection rates were produced in ArcMap (ESRI, 2011) using detection data from camera locations as a function of effort. Detection rates at camera locations were standardized with survey effort (i.e., length cameras active) giving detections per 100 trap nights at each camera location (Carbone et al., 2001; Rovero & Marshall, 2009). Mean detection rates per 100 trap days were then calculated across survey periods (camera active periods) and used in interpolation methods below. Survey periods with less than 14 total trap nights (*n = 20*), and cameras adjacent to natural mineral licks (*n = 4*) were not included in analyses.

Heat maps were interpolated across suitable habitat (defined below) using Empirical Bayesian Kriging (EBK) in ArcMAP in the geostatistical toolset to create a raster surface of predicted detection rates based on neighborhood values from camera traps. Search neighborhoods were limited to a minimum and maximum of 5 and 10 cameras respectively, with search radii equal to twice the original grid cell size (~8000 kilometers). Semi-variogram, standard error, and residual plots for parameter settings in the geostatistical toolset were visually assessed for best model fit prior to interpolation (Krivoruchko, 2012). Maps were then compared to the distribution feral horse counts to assess areas of high and low detection as a general description of relative abundance across the study area. Areas where detections are in the top decile of those across the study zone were further delineated to compare high local density with evidence from earlier studies.

Space-to-event sampling

Estimates of the abundance of horses in the Sundre EMZ were undertaken using space-to-event (STE) models from the *spaceNtime* R package. STE models are similar to time-to-event abundance models, modelling density as a function of Poisson-distributed detection events. STE models use instantaneous sampling occasions however, with density per viewshed unit (e.g., m^2) estimated as a function of exponential likelihood of space between detections (Moeller et al., 2018; Moeller & Lukacs, 2021). Total abundance for a given area is then calculated by multiplying this density by the study area (Moeller et al., 2018).

The spatial sampling frame for models was defined across all camera locations as these were deployed across the known distribution of horses in the Sundre zone (see trail camera deployment). Cameras at, or immediately adjacent to, natural mineral licks were excluded to avoid the influence of cameras that concentrate animal movement (Moeller & Lukacs, 2021). Viewshed (m^2) of each of the camera types deployed was derived during deployment. Maximum areal detection “cones” (i.e., unimpeded viewsheds) were defined by testing motion trigger distances and angles for each camera type across ten separate trials, following (Caravaggi, 2016).

Mean viewshed area across trials was then calculated for each camera type (StealthCam = 123.9 m^2; BlazeVideo = 109.6 m^2) and assumed to be consistent for each model across deployed cameras in the field. This means that total viewshed area will be smaller than that calculated, though not larger (i.e., not all cameras will have maximum viewable areas, such as those in closed forest). Detection histories were generated using a 2 s sampling window at 30 s intervals over the time period from June to August each year as this represented the greatest coverage of active cameras during the study (Ausband et al., 2022). Final abundance values for the Sundre EMZ were calculated by multiplying density estimates for each year by the area of suitable horse habitat within the Sundre EMZ. Suitable habitat was spatially defined as the area where horses have been consistently sighted during minimum aerial counts throughout the Sundre EMZ, buffered by the maximum daily movement distance as identified from telemetry data in this study (Chapter 3). Non-vegetated areas such as lakes and bedrock above 2000m (i.e., mountains) were also excluded from suitable habitat.

As STE estimators derive density based on an instantaneous sample of the total viewable area, estimates can be sensitive to temporal distribution of samples (pers. comm, A Moeller). To account for this variance, a final abundance value for each year was derived through stepwise iteration of sampling occasions by one minute, adjusting each sample detection history window. This resulted in 61 individual estimates for each year, with the mean of model estimates for each year taken as a final estimate of abundance, and the mean of standard errors used to calculate 95% confidence intervals.

Results

Over the four years surveyed, 18,836 detections of groups of horses were collected across all camera locations monitored and for all surveys. Interpolation of relative abundance (i.e., detection rate) throughout the Sundre EMZ revealed similar patterns compared with feral horse distribution from previous aerial survey years. Highest relative abundance based on detections was located in the south and southeastern regions of the EMZ (Figure 4.1). Few horses were detected in locations sampled westward of the eastern extent of the Rocky Mountains, with the highest detections across the Sundre EMZ overlapping with similar areas of Salter's original work in 1978 (Figure 4.4; see Discussion in this Chapter).

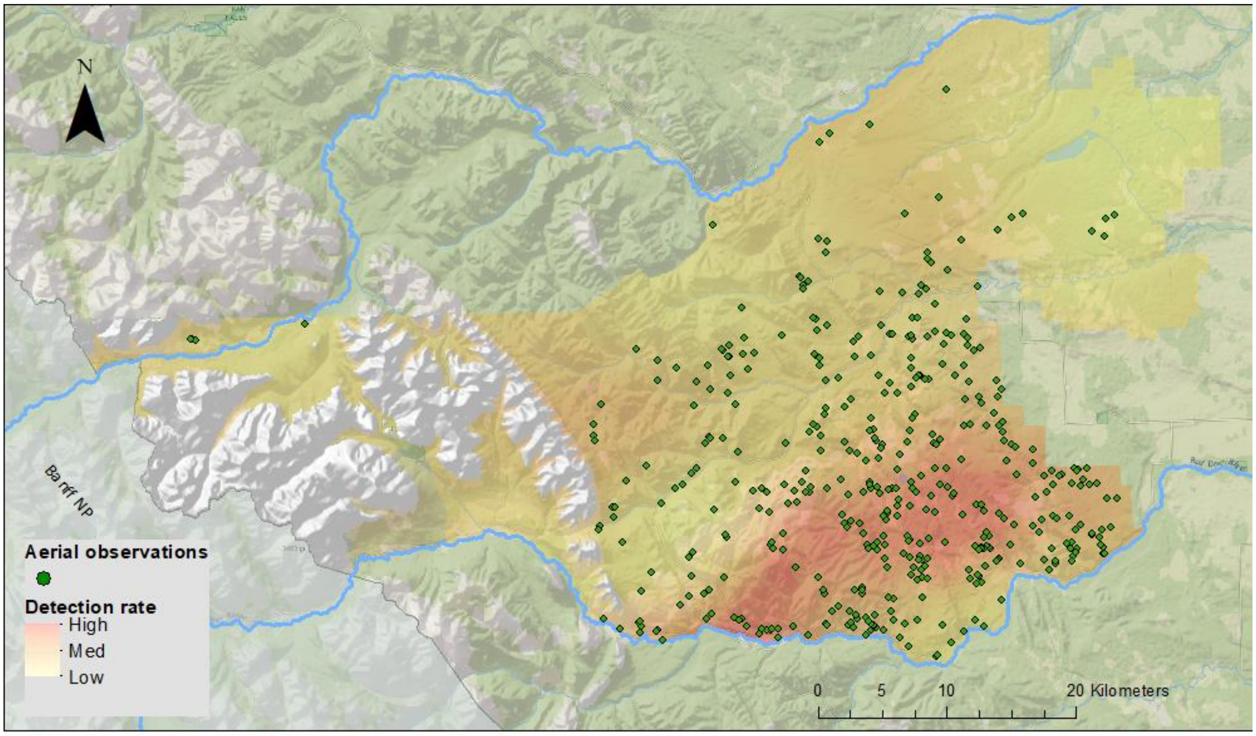

Figure 4.2. Interpolated map values for horse detections per 100 trap days from camera trap data. Aerial observations of horses are from minimum count data over the study period (2017-2019; Alberta Environment and Parks, [2021]). Clearwater and Red Deer rivers, and Banff national park are indicated to the north, south, and west of the EMZ respectively, and elevation with the Sundre EMZ above 2000m indicated in grey shaded relief. Base map sources National Geographic, Esri, DeLorme, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, iPC.

Total density estimates from STE models across the three years of study were 0.602/km^2, 0.606/km^2 and 0.522/km^2 respectively (Table 4.1), showing a decrease of approximately 14% between 2018 and 2019. Comparison of numbers with aerial minimum counts is difficult in some years as aerial counts in 2017 likely represent a methdological error (an increase of 53% over a single year is biologically unlikely; Figure 4.1), and an aerial survey in 2020 was not conducted. However, minimum count estimates were approximately 22% lower in 2021, compared with 2019.

Table 4.1. Density and abundance estimates from STE models for horses in the Sundre EMZ. Values for abundance are rounded down to the nearest animal[a].

Year	**Density (km^2)**	**Total Abundance**	**Minimum count[b]**	**Detections[c]**
2017	0.602 (0.502 – 0.702)[d]	1104 (918 – 1291)	661	3338
2018	0.606 (0.545 – 0.668)	1113 (1002 – 1223)	1015	5190
2019	0.522 (0.476 – 0.569)	959 (876 – 1041)	981	7471
2021	-	-	763	-

[a] An aerial survey and camera analysis was not conducted in 2020
[b] Data retrieved from https://www.alberta.ca/feral-horse-management/
[c] Number of detections used in STE analysis
[d] Numbers in parentheses are 95% confidence intervals

Total abundance estimates were similar to aerial counts, and confidence intervals of STE estimates overlapped with minimum counts in all concurrent years except 2017. Relative declines in abundance estimates and counts in recent years show a similar trend between the two survey methods. Confidence intervals in 2017 are larger in STE models compared with other years likely due to the influence of differential detection rates at any given camera having a larger relative influence in smaller survey sizes (Ausband et al., 2022; Moeller et al., 2018).

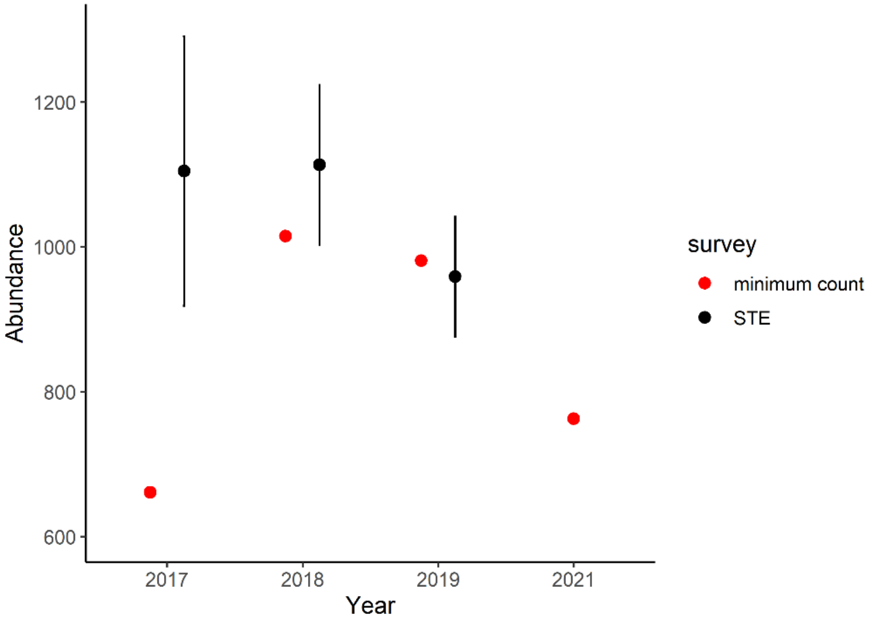

Figure 4.3. Abundance estimates and 95% confidence intervals derived from STE models. Aerial minimum counts for available years are shown for comparison. An aerial survey was not flown in 2020.

Discussion

Estimates of total abundance from STE models were similar to numbers from aerial minimum counts, and in both surveys the population appears to have recently decreased in size (Figure 4.3). Differences between estimates could arise from a number of methodological factors including negative observation biases inherent in minimum count aerial surveys (Ransom, 2012), or the non-random placement of some cameras in this study (Ausband et al., 2022). STE models are also sensitive to spatial coverage, (Loonam et al., 2021; Moeller & Lukacs, 2021), while the time period associated with each method differs (e.g., day(s) in winter [aerial survey] versus months in summer [STE]) potentially capturing seasonal patterns in animal distribution (Fleming & Tracey, 2008). Relative detection rate across the study area also varied (Figure 4.2) potentially leading to spatial biases inherent in patchy distributions of animals (Hickey & Sollmann, 2018). Despite these potential influences, abundance estimates are similar in all years except 2017, with confidence intervals of STE estimates overlapping with minimum count data suggesting the estimated abundance and detected declining trend are reliable.

Relative abundance as measured by detection rate is higher in the southern and eastern extent of the Sundre EMZ (Figure 4.2), and locations in the top decile of horse detection rates were delineated in a relatively small area throughout the Williams’ Creek and Deer Creek area on the southern border (Figure 4.4). Salter's (1978) work in the Williams' and Deer Creek areas also found horse abundance was high compared to other areas, suggesting consistent local density in these locations could lead to resource limitation and the density-dependent impacts observed in other populations (Grange et al., 2009). However, the abundance of forage in the Foothills region and the early utilization of spring growth by horses compared to later grazers (i.e., cattle) (Girard et al., 2013; Salter & Hudson, 1980) may mean the impact of high local density is low compared to less productive ecosystems, particularly given horses' ability to generalize foraging at high density (van Beest et al., 2014). For example, home range size is often associated with local resource availability in equids (Linklater et al., 2000; Schoenecker et al., 2016), yet no correlation was found between band size and home range in this study, and adjacent bands overlapped in home range considerably in these high-density areas (Figure 3.9, Chapter 3). This suggests resources are not limiting among horses in these locations despite the potential for overgrazing of grasslands being relatively high (Salter, 1978). Grazing patterns between horses and cattle are also distinct despite overlap in these areas (horses utilizing shared sites in spring vs cattle in summer) suggesting horses may be less impacted by available grassland resources where combined grazer density is high in summer (Salter, 1978). Yet clearly, these southern regions of the EMZ are utilized heavily by horses and high relative abundance here is consistent with Salter's work from four decades ago. Areas of heavy use and overgrazing, such as those around mineral licks noted by Salter, remain most likely in these high-density areas, increasing the potential for conflict among grazing species compared with other areas in the management zone (Beever et al., 2008; Beever & Brussard, 2000; Kaufmann et al., 2013).

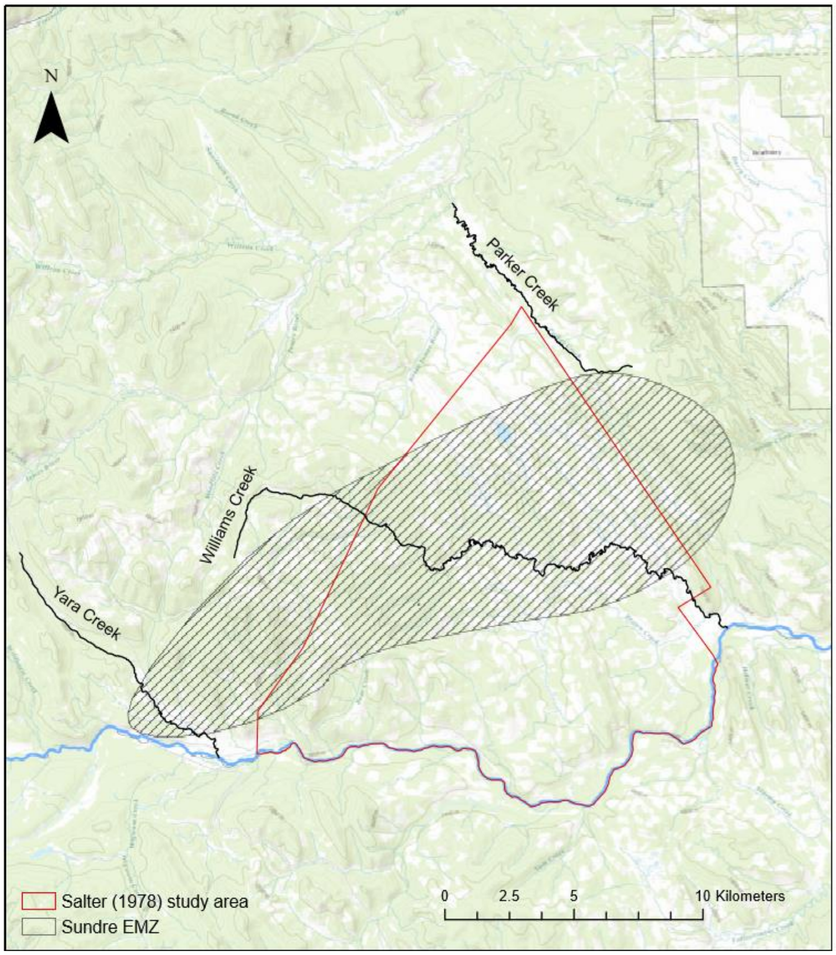

Figure 4.4. Location of top decile of relative detections across the Sundre EMZ. Salter's (1978) study area shown in the region between the Williams' and Deer creeks. Red Deer River forming the approximate southern edge of the Sundre EMZ shown in blue. Source map: ESRI, HERE, Garmin, Intermap.

The recent decline in total horse abundance estimates in Sundre is interesting following the apparent increase in the population over the preceding decade, and given that no management actions (i.e., removals or culling) have been undertaken recently (Figure 4.1). Populations of horses and other feral ungulates at high density have been observed to exhibit large population declines, with some suggestion that artificially selected life-history traits may have led to constant reproduction in females at the expense of survival (Grange et al., 2009; Regan et al., 2020). These observations typically occur in island populations where density can be particularly high (e.g., >20 horses/km^2), and the impacts of density-dependence on social characteristics, survival, and resource use can be pronounced (Cluttonbrock et al., 1987; McLoughlin et al., 2006; van Beest et al., 2016). Densities of horses greater than 20/km^2 on Sable Island for example, lead to negative consequences for adult female survival as the population became strongly male-biased (Regan et al., 2020). The Camargue horses at densities exceeding 20/km^2 showed similar patterns as high reproductive output of females continued despite severe resource shortages, leading to population decline (Grange et al., 2009). However, density in Sundre is low compared to these studies, and adult sex-ratios were similar to those observed four decades ago (Chapter 3) suggesting the density-dependent effects observed in populations such as the Sable Island horses are not occurring here. The population inhabits a large open landscape with comparatively abundant resources (Girard et al., 2013), and even at high local densities, social and spatial dispersal are possible, suggesting other factors might be contributing to the observed decline.

Severe winter weather events, particularly in northern climates have been noted to result in significant mass mortalities in feral horse populations (Ransom et al., 2016). In both the Granite (Berger, 1983a) and Pryor Mountain ranges (Garrott & Taylor, 1990) snowstorms and cold temperatures were noted to result in large (>50% in the latter case) population losses. Winter in the Sundre EMZ is both cold and subject to heavy and prolonged snowfall and indeed, deaths of four adult mares were observed to have occurred from apparent exposure during a severe winter in 2017. Mass mortality did not occur during this study however, and the multi-year decline in numbers despite less-severe winter conditions suggests winter mortality was not a major source of population change. There is also the potential that emigration of horses out of the study area has led to lower minimum count numbers, and lower numbers detected in STE models. The natural features of the Clearwater and Red Deer rivers to the north and south respectively, are not impassable for horses (Chapter 3), particularly during late fall and winter when river levels are low, and coincident forage depletion following summer grazing (Salter, 1978) may lead to emigration if density is high. Minimum count data from the Clearwater survey zone to the north of the Sundre zone was in fact 30% ($n = 42$) lower in 2019 compared to 2018 counts, then increasing by 14% in 2021 ($n = 17$) compared to 2019. In the Ghost management zone to the south, minimum counts were 2% ($n = 8$) higher in 2019, and 2021 counts were 17% ($n = 66$) compared to 2019 data. Thus, these differences alone cannot account for the total changes observed in the Sundre zone (i.e., a decline of 281 horses counted between 2019 and 2021), and additional factors may be contributing to the decline.

Increased predation is one potential contributor to the recent decline observed and horses may be experiencing elevated predation as the relative abundance of primary prey species declines. Elk populations in the Sundre area are an important prey species for all three large predators (cougars, wolves, and grizzly bears) and have been in decline for several decades (Berg et al., 2015; J. E. Berg, 2019; Hebblewhite et al., 2006, 2018). Based on aerial counts of the area, Boyce and McLoughlin (2021) estimated that as much as 188 kg/km^2 of additional biomass was provided by horses in the Sundre EMZ, when the population was estimated to be at its peak (aerial minimum count data). Strong relationships between the number of wolves and total ungulate biomass have been found in similar ecosystems (Hayes & Harestad, 2000; Kuzyk & Hatter, 2014) and increasing prey density is often followed by numerical or functional responses in predator populations (O'Donoghue et al., 1997, 1998; Sinclair et al., 2003; Sinclair & Krebs, 2002), including those involving feral horses (Andreasen et al., 2021; Ingebrigtsen et al., 2021). Predator studies in the Alberta foothills found that feral horses composed 12% of the relative biomass of wolf diets (Webb, 2009), and as much as 13% of cougar kills seasonally (Knopff, 2010) when minimum counts estimated the horse population to be less than half its current size (Figure 4.1). The relative abundance of feral horses has increased since, and both predator-prey theory and evidence from other feral horse populations suggest predators could be increasingly selecting horses, potentially leading to slower population growth (Andreasen et al., 2021; Engebretsen et al., 2021; Lagos & Bárcena, 2018).

The relationship between one such predator in particular, grizzly bears – the largest predator in the area – and feral horses is poorly understood. Some evidence of European brown bears attacking horses has been found (Cozza et al., 1996), yet only anecdotal accounts exist in North America of grizzly bears actively hunting horses (Berger, 1986). Two accounts of grizzly bear chases of horses have been captured via trail cameras in the Sundre EMZ, one of which was captured during this study (Appendix C). These observations in Sundre suggest interesting parallels with multi-prey, multi-predator systems involving feral horses elsewhere in North America (Engebretsen et al., 2021). Grizzly bears are important predators of elk in this system (J. E. Berg, 2019) and influence wolf and cougar predation on elk when they overlap (Griffin et al., 2011; Hebblewhite & Merrill, 2011).

Similar patterns have been found involving feral horses, cougars, and black bears in Sierra Nevada and the Great Basin, where cougar predation on horses increased with horse relative abundance (Andreasen et al., 2021), though was mediated in the presence of black bears due to the risk of kleptoparasitism (Engebretsen et al., 2021). Winter predation on horses by cougars was greater when bears were absent, as has been found with cougar predation on feral horses in the Sundre region (Knopff, 2010). Thus, bear species could benefit from additional prey biomass of horses, whether as effective predators of horses themselves, or, as kleptoparasites of known horse predators in the region. A recent doubling of grizzly bear populations across core grizzly bear habitat within a management zone that encompasses the Sundre EMZ (BM4 [Stenhouse et al., 2020]) could mean these predator-prey interactions involving feral horses are becoming more important in this system. While only limited evidence exists that predator populations are influenced by feral horses in the Sundre EMZ, these anecdotal accounts here, in conjunction with the observed population decline, and recent evidence from other systems, warrant further investigation of these dynamics in the Sundre population.

Conclusion

Ultimately, the cause for the recent decline in the Sundre population is difficult to assess based on the limited available data. Much about the role of feral horses in food webs and predator population dynamics requires further investigation, despite the increasing interest in the topic (Andreasen et al., 2021; Boyce & McLoughlin, 2021; Engebretsen et al., 2021; Lundgren, Ramp, Middleton, et al., 2021). Population dynamics are also inherently complex, particularly in diverse ecological communities (Krebs, 2002) and the declines in abundance observed in the Sundre feral horse population are likely the combined result of several of those factors described above. This trend is interesting however, particularly in a relatively large, open population of feral horses not subject to recent management or to the kind of resource limitation observed in island populations, or those in arid or semi-arid ecosystems. High intrinsic growth rates are typical in many unmanaged populations and are often described as an inherent invasive quality of horses (Boyce et al., 2021; Dobbie & Braysher, 1993; Garrott et al., 1991; Scasta et al., 2018). Yet the decline in the population in Sundre despite low density suggests such growth rates may instead be inherent to environments where natural limitations to horse populations are absent, rather than being inherent to populations or the species generally (Garrott et al., 1991; Garrott & Taylor, 1990; Lundgren, Ramp, Wu, et al., 2021).

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Chapter 5 Estimating resource selection and occupancy of feral horses in the Alberta Foothills.

Abstract

Understanding species occupancy and habitat use are fundamental components of ecology and provide critical information for managers. In western Canada, feral horses (*Equus ferus caballus*) overlap with many species of interest, yet, few studies have investigated feral horse habitat use in northern temperate ecosystems. I assessed seasonal habitat use of five GPS tracked feral horses in the Sundre equine management zone in Alberta, Canada, and compared summer occupancy of horses, domestic cattle, and elk (*Cervus elaphus*) using trail camera data. Variation was high among tracked individuals in selection for vegetation type, though counter to expectations, horses avoided native rangeland in summer, compared to greater selection of forestry cutblocks in all but one individual. In winter, horses selected areas closer to roads, areas of lower terrain ruggedness, and areas of higher solar radiation further from forests, suggesting habitat accessibility and thermoregulation may be important drivers of winter habitat use. As identified in other studies within this ecosystem, distance to water did not appear to be important in habitat selection in either season, or in summer occupancy. Summer horse occupancy probability was highest with increasing areal coverage of cutblocks in contrast to cattle where occupancy probability decreased strongly with increasing cutblock coverage. Cattle occupancy was also negatively influenced by terrain, though positively influenced by the presence of linear features and lower distance to roads. Elk summer occupancy increased with decreased distance to conifer forest and increasing native rangeland, though spatial coverage of elk was low compared to cattle and horses. These results have important implications for management and suggest that human-caused ecosystem disturbance and landscape-level change are important drivers of feral horse selection and occupancy and hence, feral horse management may warrant attention to industrial land uses such as forestry.

Introduction

The evolution and success of *Equus* in the grasslands of North America led to the expansion of the genus across many of the world's grassland ecosystems (MacFadden, 1994; Shoemaker & Clauset, 2014). The evolution of hindgut fermentation allows equids to efficiently process large amounts of low-quality roughage compared to ruminants (Slade et al., 1970), and populations can thrive in ecosystems where poor-quality forage is abundant (Schoenecker et al., 2016). This has resulted in present-day populations of feral horses (*Equus caballus*) surviving and expanding throughout a diversity of habitat types, including in many heavily modified ecosystems. Low research investment means understanding of feral horse habitat selection is poor however, despite horses overlapping and potentially competing with many priority species in sensitive environments (Bonacic et al., 2019; Boyce & McLoughlin, 2021). The potential for competition is particularly high in large herbivore communities that share diminishing native grasslands (Zapisocki et al., 2022), and a paucity of data regarding feral horses in these ecosystems often complicates already difficult management decisions (Scasta et al., 2018). Investigating resource use of feral horses is therefore critical to understanding the ecology of the most widespread of modern-day equids, and to the effective management and maintenance of the ecological communities of which they are a part.

As predominant grazers, habitat selection by feral horses is often linked to the abundance of grasses (Salter and Hudson, 1979). However, evidence suggests selection is complex and associated with a wide range of factors, particularly in seasonally variable ecosystems at high latitudes (Girard et al., 2013a). While horses can utilize abundant low-quality resources, high quality forage is consistently selected when available (Salter, 1978), suggesting that selection for lower-quality resources may only occur at high density or when resources are limiting (van Beest et al., 2014). In northern temperate ecosystems, biomass production and forage quality peaks in summer months (Girard, 2012; Hebblewhite, 2006; Kaufmann et al., 2013), though temporal overlap with competitors such as domestic cattle and elk (*Cervus* elaphus) during these months, may drive feral horse selection for less-preferred habitats as relative available grassland biomass declines (Salter & Hudson, 1980). Habitat selection during seasonal extremes may also relate to climatic conditions, as temperatures and precipitation fluctuate widely throughout annual cycles (Ganskopp & Vavra, 1986). Snow cover (Berger, 1986), temperature (Girard et al. 2013b), and grazing pressure during the preceding summer months (Salter, 1978), can all influence winter habitat selection, while the disturbance features (e.g., clearcut logging) present in many ecosystems, may provide alternative forage when winter resources are limiting or difficult to access (Irving, 2011; Salter, 1978). Feral horse habitat selection can therefore be complex, and patterns may be difficult to discern in highly disturbed and seasonally variable ecosystems.

In western Canada, feral horses are distributed throughout the Rocky Mountain Foothills in ecosystems that are mosaics of native and anthropogenic grasslands (Thistle, 2008), vast forestry cutblocks, intensive recreational disturbances (McFarlane & Boxall, 1996), and densely grassed linear features (Dickie et al., 2020; Irving, 2001). In Alberta, Canada, horse populations have persisted since the 1700's following the release and escape of domestic horses (McKnight, 1959). Competition between feral horses and domestic and native grazers for rangeland resources is a primary management concern (Girard et al., 2013; Hebblewhite, 2006; Kaufmann et al., 2013), though few studies have investigated habitat selection in these forested northern environments (Salter, 1978). Two studies have explicitly investigated feral horse habitat use in Alberta, Canada: Salter's widely cited 1978 study, and another in 2012 by Girard. With inference from better-studied populations in arid environments potentially not representative of habitat use in western Canada, additional contemporary research is much needed. For example, water availability is often a strong determinant of habitat selection in feral horses (Ganskopp & Vavra, 1986), and conflict between horses and cattle, and horses and native ungulates is often identified at locations where water is limiting (Hall et al., 2018). In addition, competition for limited grassland resources often leads to declines in rangeland health where feral horses overlap with other grazers (Baur et al., 2017; Beever et al., 2008). However, in the Alberta Foothills water sources are relatively widespread and distance to water has not been shown to influence selection patterns strongly (Girard et al., 2013a, 2013b). Relatively abundant and diverse forage throughout the growing season in the Foothills (compared with low-productivity ecosystems) may also mean horses can mediate direct competition temporally, selecting less-preferred though still productive habitats as grazing impacts increase (Salter, 1978; Salter & Hudson, 1979). In addition, much of the Foothills landscape is subject to heavy industrial land use (Schneider, 2002), and some disturbances may increase the available forage for feral horses. For example, forestry cut blocks are second to native grasslands and shrublands in the production of available forage biomass, compared with other vegetation types in this ecosystem (Girard et al, 2013b). With cutblocks ubiquitous throughout the Foothills (McFarlane & Boxall, 1996), this may have important consequences for feral horse distribution, particularly when competition for native grasslands is high.

Seasonal changes in available forage are also coupled with changes in grazing communities. Free-ranging cattle in Alberta are only present in summer months (Kaufmann et al., 2013), while partially-migratory elk populations may result in lesser relative overlap in summer compared to winter as portions of the elk population migrate west of presumed feral horse population range (Hebblewhite et al., 2006). Thus, where present, competition for preferred resources may be temporally variable, presumably peaking when all three species are present. Importantly, terrain, distance to water, linear features and fragmented forests, and human disturbance can have strong and variable effects on large herbivores, mediated through varying predation risk (DeCesare et al., 2014; Hebblewhite et al., 2005), mobility and access to preferred habitat (Dickie et al., 2020; Trombulak & Frissell, 2000), and behavioral avoidance of humans (Leblond et al., 2013), and factors beyond forage abundance are likely to be important when considering potential competition between species. Thus, multiple biotic and abiotic factors inherent to northern forested ecosystems in western Canada, coupled with differing foraging and digestive strategies (Janis, 1976; Preston, 1984) will lead to varying habitat use among species. With limited empirical evidence available for feral horse selection in these ecosystems, comparing habitat use among species is difficult without further study.

I assessed feral landscape-scale horse selection and occupancy in the Sundre equine management zone (EMZ) in a temperate Montane ecosystem to address two key research objectives. 1) I used resource selection analyses to quantify the relative seasonal importance of different natural and anthropogenic landscape features in horse habitat use in the Sundre EMZ and produced spatially explicit seasonal maps predicting feral horse habitat use across seasons. 2) I then assessed single-season occupancy of horses, cattle, and elk over summer, in relation to key variables identified in selection analyses and compared relative support among landscape variables in predicting occupancy of species. Broadly, I predicted that feral horse selection for grasslands would be greatest in summer when herbage productivity is highest, and that selection for relatively low-quality forage in disturbed areas would increase in winter (Girard et al., 2013b). I also predicted that occupancy of each species would be best predicted by the proportion of preferred native rangeland, and that human-disturbance features would reduce predicted occupancy among horses and elk (DeMars & Boutin, 2018; Leblond et al., 2013).

Methods

Study area

The Sundre equine management zone (EMZ) is one of six equine management zones in the Alberta foothills, located approximately 100 km northwest of Calgary, Alberta (Figure 5.1). The zone is approximately 2205 km^2 and is bordered by the Clearwater River to the north, the Red Deer River to the south, and Banff National Park to the west. The eastern boundary of the zone is comprised of a mix of grazing leases and fenced private land, with topography generally rolling or flat. Approaching the west of the study area, terrain ruggedness increases, with the eastern ranges of the Rocky Mountains bordering the western administrative boundary (Figure 4.2, Chapter 4). Abundant creeks, muskegs, ponds and sloughs are present throughout the study area, many of which are frozen in winter, while snow generally remains on the ground from November through to March, particularly at higher elevation towards the western end of the EMZ (Hebblewhite, 2006; Salter, 1978). Temperatures vary by season with minimum hourly temperatures dropping below -29°C in February (mean = -7°C) and maximum temperatures exceeding 31°C in July (mean = 16°C). Precipitation is highest in May (mean = 70mm), June (mean = 114mm), and July (mean = 82mm) with mean annual precipitation approximately 550 mm (data from 2017 – 2019 inclusive; temperature and precipitation data from the Coalcamp Creek weather station in the south of the EMZ). Botanical species in the Sundre EMZ include pine (*Pinus spp.*), fir (*Abies* and *Psuedostuga spp.*), spruce (*Picea spp.*), tamarack (*Larix sp.*), poplar (*Populus spp.*), and birch (*Betula spp.*) with (willow [*Salix spp.*], alder [*Aluns spp.*], bog birch [*Betula pumila*]), herbaceous forbs (non-graminoid dominant) and grasses/sedges (graminoid dominant [*Festuca spp.*; *Poa spp.*; *Carex spp.*) present in non-forested areas including native rangeland and cutblocks (Alberta Vegetation Inventory, 2016).

The majority of horses are present in the eastern extent of the EMZ (see Figure 3.1, Chapter 3 for distribution), which has been subject to substantial modification (Figure 5.1). Approximately 21% of the total area of the EMZ has been logged at some time, while the combined human footprint (e.g., roads, oil and gas infrastructure, transmission lines, forestry) in the EMZ is approximately 25% based on Alberta Biodiversity Monitoring Institute (ABMI) data. Vegetation inventories on public land are maintained by Alberta Environment and Parks (AEP) in the Alberta Vegetation Inventory (AVI), which is a composition of vector polygons classified from aerial photography (Alberta Agriculture and Forestry, 2016). In locations where forestry management agreements (FMA) are in place, the inventory is maintained by agreement holders. Within the Sundre EMZ, two such FMAs exist in the eastern portion of the study area, covering approximately 51% of the total EMZ. Thus, vegetation and landcover data used to characterize the study area were compiled from three separate AVI datasets: crown AVI data; and two AVI datasets provided on request from agreement holders. Aerial photograph dates within each dataset were dated to 2011/12, and changes in areal coverage of some classes (e.g., forest harvest data) since these dates were updated using 2018 data from the ABMI human footprint layer (Alberta Biodiversity Monitoring Institute, 2018).

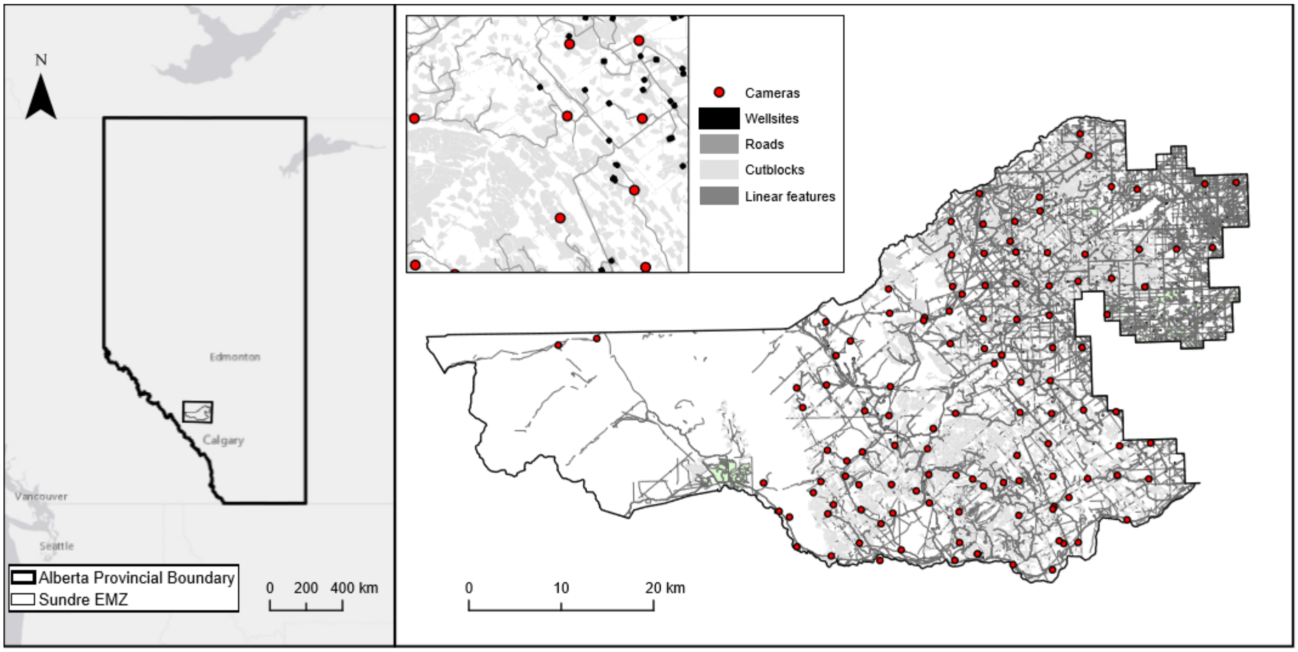

Figure 5.1. The Sundre equine management zone (EMZ) is situated in the south-western corner of the province of Alberta. The features in grey are composed of relevant human footprint features as identified in the Alberta Biological Monitoring Institute (ABMI). Main roads are shown here for visualization, though ATV trails and other recreational trails are omitted for clarity. Camera locations include all deployments and redeployments. Base map sources National Geographic, Esri, DeLorme, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, iPC.

Trail camera deployment

For additional descriptions of trail camera deployment and image classification techniques, see Chapters 3 and 4). A description relevant to Chapter 5 is provided here.

120 trail cameras (BlazeVideo© [model A252]; Stealthcam© [model PX14]) (Blaze Video Canada, 2022; Stealth Cam, 2022) were deployed from 2017/18 – 2020 across the Sundre EMZ using 4km grid spacing across the known distribution of feral horses based on minimum count observations from 2001-2016 (Alberta Environment and Parks, 2021). Cameras were set to motion-triggered detection, on the highest sensitivity setting, with 32gb SanDisk memory cards and Energizer batteries exchanged at approximately 6-monthly intervals. Cameras were mounted at waist height (1-1.5m) relative to animal movement, oriented to maximize detection of both feet and facial markings of horses. Given the ubiquitous nature of linear features and trails, cameras located adjacent to, or, on trails were oriented towards animal movement to maximize detection of animals when present in the area (Stewart et al., 2019). Several cameras and SD cards were stolen, damaged, or otherwise rendered inoperable (e.g., flipped against trees) leaving approximately 79% of the grid functioning over the study period.

Images were classified in Timelapse2 Image Classification Software using both manual classification and machine learning image recognition techniques. Approximately one third of all images were classified to species level manually by the author and undergraduate students from the University of Saskatchewan, with the remaining two thirds of images classified using Microsoft's Megadetector algorithm (Beery et al., 2019; Microsoft Corporation, Redmond, WA, United States). Following classification, I reviewed all classifications for large mammal species including those by both students and the Megadetector algorithm and corrected any misclassifications.

GPS Collar deployment

To assess resource selection, 5 GPS collars were deployed on female horses in the 2018/19 winter following the protocol described in Stover and Caulkett (2021) (University of Saskatchewan AUP – 20170117; AEP HCL: RDNS 003 2018; AEP TFAs: 182578, 185269). Collars were a combination of Lotek 7000 series (2; 12 hourly fixes) and Vectronic SURVEY (3; 3-hourly fixes) models (Lotek Wireless Inc., 2022; Vectronic-Aerospace, 2022). Collars recorded date and time, elevation, and temperature and data were periodically downloaded via satellite. All collars were initially set to record animal locations every 3 hours, though Lotek brand collars reverted to 12 hourly fixes following deployment from previous study schedules, with one Lotek collar going offline without further satellite communication. No other problems with collars were identified.

Composite landcover and additional covariates

Variables used in resource selection and occupancy analyses were selected based on evidence from previous feral horse habitat selection studies (Table 4.1) including vegetation classes, distance to water, terrain ruggedness, and disturbance features. To generate vegetation classes, AVI data were combined into broad categories of conifer and deciduous dominant forest (i.e., mixed-wood), non-forested land such as grasslands and cut blocks, and disturbance features such as roads and transmission lines. Non-forested land within the AVI encapsulates areas with ≤ 6% tree cover, but ≥ 6% vegetated cover and includes herbaceous graminoids and forbs, closed and open shrub, or bryophyte dominant classified polygons. Conifer and deciduous classes refer to the dominant tree species present as identified in the AVI, though not the absence of deciduous or conifer trees, respectively. Non-forested land previously logged (i.e., current or historic non-regenerated clear-cuts) was grouped as cleared non-forested land (cut blocks) distinct from native rangeland. Unmodified grasslands and shrublands were grouped together as native rangeland, as both classes have been shown to have high herbage production and similar patterns of seasonal horse selection within the temporal scales investigated here (Girard et al., 2013a, 2013b; Salter & Hudson, 1979). Other cleared features directly seeded with grass such as transmission lines and areas associated with geophysical exploration or extraction (e.g., pipelines) were grouped as linear features. All water features including rivers, lakes and ponds, and named streams from both the AVI, and the Alberta hydrography database (www.AltaLIS.com) were combined into a single water class, and road vector data was sourced from both ABMI data, and open source AltaLIS feature layers, and included both paved and unpaved roads and trails within the study area.

In ArcMap (ESRI, 2011), two additional covariates were derived from an Alberta provincial 25-meter digital elevation model (DEM) (Alberta Environment and Parks, 2017). A Terrain Ruggedness Index (TRI) characterizing topography was calculated following Riley et al. (Riley et al., 1999), while global solar radiation (GSR) was calculated following equations derived by (Fu & Rich, 2002) in the Solar Radiation toolset in ArcMAP (ESRI, 2011). For Step-Selection Function (SSF) analyses, individual Euclidean distance raster datasets were created for each vegetation covariate, with all classes scaled and centered prior to analysis. Covariates were examined for collinearity with variables correlated at $r \geq 0.70$, not used in the same model.

For camera data, 1000m radius buffers (Fisher et al., 2011, 2021) were created around each camera site and the percent areal coverage of vegetation classes calculated to characterize habitat. For covariates such as GSR and TRI, both the range and the mean value within the buffer were calculated, with top-ranking variables (based on AIC) from univariate models used in subsequent models (see below). For roads and distance to water data, Euclidean distance from the camera location to the nearest feature was calculated. Covariates were scaled and checked for collinearity as with raster datasets, with correlated variables ($r \geq 0.7$) not included in models together.

Season was defined from animal movement data and information from similar studies in the area based on key phenological events (Girard, 2012). K-means clustering (Zeller et al., 2019) was first used to identify different statistical clusters in mean daily movement pooled across horses and years to determine movement-based biological seasons (Zeller et al., 2019). Clusters were then visually compared to key phenological dates as identified by Girard (2012) in a similar Foothills ecosystem (i.e., Bragg Creek, AB). Two clear seasons based on movement data were defined (see chapter 3) compared to the four vegetation-derived seasons in Girard (2012). Seasons based on movement data matched closely with the winter-spring seasonal transition (May 14th), and the summer-fall transition (October 31st) described from plant phenology and snow cover in Girard (2012), and these transition dates were used to define seasons thereafter.

Table 5.1. Data sources of variables used in selection analyses.

Variable	**Description**	**Data Source**
Season	K-means cluster defined seasons	GPS collar data
Cutblocks	Non-forested land previously cleared	AVI[a] + ABMI[b]
Grasslands and shrublands	Unmodified vegetated non-forested land	AVI
Coniferous forest	Conifer dominant forest	AVI
Deciduous forest	Deciduous dominant forest	AVI
TRI	Terrain ruggedness – higher values are more rugged	Alberta DEM[c]
Linear features	Seismic lines, transmission lines, pipelines	AVI + ABMI
Roads	Trails and roads inclusive of vegetated road edges	AVI + ABMI
Solar	Global solar radiation	Alberta DEM
Water	Distance to nearest water feature	AltaLIS hydrography[d]

[a] Alberta agriculture and forestry (2016)
[b] Alberta Biodiversity Monitoring Institute (2018)
[c] Alberta Environment and Parks (2017)
[d] hydrography base-features from www.Altalis.com

Resource selection and occupancy modelling

Step Selection Functions

I assessed landscape-scale selection of feral horses (i.e., second-order selection [Johnson, 1980]) using step-selection functions. Step-selection functions are an adaptation of tradition resource-selection functions (Manly, 2002), and assess segments (steps) of animal movement as sampling units rather than static locations (as in point-location resource-selection functions), allowing the modelling of conditional selection, as a function of covariates along an animals' projected path (step) (Fortin et al., 2005). Step-selection functions are useful in highly heterogeneous environments compared to static use-available analyses (Prokopenko et al., 2017), which was an important consideration as much of the Sundre zone is a highly heterogenous complex of industrial linear features and habitat patches.

Individual step-selection functions (SSF) were derived from trajectories for each horse fitted with a GPS collar using the *amt* package in R (R Core Team, 2022) and following the equation from Fortin et al. (2005):

$$\hat{w}(\boldsymbol{x}) = exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_p x_p)$$

where coefficients β_1 to β_p derived from conditional logistic regression associated with landscape covariates χ_1 to χ_p, estimate conditional selection of steps, with steps with higher $\hat{w}(\boldsymbol{x})$ values more likely (higher odds) to be selected (Fortin et al., 2005). Sample frequencies between collars were first regularized and fifty available points per used point were randomly generated from distributions of observed step lengths and turn angles for each horse where two successive steps could be calculated based on sample frequency (i.e., minimum of three locations not longer than sample frequency; [Prokopenko et al., 2017]). Conditional logistic models were then fitted to location data using the *survival* package in R (R Core Team, 2022). Univariate selection models for covariates predicted to influence feral horse habitat selection (Table 5.1) were initially assessed and compared to a global model (i.e., unconstrained) using AIC (Anderson & Burnham, 2004). The global model including all variables and a season interaction received full model weight when compared to univariate models and was subsequently used to describe feral horse selection. Mean beta coefficients across individuals based on the global model were used to describe “population” level selection characteristics within the Sundre EMZ. Spatial predictions of habitat suitability based on mean selection coefficients for each covariate were then used to generate predicted habitat use maps across the Sundre EMZ by season.

Occupancy

Occupancy analyses are robust to variable detection rates of species and are an effective means to assess broad patterns of species distribution in relation to landscape covariates (MacKenzie et al., 2002). Combined with camera-trap data, they can provide robust inference about multiple species within ecological communities (Kays et al., 2020). I assessed occupancy of horses, cattle, and elk using an information-theoretic approach to test the relative influence of landscape covariates on summer occupancy of each species. I focused on the summer growing period of June – September, as all three species are present within the Sundre EMZ (i.e., cattle are removed in late summer/fall). This period also lies within peak rangeland biomass production (Girard, 2012; Hebblewhite, 2006) and was short enough (12 weeks) that colonization or extinction across sites could reasonably be assumed to absent (Mackenzie and bailey 2006), while long enough to provide robust estimates of occupancy (Kays et al., 2020).

Single-season occupancy models (MacKenzie et al., 2002) were fit using the *unmarked* package in R (R Core Team, 2022) with detection data discretized to weekly samples creating a detection history for each species. I first assessed global models for each species for goodness-of-fit using the Mackenzie-Baily (MB) goodness-of-fit (GOF) test (MacKenzie & Bailey, 2004). The MB goodness-of-fit test calculates a Pearson's chi-squared statistic ($\hat{c}$) to assess model dispersion using parametric bootstrapping of observed occupancy compared with occupancy fit to randomly generated detection histories. Values of $\hat{c}$ approximating 1 denote adequate model fit, and where significant ($P < 0.05$) lack-of-fit and $\hat{c} > 1$, or , < 1 is identified, model variance (SE) can be inflated based on the chi-squared statistic to facilitate more robust inference during model selection (Burnham, 2002; MacKenzie & Bailey, 2004). I estimated variance inflation factors ($\hat{c}$) for each species' global model using 1000 simulated bootstrap samples to assess global fit prior to assessment of model hypotheses and assumed fit of subsequent nested models was adequate where $\hat{c}$ was close to 1 and lack-of-fit estimates were not significant (Grant et al., 2009). Following model testing, I fit multiple single-season occupancy models within a structured candidate model set (Table 5.2). Detection probability in all models was modelled as a function of effort (continuous; total trap days) and whether the camera was adjacent to a trail or not (factor; 1, 0). I then compared models within species using AIC and where multiple models within species had ΔAIC < 2, I used model averaging to estimate the relative influence of each covariate from top models on occupancy, to reduce potential inferential bias based on a single top-ranked model (Anderson & Burnham, 2004; Burnham, 2002). Finally, I calculated evidence ratios (ER) comparing top models with second-ranked models for each species, assessing relative influence of omission or inclusion of variables in top models.

Occupancy model structure

I developed nine candidate models based on *a priori* hypotheses nested within four broad predictions characterizing habitat use of horses, cattle, and elk: key resources, topography, habitat structure, and disturbance (Table 5.2). My first hypothesis predicted that occupancy would be greatest for all species in habitats with the greatest forage biomass production (rangeland and shrublands), and that distance to water would be important for more water-dependent species such as equids (Ganskopp & Vavra, 1986; Schoenecker et al., 2016). My second hypothesis predicted that forage biomass and terrain would best describe occupancy, as Montane grasslands are often sparse and dispersed at both high elevation and slope (Girard, 2012), yet cattle are often limited by slope and elevation compared to horses and elk (Kaufmann et al., 2013). My third hypothesis predicted that habitat structure would best explain occupancy, as both elk and horses have been shown to select and avoid open habitats, potentially to reduce predation risk, or for thermoregulation purposes where solar radiation is high, respectively (Girard et al., 2013; Hebblewhite, 2006). My final hypothesis predicted that disturbance would best explain occupancy, where linear features and distance to roads strongly influence large herbivore movement and habitat selection (Dickie et al., 2020; Leblond et al., 2013), while disturbances in the Sundre EMZ that potentially increase forage biomass (i.e., cutblocks, linear features), may result in additional and more accessible forage when more preferred habitat is limiting, particularly at high species overlap in summer (Irving, 2001).

Table 5.2. Candidate models used in resource selection analyses

Model	Variables included	Description	sources
Key resources			
1	Native rangeland (NR)	Occupancy highest in habitats with greatest forage biomass production during summer (1) while access to water consistently linked to equid and cattle habitat selection (2). Montane grasslands are sparse and distributed more frequently on south-facing slopes, while forage quality in preferred habitats can also increase at higher elevations but slope can also limit some species, presumable cattle > horses > elk (3 & 4).	(Girard et al., 2013; Hebblewhite, 2006) (Hall et al., 2018; Schoenecker et al., 2016) (Ganskopp & Vavra, 1987)
2	NR + D.water (distance to water)		
Topography			
3	NR + TRI (terrain ruggedness index)		
4	NR + TRI + D.water		
Habitat structure			
5	NR + D.anyforest + GSR + D.water	(5) “Thermal” model from Girard (2013), where equid abundance and presence were influenced by global solar radiation (GSR) and distance to forest, potentially further impacted by distance to water in drier summer months. (6) Native ungulates often select preferred habitat in open spaces or at higher elevation to lower predation risk when foraging, while herbivores may select areas at increasing distance from complex forest patches (predominantly conifer in this ecosystem) and forest edges (7), where predation risk is greater.	(Girard et al., 2013a, 2013b) (Fortin et al., 2005; Ganskopp & Vavra, 1987; Hebblewhite et al., 2005)
6	NR + cutblocks + TRI		
7	NR + D. conifer forest		

Disturbance			
8	D.roads + linear features	Linear features may both increase accessibility and mobility, while providing forage in dense forested habitats or potentially increasing risk from predators (8). Disturbance generally linked with widespread disruption of habitat use in herbivores, with many species avoiding high human-use areas and lower-quality, disturbed habitat. Conversely, horses may select disturbed areas where few alternative options for forage exist.	(Dickie et al., 2020; Kaufmann et al., 2013; Latham et al., 2011) (Doherty et al., 2021; Irving, 2001; Leblond et al., 2013)
9	Linear features + D.roads + cutblocks		
Null	Intercept only	No covariates modelled	-

Results

Location and covariate data

Location data from 5 female horses was used to evaluate step-selection functions across movement-based biological seasons from 2018 – 2020, with a total of 23,821 locations collected. One horse travelled outside the southern boundary of the EMZ, crossing the Red Deer river in winter in multiple years (see Chapter 3). All other animals remained within the administrative boundaries of the EMZ. Proportional areal coverage of landscape covariates throughout the Sundre EMZ was as follows: conifer forest (~60%) > mixed-wood forest (~10%) > rangeland (grasslands and shrublands; 7%) > cutblocks (7%) > linear features (1%; note: areal coverage). A global model including all variables predicted to influence habitat selection in feral horses received the total weight (AIC *wt* = 1) compared to univariate selection models for each of the above vegetation covariates, and distance to water or roads, terrain ruggedness, or solar radiation.

Resource selection

Habitat selection of feral horses showed clear seasonal differences. Summer selection for areas further from native rangeland was strongest and consistently so across all individuals (β = 0.43, CIs = 0.07 – 0.99; Figure 5.2). Selection for areas of low solar radiation in summer relative to winter was also apparent (β = -0.20, CIs = -0.35 – 0.02), while areas closer to cutblocks appeared to be selected relative to winter (β= -0.31, CIs = -0.85 – 0.15), however, confidence intervals for these latter two covariates overlapped 0. Selection patterns in winter appeared to be stronger and non-overlapping with zero for several covariates compared with summer selection patterns. Areas closer to roads (β= -0.22, CIs = -0.46 – -0.12) and with lower terrain ruggedness values (β= -0.22, CIs = -0.41 – -0.09) were selected, while areas with greater solar radiation were selected strongly across all individuals (β= 0.52, CIs = 0.39 – 0.72). Areas further from cutblocks and conifer forest were selected more in winter relative to summer, while areas further from native rangeland, linear features, and water were avoided, though confidence intervals overlapped zero in these latter cases (Figure 5.2). Selection for all other covariates appeared weak, neutral, or were variable among individuals (Table 5.3), with greater general consistency in selection patterns in winter relative to summer.

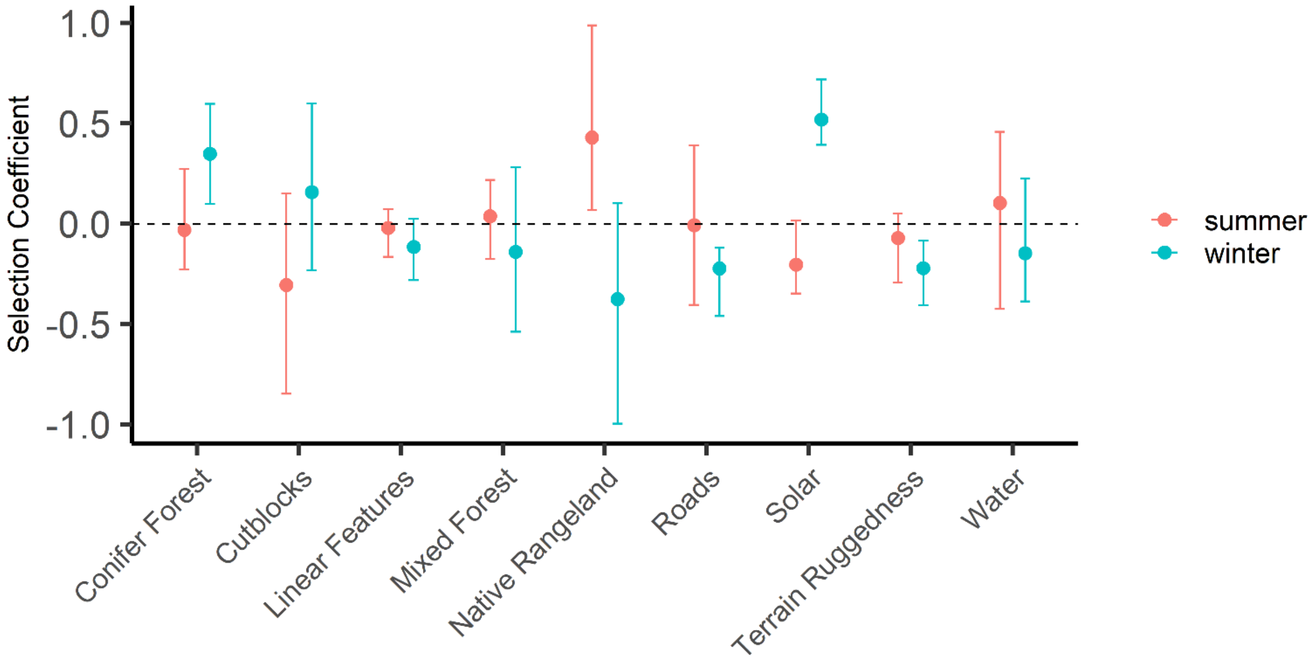

Figure 5.2. Relative strength of selection coefficients and 95% confidence intervals for landscape covariates for summer and winter in the Sundre EMZ, AB, Canada (data from 2018-2020).

Spatially explicit predictions of habitat suitability showed a more widespread distribution of suitable habitats in the eastern extent of the Sundre EMZ in summer compared to winter (Figure 5.3). Winter selection was more limited, with medium use areas in the eastern extent of the study area reflected in the general distribution of remaining rangeland and areas of highest solar radiation highlighted towards the mountains in the west, compared to the wider distribution of cutblocks throughout the EMZ in the east (see Figure 5.1). Both summer and winter predictions of suitable habitat were relatively high for areas of flat, native rangeland (note the high predicted use of the expansive Ya Ha Tinda ranch grasslands in the south-west), while the western regions characterized by higher elevation and more rugged terrain, and greater forest coverage (i.e., approaching the Rocky Mountains), indicated low habitat suitability (note the greater relative suitability within this more mountainous habitat of the grassland areas known as Harrison flats in the north-west of the Sundre EMZ [Figure 5.3]).

Table 5.3. Individual selection coefficients for each female horse in the Sundre EMZ.

Collar ID	**44420**	**44417**	**35686**	**35687**	**35734**
Summer					
Roads[1]	-0.4210	-0.2550	0.1439	0.0786	0.4183
Cutblocks	-0.0040	0.1694	-0.8871	-0.3253	-0.4807
Native rangeland	**0.3560**[2]	**0.3743**	**1.0566**	**0.3229**	**0.0420**
Conifer forest	0.2940	-0.1625	-0.1332	0.0866	-0.2334
Mixed-wood	0.2316	-0.0529	-0.1879	0.1031	0.0910
GSR	-0.0849	-0.3205	-0.3498	0.0282	-0.2937
TRI	-0.3187	-0.0140	0.0585	-0.0348	-0.0427
Linear features	-0.1754	-0.0712	0.0765	0.0218	0.0434
Distance to water	0.2213	-0.0385	0.3316	-0.4665	0.4725
Winter					
Roads[1]	**-0.1632**	**-0.1147**	**-0.1777**	**-0.1680**	**-0.4901**
Cutblocks	0.0376	-0.2622	0.3445	0.6280	0.0396
Native rangeland	-0.4099	0.1417	-1.0604	-0.2895	-0.2560
Conifer forest	**0.1131**	**0.4958**	**0.4285**	**0.0971**	**0.6082**
Mixed-wood	-0.2861	-0.5657	0.3149	-0.1311	-0.0308
GSR	**0.4851**	**0.7410**	**0.5246**	**0.3858**	**0.4586**
TRI	**-0.0777**	**-0.4188**	**-0.1472**	**-0.1655**	**-0.2948**
Linear features	-0.2935	-0.0196	-0.1358	-0.1586	0.0298
Distance to water	-0.2057	-0.4037	-0.2269	0.2702	-0.1650

[1] Individual selection beta coefficients shown for relative seasonal selection.

[2] Bolded values show consistent selection or avoidance across individuals.

Occupancy

There was no evidence of lack-of-fit for global occupancy models as assessed by the MB goodness-of-fit test. Estimates of $\hat{c}$ were close to one for each species and lack-of-fit tests were non-significant (horses = 1.02, X^2 = 4193.7, P= 0.30; cattle = 1.07, X^2 = 4375.2, P = 0.15; elk = 1.03, X^2 = 4201.2, P = 0.23 [MacKenzie & Bailey, 2004]). Naïve occupancy probability (i.e., occupancy assuming detection probability = 1; [MacKenzie et al., 2002]) across all sites during summer was 0.80 (0.65 – 0.89), 0.46 (0.36 – 0.60), and 0.19 (0.088 – 0.36), for horses, cattle, and elk respectively. Detection probability (assuming occupancy at a site = 1) was 0.44 (0.39 – 0.48), 0.43 (0.38 – 0.49) 0.14 (0.073 – 0.25), again for horses, cattle and elk, respectively. Proportion of rangeland only models were the top-ranked occupancy models for both horses and elk, whereas disturbance was the top ranked model for cattle (Table 5.4). ΔAIC values for all species showed multiple models explained occupancy reasonably (cattle $n = 2$; elk n = 3; horses

$n = 5$) and evidence ratios between top and second-ranked models were relatively low. For horses in particular, several models had ΔAIC < 2.

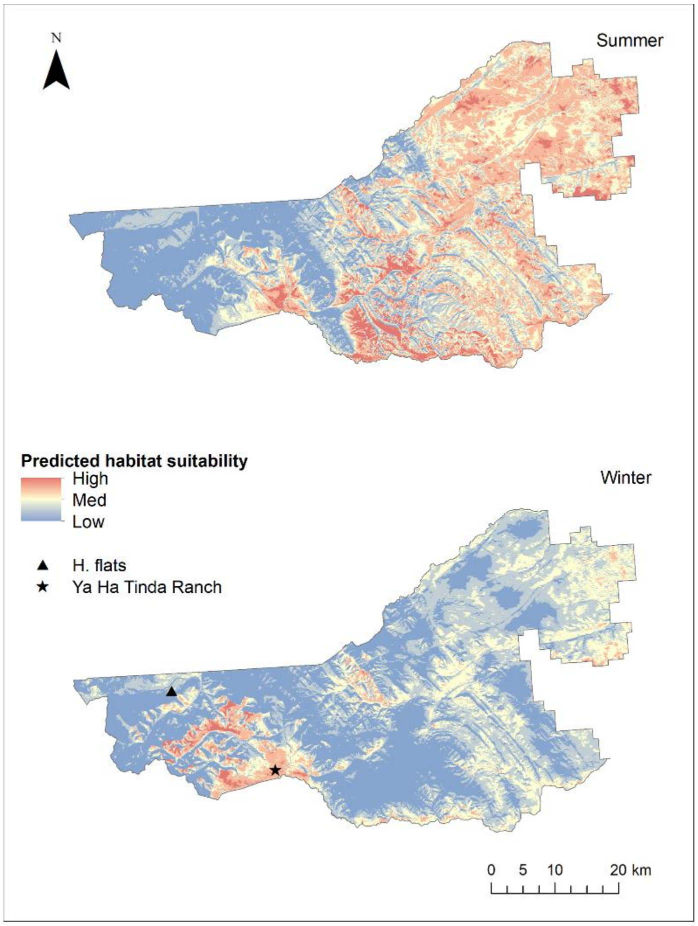

Figure 5.3. Spatially explicit habitat suitability for feral horses derived from step-selection functions from five collared mares in the Sundre EMZ, AB, Canada. H. flats refers to Harrison flats grasslands near 40-mile cabin in the northwest. The Parks Canada Ya Ha Tinda ranch and associate pastures shown in the south.

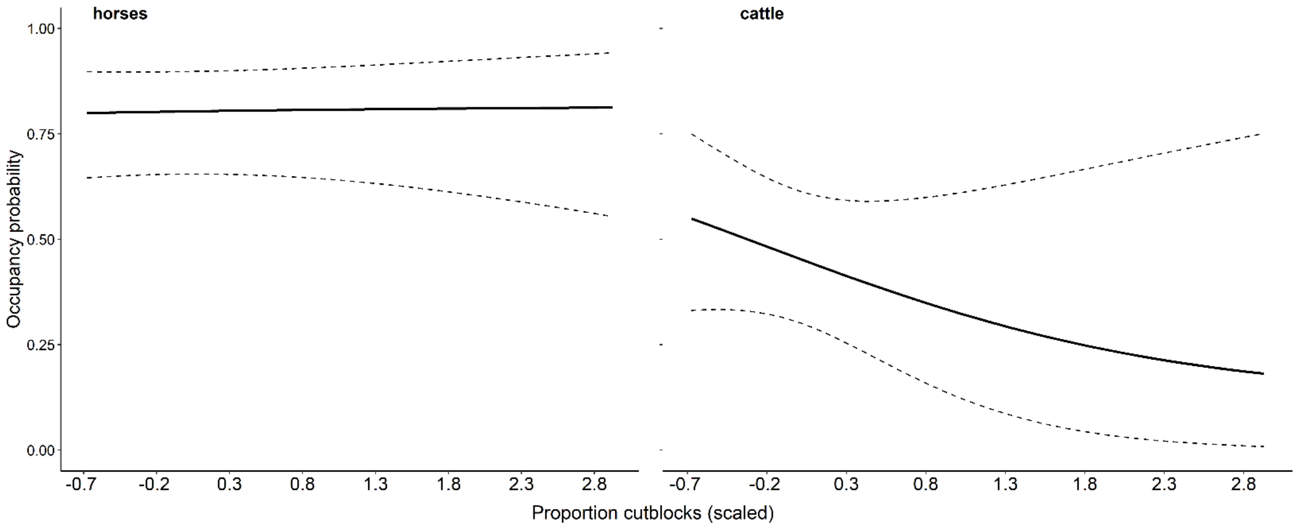

Figure 5.4. Model averaged occupancy probability as a function of the proportion of cutblocks for horses and cattle in the Sundre EMZ, AB, Canada. Model selection based on top-ranked (ΔAIC < 2). Dashed lines are 95% confidence intervals, and predictions are calculated with all other model covariates held constant.

Model averaged occupancy coefficients showed proportion of rangeland had a positive effect on occupancy for all species though this was weak for cattle compared to elk and horses (Table 5.5; Figure 5.4). Predicted occupancy decreased with increasing terrain ruggedness (-0.858) and distance from roads (-0.484) for cattle, and the proportion of cut blocks has a similarly negative effect (-0.768). Proportion of cutblocks had an opposite, positive effect for horses (Figure 5.4), and was the largest effect across all covariates for horses (0.471). Occupancy was higher with greater areal coverage of linear features for cattle (0.726), though this had the opposite effect for horses (-0.324), while elk occupancy was lower at sites further from conifer forest patches (-0.858; Table 5.5). Distance to water and terrain ruggedness had a positive effect on horse predicted occupancy, suggesting these are not limiting factors, while global solar radiation and distance to roads had minor effects. Interestingly, distance to any forest, which includes mixed-wood forests, had a negative effect on horse occupancy (-0.330), while distance to conifer forest had a weak positive effect (0.022).

Table 5.4. Relative support for models estimating occupancy of horses, cattle and elk in the Sundre EMZ.

		ΔAIC (AICwt)[a]		
Model[b]	**K[c]**	**Horses**	**Elk**	**Cattle**
Key resources				
rangeland	5	***0.00 (0.24)***	***0.00 (0.34)***	4.439 (0.04)
rangeland and water	6	1.244 (0.13)	*1.822 (0.14)*	5.986 (0.02)
Topography				
rangeland and terrain	6	***1.092 (0.14)***	*1.990 (0.12)*	4.501 (0.04)
rangeland +TRI + water	7	2.002 (0.09)	3.815 (0.05)	6.264 (0.02)
Habitat structure				
Thermal	9	3.978 (0.03)	6.845 (0.01)	9.153 (0.00)
open habitat	7	*1.906 (0.09)*	3.284 (0.06)	***1.291 (0.21)***
rangeland + conifer	6	*1.995 (0.09)*	***1.240 (0.18)***	3.532 (0.07)
Disturbance				
linear features	6	*1.485 (0.11)*	3.603 (0.06)	2.030 (0.14)
Disturbance	7	2.903 (0.06)	4.660 (0.03)	***0.00 (0.39)***
NULL	2	5.692 (0.01)	7.329 (0.00)	3.431 (0.07)
ER[d]	-	1.73	1.86	1.45

[a]All models where ΔAIC < 2 italicized, first and second ranked models bolded, with top models underlined. AIC weight of each model shown in parentheses.

[b] Full model weights and log-likelihood estimates provided in appendix C.

[c] Number of model parameters

[d] Evidence ratio calculating the relative weight between top and second ranked models for each species

Table 5.5. Model averaged coefficients of species occupancy from top ranked (ΔAIC < 2) models.

Covariate[a]	**horses**	**cattle**	**elk**
Rangeland	0.420 (0.56)	0.012 (0.44)	0.699 (0.57)
TRI[b]	0.448 (0.44)	-0.858 (0.44)	0.022 (0.57)
D.water	0.351 (0.44)	-	-0.194 (0.47)
D.roads	0.022 (0.45)	-0.484 (0.41)	-
Linear features	-0.324 (0.33)	0.726 (0.37)	-
D. conifer	0.022 (0.31)	-	-0.858 (1.3)
Cutblocks	0.471 (0.47)	-0.768 (0.42)	-
GSR[c]	0.076 (0.43)	-	-
D. any forest	-0.330 (0.31)	-	-

[a] Individual covariates included in models

[b] Terrain ruggedness index

[c] Global solar radiation

Discussion

Feral horse resource selection in the Sundre EMZ was generally consistent with other studies in similar ecosystems, showing strong seasonal effects and selection for habitats based on both biotic and abiotic factors. However, the strongest patterns of summer habitat selection indicated that horses selected areas further from native rangeland, which contrasted with expectations that horses would select the most productive habitats. Forage biomass production is greatest in native grasslands (Girard et al., 2013b; Hebblewhite, 2006a), and feral horse habitat selection is often linked to areas of greatest forage abundance (Schoenecker et al., 2016). Girard (2012) for example, found grassland and rangeland habitats were selected over more available habitat types such as conifer and mixed-wood forests. Salter's 1978 study on the Sundre population also found that grasslands were selected throughout the year, but noted key differences when cattle were present, and small contemporaneous overlap in habitat use between the two species (2%), despite strong dietary overlap (64%). Forage biomass production in cutblocks is also high relative to other habitats such as conifer or mixed-wood forest habitats (Figure 5.5; Girard et al., 2013b; Kaufmann, 2011; Kaufmann et al., 2013). In this study, though variance among individuals was high, horses appeared to select cutblocks more in summer, relative to native rangeland (Figure 5.2). Summer occupancy of horses was similar in both cutblocks and native rangeland (Table 5.5), and when compared to the strong negative effect cutblocks had on cattle occupancy in this study (Figure 5.4), greater relative selection by horses for cutblocks over rangeland in summer may reflect avoidance of competition with cattle. Utilization of cutblocks by cattle has previously been identified as low in Montane ecosystems (Kaufmann et al., 2013), and the generalist foraging strategy of equids and their greater relative mobility (Janis, 1976; Menard et al., 2002; van Beest et al., 2014a) may facilitate the use of low-quality cutblocks when spatial overlap with cattle is high, despite a preference for native rangeland (Girard et al., 2013a; Salter, 1978). This observation is also supported by greater use of rangelands in winter when cattle are absent (Figure 5.1), a pattern reflected in spatial predictions of habitat suitability (Figure 5.3), and also by Salter (1978) who found dry grasslands to be important winter habitat.

Suitable habitat in winter is more limited, and horses also appeared to select habitats that potentially ameliorate harsh winter conditions (Berger, 1986, Girard et al 2013b). For example, areas with greater solar radiation and those further from forests were selected, lending support to hypotheses that mechanisms of thermoregulation via sun exposure may drive feral horse winter habitat selection (Girard et al., 2013b). As noted by Girard et al. (2013b) however, sites with greater solar radiation may also have greater herbage growth (Willoughby et al., 1998), or reduced snow cover, increasing overall access to limited winter forage (Salter, 1978). Sites closer to roads and with less rugged terrain were also important in winter, potentially due to reduced access to habitat and general mobility when snow cover is at its peak (Whittington et al, 2005). Animals often avoid roads to reduce the risk of encounters with humans, particularly when human activity is high (Leblond et al., 2013) which, in the Sundre EMZ, peaks in summer, and indeed, selection and occupancy were neutral or weakly influenced by distance to roads in summer. In winter when human activity is low, roads may provide important movement corridors, especially in complex or difficult terrain (Underhill & Angold, 1999; Whittington et al., 2005) and may increase horse mobility between habitat patches when alternative movement corridors are limited. Roadsides can also provide important sources of forage for species, particularly grazers (Fahrig & Rytwinski, 2009), and in ecosystems where grassland availability is low, feral horses may utilize disturbance features where grass production is relatively high (Irving, 2001). Salter (1978) found similar results, where horses use of roadside forage was high in winter, as snow depth and litter cover was relatively low compared to other habitats. Thus, roads may be important habitat in winter for horses, providing both forage and access to habitat when conditions are severe.

Habitat structure – mediated by seasonality – is also an important determinant of habitat use in large mammal communities (Garrott et al., 2008; Kuijper et al., 2015; Sutherland et al., 2015), particularly in areas where predators create variable risk across landscapes (DeMars & Boutin, 2018), or human use is high (Treves et al., 2006). While horses selected areas closer to roads in winter, summer occupancy was lower where areal coverage of linear features was high (Table 4.5) and may reflect avoidance of potential encounters with humans when activity is high (Girard et al. 2013a). Large predators are also attracted to linear features (DeMars & Boutin, 2018; Whittington et al., 2005), and while predation on horses in this system is poorly quantified, cougars (*Felis concolor*) and wolves (*Canis lupus*) attack and kill horses (Knopff, 2010; Webb, 2009), and grizzly bears (*Ursus arctos*) are a potential third predator that may lead to horses avoiding linear features (Dickie et al., 2020). As seen in Girard et al. (2013b), feral horses also selected areas further from conifer forest in winter, potentially reducing the ambush risk from cougars, which predominantly kill horses in winter in this ecosystem (Knopff, 2010). These results together suggest horses may structure habitat use in part around predation risk. Cattle summer occupancy by contrast, increased in areas both closer to roads and with greater coverage of linear features (Table 4.5). While cattle tend to exhibit reduced anti-predator behavior compared to wild ungulates (Clutton-Brock, 1981; Kluever et al., 2008), they are also less mobile than horses (Ganskopp & Vavra, 1987; Kaufmann et al., 2013), and may simply be restricted to areas where accessibility is high, including linear features and relatively flat terrain (Table 4.5).

Interestingly, elk occupancy in rangeland in summer was greater as with horses and cattle, though distance to conifer forest (negative) had the largest effect on elk occupancy (Table 4.5). Elk may avoid risky predator habitat near forests (Hebblewhite et al., 2005; Laundre et al., 2001), preferring to graze in open spaces, however, may also utilize forest edges and forest cover to reduce predation risk from pursuit predators such as wolves (Mysterud & Ostbye, 1999; Hernandez & Laundre, 2005). Conifer and deciduous browse are also important for elk, including in the system (Salter, 1978), and occupancy of rangelands close to forests may provide optimal habitat balancing foraging and predator avoidance needs.

Figure 5.5. View of horses in the Williams Creek area at the east of the Sundre EMZ, AB, Canada showing typical cutblock and forest patch habitat. Rocky Mountains towards Banff National Park visible in background.

Previous studies in the Foothills ecosystem have found water not to be limiting for horses despite strong water-dependency (Schoenecker et al., 2016), and results here further support this. Distance to water appeared to have little impact on feral horse selection either in winter or summer, and little impact on horse occupancy (Tables 5.4; 5.5). Similarly, while flatter areas were preferred in winter, potentially due to accessibility (see above), terrain did not appear to be limiting in summer (Table 5.5; Figure 5.2) and may further reflect avoidance of spatial overlap with cattle, which are more limited to lowland areas (Table 5.5; [Kaufman et al., 2013]). Consistent among species was the positive effect of proportion of rangeland on occupancy (Figure 5.4; Table 5.5). This was relatively weak for cattle compared to horses and elk, though it is well-established that cattle use of rangelands can be intensive, particularly in lowland areas (Kaufmann et al., 2013). This shared use has important implications for management particularly given the rapidly diminishing native grassland habitats across the province (Zapisocki et al., 2022).

Overgrazing of native rangeland and competition between elk and horses (Hebblewhite, 2006a; McInenly, 2004), and cattle and horses (Girard et al., 2013; Salter & Hudson, 1980), are contentious issues in the Sundre EMZ. Long-term grazing pressure can have negative impacts on

Montane grasslands (Lyseng et al., 2018), and the impacts of overgrazing on rangeland health where horses and cattle overlap are common in many ecosystems (Baur et al., 2017; Beever & Brussard, 2000; Beever & Herrick, 2006). Elk in this system are also increasingly resident as opposed to migratory (Hebblewhite et al., 2006b), and dietary overlap with horses and cattle (Salter, 1978) may increase pressure on grassland ecosystems within the wider EMZ as resident elk seek forage east of their historic summer range in Banff National Park (Hebblewhite, 2006a). These impacts could be spatially variable with factors such as terrain leading to partitioned use of rangelands among species (Ganskopp & Vavra, 1987), while the preferential use of cutblocks by horses in summer suggests potential mechanisms for avoiding competition when grazing pressure is high (van Beest et al., 2014a). Cutblocks are ubiquitous and increasing in the foothills and despite recent declines in the feral horse population (see Chapter 4), dynamics of horse populations and grazers in general are closely tied to bottom-up processes (Grange & Duncan, 2006; McShea, 2005; Proffitt et al., 2014). This could have important consequences for long-term population dynamics, where density-dependent processes observed in other, smaller populations, particularly in closed ecosystems (Grange et al., 2009; Regan et al., 2020), are unlikely to impact feral horses where relative forage biomass increases through clear cut logging. These results suggest that human-caused ecosystem disturbance and landscape-level change are important drivers of feral horse selection and occupancy and hence, feral horse management may warrant attention to industrial land uses such as forestry. This is likely to have different impacts for ruminant herbivores that are less efficient at processing bulk roughage (Slade et al., 1970), though further study is needed, to accurately assess population level responses to relative resource availability for feral horses in the Foothills.

Finally, it is important to note that habitat selection (and occupancy) were examined at the landscape-scale in this study and selection at finer scales (e.g., third- or fourth-order [Johnson, 1980]) may reveal different patterns of resource use, or different degrees of variation among individuals than those identified here. Large herbivore selection can be scale-dependent in some ecosystems (Mayor et al., 2009; DeCesare et al., 2012), while in others, both coarse- and fine-grained selection have been shown relatively similar, including in horses (van Beest et al., 2014a). Data resolution at the individual level within this study precludes robust investigation of third-order or finer scales of selection, and as occupancy analyses were constrained at the level of second-order habitat selection, analysis of, and comparisons to, landscape-level selection were appropriate. However, further research is warranted regarding changing selection and occupancy patterns in relation to both horses and competing species density (i.e., density-dependent resource selection [van Beest et al., 2014b]), to the influence of abiotic factors such as linear features at finer scales (Decesare et al., 2012), and to the selection of resources at the patch-scale of varying quality and biomass (Wilmshurst et al., 1995; Hebblewhite et al., 2008; van Beest et al., 2010).

Conclusion

Despite increasing interest there remains a paucity of data regarding feral horse habitat use compared to other species and interspecific interactions are not well understood (Boyce et al., 2021). Several factors also appeared to be important in driving feral horse resource selection in the Sundre EMZ (i.e., disturbance type, forage availability/quality, habitat structure, seasonality, and the presence of cattle), and multiple models appeared to describe feral horse occupancy adequately. Variance in these results could be a function of sample size, and clearly, variation within selection data is exacerbated by the small number of animals surveyed. However, variation in selection and occupancy data may also reflect selection of a generalist large herbivore (van Beest et al., 2014) in a highly fragmented, and heavily modified ecosystem. Accurately characterizing such landscapes is also challenging (Thompson & Gergel, 2008), as heterogeneity is high at both home range and landscape scales (Crooks, 2002), complicating assessments of selection for representative covariates. Ongoing disturbance and habitat loss in the province (Schneider, 2002), coupled with a more dynamic climate (Schneider et al., 2009) and recovering predator populations (Boyce & McLoughlin, 2021; Stenhouse et al., 2020) stand to add further complexity within the wider Foothills ecosystem. The complicated nature of feral horse management (Boyce et al., 2021; Scasta et al., 2018) reiterates the need for continued study and greater understanding of feral horse ecology in this system.

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Chapter 6 Conclusion

The research that I report and discuss in this thesis responded to a critical gap in information, knowledge, and understanding about feral horse ecology in the Alberta Rocky Mountain Foothills, and is comprised of population characteristics, abundance and density estimates, and habitat use and occupancy assessments.

Caballine horses evolved as a non-ruminant grazer on the North American plains and were an abundant component of a diverse Pleistocene megafauna. As cecal digesters, horses could capitalize on bulk, low-quality forage, making them a highly adaptable generalist that could succeed in many environments relative to ruminant grazers. Horses expanded into Eurasia and were subsequently domesticated around 5500 years ago, with wild populations becoming extinct on the North America continent approximately 6,000 – 13,000 years ago. As domesticated animals, horses accompanied humans throughout their expansion across the globe and were introduced back to the North American continent following European exploration and colonization. Feral horse populations now inhabit a remarkable range of ecosystems globally and within North America. However, our close relationship with horses and the domesticated history of extant caballines makes both management and research of the species complicated relative to native wildlife. In many cases, little is known about fundamental demographic characteristics of horse populations and basic ecological understanding remains poor.

Feral horses have been present in the foothills of the Rocky Mountains in Alberta, Canada, since the 1750s, including the largest population of feral horses in Canada, west of Sundre, AB. However, prior to the research reported here, only one ecological study had been undertaken to date on the Sundre population, and combined with one other study undertaken in Bragg Creek, AB, in 2012 represented the totality of feral horse ecological research in the province. Salter's 1978 work described much about a population of horses in an area covering 200 km^2 within the wider contemporary Sundre equine management zone (EMZ) which covers more than 2200 km^2. With a lack of contemporary information and considering the increasing challenges to population management, the dearth of ecological information regarding the population has become critical given management conflicts in recent years. My research aimed to improve our ecological understanding of the Sundre population, including several key demographic and population characteristics, to estimate total abundance and density, and to assess habitat use and occupancy.

Key findings

1) Feral horse band sizes and sex-ratios were similar to those of other North American populations, and similar to that described in Salter's work. Mean band size was 4.92 and adult sex-ratios (male:female) across individually identified bands was 0.86.
2) The number of foals detected, and the mean number of foals within each band peaked from June to August and composed less than 15% of the total individuals detected each year.
3) Home range size ranged from 47 to 93 km^2 and was larger than that described by Salter, but similar to those found by Girard in Bragg, Creek, AB. Home range sizes showed no relationship with band sizes and home ranges overlapped considerably between adjacent bands. Two seasons were apparent based on k-means cluster analysis, with daily movement rates higher in summer (May 15th to October 31st) relative to winter.
4) Non-independent movement by virtue of social grouping was evident when identifying individuals and developing detection histories. Known presence despite non-detection and high social fidelity among horses is problematic for individual-based capture-recapture analyses and suggests further development of group-based capture-recapture methods will be important for highly social species such as horses.
5) Total abundance within the Sundre EMZ declined over the period of study by ~14% from 2017/2018 to 2019, supporting declining trends observed in aerial minimum counts. Abundance estimates at 2019 were 959 (876 – 1041; 95% confidence interval) with density estimated to be 0.522 (0.476 – 0.569) across the Sundre EMZ.
6) Declines in abundance were not associated with relative increases via emigration to adjacent management zones or mass mortality. Potential causes for the decline include increasing density-dependence and increasing influence of predation as relative abundance of horses increases compared with other primary prey species.
7) Detection rate (detections per 100 trap days) was highest in the eastern region, and particularly the south-eastern region of the Sundre EMZ, similar to distributions observed in aerial counts, suggesting density is highest in these areas. Areas associated with greatest detection rate (top decile) overlapped with Salter's original study area and suggest the Williams' Lake area generally has consistently contained high densities of horses.

8) Horses selected areas closer to roads, with lower terrain ruggedness, and those with higher solar radiation further from forest in winter relative to summer, suggesting accessibility and thermal regulation may be important in winter.
9) Horses selected areas further from native rangeland in summer, selected areas closer to forestry cutblocks, and summer occupancy was highest in locations with greater areal coverage of forestry cutblocks. Distance to water did not appear to influence selection strongly in either season, though horses spent the longest time (contiguous detections) at mineral licks as seen in Salter's work, ingesting quantities of soil and interacting with multiple other ungulate species.
10) Habitat selection and occupancy analyses suggest horses are using cutblocks in summer and avoiding rangeland where competition with cattle may be high, and horses may be capitalizing on the additional low-quality forage available in cutblocks. Other anthropogenic disturbances (e.g., linear features, roads etc.) were avoided by horses in summer when human activity is high.

Management Implications

There are few locations where management of feral horses is not controversial. Traditional approaches to managing feral horses are often based in ambiguous policy that delegates management to government departments which lack the clear mandates and resources required for the appropriate study of population and behavioral ecology. However, socio-political conflict arising from differing ideologies about the legitimacy of feral horses in nature, the impacts horses have on ecosystems and native and commercially important species, and how feral horse populations are managed can be intense and at times prohibitive to management action. Accurate information regarding feral horse populations will be increasingly critical to management as viewpoints become more partisan and human pressures on landscapes and wildlife habitat increase, dictating a greater need for research investment into feral horse ecology generally, regardless of arguments relating to the inherent nativeness of horses.

The horse population in the Sundre EMZ appears to have declined in recent years, in contrast to many other free-ranging populations globally and in North America. Reasons for this decline are likely many, and difficult to parse based on the limited available information. However, factors such as density-dependence resource limitation or increased predation levels associated with greater relative abundance of horses in previous years could be important and warrant further investigation. In the latter case in particular, little is known the role of predators and feral horses, yet, increasing evidence suggests horses are important prey where native prey are in decline. Anecdotal evidence observed in this study may highlight increasing grizzly bear predation in this system, in addition to known cougar and wolf predation. This has important implications for management of the horse population, and for management of other prey species in this system. Predator populations supported by horses for example, could result in greater relative predation on native species, while conversely, further management of feral horses reducing abundance could similarly impact native prey species as horse relative abundance declines and predators populations initially remain high. Such community-level factors require further study to accurately assess and could be critical in future management aimed at both decreasing feral horse populations while protecting native species. Ultimately, this study highlights that the high intrinsic growth rates often described as a typical invasive quality in unmanaged feral horse populations may instead be qualities of environments where natural limitations are absent, rather than being inherent to all feral horse populations.

Management of the feral horse population may also be influenced by industrial modification of the landscape, particularly where modification leads to greater relative abundance of available forage. A key point in this research was the apparent use of cutblocks in summer by horses, which may reflect avoidance of competition with cattle when present (which appear to strongly avoid cutblocks), or avoidance of areas heavily used by all grazers, including horses (i.e., intraspecific competition). The influence of landscape disturbance on feral horse populations has important implications for ongoing industrial modification of the landscape, where increasing cutblock areal coverage may facilitate both the spatial and population expansion of feral horses. Such competing land uses may be difficult to resolve in heavily modified ecosystems such as the Sundre EMZ, yet, these results could aid forecasting occupancy and habitat use of horses in the face of ongoing modification.

Appendix A Ecological interactions involving feral horses and predators: review with implications for biodiversity conservation.

Citation: Boyce, P. N., & McLoughlin, P. D. (2021). Ecological interactions involving feral horses and predators: review with implications for biodiversity conservation. *The Journal of Wildlife Management*, *85*(6), 1091–1103.

Abstract

For many ecosystems, feral horses are increasingly becoming an important if not dominant component of ungulate biomass and hence influence on community dynamics. Yet, we still know little of how horses contribute to key ecological interactions including predator-prey and indirect competitive relationships at a community level. Notably, feral species like horses can exhibit life-history traits that differ from that of native (mainly artiodactyl) herbivore competitors. Artificial selection for traits like increased, early, or extended reproduction that have yet to be reversed by natural selection, coupled with naturally selected differences in anatomy and behavior, in addition to unique management objectives for horses compared to other species, means that the dynamics of feral horse populations are not likely to align with what might be expected of other large herbivores. For example, evidence is emerging that reproduction in female feral horses can remain constant despite declining adult survival, skewing sex ratios that extend cycles of population growth but exacerbate declines; while differences in foraging behaviour and digestive ability means horses may not only replace ungulate biomass in ecosystems but add to it, with predictable consequences to predators like wolves which show strong relationships to kg/km^2 of ungulate biomass. Unexpected population dynamics and inherent biological asymmetries between native ungulates and feral horses may therefore impact the former not only via direct competition for shared resources, but also through enemy-mediated interactions like apparent competition. In several localities feral horses now co-exist with multiple native prey species, some of which are in decline or are species at risk. Compounding risks to native species from direct or indirect competitive exclusion by horses is the unique nature and socio-political context of feral horse management, which tends towards allowing horse populations to be limited largely by natural density-dependent factors. We summarize the inherent asymmetries between feral horse biology and that of other ungulate prey species with consequences for conservation, focusing on predator-prey and emerging indirect interactions in multi-prey systems; and highlight future directions to address key knowledge gaps in our understanding of how feral horses may now be contributing to the (re)structuring of food webs. Key findings support previous observations of patterns of rapid growth and decline, and associated skews in sex ratios of feral horse populations and illustrate a prevalence of feral horses as preferred prey particularly where native prey are declining. Predator-prey interactions in feral horse populations will be increasingly important to wildlife conservation objectives and will require understanding the role of the horses in ecosystems beyond population management.

KEY WORDS apparent competition, artificial selection, community ecology, conservation, feral horse (*Equus ferus caballus*), life history, predator-prey dynamics

Introduction

Understanding the strength and direction of species interactions is critical to biodiversity conservation (McDonald-Madden et al. 2016). We now have greater appreciation for the importance of apex predators (Hebblewhite et al. 2005, Ripple et al. 2012), trophic cascades (Hairston et al. 1960, Estes and Duggins 1995), trophic downgrading (Estes et al. 2013), and the role of both direct and indirect species interactions in governing animal behaviour (Fortin et al. 2005) and population dynamics (Wittmer et al. 2005, Burgar et al. 2019). Our understanding of how introduced, non-native species might destabilize community structure, however, is still limited (e.g., Ruscoe et al. 2011). We particularly lag in understanding how feral species now fit within the context of predator-prey interactions and food-web ecology. This is important because unlike native equivalents, in some environments feral species are likely to have superior competitive abilities due to artificially selected traits that have yet to be reversed by natural selection. Feral horses are one such species of concern.

Feral horses have expanded in range and population size throughout the world (Fig. 1) and are increasingly becoming important components of ungulate biomass in ecological systems (Andreasen 2014, Nuñez et al. 2016). Artificial selection during domestication for traits such as reproductive output (Clutton-Brock 1981) is believed to have influenced population growth rates in feral horses (Grange et al. 2009), which can grow at a natural (intrinsic) rate of increase that is unexpectedly high. For example, Eberhardt et al. (1982), modelling the dynamics of feral horses in Oregon, showed how the combination of high adult survival and shifts in age at first reproduction from 4 to 3 years of age is possible to produce observed growth rates of 20% per year—even when foal survival is 60% of adults.

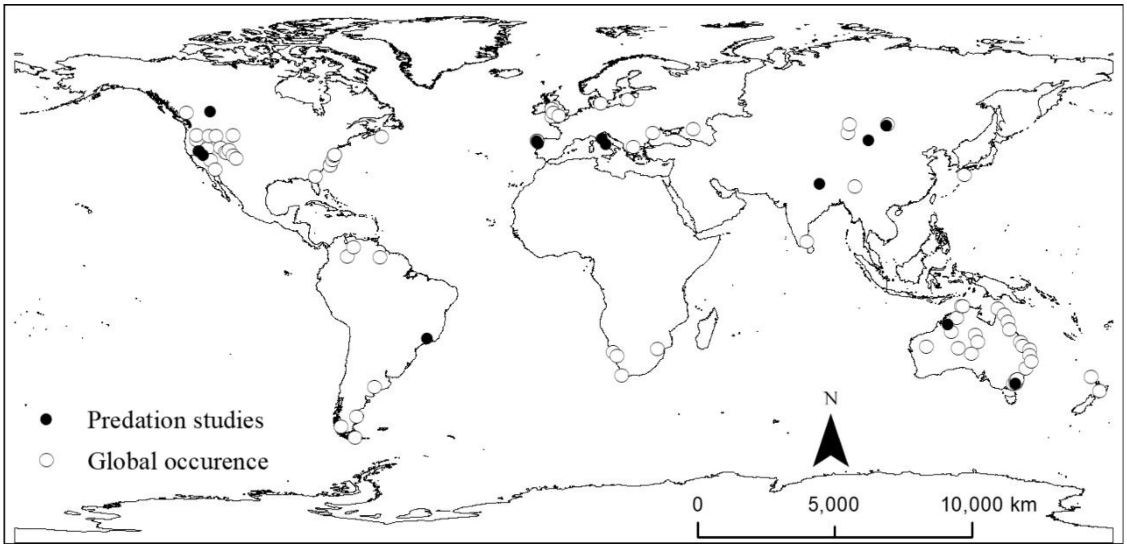

Figure A.1. Global distribution of the occurrence of feral horse populations with locations of studies assessing predation on feral horses. Occurrence data are from the thinned dataset (*n* = 76) as published in Naundrup and Svenning (2015). Continent data from Esri (Esri, Redlands, CA, USA).

High reproductive capacity in combination with high adult survival can have important consequences for interactions between feral and native species. For example, reproduction in feral pigs (*Sus scrofa*) can override the impact of high predation levels, increasing predator abundance and subsequently impacting native species (Corbett 1995, Roemer et al. 2002). In feral horses, artificial selection for increased reproduction may also mean that females continue to invest in reproduction even at a cost to their own survival, resulting in marked population fluctuations as has been observed in feral sheep (Mysterud et al. 2002, Grange et al. 2009). Natural and artificial experiments have shown the impact that rapid changes in prey availability can have on rare, native prey species (Serrouya et al. 2015); and the altered biology and subsequent population dynamics of feral horses may mirror these occurrences seen in nature by rapidly adding then removing prey biomass as populations fluctuate. Such dynamics differ from most other wild, large prey populations which typically have stable adult survival over a range of environments and where females first trade-off reproduction to preserve their own survival as density increases (Gaillard et al. 2000, Gaillard and Yoccoz 2003), and thus contrast with established models describing life-history trade-offs during periods of limitation (e.g., Eberhardt's [1977] model).

Feral horses also possess behavioral and biological traits unrelated to domestication that differ from most native prey animals. For example, long-term, female-defense polygyny and a complex social structure (Linklater 2000); an ability to use relatively high volumes of low-quality forage in addition to high-quality foods (Janis 1976); and large relative body size (Knopff 2010) may not only enhance interspecific competitive ability, but also reduce the relative vulnerability of horses to predation. While much is known about the varied environments in which horses can exploit and thrive, and how horses can displace native herbivores in direct competitive interactions (e.g., Hall et al. 2018), much less is known of how horses might interact with competitors indirectly, e.g., by sharing predators through apparent competition (Holt 1977).

In multi-prey systems the presence/absence of a shared predator is well known to play an important role in shaping community structure (Payne 1966); however, the introduction of new prey can also be significant. Numerous examples highlight how asymmetries in prey vulnerability, resource use, and indirect interactions can alter effects of predation among species and destabilize community structure. For example, Roemer et al. (2002) showed how introduced feral pigs (*Sus scrofa*), by providing abundant food, enabled golden eagles (*Aquila chrysaetos*) to colonize the California Channel Islands, subsequently preying heavily on the Endangered island fox (*Urocyon littoralis*) and releasing populations of the competitively inferior island spotted skunk (*Spilogale gracilis amphiala*). Similarly, invading white-tailed deer (*Odocoileus virginianus*) in the boreal forests of western Canada appeared to almost double wolf (*Canis lupus*) densities, increasing predation risk to alternate prey like Threatened boreal caribou (*Rangifer tarandus caribou*; Latham et al. 2011). Under these scenarios, negatively affected species can be further impacted by shared predators if the more abundant prey population crashes or is suddenly eliminated, as predators can rapidly switch to preying on remaining prey to survive (e.g., effects of mountain lions [*Puma concolor*] on caribou after moose [*Alces alces*] populations were culled; Serrouya et al. 2015). Vital to conserving vulnerable prey species is an understanding of the mechanistic pathways in which introduced species might contribute to ecosystem shifts, for example by indirectly causing predation on native species by supporting predators (Holt and Lawton 1994, Roemer et al. 2002). Effective management of native prey species therefore also requires careful evaluation of the potential unintended consequences of controlling introduced species (Ruscoe et al. 2011).

While feral horses have expanded into multiple ecosystems where large predators and native prey exist (Ransom et al. 2016), predator-prey interactions involving feral horses are not well known despite their relative abundance as prey biomass and the regularity with which horses are reported as components of predator diets. Predator preferences to prey on horses, particularly where they are abundant (Vos 2000, Gray et al. 2008, Knopff 2010, Andreasen 2014, Palmeira et al. 2015), has clear implications for conservation of native prey because of apparent competition. Yet, unique biological characteristics coupled with management challenges of feral horses means much of our understanding of predator-prey dynamics and management methods derived from natural or native predator-prey dynamics may not translate to feral horse-predator-native prey systems.

In most areas where feral horse populations have established, contention over environmental impacts and competition for resources between native species and livestock is common, while public opposition limits many typical population management strategies (Linklater et al. 2002, Nimmo and Miller 2007, Kincaid 2015, Scasta et al. 2018). Fundamental interactions between native prey, predators, and horses and the latter's relevance to conservation may be overlooked in the effort to quantify expected ecological impacts and to develop management strategies (Sundararaj et al. 2012). At the same time, biological differences in horses and peculiarities of their population ecology continue to engender largely unknown impacts on the long-term viability of competing prey species. As horses expand in range, and with rewilding proposals to actively introduce horses into ecosystems alongside large predators and rare native species (Cromsigt et al. 2018), knowledge gaps stand to exacerbate management challenges.

Here we review important aspects of feral horse ecology and evolution as they apply to management and the conservation of native biodiversity, with emphasis on the often overlooked, indirect interaction of apparent competition We discuss the negative conservation outcomes that might emerge due to knowledge gaps regarding the now *de facto* place of horses within terrestrial food webs against the backdrop of management practices for horses relative to that of other wild ungulates. We conclude by proposing several key questions aimed at filling these current knowledge gaps, particularly around interactions between feral horses and predators, and the relevance of these interactions to wildlife management.

Methods

Our review was based on a comprehensive literature search of the ecology and management of feral horses using the academic search engine Google Scholar, further to ISI Web of Knowledge (© 2020 Clarivate Analytics), and the University of Saskatchewan library database for dissertations and theses. We included in our search numerous key words including those assigned to this article, as well as “feral”, “free-ranging”, “wild”, “semi-feral”, “equid”, “horse”, “predator”, “predation”, and “depredation.” To compile data on the prevalence of predation-prey interactions regarding feral horses (Table A1), we screened publications and unpublished reports for their inclusion of feral horses in predator-diet analysis or inclusion of kill rates. Studies which quantified predation rates, or dietary composition that included feral horses were then selected, excluding those that did not provide any quantification of predation. Those that explicitly measured and stated values with dietary analyses or predation rates (e.g., frequency of occurrence; livestock kill rates) were included, with studies that noted only anecdotal or unquantified predation on horses excluded. Studies where feral horses were not free-roaming in a predator-prey system for at least part of the year (e.g., within fences or enclosures year-round) were also excluded.

Artificial Selection and Population Dynamics of Feral Horses

While much of the evolution of the modern caballine horse (*Equus ferus* spp.) took place in North America, horses went extinct in the wild in North America during the late Pleistocene and more recently in Eurasia, excepting reintroductions of the Prezwalski sub-species (Haynes 2009, Barrón-Ortiz et al. 2017). Modern descendants of wild horses (*E. f. caballus*; first domesticated around 5500 B.C.E. [Outram et al. 2009]) appear relatively unchanged from their wild ancestors in both morphology and behavior (Clutton-Brock 1981, Linklater 2000, Barrón-Ortiz et al. 2017). Artificial selection for reproductive traits in horses, however, may have increased fecundity and resulted in life history trade-offs that depart from typical expectations of large herbivores. Grange et al. (2009) showed that prime-aged Camargue mares continued to invest in reproduction at a cost to their own survival under density-dependent food stress, which was unexpected for a large mammal. Stability in reproductive output at the expense of survival departs from Eberhardt's (1977) empirically supported model describing self-regulation in large mammal populations, and counters typical investment strategies of survival over reproduction in *K*-selected species (*sensu r*- and *K*-selection, Sinclair 2003).

Theory suggests that selection for high reproduction at the expense of survival should increase instability in feral populations (Barraquand et al. 2015), and this may be responsible for the steep decline and rapid growth observed in some feral horse populations (Grange et al. 2009). Similar population dynamics have recently been observed for feral horses on Sable Island, Nova Scotia, Canada. Over its >250-year existence, the Sable Island population has shown wide fluctuations since records have been kept, declining by approximately 50% in cases over brief (1–2 year) periods, followed by rapid growth before plateauing and subsequent population decline (Fig. 2). While the mechanisms causing these historic cycles had not been studied, new research shows that during the most recent population increase from approximately 130 individuals in 2003 to a peak at 579 individuals in 2019, while foal survival declined (Laforge et al. 2016), this was also accompanied by a strong shift from roughly equal sex ratios towards a strong male bias in the adult (4+ year old) population. For example, by 2017 there were 1.7 males for every female on the island, which coincided with decreased adult female survival and female reproduction (Regan et al. 2020). Male-biased adult sex ratios have obvious implications for most populations, though dynamics in feral horses may be exaggerated, with effects such as female harassment under female-defense polygyny further negatively impacting female survival (Linklater et al. 1999, Rubenstein and Nunez 2009). Such dynamics in predator-free Camargue and Sable Island horse populations have been explained as an unexpected life-history trade off arising from a hold-over of artificial selection (Grange et al. 2009) that has yet to be reversed by natural selection. Even if maladaptive over the long term, the consequences of release into the wild of artificially selected feral animals is not likely to be trivial to interacting competitors and predators on ecological time scales.

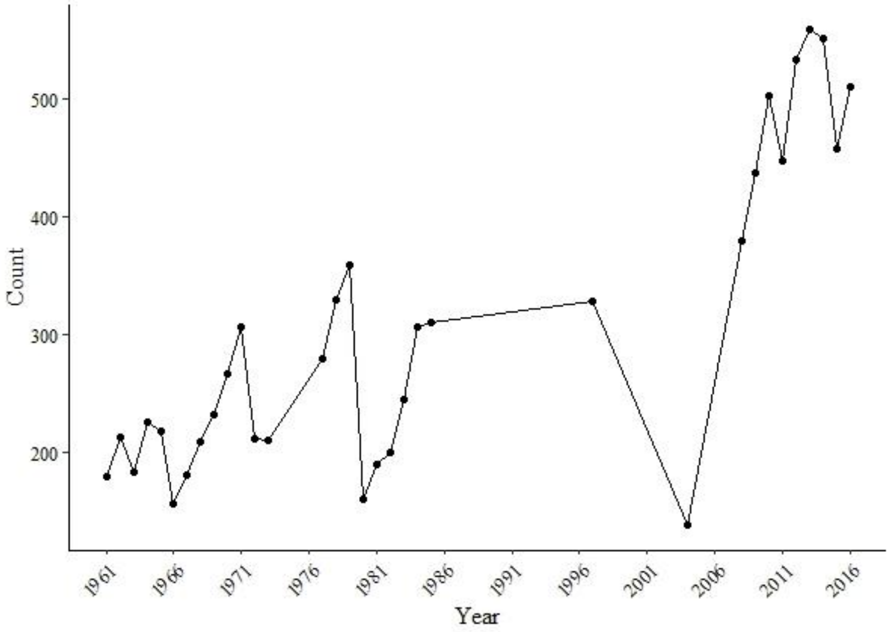

Figure A.2. Direct population counts of feral horses on Sable Island, NS, Canada from 1961 to 2019. Data since 2008 collected by the authors. Data prior to 2008 obtained from air photo interpretation in 2004 (Parks Canada Agency, unpublished data) and as published in Frasier et al. (2016).

The high, intrinsic rate of increase of feral horse populations (Eberhardt et al. 1982) and unique sex-structuring that can result at high density (Grange et al. 2009) may have important consequences for predator-prey dynamics in other settings, especially if differential mortality between sexes in feral horses at high density is exacerbated by predation (Berger and Gompper 1999, Grange et al. 2009). For example, where predation is higher on females compared to males as is seen in some native (Kruuk 1976, Berger 1983b) and feral equids (Knopff 2010), we can expect accelerated population declines if environmental conditions are disproportionately impacting reproductive females (Grange et al. 2015). In multi-prey systems, accelerated declines of one prey species have been known to generate conditions for apparent competition that can be strongly detrimental to vulnerable native prey (other ungulates), if the former has been supporting predators (Wittmer et al. 2013). Here, differing rates of decline in deer (*Odocoileus* spp.) and moose resulted in differing rates of mountain caribou predation whereby rapid reductions of deer as primary prey for mountain lions increased caribou mortality. In contrast, gradual declines in moose populations were matched in numerical responses of wolves, and sympatric caribou populations remained stable (Serrouya et al. 2015). Regular cycles of rapid growth and steep decline in feral horses, which are likely characteristic both as an introduced species (Abrams and Matsuda 1996) and given historical artificial selection, are expected to have important consequences for both predators and prey overlapping with feral horse populations.

Predator-prey interactions are system specific (Messier 1995); hence, what constitutes rapid and gradual declines within a given system will be dependent on system characteristics (Holt 1977). Population oscillations in unmanaged populations of feral horses, however, suggests potential for apparent competition to occur in multi-prey systems where feral horses are present. Moreover, if feral horse reproduction (and its subsequent impact on survival) is more influenced by environmental conditions as predicted for species exhibiting these life-history traits (Barraquand et al. 2015), conditions sufficient to impact on body condition may arise within relatively narrow environmental ranges for feral horses (Berger 1983a, Grange et al. 2009). In fact, significant mortality (e.g., >50%) in both native and feral equid populations can occur during periods of heavy snow or rainfall, or drought (Ransom et al. 2016), with female-biased mortality occurring in some cases (Garrott and Taylor 1990, Dobbie and Braysher 1993, Scorolli et al. 2006). In feral horses, poor-condition mothers and their offspring may therefore be more accessible to predators during severe environmental or high-density conditions (Barraquand et al. 2015, Grange et al. 2015), effectively increasing prey biomass over otherwise limiting conditions, where other ungulates are less impacted (Novaro et al. 2000, Scorolli et al. 2006). Such supplementation of predator populations during conditions that would typically reduce reproduction and associated survival costs in native prey species (Festa-Bianchet and Jorgenson 1998) may be an overlooked but important driver of apparent competition in systems containing feral horses.

Resource Use and Environmental Vulnerability

Habitat modification can favor introduced species and create asymmetries with native prey that drive apparent competition (Sinclair et al. 1998, Festa-Bianchet et al. 2011). For example, exotic ungulate species in Patagonia exploited modified habitats that negatively impacted native species, elevating predator populations and increasing guanaco (*Lama guanicoe*) mortality (Novaro and Walker 2005); while habitat change in Alberta, Canada, facilitated invasions of white-tailed deer increasing wolf numbers in regions supporting Threatened caribou populations

(Latham et al. 2011). The ability of horses to exploit high-volume, low-quality forage (Grange et al. 2004, Schoenecker et al. 2016) means habitat modifications that otherwise reduce the abundance of quality forage or fragment habitat for native species may do less to impact on relative resource availability to horses (Beever and Brussard 2000b, De Villalobos and Zalba 2010, Girard et al. 2013). Indeed, where habitat alteration increases the carrying capacity for feral horses, prey biomass and predator abundance may increase in response to growing horse populations despite declines in native prey species (McShea 2005).

Landscape complexity in fragmented environments can also impede animal movement and hence have strong but variable effects on different species and their relative vulnerability to predators (Wittmer et al. 2007). Flight from predators, for example, can be hindered in landscapes with hard edges, rugged terrain, or extensive tree fall (Bergman et al. 2006). In Yellowstone National Park, larger and more aggressive bison were less vulnerable to these habitat differences than were elk, and only suffered predation when elk numbers dropped substantially relative to bison (Garrott et al. 2008). In predator-prey systems where horses are now present, horses are one of, if not the largest (kg) and hence potentially least vulnerable prey species (Gula 2008, Webb 2009, Knopff 2010, Forsyth et al. 2019). Horses may also not rely on flight to defend against natural predators, rather adopting assertive anti-predator behaviors (i.e., behaviors that increase exposure to a predator or decrease the distance between an animal and a predator on encounter; Dorn 2009) that are weapon-based (striking, biting and kicking; Feh et al. 1994) in concert with social-group defence. Habitat alteration may therefore exacerbate inherent advantages of horses compared to alternate prey species through two mechanisms: 1) the provision of additional resources and hence reduced vulnerability to predation at a population scale (Holt and Bonsall 2017); and 2) via lower relative vulnerability for individual animals and anti-predator behaviors as a result of inherent morphology and behavior.

Where human modification of habitat facilitates feral horse population growth (e.g., forest conversion to grassland, or where rangelands are actively managed for large grazers including cattle), grazing pressure may induce plant-community feedbacks (Forsyth and Caley 2006). Increased abundance of horses is known to reduce plant biodiversity but increase overall productivity (Beever et al. 2008, De Villalobos and Zalba 2010), supporting higher grazer abundance (McShea 2005) and in turn maintaining altered successional trajectories and vegetation states (Sinclair 2003). Such shifts are likely to reduce (relative) resource limitation for feral horses with unknown but likely negative consequences for browsing native prey like deer, moose, and at times elk, all of which feed on woody browse especially in winter. Both elk (Christianson and Creel 2010) and feral horses will, however, use graminoids in greater proportion to availablity (King and Schoenecker 2019), and so the effects of landscape conversion in favour of graminoid abundance may reduce (winter) habitat suitability for deer and moose, but also lead to direct competition between elk and feral horses (as well as other grazers including bison and cattle).

The role of humans in modifying the influence of resource limitation in favor of horses vs. other ungulate prey is not restricted to actions of landscape or rangeland management, however. In contrast to most native prey populations, feral horses may also benefit strongly from competitive subsidies of forage and water intended for domestic species. In some cases, direct supplementation of horses may be a legislative requirement (Scasta et al. 2018) to reduce mortality in populations experiencing resource limitation (Nuñez et al. 2016). Artificial supplementation undoubtedly benefits horses relative to native prey species, particularly where inherent equid biology would otherwise disadvantage the species (e.g., water dependency; Dobbie and Braysher 1993). Management requirements for some feral horse populations may facilitate apparent competition with native species, particularly in arid environments, e.g., as observed in African multi-prey systems containing native equids. Roan antelope (*Hippotragus equinus*) declined sharply following artificial water supplementation in Kruger National Park where water-dependent zebra and wildebeest (*Connochaetes taurinus*) populations increased markedly, in-turn increasing predator numbers and predation on antelope (Harrington et al. 1999). Similar dynamics could be predicted for systems including feral horse populations where resource limitation which would otherwise limit abundance (Scasta et al. 2016). As habitat alteration, climate change, and management approaches continue to shift vulnerability of environmental limitation in favor of horses, negative effects of both direct and apparent competition on native prey species are likely to be non-trivial.

Horses as Prey

Most feral horse populations are not subject to significant predation simply because of a lack of large predators (Ransom et al. 2016). However, continued range expansion of feral horses and direct introduction of feral horses in trophic rewilding projects (Donlan et al. 2006, Cromsigt et al. 2018), coupled with the reintroduction of and growth in growth in populations of large predators including wolves (Ray 2005, Wolf and Ripple 2018), means that predation is likely to increase in importance as an ecological interaction where feral horses occur. Despite widespread extirpation of large carnivores, generalist predators capable of attacking and killing both adult horses and foals now do so in several ecosystems (Table A1).

Table A.1. Locations of studies reporting predation on feral horses (FH). Total numbers (*n*) of horses sampled in the study and horse density (horses/km^2) taken directly from study descriptions (Search criteria available in S1). Percent of feral horses (%FH) represented in predator diets relates to particular analysis method stated (FO = frequency of occurrence; NS = not stated).

Location	*n* / horses/km^2	Predator(s)	% FH in diet[a]	alternative prey[d]	Analysis	References
Europe						
Spain, Galicia a) Eume river valley b) Dorsal Galega	C) 448 / 1.48 b) 215 / 0.83	Wolf[p]	C) 37.13 b) 33.93	domestic and commercial livestock	FO	Lagos and Bárcena (2018)
Italy, Appennine Mountains a) N. Appennines b) Abruzzo Nat. Park	a) 400 / 0.80 b) 200 / 11.7	Wolf[p]	a) 1.3 b) 7[c]	deer sp., mouflon, wild boar, livestock	% scat volume	Meriggi et al. (1996) Patalano and Lovari (1993)
Portugal, Peneda-Gerês National Park	895 / 3.7	Wolf[p]	41.3	Livestock	FO	Vos (2000)
North America						
NV, USA a) Virginia Range b) North area	a) 1500 / 1.03 b) 1185 / 0.18	Cougar[p]	a) 77 b) 45	Mule deer[e], bighorn sheep[e], feral goats, pronghorn[e], livestock	% kill site prey species	Andreasen (2014) Gray et al. (2008)
U.S.A.,California	162 / 0.27	Cougar	48	mule deer	% foals killed	Turner et al. (1992)
Canada, Alberta[b]	749 / 0.05	a) Cougar[p] b) Wolf[p]	a) 10-13 b) 12	Elk[e], deer, moose	a) frequency b) relative biomass	Knopff (2010) Webb (2009)
South America						

Brazil, Serra da Mantiqueira[c]	279 / NS	Puma[p]	51	Livestock, native small mammals	% livestock predation	Palmeira et al. (2015)
			Asia			
Mongolia[c] a) Hustai Nat. Park b) South Gobi	C) NS b) 120 / 0.07	C) Wolf b) S. leopard	C) 32 b) 12	a) Prezwalski horses[e], red deer, livestock b) Ibex, argali, livestock	a) relative biomass b) % kill site prey species	van Duyne et al. (2009) Johansson et al. (2015)
Nepal, Himalayas	NS / 1.24	a) S. leopard[p] b) H. wolf	a) 11.46 b) 9.03	Bharal, Himalayan thar, Tibetan argali, Tibetan gazelle, kiang, livestock	relative biomass	Chetri et al. (2017)
			Oceania			
Australia[g] a) Kosciuszko Nat. Park b) Kimberley	NS NS	Dingo	a) 3.1 b) 5.0	feral and domestic ungulates, native small mammals	FO	Newsome et al (1983) Brook (2013) Forsyth et al. (2019)

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[a] Where a range of values are reported, for instance when diet composition of predators is separated by sex, age, season, maximum rates are reported. All other values are averages or as reported in publications. [b] Horse density values used from (Webb 2009). [c] Free-roaming domestic horses or grouped with domestic/livestock ungulates. [d] Additional ungulate prey species (common names) only included here for brevity. [e] Declining, rare, or of conservation concern. [f] Values from survey data. [g] A range of values from Australian data are reported for multiple locations across Australia in Forsyth et al. (2019). Locations of highest values identified in Brook (2013), and Newsome (1983) are alone displayed in Table A1 for clarity. [p] Indicates where preference or selection for horses was inferred. S. leopard = snow leopard (*Panthera uncia*), H. wolf = Himalayan wolf (*Canis lupus chanco*).

In the Sierra Nevada mountains of the United States, mountain lions have taken up to 48% of foals born, potentially limiting growth in small feral horse populations (Turner et al. 1992); while several individual lions are known to specialize in hunting both adults and young in areas where horses are abundant (Gray et al. 2008, Andreasen 2014). In the Canadian Rockies, feral horses live with mountain lions, wolves, and grizzly (brown) bears (*Ursus arctos*); comprise significant proportions of the available prey biomass; and are the sole prey hunted by some individual (lion) predators (Knopff 2010). Free-roaming domestic horses in Mongolia live alongside recently reintroduced Przewalski horses (*E. f. przewalskii*), where wolves regularly hunt and kill both populations (van Duyne et al. 2009); while snow leopards (*Panthera uncia*) in Nepal show a preference for free-roaming horses among a suite of wild and domestic prey including the rare native equid, kiang (*Equus kiang* [Chetri et al. 2017]). In several European regions, horses both feral and free-roaming (domestic) are present in predator diets including brown bears and wolves (Cozza et al. 1996), with preferences for horses observed in multiple wolf packs (Vos 2000). As in well-studied native systems (Owen-Smith and Mills 2008b), relative abundance, predator preference, and changing vulnerability play significant roles in determining predation rates on horses (Cozza et al. 1996, Schiess-Meier et al. 2007) and the potential negative interactions of shared predation among alternate prey. Parameterization of even simplistic equations regarding predator-prey interactions (e.g., exclusion criteria, Holt 1994), from the perspective of horses as prey is notably lacking, compared to the abundance of information regarding competition among native prey and horses—processes which are intimately linked (Chase et al. 2002).

Much of the literature regarding predation on feral horses is limited to predator dietary analyses, making inference about the impact of predator-prey interactions difficult (Ransom et al. 2016). Key differences in feral-horse biology compared to that of native-ungulate prey species, however, means predator-prey interactions involving horses are likely to differ from those of sympatric prey. For example, availability of foals to predators may occur over extended periods throughout the year compared to distinct and synchronous pulses of fawns, kids, and calves in native ungulates, as gestation is long in horses (~11 months) and produces a single offspring (Berger 1986, Grange et al. 2004). Differences in birthing intervals between horses and other ungulate prey can be significant, with foaling periods extending over 6 months in the Canadian west (Salter and Hudson 1982); while intervals in sympatric ungulates such as elk and moose may only range over 2 months (Poole et al. 2007, Hebblewhite and Merrill 2011). Such extended birth periods mean new foals arrive before juveniles reach sizes sufficient to defend against predators (Gray et al. 2008), and such a prey base may be consistent during environmental conditions that would otherwise reduce availability of native juveniles (section above). The provision of predator populations with a feral horse prey-base, then, even where horses and native prey are spatially or temporally separated, could mean predators are effectively bridged throughout the year, where there would usually be distinct gaps in native prey availability (e.g., seasonally or over extended periods of severe environmental conditions; Holt and Lawton 1994).

Similarly, behavioral responses and anti-predator strategies are poorly understood in feral horses compared to those for native-prey species, with much inference being drawn from African equids (Brubaker and Coss 2015). Intra- and interspecies variations in predator hunting tactics differentially impact sexes and age groups of prey species including native equids, reducing resource use (Kruuk 1976, Thaker et al. 2011) and increasing grouping behavior in predator dense areas (Feh et al. 1994, Hebblewhite and Pletscher 2002); while aggressive anti-predator responses can reduce predation risk (Garrott et al. 2008, Forsyth et al. 2019). Effective anti-predator behaviors by equids vary in response to seasonal resource availability, relative prey composition and abundance, and dynamic predator responses (Bowen 1981, Grange and Duncan 2006, Owen-Smith and Mills 2008a, Owen-Smith and Mills 2008b). While African equids provide broad inference for feral horses, predator-prey interactions (Diedrich 2010, Brubaker and Coss 2015), predator and prey guilds, and ecosystem types in the Americas, Australia, and Europe, differ greatly. Bears (*Ursus* spp.) and wolves and mountain lions dominate predator guilds in North America and Europe, for example, and feral horse habitat varies from high-elevation forested landscapes (Salter 1978) to arid canyons (Gray et al. 2008). In montane forests, landscape factors such as elevation, snow depth, and tree cover may prove important in minimizing predation risk from some predators such as bears and wolves (Poole et al. 2007, Kittle et al. 2008), and this relative risk will fluctuate seasonally with the migratory movements of sympatric prey species such as elk (Hebblewhite and Merrill 2011). While volumes have been written on native ungulate prey and predator population ecology, we know little about how feral horses are impacted by predation despite their presence in many of the same ecosystems as native prey; or how human modification of habitat can influence predator efficiency or functional responses.

Habitat fragmentation is common where feral horses occur, and this may further increase variation in species vulnerabilities to predation risk (Novaro and Walker 2005). Typical anti-predator strategies of ungulates such as flight (Brubaker and Coss 2015) can be precluded in mosaics of clear-cuts and linear features where deadfall and hard-habitat edges are prevalent (e.g., western Canada; Garrott et al. 2008, Latham et al. 2011), meaning anti-predator behaviors used by horses (Feh et al. 1994, Dorn 2009) may become relatively more important for survival. Spatial refugia through proximity to human activity can also reduce predation risk (Hebblewhite et al. 2005), and feral horses are often habituated to humans and human activities due to intense interest from observers and the near absence of human hunting of horses (Linnell et al. 2016). While large predators may avoid proximity to people, feral horses existing in a complex mix of predators and people can still be successfully hunted by predators (Vos 2000, van Duyne et al. 2009, Knopff et al. 2010); but the relative vulnerabilities of native large herbivores compared to horses are not well known.

Despite many unknown aspects of predator-horse interactions, it remains an assumption that adult feral horses are relatively invulnerable to predators due to their size alone (Knopff 2010, Andreasen 2014, Forsyth et al. 2019). Relative predator and prey size does not necessarily govern prey selection in multi-prey systems however (Owen-Smith and Mills 2008a), and as expected, when feral horses comprise the dominant portion of prey biomass, predator diets can be composed solely of horses (Vos 2000, Andreasen 2014). Selection or preference for horses has been inferred in multiple studies where relative feral horse biomass has increased (Table A1). The data suggest, however, that presumptions in the literature around unprofitability and risk to predators in hunting horses appear to be unfounded, not least in generalist predators' ability to adapt to novel prey (Holt and Lawton 1994, Weitz and Levin 2006). Increases in pack size in canids has been inferred as a potential mechanism to better handle large prey including feral horses for example (Bowen 1981, Gula 2008, Forsyth et al. 2019) and moreover, large body size may be less relevant as an inherent defence in feral horses if survival and annual mortality expectations for large-bodied prey are not met in feral horses (Owen-Smith and Mills 2008a, Grange et al. 2009).

Where apparent competition limits native prey populations, population modelling and predator-prey theory suggest that populations of predators and/or non-native prey may need to be eradicated or severely reduced in size (e.g., Courchamp et al. 2003). The social and political realities of feral horse management (and their predators), however, clearly indicate that removal of entire horse populations is very likely impossible (Scasta et al. 2018), demonstrating a need for more detailed understandings of predator-prey interactions involving feral horses. Top predators are capable of hunting and killing male and female feral horses both adult and young, and there is little evidence to suggest that predation will not increase in populations where predation is minor or incidental, particularly in the context of declining populations of native ungulate prey (Owen-Smith and Mills 2008a). Apparent competition (or positive indirect effects, discussed below) with feral horses should therefore be expected (Garrott et al. 2008, Gower et al. 2008, Dunkley et al. 2012); however, increasing our understanding of feral horse predator-prey ecology remains an outside priority for most government mandates.

Conservation Consequences

While expansion and growth in feral horse populations may be controlled, once established horses have proven to be resilient and permanent components of food webs. The distinct nature of feral horse biology, ecology, and our approaches to managing horses relative to other wildlife precludes many of the typical strategies directed at minimizing negative ecological interactions, including those used in native large-mammal systems like culling or harvest management (Symanski 1996, Beever and Brussard 2000a). At the same time, discounting of the importance of feral-horse biomass to community ecology because of how horses are categorized (e.g., as escaped or free-ranging domestic livestock) circumvents questions over their relevance in wider predator-prey systems. Increasingly, however, free-roaming horses can comprise significant portions of seasonal or year-round prey bases, with predators often showing strong preference for horses particularly in areas supporting reduced availability of native prey (Patalano and Lovari 1993, Meriggi and Lovari 1996, Mishra 2002, Palmeira et al. 2015, Chetri et al. 2019).

For many native species such as elk or caribou in North America, guanacos in South America, or the reintroduced Prezwalski horse in Mongolia, potential apparent competition with feral or free-roaming horses presents real conservation risks. Declining populations of elk in the eastern Rocky Mountains of Canada (Berg et al. 2016) contrasts strongly with a rapidly increasing sympatric feral horse population. Indeed, horses in the region are now adding as much as 188 kg/km^2 of live-weight biomass to prey bases in the system (weights from Andreasen [2014]; abundance estimates from Alberta Environment and Parks [2019]). Ungulate biomass is widely accepted (and predictively modelled) to be positively related to wolf density at a macroecological scale (Kuzyk and Hatter 2014). At 188 kg/km^2 (roughly 2 relative ungulate biomass values per km^2), a wolf population as high as 10 wolves/1000 km^2 may be supported by feral horses alone (quadratic model of Kuzyk and Hatter [2014]). While predator subsidization by horses to the detriment of native elk, moose, and deer populations may increasingly become important in places like Alberta, habitat loss and apparent competition with native prey is already impacting threatened woodland caribou populations in closely adjacent ecosystems (Wittmer et al. 2007, Hervieux et al. 2013). There is little to suggest that feral horses will not also eventually colonize mountain or even woodland caribou ranges in western Alberta and eastern British Columbia, imparting further stresses on the at-risk species.

Multiple asymmetries in predator vulnerability and resource use between horses and native species favor horses in areas of sympatry (Garrott et al. 2008) satisfying conditions for apparent competition (Holt and Lawton 1994), further to issues regarding resource competition which receives more attention. However, high relative abundance, variable vulnerability emergent as a result of artificial selection, and predator preference in systems where feral horses are present may not necessarily translate into negative effects for sympatric, native ungulate competitors. Predators may be drawn away from quality native prey habitat into areas where horses are abundant as seen with livestock and rare prey (Sundararaj et al. 2012). Similarly, predation on horses may facilitate persistence of native prey through sheer division of total predation (Abrams and Matsuda 1996), or preference for the species less invested in survival (i.e., horses) when environmental conditions are severe (Barraquand et al. 2015). Maladaptive trade-offs for survival recognized in feral horse populations (Grange et al. 2009) and discussed above as a potential negative outcome of predator-prey interactions, may in fact benefit alternate prey species and support coexistence, particularly where numerical responses of predators to horse abundance are low (Holt and Bonsall 2017). Potential positive effects of horses, e.g., as diversionary prey, however, are unknown and largely speculative.

Developing an understanding of feral horse predator-prey dynamics will have further value as the reintroduction and natural range expansion of large predators into areas in both Europe and North America continues (Wolf and Ripple 2018). In some cases, feral horses are also being used directly in rewilding efforts, as surrogates for extinct native grazers to re-establish large-grazer trophic interactions (Donlan et al. 2006, Rubenstein et al. 2006, Corlett 2016). Longer-term objectives that aim to establish grazing communities using horses inclusive of apex predators will certainly depend on understanding predator-prey dynamics of feral horses. Even scenarios where herds of domestic horses that range freely are preyed upon, such as those in Mongolia (van Duyne et al. 2009) and Iberia (Vos 2000), provide vital information about profitability and risk as horses in systems are components of fluctuating native prey bases (Holt and Lawton 1994). As reintroduction or rewilding efforts introduce horses into prey bases, and as free-roaming horse and predator ranges naturally expand, information from established predator-prey studies involving horses may provide novel avenues for population management (Gray et al. 2008) and provide tools for the conservation of vulnerable native species, both predator and prey (Sundararaj et al. 2012). We encourage this work.

Evolutionary Consequences

Our review has focused on the management and conservation implications of indirect ecological interactions involving feral horses. The evolutionary context of predator-prey interactions in free-roaming horse populations, however, also has both historic and current relevance. Much about feral horse behavior and sociality may not have been altered during domestication to the extent that traits of reproduction have (Clutton-Brock 1981, Linklater 2000). Natural selection among directly and apparently competing horses and prey species may be recognizable among contemporary distribution patterns, species composition and behavior, concomitant with specific physical traits (Holt and Bonsall 2017). Predators might select a particular coat color in horses, for example, which may be related to primary prey abundance (Turner et al. 1992) thus operating in opposition to artificial selection. Similarly, although anti-predator behaviors in feral horses are likely maintained, or at least quick to re-establish (Sih et al. 2010), deeper investigation into predator-prey dynamics of feral horses provides an avenue to study antagonism between natural and artificial selection for traits such as docility (Sundararaj et al. 2012, Brubaker and Coss 2015, Cabrera et al. 2017). Ultimately, for many feral horse populations, particularly in North America, similar predator guilds, although less diverse and smaller in size, exist as those present among megafaunal communities prior to widespread megafaunal extinctions (Haynes 2009). Little is known about predator-prey interactions in extinct species from Late Pleistocene herbivore communities (Lundgren et al. 2020). However, the close relatedness, behavior, and morphology of feral horses to the extinct Pleistocene equids (Barrón-Ortiz et al. 2017) provides a unique opportunity to answer general questions such as those regarding adaptive foraging, ontogeny and body size, or social and inter-species organization among feral horses under predation (Holt and Bonsall 2017) and their role in community dynamics.

Future Directions

With horses already established as *de facto* permanent components of predator-prey systems in many areas, increasing our knowledge base of predator-prey and indirect interactions involving feral horses will be critical to managing expanding feral horse populations and, by extension, native-species conservation. Outstanding questions we identify as being the most important for addressing current knowledge gaps on this topic include:

1. To what extent and in which environments has artificial selection and inherent equid biology (e.g., foraging and survival strategies) shaped differences in competitive ability between horses and native ungulate prey on shared landscapes from direct and indirect competition. That is, what is the potential for horses to exclude competitors through both competition and apparent competition? Few researchers have yet to think about the invasion ecology of horses in the context of Lotka-Volterra-type or agent-based competition modelling (Donalson and Nisbet 1999, Haerter et al. 2016), but it may be possible to predict the exclusionary effects of horses and scenarios of management that help promote coexistence.
2. Are there sex-differences in predation vulnerability among adult horses, and how does this vary with age, reproductive status, and environmental conditions? Differential predation among sexes could exacerbate declines in feral horse populations given observed trends in female life-history trade-offs. Quantifying differential predation rates between sexes, and how these change with density dependence requires methods beyond dietary analyses of predators, such as rapid kill-site investigation in predator studies (Knopff 2010) and individual-based monitoring of feral horse populations under predation (Grange et al. 2015).

3. How does vulnerability to predation in horses change across landscapes and by predator species, and are anti-predator behaviors related to these factors? Habitat type and spatial distribution has a significant impact on prey vulnerability, and these change with predator type and anti-predator behavior (Schneider 2001, Garrott et al. 2008). Determining relative predation risk in the range of landscapes and across the diversity of multi-prey systems that feral horses now occupy requires both behavioral observation of predator-prey interactions and quantification of predator success rates in differing habitats (Forsyth et al. 2019).
4. What role does asynchronous foaling play in relation to fluctuations in native-prey availability, i.e., via apparent competition? Foals can be born at any time of the year, and this may prove critical in the maintenance of predator populations during declining abundance of native prey (Gray et al. 2008); however, the importance of this is not known.
5. What role might predation play in modulating the population oscillations observed in predator-free (mainly island) feral horse populations? Predators can limit growth of feral horse populations under certain circumstances (Turner et al. 1992, Ransom et al. 2016), and this may prove critical in mitigating the impacts of density on population dynamics (Grange et al. 2009). Predators may also exacerbate population fluctuations by capitalizing on poor quality females and their young, particularly under high density or severe environmental conditions, resulting in higher predation rates on alternate prey species (Barraquand et al. 2015). Quantifying factors such as handling time, search rates, and foraging efficiency of predators regarding feral horses has general utility but may also highlight fluctuating profitability throughout population cycles.
6. Do predators alter resource-use patterns of feral horses, and how might this relate to availability of alternate prey species? Predators can significantly alter prey use of resources and the landscape through indirect effects (e.g., Laundre et al. 2001). Resource-use and expansion in feral horses may therefore be determined in part by predation risk, yet this can only be determined through detailed analysis of feral horses (e.g., using radio-telemetry data) in landscapes with predators.

Management Implications

While little is currently known of the place of the feral horse in the context of community ecology relative to other large (native) ungulates, lack of understanding of fundamental horse ecology in modern landscapes and food webs has important consequences for conserving biodiversity where populations of horses have established or are likely to establish. Feral horses differ in many ways from native ungulate herbivores in morphology, behavior, ecology, but also evolution (including history of artificial selection), with the consequence that horses can be highly competitive in anthropogenically disturbed ecosystems relative to native prey species—particularly where given special protections to do so. Superior competitive ability, however, arises not only from direct competitive interactions founded in interspecific differences of behavior, morphology, and life history, but also indirect interactions including apparent competition of which very little is known in the context of horses. Increasing horse biomass can have predictable effects on predator numbers with implications for regions undertaking large predator reintroduction programs that may be unknown for native prey because of apparent competition. Where horse biomass comprises an increasing relative share of ungulate biomass on landscapes, understanding the strength and direction of both direct and indirect ecological interactions between horses and other prey species should be of concern for both community ecologists and managers especially where native-ungulate prey may be rare or declining.

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Appendix B The need for formal reflexivity in conservation science.

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Abstract

Conservation issues are often complicated by sociopolitical controversies that reflect competing philosophies and values regarding natural systems, animals, and people. Effective conservation outcomes require managers to engage myriad influences (social, cultural, political, and economic, as well as ecological). The contribution of conservation scientists who generate the information on which solutions rely is constrained if they are unable to acknowledge how personal values and disciplinary paradigms influence their research and conclusions. Conservation challenges involving controversial species provide an opportunity to reflect on the paradigms and value systems that underpin the discipline and practice of conservation science. Recent analyses highlight the ongoing reliance on normative values in conservation. We frame our discussion around controversies over feral horses (*Equus ferus caballus*) in the Canadian West and New Zealand and suggest that a lack of transparency and reflexivity regarding normative values continues to prevent conservation practitioners from finding resilient conservation solutions. We suggest that growing scrutiny and backlash to many normative conservation objectives necessitates formal reflexivity methods in conservation biology research, similar to those required of researchers in social science disciplines. Moreover, given that much conservation research and action continues to prioritize western normative values regarding nature and conservation, we suggest that adopting reflexive methods more broadly is an important step toward more socially just research and practice. Formalizing such methods and requiring reflexivity in research will not only encourage reflection on how personal and disciplinary value systems influence conservation work but could more effectively engage people with diverse perspectives and values in conservation and encourage more novel and resilient conservation outcomes, particularly when dealing with controversial species.

Introduction

Conservation science operates at the interface of ecological research and human relationships with the natural world. The conservation sciences are a suite of values-based disciplines, wherein value judgements about types of biodiversity and ecologies preempt and accompany their measurement (Soulé 1985; Kareiva & Marvier 2012). Conflicts arise when the values of one conservation paradigm framing research and practice differ from the values of other people with interests regarding the same animals or environments (Bennett et al. 2017a). Despite extensive scholarship regarding the influence of values on science (Longino 1990; Rooney 1992; Pielke Jr 2007; Mattson et al. 2012), many conservation biologists still lack the methodological tools and support to transparently identify their underlying normative values and beliefs (including personal and group biases) and the influence those have on their research and practice. In the social sciences, developing such an awareness is called reflexivity: individuals or groups sharing their positionality or a self-critique about their a priori values and assumptions (Nicholls 2009).

Conservation controversies commonly erupt over species and habitat management, and scientists must conduct research and management in situations fraught with conflict (Bennett et al. 2017b), resistance, and scrutiny (Perry & Perry 2008; Scasta et al. 2018). Such scrutiny exposes the normative value systems within conservation biology that exacerbate conflict, particularly the a priori assumptions about wildlife and ecosystems that evaluate their worth and sometimes their ecology (Yanco et al. 2019). The conflict caused often slows progress and reduces the likelihood of achieving long-term conservation objectives (Davis et al. 2011; Crowley et al. 2017).

Being unable to acknowledge how values shape and drive their research also limits conservation scientist’s ability to navigate toward solutions amidst conflict (Longino 1990). Through a lack of transparency around the normative values and assumptions that underpin and influence the discipline and by continuing to present conservation research and management frameworks as only evidence-based, conservation scientists often make it more difficult to engage with the diversity of peoples and perspectives typical in conservation conflicts. People who might otherwise engage in conservation can feel antagonized, leading to slower progress or failure to implement conservation actions (Crowley et al. 2017; Yanco et al. 2019).

There is significant scholarship addressing the influence of values in science in general (Proctor 1991; Elliot 2017), and conservation science specifically (Vucetich & Nelson 2012), along with explorations of reflexivity and inclusivity in conservation (Bennett et al. 2017b). Yet there remain substantial gaps in the application, reach, and uptake of formal reflexivity in conservation science. For example, necessary changes to Soulé's (1985) normative values and functional postulates for conservation in the twenty-first century have been highlighted (Kareiva & Marvier 2012). Yet debate continues to focus largely on the empirical evidence supporting paradigmatic conservation solutions, rather than also addressing the underlying values that drive the debate (e.g., Hayward et al. 2019; Anderson et al. 2019; Wallach et al. 2020). Without broader disciplinary acknowledgement and more robust methodological accounting for the influence of values on research and the management processes it informs, conservation scientists risk exacerbating conflicts and failing to find durable conservation solutions.

Unacknowledged values become problematic and the origin of substantial conflict, partly because Western conservation biology is rooted in the ethics of a colonialist society (Martinez 2003; Kareiva & Marvier 2012; Bhattacharyya & Larson 2014). On continents with a history of recent European settlement, like Australasia and North America, colonial values and norms concerning nature continue to underpin much of the work in the conservation sciences (Artelle et al. 2019), despite the broad composition of cultures and peoples practicing and affected by conservation (Kareiva & Marvier 2012) and rapidly changing contemporary ecological conditions (Hobbs et al. 2009).

We addressed these issues to contribute to the discourse by discussing the controversy over feral and free-ranging horses (Equus ferus caballus) in the Canadian West (Bhattacharyya & Murphy 2015; Boyce et al. 2021) and New Zealand (Linklater et al. 2002). We first considered certain assumptions and paradigms that continue to underpin normative value systems within conservation biology about feral horses in these regional contexts and then widened this discussion to conservation science and practice. Second, we devised recommendations to improve reflexivity and transparency in conservation research. We suggest such measures are increasingly critical to scientists conducting rigorous, ethical, and broadly useful science and navigating political impasses amidst cultural diversity.

Positionality

Our positionality and values pertaining to the subject are outlined below, in accordance with the framework discussed at the end of this essay. We are 2 men and 1 woman: New Zealanders of European ancestry and first-generation Canadian of Indian and European descent, respectively. We all currently live and work in unceded, colonized Indigenous territories in North America.

Individual and interpersonal reflexivity:

This article was motivated by our respective professional and research experiences, as well as personal ethics and values. Our professional research backgrounds include training and experience in the applied biological and social sciences of conservation ecology (freshwater and terrestrial ecosystems, ethno- and wildlife ecology). We each have independent research experience regarding feral horse behavior, ecology, and management. We are influenced by personal values and beliefs that resolving disagreements about free-ranging horses and making progress on many conservation issues depends on engaging the diverse values of multiple peoples and agencies and considering ecosystems as not only physical and biological environments, but also sociocultural landscapes (i.e., home to biocultural communities). We believe conservation can and should serve these communities and provide them with agency in decision-making, while maintaining wider ecological objectives in a 21st century context. We are therefore motivated by personal moral imperatives to protect wild spaces and animals, while addressing issues related to cross-cultural social justice, ethics, and biocultural diversity.

Collective reflexivity

Our experience in free-roaming equid research leads us to a shared recognition of the impacts that non-native species can have and often the need for their management. We also have direct experience of how normative assumptions about introduced species influence and limit the research questions asked, funding, interpretation of results, and use of conclusions. Hence, we are motivated by a shared desire to critically examine and overcome some of the most limiting norms in order to diversify contributions to, and outcomes from, the conservation sciences.

Feral Horses and Conservation Conflict

Feral horses and their management typify how conservation controversies are rooted in conflicting value systems. Controversies over feral horses illustrate the limitations of some dominant paradigms within conservation science and serve as a good example for our argument and recommendations.

Few species match feral horses in the interest, attention, and compassion they receive from people of diverse backgrounds and localities. Seldom are people indifferent to their management (Scasta et al. 2018). Horse-human relationships reflect contemporary emotional connections and a shared cultural history dating back over tens of thousands of years. From horses being sources of food (i.e., prey), to their taming and domestication (Outram et al. 2009), to their extensive use for transportation, warfare, work, recreation, and agriculture (Scasta 2019), horses have been and are many things to humans. They are deeply bonded companion animals, irreplaceable work partners, symbols of power, prestige and freedom, and valuable components of ecosystems as wildlife. It is this deep personal connection to horses that fosters concerns for horse welfare and their persistence in the wild (Robinson 1999).

Human relationships with horses are evidenced in numerous effective lobby groups that advocate for feral horses and force researchers to engage with value systems outside dominant conservation paradigms about non-native species (Scasta et al. 2018). At the same time, horses are large grazing mammals that can significantly affect ecosystems, sometimes requiring management and conservation intervention (Beever 2003; Bradshaw et al. 2007; Baur et al. 2017). The extraordinary conflicts over feral horses, and their role and place in contemporary ecosystems, illuminate the ways in which conventional conservation paradigms – including normative narratives about species legitimacy – can exacerbate conflict and hinder progress toward conservation solutions.

Normative values and feral horses in conservation

Feral horse populations introduced or descended from domestic stock now inhabit all continents except Antarctica (McKnight 1959). Within conservation science, whether or not horses are considered to contribute to desirable biodiversity is a value judgement (Dalke 2011) that varies by region and context. In Europe horses are often viewed as a species that contributes to rewilding of biodiversity – or at least as ecological surrogates for wild ancestors (e.g. the extinct tarpan [Equus ferus]) – and have been reintroduced in some areas to restore large grazers to landscapes and ecosystems that have been denuded of many large native mammals for centuries (Keulartz 2009; Bakker & Svenning 2018). By contrast, in North America, where much of equid evolution occurred, free-ranging horses are often judged non-native by the narrative that favors biogeographic species distributions and ecosystems as they are imagined to have been prior to European colonization (Collin 2017) or against narratives that favor the open-range ranching economy (Bhattacharyya et al. 2011; Kincaid 2015; Thistle 2015). Outside North America and Europe, in areas such as New Zealand, Australia, South America, and southern Africa, support for horses is largely related to the regional history and heritage they represent, rather than their ecological function as natives or surrogates (Linklater et al. 2002; Muller & Bourne 2018; Scorolli 2018).

Conservation controversies like those over feral horses evoke sociopolitical values that influence research and management more than most ecological factors (Rikoon 2006; Scasta et al. 2018). Although it is commonly acknowledged by conservation scientists that research participants, stakeholders, and subjects are influenced by sociocultural and political factors, reflecting on how the people conducting a study are influenced by normative values within this context is far less common (Heger et al. 2019). For example, a recent analysis of a conservation dilemma involving feral goats suggested that conservation scientists be aware of the dominant role conservation paradigms play in decision-making and their role in conservation conflict (Yanco et al. 2019). By cautioning conservation biologists about the influence of personal and professional value systems on conservation outcomes, Yanco et al.'s (2019) analysis indirectly illustrates the ongoing impact of an absence of formal methods and expectations regarding reflexivity among conservation science practitioners.

Values that become paradigms and unacknowledged norms in science can be problematic in several ways, such as when they support dichotomies associated with conservation ideologies (e.g., native, non-native or invasive) (Davis et al. 2011). When unexamined, such dichotomies can shape one's work and understanding of nature, becoming deductive surrogates for evidence-based evaluation, and reducing scientific rigor (Yanco et al. 2019). Many dominant conservation science ideologies are informed by early conservation biology philosophy, which outlined several broad normative values (i.e., determining what is desirable or undesirable) based on an "…ethic of appropriate attitudes toward other forms of life…" (Soulé, 1985: 730). Statements such as diversity of organisms is good and evolution is good reflect values and were acknowledged as unprovable, but were presumed to be shared by conservationists and proposed as guides to assess conservation action. Contemporary conservation biology, however, often attributes normative values to ecological processes (*sensu* Soulé's [1985] functional postulates). For example, if a species is classified as non-native it is often, even in the absence of evidence, presumed to be bad (i.e., negatively affecting native biodiversity and evolutionary processes), whereas native biodiversity is presumed to be good and better off absent of non-native species.

There is widespread recognition that the sociopolitical context of novel ecosystems influences conservation biology and, in particular, the related practice of restoration ecology (see Hobbs et al. [2014] and Bennet et al. [2017] for literature reviews). In colonized landscapes, however, like North America and New Zealand, although restoration scientists have considered the management implications of novel ecosystems (Seastedt et al. 2008), much conservation biology work remains framed around reference states attached to specific historic moments (Harris et al. 2006; Kareiva & Marvier 2012). This predominantly western conservation philosophy (Wilshusen et al. 2002) tends to classify and value species based on suppositions about pre-European reference ecosystems, while ignoring or devaluing the role that Indigenous peoples' stewardship had in creating those ecological conditions (Artelle et al. 2019; Loring & Moola 2020). Within this western conservation paradigm, certain introduced species are widely evaluated as indicators of ecosystem decline even in areas where their impacts have not been assessed (e.g., feral horses) (Shackleford et al. 2013), while other introduced species are accepted despite their impacts because of their economic value to members of the economically dominant society (e.g., cattle).

Without a reflexivity framework to acknowledge and examine underlying values, conservation research is vulnerable to a biased approach that primarily confirms preconceived assumptions about species like feral horses, contributing to conflict (Davis et al. 2011). Several authors have proposed various methodological approaches to mitigate decision-making that relies solely on normative values (e.g., Shackleford et al. 2013; Yanco et al. 2019), but it is also vital to acknowledge the implicit assumptions that influence researchers (e.g., the so-called undesirability of non-native species) and the evidence base they subsequently compile.

Seldom in Canada and New Zealand have data been sought that fully assess the role feral horses play in ecosystems, consider whether those roles might be neutral or even positive regarding ecological resilience and biodiversity, or understand the impact of their removal. Instead, much of the research has been framed around a conservation paradigm that non-native horses will have negative impacts on ecosystems and other species. Our research experiences to date in the regions we have studied feral horses highlight a general lack of scholarly interest in research extending beyond population control or quantifying negative impact, and feral horse ecology plays a minor role if any in decision-making processes (Linklater et al. 2002; Bhattacharyya & Murphy 2015; Boyce et al. 2021). This approach to feral horse research validates preexisting assumptions and the dominant conservation paradigm in each place. It may also distract resources from effecting more meaningful change through conservation research to tackle the powerful and complex industrial, economic, and political drivers that most severely affect and degrade ecosystems where feral horses live (Alagona et al. 2012).

Conventionally dominant conceptualizations of nature and wilderness are increasingly challenged as but one value system among many regarding feral horses. In the context of climate change and pervasive human impacts, conventional conservationists' singular views of nature are brittle representations of not only ecological systems, but also political reality (Folke 2006; Corlett 2016). Such paradigms, left unexamined, risk predetermining research outcomes and limiting management options by overlooking potential approaches and questions that do not fit this normative epistemology and contradict a major tenet of conservation biology that objective evidence should guide decision-making (Yanco et al. 2019).

Engaging with Diverse Peoples and Values

Conservation research and practice affect and are influenced by diverse peoples who hold equally diverse philosophies, worldviews, values, and knowledge systems (Kareiva & Marvier 2012). Effective conservation action and outcomes require that conservation scientists and managers engage with those diverse peoples and views (Bennett et al. 2017a). Yet when confronted with value systems that differ from dominant conservation paradigms, our experience has shown that scientists often close ranks around paradigms they view as self-evident and dismiss other views and value systems as less valid and unsupported by evidence.

In the case of feral horses, by a priori classifying some animals as invasive and damaging, regardless of their actual ecological and biocultural role (Lundgren et al. 2021), conservation science risks perpetuating an ideology that seeks to define the ecological legitimacy of ecosystem characteristics for other peoples, thus continuing to colonize social-ecological systems (Bhattacharyya et al. 2011; Bhattacharyya & Larson 2014; Collin 2017). This approach that classifies some animals as inherently negative also reinforces a conservation dogma that wages war on non-native species, predetermining how local people ought to engage with animals and the environment (Vucetich & Nelson 2013; Duffy 2016).

Scientists' ability to understand and transparently acknowledge their own motivations and paradigms affects their ability to engage with the diverse people and groups involved in conservation and to develop trusting, equitable, and productive relationships (Treves et al. 2006; Crowley et al. 2017). Once public trust in scientists is lost, an increasing trend in general (3M. 2019, Pew Research Centre 2019), the inability of scientists to critically review or acknowledge their own paradigms can lead others to characterize research itself as partisan. This breakdown has particular relevance in controversial conservation issues (Bennett et al. 2017a). However, when scientists can and do reflexively acknowledge their own values, they are better positioned to engage respectfully, collaboratively, and in a socially just way with other people whose views differ, thus building stronger social foundations for shared conservation outcomes (Artelle et al. 2019).

Research and management that counter accepted norms remain heavily contested, despite increasing acknowledgement that values influence conservation science and that social inequities in participation (historical and ongoing) are inherent in conservation and related restoration ecology ideologies (Mool & Roth 2018; Yanco et al. 2019). Accepted normative ideologies continue to receive the most empirical support through self-reinforcing research paradigms (Heger et al. 2019) and continue to dominate approaches to conservation in situations fraught with values-based conflict and social inequity (Cumming 2018). Conservation scientists lack a disciplinary directive and supporting framework or frameworks to adapt and adjust this practice, to genuinely engage with reflexivity, and many remain untrained to work effectively and equitably in situations involving diverse peoples and perspectives.

Incorporating Formal Reflexivity in Conservation Science

To address the challenges outlined above, we suggest that the best practice recommendations cited above (cf. Yanco et al. 2019) be built on to develop principles, methodologies, and practices of reflexivity that are more broadly adopted, shared, and required where appropriate by conservation scientists and conservation biology as a discipline. The adoption of more formalized reflexive methodologies in conservation biology would improve the rigor of conservation science research and practice. By formalized methodologies" we refer to those that would encompass accepted principles and frameworks, developed through disciplinary collaboration, for explicit reflexivity as part of the design, process, and reporting phases of research. Such methods, evidenced through reflexivity statements would warrant clear expectations from academic, publishing, and funding institutions intending to communicate the results and implications of research.

Methodologies to support scientists acknowledging their positionality and being transparently reflexive are required as a convention in some disciplines (e.g., anthropology) and supported by peer review as a form of rigor (Peterson et al. 2010; Lichterman 2017). There is an established discourse on reflexivity in the conservation social sciences (Bennett et al. 2017b) and a growing engagement with such practices in related interdisciplinary areas of scholarly research (e.g., ethnoecology, community-based participatory research). Increasingly, some expression of reflexive transparency or positionality is required in conservation work done with Indigenous partners or that engages Indigenous research methodologies (Nicholls 2009; Reid & Sieber 2020). However, natural science disciplines, such as conservation biology, have yet to adopt methodologies that support or require researchers to reflect on and disclose the ways in which their own values may influence their research. Without these methodologies, conservation scientists will not be trained, motivated, or supported to reflect on how their own values may be influencing their work or the effectiveness of their conservation efforts.

Applying principles for reflexivity developed by Nicholls (2009) in health sciences, we suggest that reflexive methodologies for conservation scientists be developed, applied, and required at three levels: self, interpersonal, and collective reflexivity.

Individual self-reflexivity and Inter-personal reflexivity require that scientists identify personal beliefs and biases relevant to the research. A rigorous, inclusive process to guide transparency around personal beliefs and values is appropriate to 21st century conservation science best practices and is necessary to help conservation biologists engage ethically and honestly with others, including those whose views may differ from their own. Engaging in such a practice will encourage conservation scientists to subject their own beliefs to scientific evaluation as one does those of others, while also potentially finding shared or similar interests among diverse peoples. This practice in conservation research, as we have proposed it in this article, would relate to statements of normative values and interests regarding relevant conservation issues. Such statements provide peers with an understanding of motivations, relevant research experiences, and perceptions about species and ecosystems that could influence research design or interpretation. For example, a statement could read as follows:

My experience as a botanist and grassland ecologist has highlighted the influence of overgrazing, particularly by domestic and non-native ungulates. I believe management of these non-native species and mitigating their impacts is imperative to maintaining the function of native ecosystems.

Collective reflexivity asks the question what norms and values-based paradigms influenced the research question, design, and its conclusion? Are blind spots being perpetuated or is there a failure to seek evidence to support decision-making based on assumptions about what merits research and what does not or which questions or results are valid? Challenging normative assumptions and being explicit about the influence of paradigms on science could better equip scientists to engage in research and management processes that factor in sociopolitical complexities and engage with diverse peoples and perspectives. This wider reflexivity should include the acknowledgement by conservation scientists that their research or interpretation has been informed by particular disciplinary or institutional settings. Departmental mandates for example, might dictate the kinds of research undertaken or the interpretation of research results. For example, a collective statement could read as follows:

The department of ecology and evolution aims to research the impacts of native biodiversity loss. Members of the department maintain the position, through our extensive research background, that the loss of native species and their replacement by invasive, or non-native species, will inherently reduce the capacity for ecosystems to function, and will degrade the integrity of natural environments.

Developing and formally adopting reflexive practice will require not only new practices on the part of individuals, but also support for new methodological conventions from the conservation community as a whole. Determining which methodological conventions and when their application is appropriate within conservation science will require collaborative disciplinary discourse. In doing so, conservation scientists will possess a tool to access more varied and nuanced information and understandings of socioecological systems through knowledge sharing and potentially become more agile in our ability to effect conservation outcomes (Bennett et al. 2017b).

A more reflexive conservation science will also challenge conservation biologists to dig more deeply into their understanding of ecology, seek socially contextualized solutions to environmental challenges, and address some of the inherently colonial biases in disciplinary practice. In locations where conservation scientists have studied free-roaming horses as wildlife and engaged with other perspectives on horses it has not precluded horse population management. Free-roaming horses, for example, can offer conduits for conservationists to engage with diverse peoples and a broad public through ecological research and landscape-level conservation, as with the ?Elegasi Qayus Wild Horse Preserve, initiated by the Xeni Gwet'in First Nation and a volunteer conservation group in Tsilhqot'in territory, Canada (Bhattacharyya et al. 2011). Reflexive practice can then encourage conservation outcomes that are realistic and meaningful and thus are future resilient in vastly altered and rapidly changing landscapes where many people's passions and values are held in humanity's dynamic relationship with animals and wild places (Papworth et al. 2009; Thistle 2015).

Conclusion

Achieving conservation outcomes across the diversity of global ecosystems, cultures, and societies necessarily requires flexibility in conservation ideology, rather than strict adherence to normative values about species and ecosystems. To achieve conservation objectives as socioecological systems continue to change, reckoning with personal and professional ideologies that are inclusive of biocultural diversity will become a valuable disciplinary tool (Gavin et al. 2015).

Horses can be detrimental to ecosystems when overpopulated. However, there are gaps in research and empirical data regarding the ecology of feral horses in Canada and New Zealand, which make nuanced inference about their impacts difficult. Within these contexts we have also confronted a common, a priori conclusion that horses must be eradicated because they are non-native and therefore have negative impacts on ecosystems. This departure from an empirically based approach to research, impact assessment, and decision-making regarding feral horses indicates that conservation ideologies and research can be self-fulfilling and suggests that requests from advocates for scientists to validate their nominally objective claims about wild horses are warranted.

People’s complex relationships and attitudes toward horses characterize their management and research. Researchers who adopt positions founded in conservation paradigms that predefine free-roaming horses as illegitimate have alienated many local communities, cultures, and stakeholder groups, as well as Indigenous title and rights holders, who might otherwise have collaborated with scientists in conservation and stewardship (Cowley et al. 2012). Conventional conservation paradigms thus offer a limited toolbox to address contemporary ecological challenges in ways that support a greater diversity of peoples’ values (Bennett et al 2017b). Implementing formal methodologies that require and encourage researchers and practitioners to reflexively address biases and value systems within conservation science could offer new opportunities and solutions to a variety of conservation dilemmas beyond the examples we focused on. Participatory research already shows the benefits and necessity of local buy-in and collaboration (Clark 2002; Clark et al. 2016). Through improved methods for reflection on the influence of paradigms and personal values, conservation scientists can acknowledge the lens through which they tend to view nature, wildlife, and socioecological systems and engage more honestly with people who approach these concepts from different perspectives.

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Appendix C Supplementary figures and tables, and relevant trail camera images.

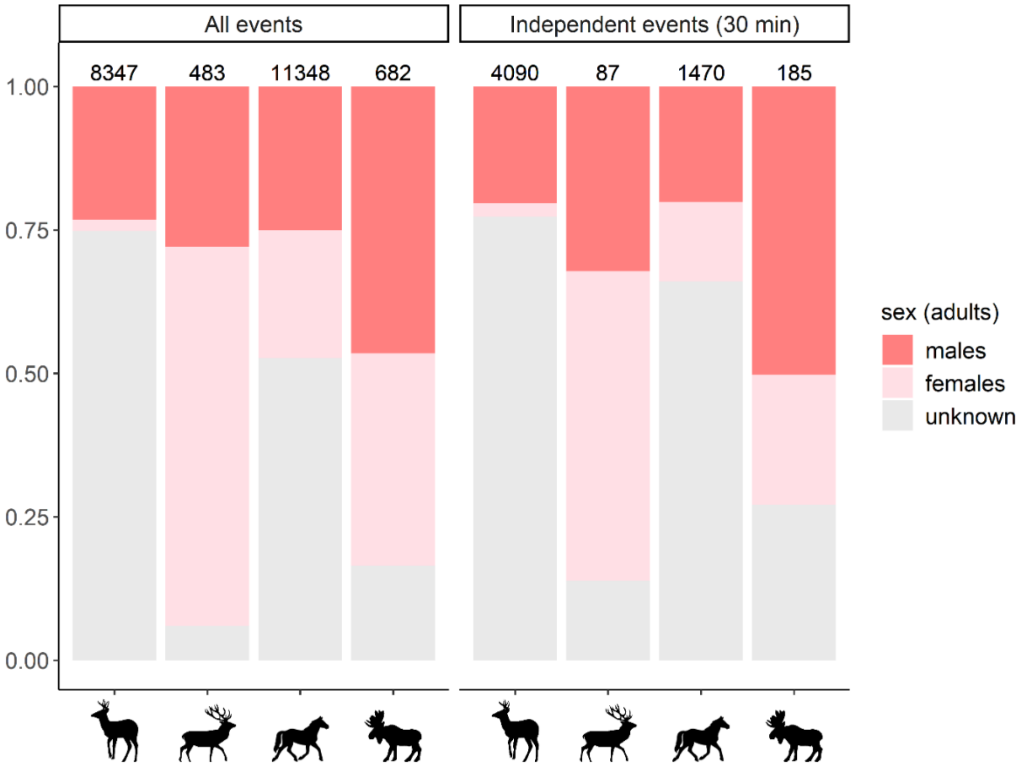

Figure C.1. Proportion of sexes of four ungulate species in the Sundre EMZ. Data pooled across sites and years.

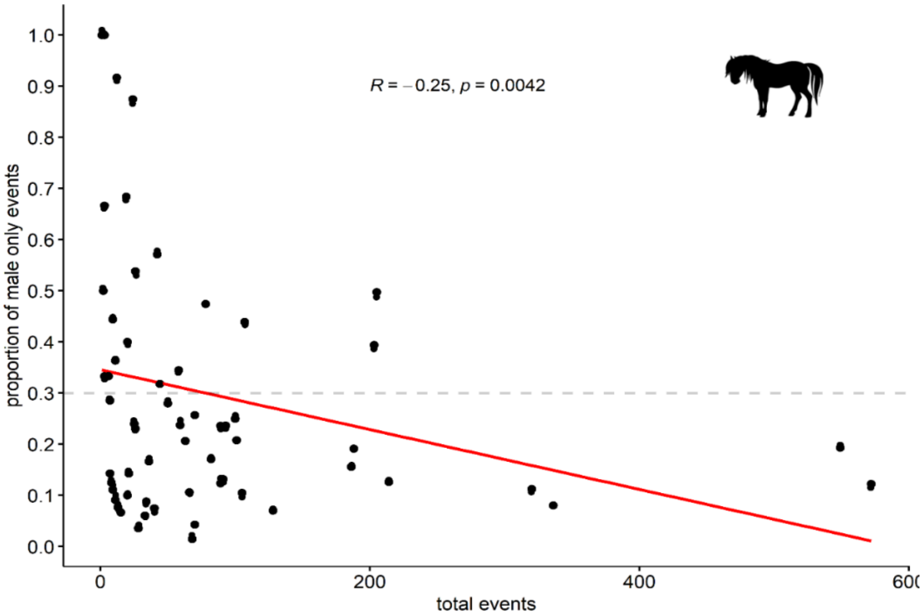

Figure C.2. Proportion of male only (bachelor) events compared to total events across all detections. Red line is Kendall correlation.

Figure C.3. Age and sex classes representing proportions of band size change in subsequent detections. Each point is a consecutive detection of a known band at a camera location.

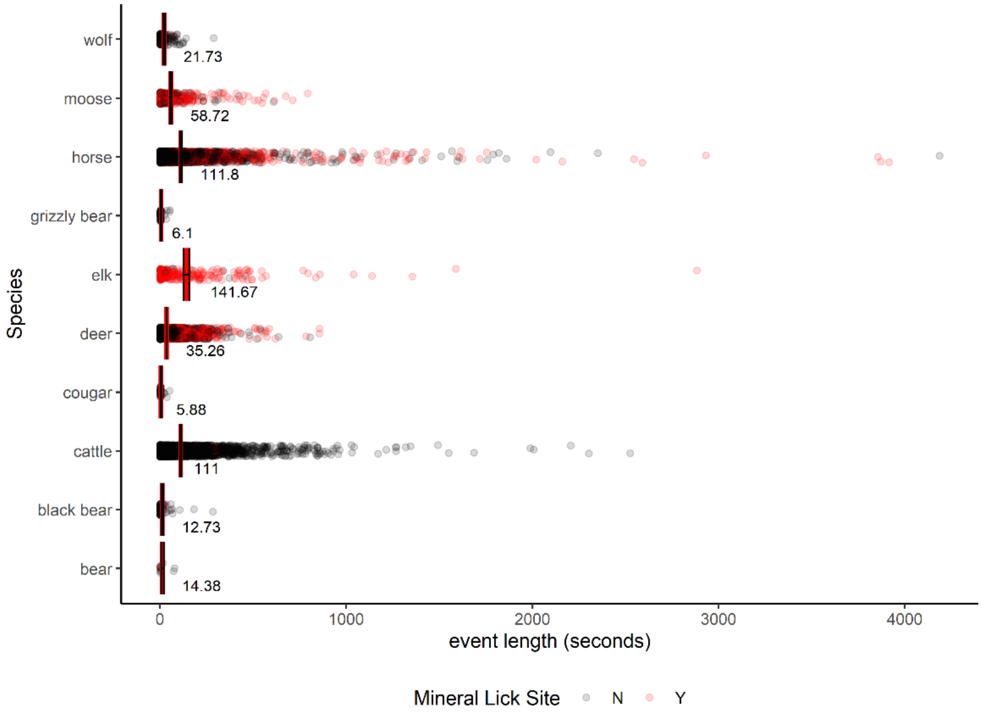

Figure C.4. Event length of different species in the Sundre EMZ at sites characterized as mineral licks and not. Note, predators and cattle were rare at mineral lick sites, whereas some species such as elk were detected predominantly at mineral sites. Red lines and numbers represent mean values.

Table C.1. Mean group size of different species in the Sundre EMZ.

Species[a]	**Mean group size**
Horse	3.41
Elk	2.86
Moose	2.17
Deer	2.37
Wolf	3.11
Grizzly bear	1.13
Cougar	1.31
Black bear	1.22

[a] Group size data for ungulate species includes a minimum of two animals to characterize group size. group size for predator species includes solo animals, except wolves where a minimum of two wolves was used to avoid the influence of solo wolves. Data from mineral lick sites where multiple groups congregate excluded.

Table C.2. Total monthly captures per 100 trap nights for species of interest. Data are pooled across cameras and years (supplement to Figure 3.2, Chapter 3).

Month	**cattle**	**cougar**	**deer**	**elk**	**grizzly bear**	**horse**	**moose**	**wolf**
Jan	0.17	0.08	15.37	0.17	0.39	21.00	1.97	1.02
Feb	0.41	0.09	12.74	0.00	0.00	7.20	2.53	0.28
Mar	0.18	0.55	11.57	0.00	0.00	5.67	3.23	1.06
Apr	0.50	0.50	15.60	0.00	0.72	20.45	1.12	0.56
May	0.67	0.54	57.15	1.35	0.76	47.49	1.35	1.68
Jun	11.28	0.40	106.33	1.96	1.72	47.85	2.89	1.56
Jul	37.63	1.63	183.44	9.74	1.48	62.96	13.12	4.70
Aug	45.91	1.24	102.90	4.56	2.96	58.32	7.88	6.12
Sep	51.47	1.10	70.36	1.04	2.33	62.27	7.73	4.38
Oct	26.07	1.21	67.67	0.52	0.97	62.64	8.27	4.34
Nov	4.74	0.23	43.95	0.08	0.40	20.99	3.57	1.94
Dec	0.24	0.32	20.60	0.08	0.17	28.67	2.31	0.80

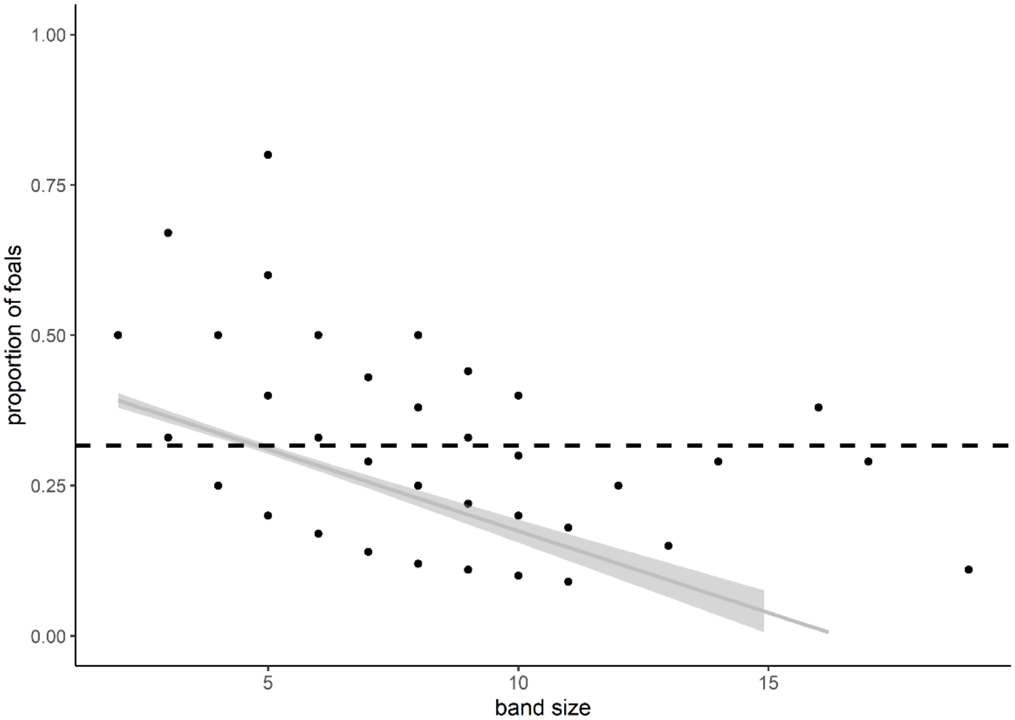

Figure C.5. Proportion of foals in a band relative to band size. Grey line and ribbon show Kendall correlation (-0.53, p<0.001) and confidence intervals.

Table C.3. Full model weights and log-likelihoods for summer occupancy models.

Model	**K**	**AIC**	**∆ AIC**	**Model likelihood**	**AIC Weight**	**Log-likelihood**	**Cumulative weight**	**2 log-likelihood**
<u>Horses</u>								
rangeland	5	618.1002	0	1	0.241369	-304.05	0.241369	-608.1
rangeland and terrain	6	619.1919	1.091735	0.579339	0.139834	-303.596	0.381203	-607.192
rangeland and water	6	619.3444	1.24417	0.536824	0.129573	-303.672	0.510776	-607.344
linear features	6	619.5852	1.484978	0.475928	0.114874	-303.793	0.62565	-607.585
open habitat	7	620.0064	1.906203	0.385543	0.093058	-303.003	0.718709	-606.006
rangeland + conifer	6	620.0951	1.994916	0.368816	0.089021	-304.048	0.807729	-608.095
rangeland +TRI + water	7	620.1024	2.00224	0.367468	0.088695	-303.051	0.896425	-606.102
Disturbance	7	621.0034	2.9032	0.234195	0.056527	-303.502	0.952952	-607.003
thermal	8	622.0779	3.977705	0.136852	0.033032	-303.039	0.985984	-606.078
NULL	2	623.7924	5.692244	0.058069	0.014016	-309.896	1	-619.792
<u>Elk</u>								
rangeland	5	108.8927	0	1	0.336442	-49.4464	0.336442	-98.8927
rangeland + conifer	6	110.1329	1.240181	0.537896	0.180971	-49.0664	0.517413	-98.1329
rangeland and water	6	110.7148	1.822112	0.402099	0.135283	-49.3574	0.652697	-98.7148
rangeland and terrain	6	110.8831	1.990377	0.369654	0.124367	-49.4415	0.777064	-98.8831
open habitat	7	112.1771	3.284363	0.193557	0.065121	-49.0885	0.842185	-98.1771
linear features	6	112.4957	3.602936	0.165056	0.055532	-50.2478	0.897717	-100.496
rangeland +TRI + water	7	112.7077	3.814936	0.148456	0.049947	-49.3538	0.947664	-98.7077
Disturbance	7	113.5523	4.659624	0.097314	0.032741	-49.7762	0.980404	-99.5523

thermal	9	115.7381	6.845351	0.032625	0.010976	-48.869	0.991381	-97.7381
NULL	2	116.2216	7.328833	0.025619	0.008619	-56.1108	1	-112.222
<u>Cattle</u>								
Disturbance	7	389.0308	0	1	0.391296	-187.515	0.391296	-375.031
open habitat	7	390.3221	1.291311	0.524319	0.205164	-188.161	0.59646	-376.322
linear features	6	391.0609	2.030083	0.362387	0.141801	-189.53	0.738261	-379.061
NULL	2	392.4624	3.431576	0.179822	0.070364	-194.231	0.808625	-388.462
rangeland + conifer	6	392.5631	3.532271	0.170993	0.066909	-190.282	0.875533	-380.563
rangeland	5	393.4693	4.438536	0.108689	0.042529	-191.735	0.918063	-383.469
rangeland and terrain	6	393.5316	4.500837	0.105355	0.041225	-190.766	0.959288	-381.532
rangeland and water	6	395.0171	5.986328	0.050129	0.019615	-191.509	0.978903	-383.017
rangeland +TRI + water	7	395.2952	6.264352	0.043623	0.017069	-190.648	0.995972	-381.295
thermal	8	398.1834	9.152552	0.010293	0.004028	-191.092	1	-382.183

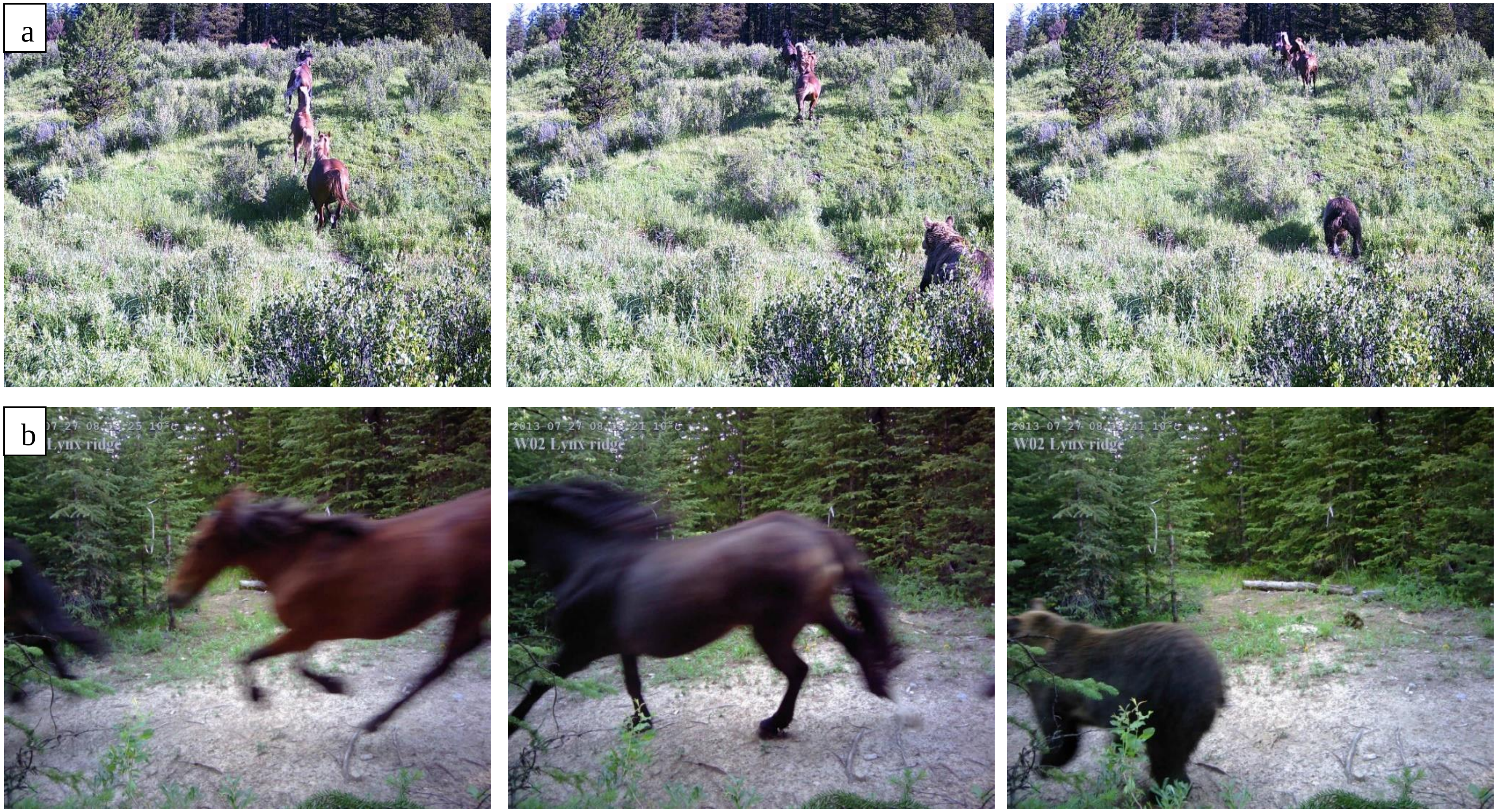
a
b
07-27 08:
Lynx ridge
2013-07-27 08:
W02 Lynx ridge
2013-07-27 08:
W02 Lynx ridge

Plate C1 (pages 196 – 197). Top (a) and center (b) series are grizzly bear chases captured in different camera trap surveys in the Sundre EMZ. The centre series is from the Ya Ha Tinda elk project study (Berg et al., 2015). Lower series (c) are examples of other interactions with predators observed. From left: horses observing a wolf pass in proximity (shadows at right of images are horses); example of heavy scarring from presumed predation attempt; injuries to collared mare from predator attack (horse was euthanized [credit: D. Glover]).


a
b

Plate C2 (pages 198 and 199). Panels a and b are examples of space use by horses and other ungulates and interactions at mineral licks/wallows, . Mineral licks and wallows are shown top and center where interactions appeared to follow expected body mass hierarchies at limiting resources (Hall et al., 2018; Lundgren et al., 2021); grazing with cattle showing in lower series (images are from separate events). Panel c shows horses pawing in snow in winter; deep snow fall in winter; and low temperatures occurring in late winter.

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Hall, L. K., Larsen, R. T., Knight, R. N., & McMillan, B. R. (2018). Feral horses influence both spatial and temporal patterns of water use by native ungulates in a semi-arid environment. *Ecosphere*, *9*(1). https://doi.org/10.1002/ecs2.2096

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