Using remote camera traps to monitor population demographics and community ecology of divii (Dall's sheep): Part of a community-based monitoring program in the Northern Richardson Mountains, NT

By

Sydney Lee Goward
Bachelor of Natural Resource Science, *Honours*, Thompson Rivers University (2018)

A thesis submitted in partial fulfillment of the requirements for the degree of

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SUPERVISORY COMMITTEE

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Supervisory Committee

Dr. Jason T Fisher, School of Environmental Studies
Co-Supervisor

Dr. Trevor C Lantz, School of Environmental Studies
Supervisor

ABSTRACT

The warming Arctic is undergoing rapid ecological change, influencing wildlife populations, mammal community interactions, and ultimately, the persistence of many species. Collecting the species monitoring data required for sound stewardship decisions in these remote areas is a major challenge. Remote wildlife cameras, facilitated through community-based monitoring programs, offer a solution to provide these critical data. In this thesis, I employed novel methods in remote camera trapping as part of a community-based monitoring program to investigate Dall's sheep population demography and predator-prey dynamics with grizzly bears. In Chapter 2, I explored the ability of remote wildlife cameras to estimate population demographics (lamb:nursery, ram:nursery, and ram classification proportions), as compared to currently standardized aerial surveys. These metrics are imperative to assessing population status and predicting population trends. I found that camera data, accumulated sufficiently through time and discretized in appropriate biological seasons produced reliable lamb:nursery, ram:nursery, and ram classification proportions comparable to those obtained from aerial surveys, and produced similar population status trends between the two methods. To my knowledge, this is the first study employing remote cameras to estimate productivity (lamb:nursery ratio) and adult sex ratios in a wild, un-marked sheep population, and marks a significant advancement in wildlife monitoring with remote cameras. In Chapter 3, I examined the temporal coexistence of Dall's sheep and grizzly bears, in a core habitat area, at different times of the year. I used remote camera data to derive a time-to-event model investigating if and how grizzly bears are tracking nursery groups and ram bands. I also evaluated the differences and similarities in diel activity patterns between the species to estimate temporal niche partitioning. I found clear temporal segregation of nursery groups and grizzly bears, and showed that grizzly bears were more closely tracking nursery groups than ram bands, especially early in the spring when lambs are most vulnerable to predation. The results indicate that camera traps can yield fine-resolution insights into predator-prey relationships. This study provides a new method to monitor Dall's sheep population demography, as well as new information on Dall's sheep and grizzly bear relationships. Incorporating a remote camera system into wildlife monitoring programs allows for a more comprehensive examination of demography, while fostering an opportunity to explore further questions related to community-based monitoring and management.

TABLE OF CONTENTS

LIST OF TABLES

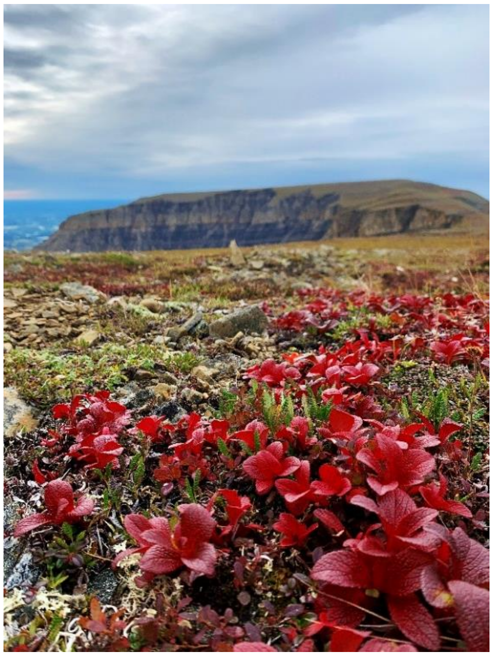
LIST OF FIGURES

ACKNOWLEDGMENTS

I have a lot to say here. I have tried to be as concise as possible, but when you are part of a large, collaborative project like this, there is so much recognition to give to others, and I think this actually reflects a very special part of my grad school experience. So here we go.

At the University of Victoria, I was fortunate to find a community of creative and engaging researchers. It was an absolute pleasure to be co-supervised by two exceptional scientists and mentors: Dr. Jason Fisher and Dr. Trevor Lantz. I'm proud to have been trained by you both in the fine art of science. I recognize I put you through perhaps a more non-traditional grad student supervisory experience, but thank you for ebbing and flowing along with me the whole way. Your willingness to oblige my way of learning and working, while issuing you experiential errs of caution, allowed me to stay true to myself, while also developing as an academic and as a person. Thank you both, truly so much, for brining me onto this project. To each and every ACME & ALE lab mate, and the "Sea Buckthorn" cohort: you challenged and supported my work in such diverse ways, and I'm grateful for the relationships I've made in the process – thank you. To my thesis-pal Becca Smith: thank you for pushing side-by-side through this insanely wild time, and for the many nights separated by a half wall in your studio apartment providing late-night counsel. To Laura Eliuk: you inspired and mentored me in so many ways: teaching me how to deploy cameras, teaching me all I know about tagging camera data, and preparing me for far too much time spent in R Studio processing said camera data. But more so, thank you for all the laughs along the way. I appreciate you so much. To Andrew Barnas (my invaluable co-author and international conference travel buddy, but more importantly, a great mentor and pal): you saved this thesis in some of the darkest moments during grad school, so cheers to you.

The Gwich'in Renewable Resources Board (GRRB), and the University of Victoria have worked hard to form an exemplary partnership in collaborative research. I am so grateful to have been able to both support and learn from this collaboration. To all the GRRB staff (both past and present) who supported this work and myself, whether through personal encouragement, managing our finances, or being a friendly face at the office – Hai' Cho! To Steve Andersen: you exceed any expectations I could have had of a study partner. Your leadership and commitment to the divii project truly made this research and partnership possible. I can't thank you enough for all the above and beyond support and mentorship you provided from start to finish. It's been such a pleasure to know you and work with you, and I will miss our time together dearly! To Édouard Bélanger: thank you for your dedication to this project, right from its conception to where it is today. It is so cool to know the history of where this project started, and to see the research now developed, which has been largely inspired by from your dedication to pursue community interests around divii. You make me excited about this work, and I thank you so much for staying on board with our team throughout the whole process. To Kristi Benson: I am truly grateful to have met and shared space with you. Whether it was our road trips together to community or connecting virtually from a far, I received some of the most valuable mentorship in these times. Having the opportunity to connect with the divii traditional knowledge study side of the divii project was fundamental to the way I conducted myself as a non-local, non-Gwich'in scientist studying Gwich'in land and animals, and I am so truly grateful for that. Your work with the Gwich'in Tribal Council is inspiring, and I hope I've paid tribute to your hard work on the divii project in this thesis.



It is a privilege not taken lightly to be able to learn from the land, animals, and people of Gwich'in and Inuvialuit lands, where this research took place. Before my involvement in the divii project, there was extensive work put in from the community members and local organizations. You could say this is expected from a community-based monitoring program like the divii project, but I can tell you - these people are beyond passionate and dedicated. Their culture, tradition, and deep ties to this land are so obvious to an outsider like me, and it is with the deepest sincerity that I say Hai' Cho, and respectfully admire the work and heart that has been put into this project. There is a long list of individuals who are the root of the success of this work; I hope I have not missed anyone! Thank you to: Freddie Furlong, Edward McLeod, Dale Semple, Trisha Greenland, Jordan Norman-Goose, Edward Lazarus, Charles Wright, Perry Villebrun, Jamis Charlie, Kristen Callaghan, Tyler Sittichinli, Davie Edwards, Jameson Wright, Anthony Kay, Robert Neyando, Jim Kay, Jessi Pascal, James Blake, Ian McLeod, Eugene Pascal, Sandra Hamel, Sam McLeod, Devon Arey, Cody Kogiak, Eugene Pascal, Crystal Koe, and Laura Nerysoo.

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And of course, my family: I'd like to take this opportunity to first apologize for putting you all through another degree. It is not lost on me how lucky I am to have such patient, loving, and supportive family, constantly rooting for my success. To my parents, sister, extended family, and close friends that feel like family: thank you - I love you all so much. To Frederick: living life together through this season has been an absolute blessing. These past (almost) three years of grad school encapsulate a truly interesting time of flexibility, growth, and experiences that I'm sure we will look back on with some really fond memories. Thank you for encouraging and supporting this work and my personal development in so many wonderful ways. An honourable mention of acknowledgement is also owed to the HarberCraft for providing unreasonably good times chasing salmon, a sanity sanctuary on the water, and a compelling reason to not work on my thesis.

It's curious how sometimes the people who were not directly involved in a particular experience can have such an impact on the experience itself. Those are the people who have maybe opened a door or said something encouraging or influential in years past, seemingly unrelated to the experience at hand. To Karl Larsen and Laura Trout – I wouldn't have ever considered ever going to grad school if it wasn't for you. May you both know the impact that your presence in years past of my life has had.

Finally, to the wild sheep community at-large (the hunter-conservationists, the non-profit organizations, the government biologists, and the wild sheep enthusiasts alike): it's been such an incredible journey stepping into this community and being fully embraced by all who share the admiration and commitment to wild sheep. It was truly the experience of a lifetime to devote so much time and space to studying these incredible mountain monarchs, and meeting the most passionate people along the way, that have dedicated their lives to conserving and appreciating these animals. There is no species I'd feel more honoured to learn from than the iconic Dall's sheep.

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DEDICATION

To the people and the sheep.

"The universe is wider than our views of it."

– Henry David Thoreau in Walden

ABBREVIATIONS

ACME -------- Applied Conservation and Macro Ecology (lab)
ALE ----------- Arctic Landscape Ecology (lab)
CBM ---------- community-based monitoring
GCLCA -------- Gwich'in Comprehensive Land Claim Agreement
GRRB ---------- Gwich'in Renewable Resources Board
GNWT--------- Government of the Northwest Territories
GSA ----------- Gwich'in Settlement Area
GTC ----------- Gwich'in Tribal Council
NT ------------- Northwest Territories
UVic ---------- University of Victoria
YT ------------- Yukon Territory

CHAPTER 1. INTRODUCTION

1.1 COMMUNITY-BASED WILDLIFE MONITORING

Wildlife populations are facing challenges, unprecedented in our time, from anthropogenic developments, natural disturbances, and global climate change, the impacts of which are often interconnected and cumulative (Fisher and Burton 2018, Venier et al. 2021). Monitoring wildlife populations is a fundamental precursor to informed stewardship decisions - decisions which have never been more complex or critical to the persistence of many wildlife populations. However, wildlife monitoring presents vast challenges, from acquiring to interpreting data in a locally relevant but scalable manner (Steenweg et al. 2017). Furthermore, it is not science in isolation that best informs stewardship decisions (Decker et al. 2016). As pressures on wildlife populations accumulate, our solutions to these problems must also be cumulative, featuring a collection of science, local knowledge, Indigenous traditional knowledge, and sociopolitical objectives (Henri et al. 2018, Hessami et al. 2021).

Community-based wildlife monitoring programs are based on community-specific values and priorities. Community-based monitoring (CBM) programs can improve the effectiveness and sustainability of modern wildlife monitoring (Berkes et al. 2007, Conrad and Daoust 2008, Popp et al. 2019, Fisher et al. 2021, Yarchuk 2023) and generally employ a blend of methods from classic biological science, social science, and Indigenous traditional knowledge (Conrad and Daoust 2008, Wong et al. 2017, Popp et al. 2019). Today, there is an increasing recognition of the role of Indigenous knowledge systems and reconciliation in ecological research (Jessen et al. 2022), and CBM is increasingly recognized as an expression of self-governance and traditional land stewardship (Reid et al. 2021, Lamb et al. 2022, Yarchuk 2023).

Wildlife monitoring in the Canadian Arctic is a scenario that illustrates the pressing need for efficient community-driven monitoring programs, especially for species of significant cultural and economic value. Temperatures in the Arctic are increasing at a rate nearly four times the global average

(Rantanen et al. 2022), disproportionately impacting wildlife and Indigenous peoples residing in these landscapes (Ford and Smit 2004, Parkinson and Berner 2009, Brinkman et al. 2016) and creating an imminent need to better understand these landscapes and set up more robust monitoring programs. Climate change is altering tundra vegetation productivity and phenology, modifying snow conditions, and increasing the frequency and severity of extreme weather events (Mann et al. 2017, Myers-Smith et al. 2020). These changes are impacting vertebrate species in ways that are currently not well understood, due to the remoteness and inherent difficulty in studying arctic wildlife.

1.2 THE CASE OF DALL'S SHEEP

Dall's sheep (*Ovis dalli dalli*), a species of cultural, ecological, and economic significance (Gwich'in Elders 1997, Benson 2023), is an example of one such species, where uncertainty about population demographics, predation, and competition complicate stewardship decision-making (Aycrigg et al. 2021). Dall's sheep thrive in some of the harshest terrestrial environments, but rapid climate and ecological change in these landscape (Myers-Smith et al. 2020, McCrystall et al. 2021) is creating uncertainty about Dall's sheep population stability (Rattenbury et al. 2018, Van de Kerk et al. 2020).

A crucial element of monitoring Dall's sheep is regularly estimating population demographics, i.e., the age and sex structure of a population. Population demography data are expensive and difficult to obtain, but are critical in understanding population fluctuations and modelling future trends. Dall's sheep herds exist in a state of fission-fusion dynamics, where their range use varies seasonally and by sex (Rachlow and Bowyer 1998, Van de Kerk et al. 2020, Aycrigg et al. 2021), further complicating our ability to monitor these populations. Aerial surveys are currently the accepted method for determining key population demographics of wild sheep, but detecting both short- and long-term fluctuations is difficult to confidently assess (Whitten 1997, Udevitz et al. 2006). Helicopter surveys also cause significant stress to wild sheep (Frid 2003), limiting the amount of data that can be collected, while limiting local community participation in wildlife monitoring. Further, aerial surveys do not offer a method to concurrently understand how the broader mammal community co-exists on the land, yet understanding these relationships is key to conservation and stewardship of the species.

Owing to the remoteness and inherent difficulty in studying Dall's sheep, we have limited consistent population monitoring and a limited understanding of the factors that may influence populations, such as predation, competition, and climate change (Aycrigg et al. 2021). Predator-prey interactions between Dall's sheep and an apex predator, the Grizzly bear (*Ursus arctos*), are widely recognized as important, but poorly understood (Frid 1997, Rachlow and Bowyer 1998, Benson 2014, Lambert Koizumi and Derocher 2019, Benson 2023). These two iconic species are highly valued by both Indigenous and non-indigenous communities for cultural, economic, and ecological reasons (Benson 2014, 2023), but concerns exist regarding their stable coexistence in the wake of cause-uncertain sheep population declines (Lambert Koizumi and Derocher 2019). Habitat selection, seasonal migration patterns, and sexual segregation have been well studied in Dall's sheep, (Hoefs 1978, Barichello et al. 1987, Rachlow and Bowyer 1998, Nagy et al. 2013, Van de Kerk et al. 2020, Aycrigg et al. 2021), but details of their temporal behaviour have received little attention. As a result, there are currently important knowledge gaps in resource partitioning of Dall' sheep with other species, such as grizzly bears, and how these relationships may impact the population (Lambert Koizumi et al. 2011, Benson 2023). These mechanisms are important for the conservation and management of both predator and prey species in mammal communities (Linnell and Strand 2000, Gómez-Ortiz et al. 2019).

1.3 I SPY THROUGH A CAMERA'S EYE: REMOTE MONITORING SOLUTIONS

Remote wildlife cameras offer not only a solution to data collection in remote environments, but also to the complex questions facing community-based monitoring programs. With continuous longitudinal sampling, cameras provide a method for monitoring population demography and densities

(Becker et al. 2022, Foley et al. 2023), habitat selection (Dertien et al. 2017), mammal responses to disturbances and restoration (Dickie et al. 2023), and mammal community interactions such as predator-prey relationships (Tattersall et al. 2020, Amir et al. 2022, Frey et al. 2022). Compared to other science-based tools for wildlife monitoring such as aerial surveys or telemetry, remote cameras are relatively inexpensive and easy to implement by individuals and communities, and thus “democratize” research (Fisher et al. 2021). Furthermore, cameras provide additional eyes on the land year-round, allowing the animals and the land to tell their stories, which are of great value and importance to communities.

1.4 THESIS OBJECTIVES

The solutions to assessing Dall’s sheep must be cost effective, properly designed to optimize data quality, and minimize disturbance (Lambert Koizumi et al. 2011). Incorporating a remote camera system into a monitoring program allows for a more comprehensive examination of demography, with additional benefits, such as examining predator-prey relationships that may be influencing the population. In this thesis, I examine Dall’s sheep population demography and predator-prey interactions, as part of a broader Gwich’in-led community-based monitoring program. In Chapter 2, I explore the ability of remote wildlife cameras to estimate population demographics, as compared to aerial surveys. In Chapter 3, I examine the coexistence of Dall’s sheep with a well-known predator, grizzly bears. In Chapter 4, I share my experience of observing the land and animals for a camera-day equivalent of 14,604 days. I share stories of the unique observations I made, and examine additional questions of interest brought forth by communities that do not fit a typical scientific inquiry. Finally, I provide my concluding remarks on what this project has taught me of wildlife stewardship in it’s broadest conceptualization.

1.5 CRITICAL CONTEXT

In application, social and biological sciences are wholly connected, and due care must be given in a project like this to set the social foundation for meaningful scientific work. Though the data chapters rely on the sharp corners of classic science, I have been exploring opportunities to soften those corners, with careful consideration of knowledge dissemination and community values. People are part of ecosystems, and emotional and physical relationships exist between people and the land. These elements must be considered when designing a study and interpreting results. Although I submit this thesis in partial fulfillment of the requirements of the *Master of Science degree*, there is a critical human context to this study that focuses on the importance of language, the community interest in this science, and the sociopolitical landscape of this research.

1.5.1 The divii project

The Northern Richardson Mountains in the Northwest Territories are home to the northernmost population of Dall’s sheep in Canada. According to local community members and Gwich’in knowledge holders, this population of sheep has been considered healthy and of low conservation concern until recent years (Benson 2023). This population has shown dramatic fluctuations since population surveys commenced in the 1980s (Davidson et al. 2018). Extremely low numbers in 2014, limited demographic data, and unknown factors causing population fluctuations have prompted significant concern from local communities and governments (Lambert et al. 2011, Environment Yukon 2019). A draft management plan for this population identified that future monitoring programs for Dall’s sheep should address knowledge gaps, such as more robust population monitoring, and research into the factors that may be driving the population such predation, competition, emerging diseases, and climate change (Working Group for Northern Richardson Mountains Dall's Sheep 2008, Lambert Koizumi et al. 2011).

My research is part of a broader, community-based monitoring program, *the divii project*, aimed at filling gaps in the current knowledge of Dall’s sheep (*divii* in Gwich’in language) in the Northern

Richardson Mountains. The divii project is led by the Gwich'in Renewable Resources Board[1] (GRRB) and Ehdiitat Renewable Resource Council (ERRC), and is driven by community values and research interests. The divii project consists of two major components: 1) a traditional knowledge study led by Kristi Benson and Sharon Snowshoe of the Gwich'in Tribal Council (GTC) Department of Culture and Heritage (Benson 2023), and 2) a scientific camera-trapping program led by the GRRB and ERRC. The objectives of the camera-trapping program are to:

1. Determine annual and seasonal population demographics of divii using cameras
2. Model annual changes to these demographic parameters
3. Compare the camera demographics to those obtained from aerial surveys
4. Examine habitat changes, predation, or other variables that are known to affect populations
5. Provide recommendations that will inform the community-based monitoring program

My research in this thesis specifically relates to the camera trapping component of the divii project, and was thus conducted in a collaborative partnership with the GRRB and in communication with the four Gwich'in Renewable Resource Councils (Ehdiitat, Tetlit, Nihtat, and Gwichya Gwich'in). I also maintained communication with contacts at the GTC throughout the research to ensure that this work was complementary to the traditional knowledge study component of the divii project, as future stewardship decisions made by communities and co-management governments will likely be informed by the braiding of knowledge from both projects.

As a non-Gwich'in and non-local researcher invited to the GSA for the purpose of working on the camera array portion of this project, I have the responsibility of ensuring I am doing my work in a way

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[1] The GRRB is the main instrument for wildlife, fish, and forest management in the Gwich'in Settlement Area (GSA), established under the Gwich'in Comprehensive Land Claim Agreement (GCLCA) (*Gwich'in Comprehensive Land Claim Agreement* 1992). The GCLCA further established the current co-management structure between the Government of the Northwest Territories and the GRRB, of natural resources for the GSA.

that respects Gwich'in people, culture, and values. To pay respect to this unique project, I have leaned on my diverse background, supported by academic creativity, to hopefully bring a unique approach to the natural sciences. Ecological research is not always about discovery, but is about searching for knowledge that already exists (Absolon 2011). In this study, I respect that the knowledge I seek is already known to animals, plants, and land. It is my job to listen to them with the tools I have (primarily tools of modern science, as detailed in the following chapters), carefully phrase those observations, and respectfully share these stories.

1.5.2 The Gwich'in Settlement Area

The Gwich'in Settlement Area (GSA), covering approximately 56,935 km^2 of land in Canada's Northwest Territories, was established after the signing of the Gwich'in Comprehensive Land Claim Agreement (GCLCA) in 1992 (*Gwich'in Comprehensive Land Claim Agreement* 1992). The GSA is situated on the traditional territories of the Gwich'in and Inuvialuit people, and prior to the GCLCA this land was largely part of Treaty 11 (established in 1921). The GSA is home to approximately 5,100 Gwich'in, Inuvialuit, Métis, and non-Aboriginal people, in the four modern-day settlements of Inuvik, Aklavik, Fort McPherson, and Tsiigehtchic (Aporta et al. 2014). With the signing of the GCLCA, the Gwich'in people and land are no longer under treaty, and are now "Gwich'in Comprehensive Land Claim Agreement participants". Aklavik and Inuvik are also part of the Inuvialuit Settlement Region, which was established under the *Inuvialuit Final Agreement* in 1984. The land of the GSA features a striking blend of boreal forest, arctic and alpine tundra, the Mackenzie River delta, and prominent mountain ranges (the Mackenzie Mountains and the Northern Richardson Mountains). These unique environments are home to a variety of fish, wildlife (Figure 1), and plant species that maintain their vast cultural and ecological value to this day (Gwich'in Elders 1997, Aporta et al. 2014).

Figure 1. Some animals of the Northern Richardson Mountains in the Gwich'in Settlement Region, as captured by remote wildlife cameras in the divii project. Left to right, top row: Dall's sheep lambs, Lynx. Bottom row: Muskoxen, Grizzly bear. Credit: Gwich'in Renewable Resources Board.

1.5.3 Sharing Gwich'in language in this thesis

Throughout this thesis, I have included certain words in Gwich'in language, mainly in the communication of animals and places. In general, I have provided English words in regular font and Gwich'in in *italics.* There are several Gwich'in dialects in this region. I have indicated which dialect I use (Gwichya Gwich'in (G) or Teetl'it (T)), where specified.

As a non-Gwich'in person, sharing Gwich'in language respectfully and appropriately is of critical importance. In 2022, I received a teaching from a Saulteau First Nation community leader that *language is a gift, and sharing it is a gift*, and so it is my intention that by including Gwich'in words, I am respectfully recognizing and affirming the deep connections and stories of the places and animals I refer to. All Gwich'in language I use has been shared verbally or in open-source Gwich'in resources (Gwich'in

Elders 1997, Gwich'in Social & Cultural Institute 2003, Aporta et al. 2014, Benson 2023) and is shared in my writing with the utmost respect. Conversations about the importance of language and what to share have been discussed with the GRRB and the GTC on an ongoing basis. I am grateful to have received advice and direction regarding sharing language from Gwich'in elders and Gwich'in Tribal Council (GTC) mentors (Alestine Andre, Kristi Benson *pers. comm*.). I recognize that these Gwich'in words are truly a gift to have been shared, and I hope the readers of this thesis will receive them as such as well.

A note on language surrounding sheep

The Gwich'in word for Dall's sheep is *divii*; however, throughout this thesis, divii is not given as a direct translation for "wild sheep" or "Dall's sheep". As Indigenous languages are so tightly connected to place and story, it would be inappropriate to use when referring to Dall's sheep as a species (who's range spans many traditional territories in four American and Canadian states, provinces, and territories), therefore divii is only used in reference to Dall's sheep specially on Gwich'in land (i.e., our study population in the Northern Richardsons). I use the standard English name "Dall's sheep" when referring to species more broadly, anywhere across their natural range not exclusive to Gwich'in lands (note: in Chapters 2 and 3, which have been written for publication, I generally maintain consistency with the English common name and do not use "divii" throughout the papers). I have used the term "wild sheep" when referring to multiple species of wild sheep (i.e., any combination of Dall's sheep, Stone sheep, Bighorn sheep, etc.). For example, much of the methodology in this project could be applied to multiple species of sheep; therefore, in those cases, I use the term "wild sheep".

CHAPTER 2. REMOTE CAMERAS SAMPLE MOUNTAIN UNGULATE POPULATION DEMOGRAPHY, AS COMPARED TO AERIAL SURVEYS, IN AN INDIGENOUS-LED COMMUNITY-BASED MONITORING PROGRAM

This manuscript is in progress for publication with Remote Sensing for Ecology and Conservation with co-authours Dr. Andrew Barnas[1], Édouard Bélanger[2], Steve Andersen[2], Dr. Trevor Lantz[1], and Dr. Jason T Fisher[1].
[1]*Department of Environmental Studies, University of Victoria*
[2]*Gwich'in Renewable Resources Board*

2.1 ABSTRACT

Wildlife demography is a crucial parameter in monitoring and modelling a population's persistence through time. Historically, aerial surveys have been the most common method for obtaining demographic data for large mammals, but they come with limitations such as sample size, temporal constraints, costs, and cause significant disturbance to wildlife. Remote cameras are an emerging non-invasive alternative to wildlife monitoring, providing continuous longitudinal and repeated sampling of a population, but are challenged by species that aggregate in fission-fusion dynamics, such as Dall's sheep (*Ovis dalli dalli*). Through an Indigenous-led, community-based monitoring program, this study compared two methods of acquiring Dall's sheep population demography data over three years. The objective was to determine the variability of lamb:nursery and ram:nursery ratios, and ram classification as captured by remote cameras and aerial surveys and to assess the reliability of the foremost for three years. We found that camera data accumulated sufficiently through time and discretized according to biological seasons produced reliable lamb:nursery, ram:nursery, and ram classification proportions (as compared to aerial surveys) ultimately indicating similar population status trends between the two methods. Incorporating a remote camera system into the monitoring process supports a comprehensive examination of demography, while fostering an opportunity to explore further questions related to community-based monitoring and management.

2.2 INTRODUCTION

Monitoring wildlife in the world's rapidly changing ecosystems is of chief importance, but is notoriously difficult. Demography is a key parameter for monitoring wildlife population persistence, as it describes the composition of a population (such as age and sex structure) and informs growth forecasts, underpinning most management decisions (Sandercock 2006, Lebreton and Gaillard 2016, Taylor et al. 2022, Foley et al. 2023). However, wildlife demography is often difficult to quantify because of survey logistics and species ecology, particularly immigration, emigration, and seasonal habitat use. Furthermore, for species that aggregate in fission-fusion dynamics - the process of groups forming and separating over time within a population (Cross et al. 2005) -, any given demographic sample is likely non-representative of the whole population, a noted challenge in quantifying demography (Johnson et al. 2010, Lebreton and Gaillard 2016, Foley et al. 2023).

In any demographic sample, it is critical to consider both the true biological state, and the observed state, which deviates from the truth as a result of sampling error (MacKenzie et al. 2002). Understanding variability in sampling is crucial for precisely estimating biological processes. Temporal variability in sampling affects ecological inferences, as samples vary in time. However, in a robust state sampling design with repeated measures over the right timespan, samples should converge on a value that reliably approximates the state process (MacKenzie et al. 2002, Fischer 2011).

Aerial surveys by observers in fixed-wing aircraft or helicopters are the most common method for obtaining demographic data from many large mammals species, and despite their many benefits, they come with limitations (Gonzalez-Voyer et al. 2001, Udevitz et al. 2006, Lubow and Ransom 2016, Foley et al. 2023). Though spatially extensive enough to capture a large sample of the population, aerial surveys provide only a single snapshot of data for one point in time (Udevitz et al. 2006), are expensive, and largely exclude community member participation in research and monitoring. Further, aerial surveys cause disturbance to wildlife (Udevitz et al. 2006, Foley et al. 2023), and can be dangerous for wildlife biologists (Sasse 2003). Thus, there is a need for alternative methods to investigate wildlife demography which addresses the limitations of aircraft surveys.

To address these issues, remote cameras offer an alternative non-invasive approach to wildlife monitoring. Cameras can be used to gain a more comprehensive understanding of ecology, including reliable population density estimates (Burgar et al. 2018, Becker et al. 2022), predator prey interactions (Arthur and Prugh 2010, Kemna et al. 2020, Amir et al. 2022, Barnas et al. 2022a), and changes in behaviour in response to anthropogenic or environmental disturbance (Caravaggi et al. 2017, Bell et al. 2023). Simultaneously, cameras also collect data on habitat use, occupancy rates, mammal community interactions, and other variables impacting populations, something lacking in aerial surveys (Becker et al. 2022). With their unique continuous sampling, cameras may also offer a method superior to periodic aerial surveys for demographic inferences. Many ungulate species form loose ephemeral groups in time and space, and these fission-fusion dynamics have made point estimates intractable: camera traps overcome this problem and provide an avenue for better understanding such dynamics. However, each camera contributes only a small sample of a population. Samples will vary temporally based on factors including temporary emigration (Stewart et al. 2018), fission-fusion dynamics, sexual segregation, seasonal habitat use (Dertien et al. 2017), mortality, and birth. The population itself also varies seasonally via mortality, birth, immigration, and dispersal. By integrating samples across time periods defined by species biology, we can use cameras to assess demography and understand fission-fusion dynamics over time.

Mountain ungulates - which predominantly exhibit complex fission-fusion dynamics - such as Bighorn sheep (*Ovis canadensis*), Stone's sheep (*Ovis dalli stonei*), Mountain goat (*Oreamnos americanus*), Ibex (*Capra ibex*), and Chamois (*Rupicapra rupicapra),* have recent monitoring histories dominated by aerial and transect surveys (Gonzalez-Voyer et al. 2001, Brambilla et al. 2020). One such species is Dall's sheep *(Ovis dalli dalli).* Native to northern British Columbia, Yukon Territory (YT), Northwest Territories (NT), and Alaska, Dall’s sheep are of rich cultural, ecological, and economical value (Lambert Koizumi and Derocher 2019, Benson 2023). The status of sheep populations is generally assessed via periodic aerial surveys, producing a total minimum count, productivity ratio (lambs per 100 nursery sheep), sex ratio (rams per 100 nursery sheep), and the proportion of rams in each horn curl category (half, three-quarter, or full curl) (Bunnell 1978, Hoefs and Bayer 1983, Simmons et al. 1984, Harris et al. 2008, Nagy et al. 2013, Environment Yukon 2019).

In the Northern Richardson Mountains of the Canadian Arctic (YT and NT), there is a Dall’s sheep population that has been steadily monitored via periodic aerial surveys every three to five years, since 1984. This population has shown significant fluctuations in minimum counts and demographic ratios, and is presently at low numbers based on historical fluctuations (Lambert Koizumi et al. 2011, Nagy et al. 2013, Bélanger and Davidson 2022). However, the accuracy of these aerial surveys for estimating demographic parameters is not well documented, leading to uncertainty regarding population size and age and sex structures (Lambert Koizumi et al. 2011, Nagy et al. 2013, Bélanger and Davidson 2022). Thus, there is significant concern for the population from local communities and co-management organizations. In response to this concern, the Gwich’in Renewable Resources Board (GRRB) and the Ehdiitat Renewable Resource Council (ERRC) launched a community-based monitoring program in 2018, focusing on testing remote cameras as a solution to monitoring concerns (Bélanger and Davidson 2022). The program directly involves local community members, and is rooted in traditional knowledge, providing an increased robustness in knowledge acquisition, and directly improving management outcomes (Smith 2005, Berkes et al. 2007, Brook et al. 2009, Johnson et al. 2015, Fast and Kovach 2019, Hovel et al. 2020, Thompson et al. 2020). For the scientific community, this approach offers a unique opportunity to test the effectiveness of remote camera programs to monitor a species exhibiting complex fission-fusion dynamics, such as Dall’s sheep.

The objective of this study is to compare estimates of demographic parameters in Dall's sheep from remote camera and aerial survey data collected as part of an Indigenous-led, community-based monitoring program. We investigated three key demographic metrics: lamb:nursery and ram:nursery ratios, and ram classification by selecting sampling periods that best represent the biological and statistical temporal variability in survey data. We hypothesize that the demographic proportions captured by the cameras will be similar to those captured by the aerial surveys.

2.3 METHODS

2.3.1 Study area

The sampling frame for this study is the Northern Richardson Mountains, along the northern YT-NT, Canada border. This rugged mountainous terrain is dominated by alpine tundra and exposed rock and is underlaid by continuous permafrost (Danks et al. 1997). Located in the high subarctic zone of the tundra cordillera ecological region, the elevation ranges from 400-1200 m, with a 300 m treeline (Ecosystem Classification Group 2010). Dall's sheep typically occupy high elevations in rugged alpine areas that offer both refuge from predators and foraging opportunity (Lambert Koizumi et al. 2011, Environment Yukon 2019, Lambert Koizumi and Derocher 2019). These mountains host approximately 4,000 km^2 of Dall's sheep habitat, which has been surveyed aerially since 1984 in 12 stratified survey blocks. Since aerial surveying commenced, this population has fluctuated from max = 1573 in 1997 to min = 496 in 2014 (Davidson et al. 2018).

Within this frame, the 'Mount Goodenough' survey block (approximately 200 km^2) is located in the northeastern Northern Richardson Mountains, west of the Mackenzie River approximately 50 km from Aklavik, NT. Previous Dall's sheep research in the area (Lambert Koizumi and Derocher 2019) and recent traditional knowledge interviews (Benson 2023) indicate the area is home to a semi-isolated sub-population of sheep. The two most recent government surveys of this block (2017 and 2022) indicate a slightly declining to stable growth rate (λ = 0.98), with a minimum count of 157 individuals in 2022 (Environment Yukon – in progress).

In this study, we sampled a portion of the 'Mount Goodenough' survey block, approximately 75 km^2, near Black Mountain (*Chigwaazraii* in Gwich'in language). This area was selected for the community-based monitoring program by the GRRB, in consultation with local knowledge holders and Gwich'in Renewable Resource Councils (RRC) (Figure 2). Significant traditional knowledge exists of the land and wildlife in the Black Mountain area, which is well-known as productive Dall's sheep (*divii* in Gwich'in language) habitat year-round (Gwich'in Elders 1997, Benson 2023). This sample represents an *ad hoc* selection, describing the study area without probabilistic extrapolation to a larger area.

2.3.2 Camera image collection and review

We deployed an array of remote wildlife cameras (Reconyx Hyperfire 2 Professional & Reconyx PC900, Holmen, WI, USA) at sites used by Dall's sheep for forage, travel, lambing, etc., identified in part by previous research (Lambert Koizumi and Derocher 2019), but primarily by traditional knowledge and local knowledge of hunters, trappers, and community members during workshops in 2014 and 2018. Subsequently, a team of biologists and community knowledge holders visited the proposed sites and then deployed cameras at snowmobile-accessible sites with high evidence of sheep use. Hence, sites were selected based on known high occurrence of Dall's sheep to sample the population, not spatial distribution, as is common in other camera-trap studies (Burton et al. 2015)

Data were collected from 20 sites using 15 cameras between January 1, 2019, and December 31, 2021 (Figure 2). We employed this small number of camera sites to strike a balance between sample size and community capacity for maintenance of this very remote camera array. With a focus on temporal replication, not spatial replication, the array is intended to capture variation in fission-fusion dynamics, across known sheep locations, not spatial heterogeneity. Cameras were mounted on steel poles embedded in the permafrost, approximately one meter above ground, with a mean spacing between sites of 2,100 m ±SD 1,360 m (range: 580 - 4,750 m). Cameras were generally set to a high sensitivity, taking five rapid-fire images when triggered. The use of timelapse settings varied by deployment due to fieldwork errors, but most cameras were set to take three daily timelapse photos, five minutes apart, at 01:00 and 13:00. Images were stored on SD cards, collected and replaced when the cameras were serviced annually in February or March by community members and GRRB staff.

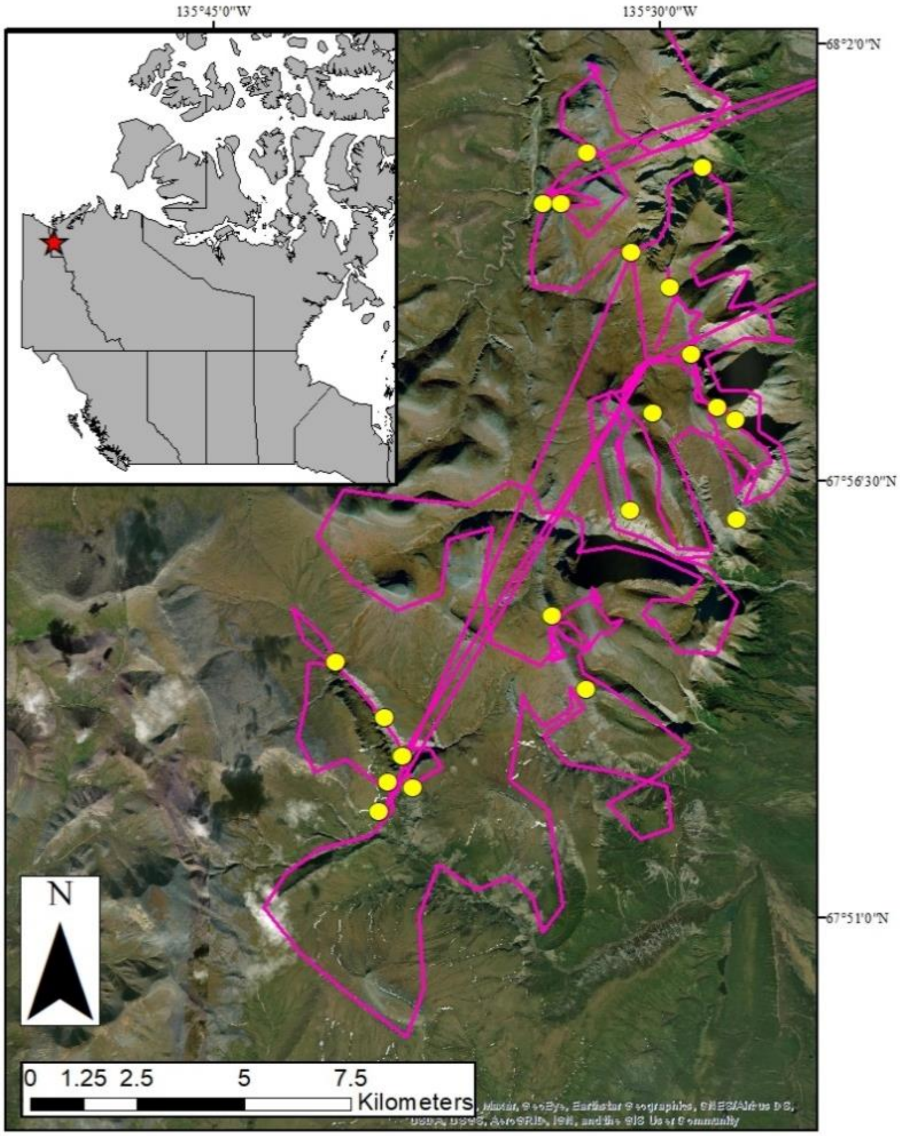

Figure 2. Map of the study location in north-western Northwest Territories, Canada. Locations of remote cameras are represented by the yellow dots (n = 20) and an example aerial survey flight path is shown in pink. The inset map identifies the general location of this area (red star) in reference to Canada. Credit: Canadian provinces and territories layer and base map accessed from ESRI online.

Raw images were initially processed using MegaDetector (MDv4 and MDv5), an artificial intelligence object detection model, to identify empty photos triggered by the sun, snowstorms, and vegetation (Beery et al. 2019, Leorna and Brinkman 2022). Images containing animals with a ≥ 0.25 probability were processed manually by a single reviewer using Timelapse 2.0 Image Analyzer software (Greenberg 2022). For each event of a Dall's sheep detection, we recorded date, time, temperature, and a count of individuals in the group. Demography data (sex and age class) was recorded for each individual in the group. Events were defined as starting when the camera is first triggered by the animal and ending once the animal leaves the frame, or when at least two minutes passed between camera triggers. Groups rarely stayed static from one two-minute sample to the next, as the sheep are always moving relative to one another. Thus, sum counts from the cameras do not represent the total number of individuals in the population, but of group demography, sampled with replacement.

2.3.3 Aerial surveys

Aerial surveys were completed in 2019 (August 25), 2020 (August 22), and 2021 (September 13), using an AStar B2 helicopter, following ridges, cliffs, and valleys (Figure 2). Aerial surveys were conducted in late August each year to target a stable lamb survival period (Bélanger and Davidson 2022): lambing season typically occurs between May 1 – June 15, with a birth peak in mid to late May, followed by an estimated 65% of mortality occurring in the first 60 days of life, with mortality stabilizing by the late summer (Nolan and Kelsall 1977, Nichols 1978, Barichello et al. 1987, Scotton 1998). The survey route was selected based on the locations of the cameras and the known distribution of Dall's sheep in the area. Sheep were counted and classified from either the helicopter or using photographs taken during the surveys (Bélanger and Davidson 2022). The same biologist performed all classifications.

2.3.4 Demographic data extraction

In both aerial and camera data sets, sheep were classified into the following categories: 1) nursery sheep (includes ewe-like sheep, yearlings, and quarter curl rams), 2) rams (further classified based on horn size to half curl, three-quarter curl, and full curl horns), 3) lambs (for camera data, we defined these as ≤ one calendar year of age, i.e., using January the following year as the cutoff between lambs and yearlings for the cameras), and 4) unclassified sheep (Figure 3).

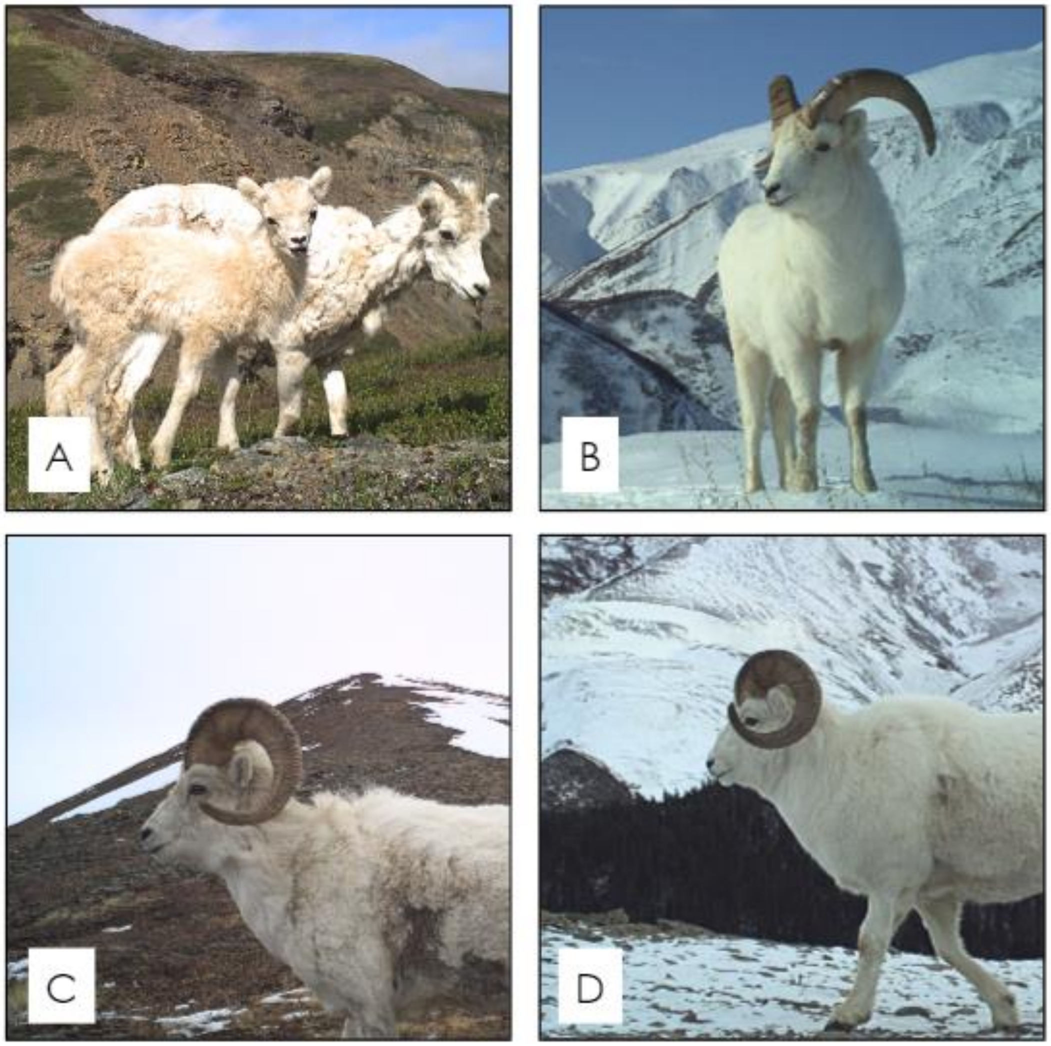

Figure 3. Demography categories for Dall's sheep classification, standardized use for aerial surveys and remote camera images. A. Left: Lamb; Right: Nursery sheep (includes all ewe-like sheep, yearlings, and young quarter-curl rams) B. Half Curl Rams C. Three Quarter Curl Rams D. Full Curl Rams.

To limit inter-observer error, all aerial classification was performed by one trained person. The classification of camera trap images was performed by a single (different) observer using the same criteria. To assess the amount of potential observer bias between the two individuals, an informal classification test was conducted and suggests that there was alignment between the two data sets.

2.3.5 Statistical analysis

The phenology of demographic sampling is a critical consideration for animals displaying fission-fusion dynamics. Using group-count camera data accumulated (Figure 4) and discretized into biological seasons for each year (Figure 5), we calculated lamb:nursery ratio, ram:nursery ratio, and ram classification composition. Seasons were defined based on Dall's sheep ecology in the study area (Lambert Koizumi et al. 2011, Dertien et al. 2017, Environment Yukon 2019, Lambert Koizumi and Derocher 2019).

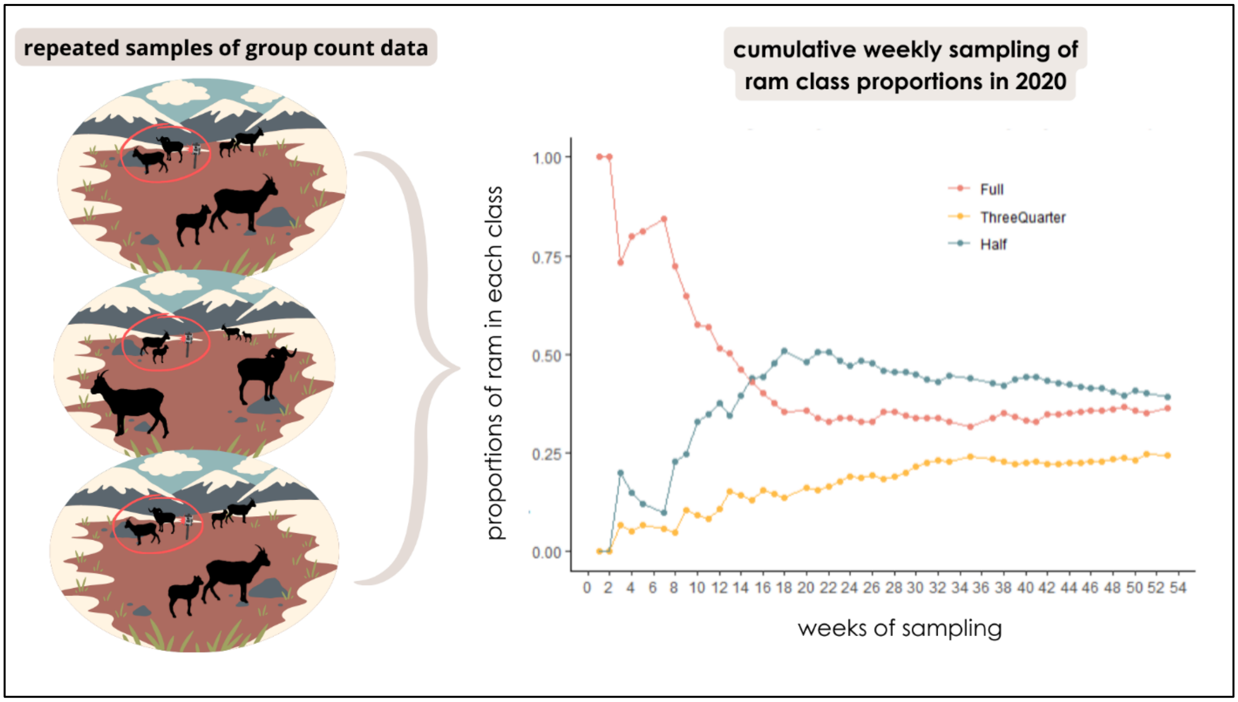

Figure 4. Cameras capture many samples of demography (left), which, when accumulated over time, converge on a true mean, as demonstrated on the right by the proportions of rams in each class (full, three quarter, and half curls).

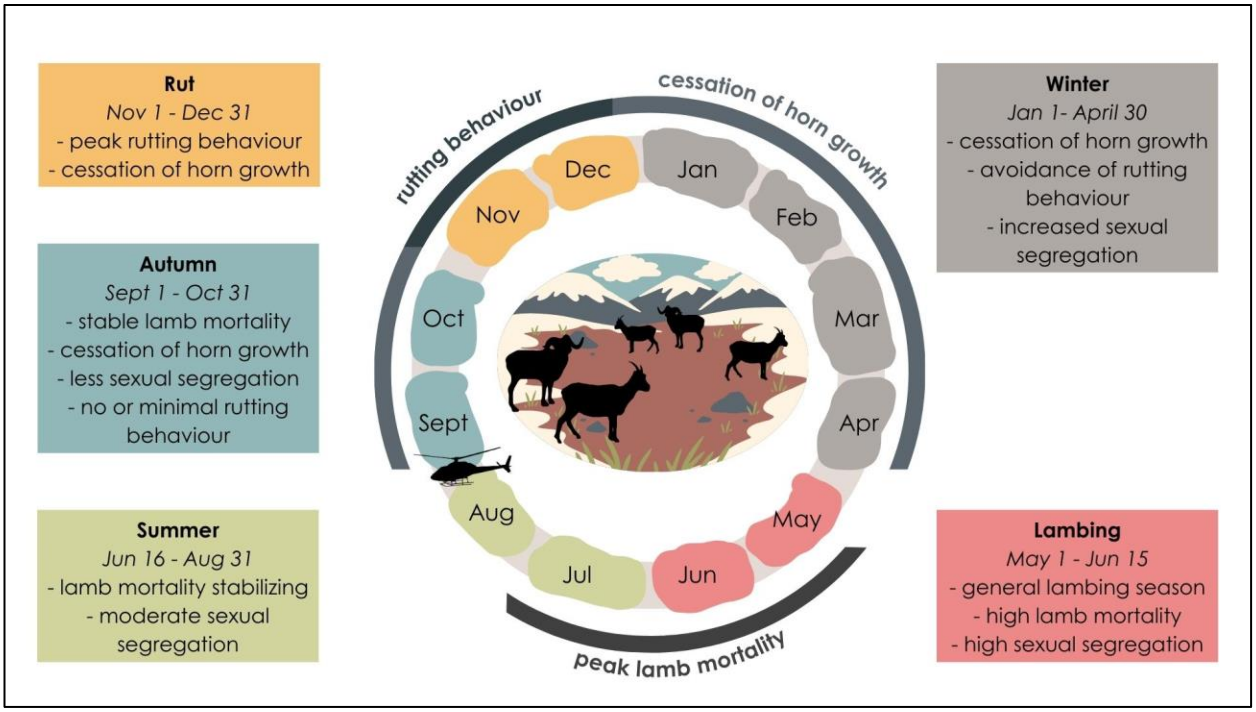

Figure 5. Grouping camera trap observations into seasons based on Dall's sheep ecology in the Northern Richardson Mountains.

Lamb to nursery ratio (an estimate of productivity)

To compare the camera data to the aerial survey data, we calculated the lamb and nursery proportions using data from the 2019, 2020, and 2021 aerial surveys, and corresponding camera data between September 1 and October 31 (autumn) of each year. This season was selected for comparison because factors such as lamb mortality, adult sexual segregation, and behaviour patterns, that could impact demographic ratios, are similar to the conditions at the time of the aerial survey (Figure 5). The proportion of lambs and nursery sheep was calculated, for both the camera data and the aerial survey data for each year:

Lamb proportion = total lambs ÷ (total lambs + total nursery)

Nursery proportion = total nursery ÷ (total lambs + total nursery)

A lamb:nursery ratio was also calculated to compare the population trends estimated from the camera and survey data. We consistently rounded partial sheep counts down. Lamb:nursery ratio is expressed as the number of lambs per 100 nursery sheep, calculated using a standardized formula in Dall's sheep monitoring (Environment Yukon – in progress):

Lamb value = (total lambs ÷ total nursery) x 100

A lamb:nursery ratio estimates the vigour of a population and provides an important indicator of population status (Geist 1971, Hoefs and Bayer 1983, Harris et al. 2008). When measured in the late summer, a ratio of 30 – 40 lambs per 100 nursery sheep generally indicates a stable population; a low ratio (< 30:100) may signal a population decline, and a high ratio (> 40:100) indicates potential growth (Whitten 1997, Demarchi and Hartwig 2004, Hengeveld and Cubberley 2012, Nagy et al. 2013). We interpreted the population trend of each year as stable, declining, or increasing based on these thresholds. To demonstrate the variability of demographic ratios in the camera data, we additionally present the ratios from all seasons where data was available, however these were not used to compare to the aerial survey as the seasonal timing was not appropriate (Figure 5).

Ram to nursery ratio (adult sex structure)

To compare the camera data to the aerial survey data, we calculated the ram and nursery proportions using data from the 2019, 2020, and 2021 aerial surveys, and corresponding camera data from between September 1 and October 31 (autumn), of each year. This season was selected for comparison in an attempt to stabilize the annual variation in adult sexual segregation, rutting behaviour, and horn growth that could impact demographic ratios, ensuring alignment with conditions at the time of the aerial survey (Figure 5). The proportion of rams and nursery sheep was calculated, for both the camera data and the survey data for each year:

Ram proportion = total rams ÷ (total rams + total nursery)

Nursery proportion = total nursery ÷ (total rams + total nursery)

A ram:nursery ratio was also calculated to compare the population trends estimated from the camera and survey data. We consistently rounded partial counts down. Ram:nursery ratio is expressed as the number of rams per 100 nursery sheep, calculated using a standardized formula in Dall's sheep monitoring (Environment Yukon – in progress):

Ram value = (total rams ÷ total nursery) x 100

The ram:nursery ratio represents the adult sex structure of a population and is a potential indicator of sex-skewed mortality with genetic and reproductive consequences (Hoefs and Bayer 1983, Hoefs and Nowlan 1994). We interpreted a ratio of 50:100 as normal, and low ratio when below 40:100 (Hoefs and Bayer 1983). A ram:nursery ratio was also calculated for every seasonal bin of data as well as a year total, using the summed counts from the autumn camera data and aerial survey data. To demonstrate the variability of demographic ratios in the camera data, we additionally present the ratios from all seasons where data was available; however, these were not used to compare to the aerial survey as the seasonal timing was not appropriate (Figure 5).

Ram classification

Rams were further classified into age classes, using a consistent judging method based on horn size (Bélanger and Davidson 2022). Adult rams were classified based on the degree of horn curl: half curl (180°, Figure 2B), three-quarter curl (270°, Figure 2C), full curl (horn exceeds the nose from a side-view or the horn reaches or extends beyond the base of the horn from a front-view, Figure 2D), as measured from a side profile, using the base of the horns as 0°. Classification was estimated conservatively and consistently in instances where a ram's position made it challenging to select a class. For data consistency, young rams classified as a quarter-curl (90°) were classified as nursery sheep, as it is difficult to tell the difference between these young rams and older ewes in aerial surveys; this is standard across aerial survey techniques for Dall's sheep (Environment Yukon 2019).

Ram classification was judged during the cessation of horn growth, which occurs from September through April, as foraging resources become scarce and rams transition from foraging to rutting (Bunnell 1978). We used camera data from January 1 to April 30 of the calendar year immediately following each aerial survey, which ensured consistent horn growth and avoided the increased detection rates of older rams during rutting behavior in the autumn (Geist 1966, Bunnell 1978). We combined all camera sites and calculated the weekly sum of ram detections in each age class (half curl, three-quarter curl, and full curl), then calculated the proportion of rams in each age class.

Goodness-of-fit tests

We performed Chi-square goodness-of-fit tests (Cochran 1952, Thomas and Taylor 1990) to inform how different the proportions derived from the cameras (observed values) were to the proportions calculated from the aerial surveys (expected values), for: a) the proportions of lambs per 100 nursery sheep, b) the proportion of rams per 100 nursery sheep, and c) the proportions of rams in each horn size classification category. We examined p-values to understand the degree to which the observed values conformed to the expected values, where smaller values indicate less conformance. We considered a threshold of α = 0.05 to aid statistical interpretation. All analyses were done in RStudio v4.2.2. (RCoreTeam 2017), using the ‘lubridate’ package for datetime data (Grolemund and Wickham 2011), ‘dplyr’ and ‘tidyr’ for general data manipulation (Wickham et al. 2023, Wickham and Vaughan 2023), ‘ggplot2’ for data visualization (Wickham 2016), and ‘cumstats’ for sample period exploration and calculations (Erdeley and Castillo 2017).

2.4 RESULTS

2.4.1 Aerial surveys

The flight time to cover the approximately 320 km survey route was around three hours. The flight in 2021 was hindered by poor weather and as a result, there was an impaired ability to spot sheep groups and poor geographical coverage (see discussion). Counts and classifications varied among years (Table 1).

Table 1. Summary results of aerial surveys of Dall's sheep in the Black Mountain, NT area in 2019, 2020 (Bélanger and Davidson 2022), and 2021.

Flight Date	**August 25, 2019**	**August 22, 2020**	**September 13, 2021***
Nursery	123	135	90
Lambs	49	30	28
Lamb:Nursery	*40:100*	*22:100*	*31:100*
Total Rams	53	44	20
Half curl	25	12	10
Three-quarter curl	19	21	10
Full-curl	8	11	0
Ram:Nursery	*43:100*	*33:100*	*22:100*
Unclassified	18	0	0
Total Sheep	242	209	138

*potentially unreliable due to unfavourable weather and poor geographical survey coverage (see Discussion).

2.4.2 Remote cameras

From January 1, 2019, to December 31, 2021, cameras were deployed for an average of 679 days +/- 352 (range: 135 - 1,088 days), representing 12,908 total camera days. We collected 337,292 total images. From the 77,801 images containing Dall's sheep, we classified 3,056 independent group detections.

2.4.3 Lamb to nursery ratio

There was a high level of conformance between the lamb and nursery camera data (observed values) and aerial survey data (expected values) in 2019, 2020, and 2021. This indicates similar proportions of lambs and nursery sheep were derived from both data sets. The lamb:nursery ratios, though different, indicate similar population trends for each sample year (Table 2). The camera lamb:nursery ratio demonstrated variability among seasons (Table 3).

Table 2. Lamb:nursery counts, proportions, and ratios for camera data (September 1st to October 31st of each year) and aerial survey data (August 25, 2019, August 22, 2020, and September 13, 2021). Note the aerial counts are true counts of sheep in the specified class, whereas camera counts are the sum count of sheep in each class detected over the specified time period. Population trend is interpreted from the ratios, based on thresholds available in the literature.

	2019		**2020**		**2021**	
	🚁	📷	🚁	📷	🚁	📷
Nursery count (proportion)	123 (0.72)	89 (0.74)	135 (0.82)	219 (0.84)	90 (0.76)	135 (0.79)
Lamb count (proportion)	49 (0.28)	31 (0.26)	30 (0.18)	42 (0.16)	28 (0.24)	36 (0.21)
Chi-square (df)	$\chi^2(1) = 0.279$ $p < 0.59$		$\chi^2(1) = 0.644$ $p < 0.42$		$\chi^2(1) = 0.814$ $p < 0.36$	
Lamb: nursery	40:100	34:100	22:100	19:100	31:100	26:100
Population trend	stable - increasing	stable	decreasing	decreasing	stable	decreasing

Table 3. Lamb:nursery ratios (number of lambs per 100 nursery sheep) calculated for each seasonal bin of camera data in 2019, 2020, and 2021, to demonstrate the variability in sampling periods. Note the winter season is not provided because lambs were not classified during this period (see section 2.3.4).

Camera Sample	**2019**	**2020**	**2021**
Lambing	35:100	9:100	29:100
Summer	30:100	14:100	32:100
Autumn	34:100	19:100	26:100
Rut	25:100	25:100	42:100

2.4.4 Ram to nursery ratio

In 2019, there was limited conformance between the observed and expected ram and nursery proportions, with the camera data indicating there were more nursery sheep and fewer rams than the aerial survey data. However, there was a high level of conformance in 2020 and 2021, indicating similar proportions were detected in the later two years but not 2019. All the ratios (with the exception the 2019 aerial survey) are consistently lower than expected (Table 4). The camera ram:nursery ratio demonstrated variability among seasons (Table 5).

Table 4. Ram: nursery counts, proportions, and ratios from camera data (September 1st to October 31st of each year) and aerial survey data (August 25, 2019, August 22, 2020, and September 13, 2021). Note the aerial counts are true counts of sheep in the specified class, whereas camera counts are the sum count of sheep in each class detected over the specified time period. Interpretation of the ratio is based on thresholds available in the literature.

	2019		**2020**		**2021**	
	🚁	📷	🚁	📷	🚁	📷
Nursery count (proportion)	123 (0.64)	89 (0.77)	135 (0.75)	219 (0.76)	90 (0.82)	135 (0.87)
Ram count (proportion)	70 (0.36)	26 (0.23)	44 (0.25)	68 (0.24)	20 (0.18)	20 (0.13)
Chi-square (df)	χ2(1) = 8.951 p < 0.005		χ2(1) = 0.261 p < 0.61		χ2(1) = 2.728 p < 0.099	
Ram: nursery	57:00	29:100	33:100	31:100	22:100	14:100
Interpretation	high	low	low	low	low	low

Table 5. Ram:nursery ratios (number of rams per 100 nursery sheep) calculated for each seasonal bin of camera data in 2019, 2020, and 2021, to demonstrate the variability in sampling periods.

Camera Sample	**2019**	**2020**	**2021**
Winter	20:100	11:100	23:100
Lambing	2:100	13:100	19:100
Summer	10:100	26:100	22:100
Autumn	29:100	31:100	14:100
Rut	110:100	161:100	19:100

2.4.5 Ram classification

In the 2019 survey season, there was limited conformance between the observed and expected data, with the observed camera data indicating there were fewer three-quarter-curl rams than the aerial survey data. However, there was a high level of conformance in the 2020 survey season between proportions derived from the two methods (Table 6).

Table 6. Ram classification (half, three-quarter, and full curl) counts and proportions, for all types (aerial and camera) and years (2019, 2020, 2021) of data analyzed. Note the aerial counts are true counts of sheep in the specified class, whereas camera counts are the sum count of sheep in each class detected over the specified time period.

	2019	2020	2020	2021
	🚁	📷	🚁	📷
Half Curl count (%)	25 (48%)	20 (40%)	12 (27%)	23 (35%)
Three Quarter Curl count (%)	19 (37%)	10 (20%)	21(48%)	31 (48%)
Full Curl count (%)	8 (15%)	20 (40%)	11(25%)	11 (17%)
Total Rams count	52	50	44	65
Unclassified count (%)	18 (26%)	-	0	-
Chi-square (df)	χ2(2) = 25.405, p < 0.001		χ2(2) = 3.390, p < 0.184	

2.5 DISCUSSION

We compared camera data with annual aerial survey data over a three-year period to assess the effectiveness of using camera traps for estimating wildlife demographics. We found camera traps accurately estimate key demographic parameters in wild sheep populations compared to aerial surveys, which is a significant advancement in wildlife monitoring, as to our knowledge, this is the first study employing remote cameras to estimate recruitment and sex ratios in a wild, un-marked sheep population. While annual and periodic aerial surveys can provide valuable single-sample data such as minimum counts (Gonzalez-Voyer et al. 2001, Udevitz et al. 2006, Foley et al. 2023), continuous camera data, compounded to overcome daily heterogeneity induced by loose grouping behaviours, provide a comprehensive picture of population dynamics. This is relevant in many wildlife monitoring situations, but is especially of interest in remote areas with limited budgets and difficult survey conditions (Mallory et al. 2018).

Lamb:Nursery ratios were similar from cameras and aircraft, and indicate variable productivity.

In the most recent government surveys in June 2017 (Davidson et al. 2018) and June 2022 (Environment Yukon – In Progress), the lamb:nursery ratios are reported, in draft, as 36:100 and 35:100, respectively, indicating a stable population. However, between these data points, we were able to derive ratios that showed substantial variation in the lamb: nursery ratios. Utilizing cameras to estimate population demography can fill the gaps in aerial survey periods, and may help decision-makers notice important population shifts otherwise obscured by long sampling periods, especially where increasing the frequency of aerial surveys is not a viable option.

When interpreting population trends from lamb:nursery ratios, it is important to be aware of the season of measurement and the definition of nursery sheep. Additionally, reproduction is density-dependent, and time lags can result in misleading lamb:nursery ratios for predicting population stability (McCullough 1994) so caution must be applied. Different jurisdictions also have different management thresholds for interpretating population status, thus interpreting population status is relatively population specific (Demarchi and Hartwig 2004, Nagy et al. 2013, Environment Yukon 2019, Thinhorn Sheep Indigenous Perspectives and Thinhorn Sheep Management Teams 2022).

Ram:Nursery ratios were difficult to capture and generally low.

Both the cameras and aerial surveys generally produced a low, and decreasing, ram:nursery ratio. A low ram:nursery ratio can have negative consequences for genetics and reproduction, and may be caused by variable lamb production, overharvest of rams, or other factors resulting in male-biased mortality (Hoefs and Bayer 1983, Simmons et al. 1984, Hoefs and Nowlan 1994, McCullough 1994, Whitten 1997, Lambert Koizumi et al. 2011, Environment Yukon 2019). In the 1970's, there were concerns of overharvesting of sheep in the Northern Richardson Mountains (Barichello et al. 1987). The impacts of overharvest of sheep, especially over a prolonged period, can result in genetic implications for a population (Festa-Bianchet 2017, Festa-Bianchet 2019). More recent reporting suggests that current harvest levels are low and not sex-selective (Working Group for Northern Richardson Mountains Dall's Sheep 2008, Lambert Koizumi et al. 2011). Alternatively, a decreasing ratio could result if nursery numbers have increased while rams have remained constant, or if both classes have increased but rams less so (McCullough 1994). These results must be treated cautiously, as obtaining an accurate adult sex ratio is difficult due to the dispersal of ram groups outside the rut season and the variable sight-ability of these groups (Cubberley 2008).

Ram classification proportions were similar from cameras and aircraft.

The distribution of ram classes is relevant to the natural preservation of the social and biological roles in a population, especially those played by older rams (Geist 1971). Ram classification data is primarily of interest in managed sheep populations with hunting opportunities, as hunting regulations typically base harvest rates on a conservative portion of a specific ram age class (Environment Yukon

2019, Thinhorn Sheep Indigenous Perspectives and Thinhorn Sheep Management Teams 2022). This study is not intended to provide management recommendations, and this population is not currently open to licensed hunting; however, we examined ram classifications to ensure practical application of our methods to other populations. Working with a single sex also simplified the ecological considerations for binning data, making it a simple and effective data set to test camera data against aerial surveys.

Cameras highlight importance of temporal sampling in fission-fusion ungulate populations.

This study highlights the importance of considering the temporal nature of sampling wildlife populations (Frey et al. 2017, Kemna et al. 2020, Wiskirchen et al. 2022). The cameras' continuous sampling provided an opportunity to calculate demographic parameters for multiple sample periods, unlike aerial data, which provided a single annual sample. Obtaining precise demographic ratios were heavily reliant on multiple samples, as variation can be drastically reduced with accumulation (Figure 4) (Fischer 2011, Burton et al. 2015, Lebreton and Gaillard 2016). The seasonal variation demonstrates the value of selecting appropriate samples for ecological survey methods. The sample that best reflects true populations state should be selected based on knowledge of behaviour and movement, the two factors affecting fission-fusion dynamics and the sample variation it imparts (Cross et al. 2005).

Community-based monitoring at the root of success.

The use of a limited number of cameras was found to be highly effective in capturing a high volume of sheep detections, which was achieved through the collaboration of local community partnerships and the application of local knowledge. The work and expertise of local knowledge holders in selecting high-use sheep trails was critical to the successful accumulation of demography samples.

A community-based approach to research in a cross-knowledge collaboration improves the effectiveness, sustainability, management outcomes of wildlife monitoring programs by integrating diverse knowledges and perspectives, focusing on holistic values, and localizing stewardship decisions (Berkes et al. 2007, Conrad and Daoust 2008, Wong et al. 2017, Henri et al. 2018, Popp et al. 2019, Fisher et al. 2021, Hessami et al. 2021, Yarchuk 2023). Founded on community-specific values and priorities, community-based wildlife monitoring is one expression of self-governance and traditional land stewardship, which has been shown to greatly improve local management outcomes (Reid et al. 2021, Lamb et al. 2022, Yarchuk 2023). Further, remote cameras are inexpensive compared to other methods of wildlife monitoring and easy to implement by individuals, and so democratize research, lending themselves to a community-based approach to scientific research (Fisher et al. 2021). Cameras provide additional eyes on the land year-round, allowing the animals and the land to tell their stories. As such, cameras have the ability to engage people in profound ways, for example, by bringing people out on the land and inspiring local youth as the next generation of stewards.

Caveats and limitations.

Vagaries in aerial surveys: Disturbance caused by the helicopter (Krausman and Hervert 1983) during the 2019 aerial survey resulted in a sampling error of rams (Bélanger and Davidson 2022), thus a comparison between the camera data and aerial survey data should be interpreted with caution. Eighteen sheep, all highly suspected rams, were mixed into already classified groups before they were classified. If the ram band was biased to a particular ram age class, it would have the potential to impact the results of the ram class proportions. In the 2021 aerial survey, a comprehensive sample of the study area was not obtained due to unsafe flying weather and low fog, resulting in poor geographical coverage and difficulty in observing sheep.

Assumptions about seasonality: We defined seasons based on best available knowledge about Dall's sheep biology, but this knowledge remains imperfect. Additionally, we recognize that for older rams, their relatively high energy expenditure during the rut can result in increased winter mortality

(Singer et al. 1991) which may impact the accuracy of the ram classification from winter camera data in comparison to the fall aerial surveys.

Non-representative sampling: Non-representative sampling in both aerial surveys and camera data is a potential limitation due to factors such as sexual segregation of adults at different times of the year (Nagy et al. 2013, Dertien et al. 2017, Lambert Koizumi and Derocher 2019), the surveyor's ability to detect sheep (Udevitz et al. 2006, Bélanger and Davidson 2022), and the potential influence of the cameras' novelty on animal behavior (Meek et al. 2015, Caravaggi et al. 2020). We noticed during image tagging that sheep age may play a role in their response to camera novelty. Lambs were particularly curious about the cameras, and their investigation of the unit sometimes blocked the field of view, potentially forcing missing detections of sheep passing through in the background. We also noticed behaviour around the cameras may have differed by sex. Nursery groups generally appeared to spend more time in an area, whereas ram groups appeared to be travelling through. By intentionally placing cameras in areas with high-use evidence, we may have biased the sampling against rams, who frequently use habitat that would have fewer signs of heavy sheep use. Cameras also have limitations in detecting animals in or near their viewshed, and counting herding animals is a special case of this problem. For example, some images captured only images of lambs (unlikely orphans) or only nursery sheep without lambs. Although multi-state occupancy models can estimate missed detections and estimate occupancy adjusted for these factors (Fisher and Bradbury 2014, Fisher et al. 2014) these models require additional spatial design considerations (Bailey et al. 2007) which were not incorporated in this targeted design. Future analysis could help determine possible detection biases and limit this potential source of error.

2.6 CONCLUSIONS

Remote cameras can estimate demographic parameters using an approach that carefully considers fission-fusion dynamics, seasonality, temporary emigration, and behaviour. This is the first study employing remote cameras to estimate productivity (lamb:nursery ratio) and adult sex ratios in a wild, un-marked sheep population. Despite challenges and assumptions in compiling and interpreting demographic parameters for wild mammal populations, they remain key for empirically assessing population status and managing species. Incorporating a remote camera system into wildlife monitoring programs allows for a more comprehensive examination of demography. Our methods could apply to any population of social ungulate, where sufficient knowledge exists on high-use sites and seasonal habitat use. Moreover, we demonstrate that an array within a community-based monitoring program framework can obtain this demography data, critical to proper, proactive wildlife management.

2.7 SUPPLEMENTAL INFORMATION

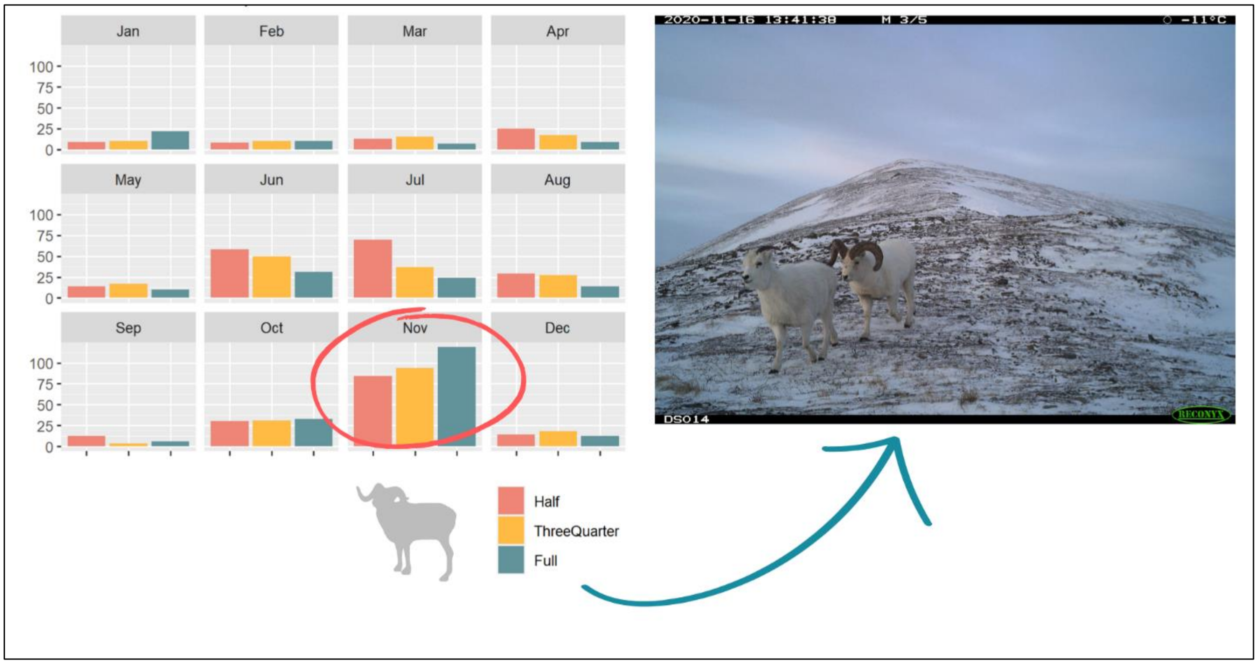

Figure 6. Illustration of increased detections of rams, particularly older, full-curl males, during the peak rutting period in November.

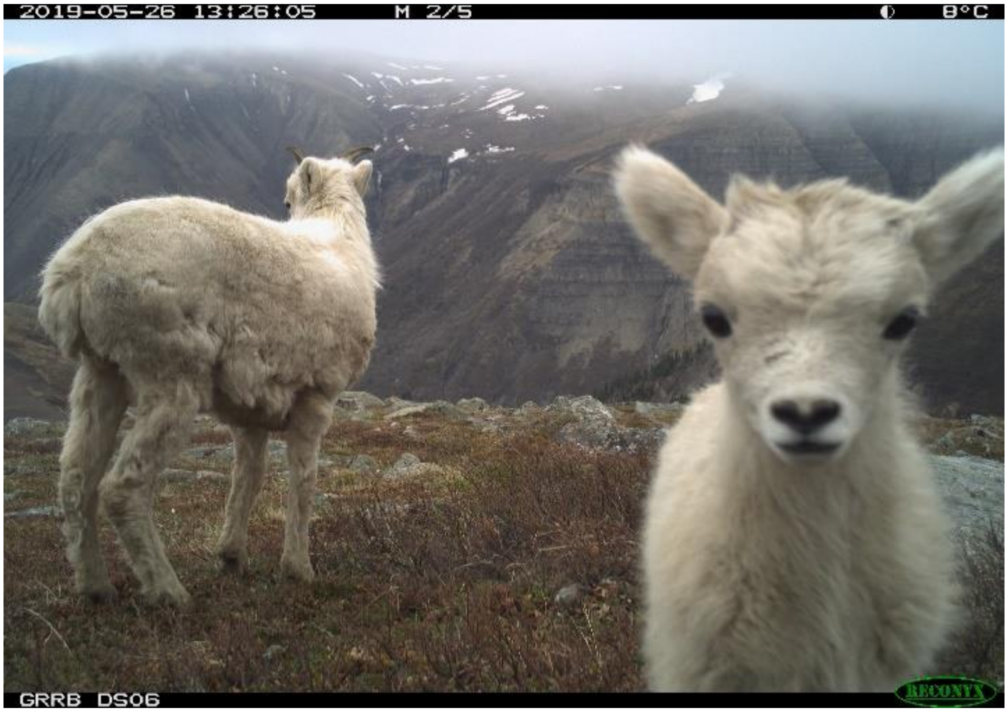

Figure 7. Example of a lamb showing particular interest in the camera (approaching), while the ewe-like sheep grazes or looks elsewhere.

Figure 8. Example of a sheep partially blocking the field of view while examining the camera. This is also an example of an "unclassified" sheep because we can only speculate on the sex or age from this picture in the absence of horns.

Figure 9. Example of a detection of only lambs without their accompanying nursery group.

CHAPTER 3. SHARING THE LAND: A TEMPORAL EVALUATION OF DALL'S SHEEP AND GRIZZLY BEAR CO-OCCURRENCE

3.1 ABSTRACT

Temporal partitioning, or how sympatric species divide up time as a resource, provides valuable information on how species coexist, and reflects animal behaviour. Predator avoidance by prey often drives temporal partitioning for species that exist in the same space. Understanding the temporal mechanisms of predator-prey interactions is of key importance to our broader understanding of mammal community assembly and niche partitioning, but is particularly difficult to study in remote ecosystems such as the Canadian Arctic. Here, ungulates and carnivores are uniquely adapted to harsh conditions and must also contend with each other. Predator-prey interactions between Dall's sheep and grizzly bears are known to occur but a comprehensive understanding is lacking. This study evaluates the temporal partitioning of these sympatric species through a time-to-event analysis (TTE) and activity pattern analysis (APA), to better understand temporal predator-prey attractance (how grizzly bears follow Dall's sheep), and avoidance (how Dall's sheep escape grizzly bears). We found that grizzly bears are more closely tracking sheep nursery groups than ram bands, a relationship that is most profound during the early spring, when lambs are most vulnerable to predation. Our results also show that nursery groups consistently occupy a different temporal niche than grizzly bears. Though ram bands and grizzly bears occupy a different temporal niche in the spring and early summer, they share a temporal niche in the later summer and early fall. Our research on the temporal relationship between Dall's sheep and grizzly bears using remote camera trapping provides nuance and context to other wildlife monitoring tools, such as GPS collars and stable isotope analysis. With a small camera array in a community-based monitoring framework, we were able to investigate fine-scale temporal relationships between Dall's sheep and grizzly bears, which is an important advance in wildlife monitoring in the face of unprecedented landscape change.

3.2 INTRODUCTION

Niche theory plays a pivotal role in shaping our understanding of species interactions and community assembly within the field of ecology. Niche theory, a core concept in ecology, describes the relationships between a species and its required resources, and provides a framework for examining the roles of, and interactions between, sympatric species in an ecosystem (Kronfeld-Schor and Dayan 2003). Niches describe the required resources and tolerances of individual species in ecological communities. Niche partitioning describes a process where species alter resource use (either in time or space) to limit overlap and competition with other species, for example, competitors and predators. A species’ niche may be partitioned in both space and time (Schoener 1974), and temporal partitioning – or how species use time as a resource – is particularly understudied, especially in remote mammal communities (Pocheville 2015, Kemna et al. 2020). Temporal partitioning, such as a species’ diel activity pattern is often a factor in the stable coexistence of predator and prey species (Kronfeld-Schor and Dayan 2003) through predator avoidance (Leech et al. 2017, Cunningham et al. 2019) and attractance to prey (Santos et al. 2019). For many species, temporal partitioning is influenced by the presence of other species (Cunningham et al. 2019, Ikeda et al. 2021), environmental conditions (van Beest et al. 2020), and landscape disturbances (Frey et al. 2022, Khan et al. 2023), which in turn may influence relationships between predators and prey. For example, in Canada’s boreal forest, treatments to reduce wolf densities resulted in a decrease in activity overlap between wolves and other species such as moose and white-tailed deer, indicating a reduced potential for wolves to interact with prey species (Frey et al. 2022). In the Canadian Rocky Mountains, predators such as wolves appear to shift diel activity patterns in response to increasing anthropogenic landscape disturbance, but the rippling effects on the broader mammal community remain unclear (Khan et al. 2023). Thus, understanding the temporal mechanisms of predator-prey interactions is of key importance to our broader understanding of mammal community assembly and niche partitioning. This is especially true as we strive to understand the ecology of remote, understudied systems, including Arctic systems. One such system is the Canadian arctic, where ungulates and carnivores, uniquely adapted to harsh conditions, must also contend for coexistence with each other.

In the Arctic, predator-prey interactions between the social mountain ungulate, Dall's sheep (*Ovis dalli dalli*), and an apex predator, the Grizzly bear (*Ursus arctos*) - are widely recognized as important to coexistence, but have not been temporally examined (Frid 1997, Rachlow and Bowyer 1998, Benson 2014, Lambert Koizumi and Derocher 2019, Benson 2023). These two iconic species are of high cultural, ecological, and economic (Simeone 2007, Heffelfinger et al. 2013) value for both Indigenous (Benson 2014, 2023) and non-Indigenous communities, but concerns exist regarding the stable coexistence of these two species in the wake of recent cause-uncertain population declines (Lambert Koizumi and Derocher 2019). Habitat selection, seasonal migration patterns, and sexual segregation have been well studied in Dall's sheep, (Hoefs 1978, Barichello et al. 1987, Rachlow and Bowyer 1998, Nagy et al. 2013, Van de Kerk et al. 2020, Aycrigg et al. 2021), but details of their temporal behaviour have received little attention. As a result, there are currently important knowledge gaps in resource partitioning of Dall's sheep with their predators such as grizzly bears, and how these relationship may be impacting the population (Lambert Koizumi et al. 2011, Benson 2023). These mechanisms are important to conservation and management of both predator and prey species in mammal communities (Linnell and Strand 2000, Gómez-Ortiz et al. 2019).

In general, a prey species' temporal niche is the result of the need to balance both acquiring resources and avoiding predation. Forage acquisition must be weighed against predation risk (Rachlow and Bowyer 1998, Hamel and Côté 2007), especially predation of neonates - as neonate survival is needed for population stability (Hoefs and Nowlan 1994, Whitten 1997, Demarchi and Hartwig 2004, Environment Yukon 2019). Dall's sheep exhibit sexually segregated fission-fusion dynamics, where loose groups of different age/sex classes form and break up in time and space; perceived predation risk is well-known to influence habitat selection and spatiotemporal behaviour (Frid 1997, Corti and Shackleton 2002, Hopewell et al. 2005, Walker et al. 2007, Forshee et al. 2022). Dall's sheep lambs experience the majority of mortality in the first weeks and months post-lambing, with mortality rates stabilizing late summer and into the fall (Rachlow and Bowyer 1991). During this "peak season" of lamb vulnerability, habitat selection for nursery groups (ewes and lambs) notably trends to favouring escape terrain in the spring and summer likely to limit predation risk (Frid 1997, Rachlow and Bowyer 1998). In contrast, ram habitat selection is closely related to optimizing forage, with less need to balance predation risk. By the autumn as mating season approaches, sexes co-occur in anticipation of mating season (Lambert Koizumi and Derocher 2019).

Grizzly bear behaviour and habitat use patterns are highly correlated to phenological development of plant foods (MacHutchon 2001), though their diets are known to vary markedly between individuals (Edwards et al., 2011). It is common for bears to target ungulate neonates during the spring, early in the lambing season, posing a large risk to nursery groups of Dall's sheep in particular. As the summer progresses other food sources become available, grizzly bear foraging behaviour appears to shift to a focus on plant foods (MacHutchon 2001, Edwards et al. 2011). Despite a relatively limited effort on predation and a greater focus on forging plant foods, the spatiotemporal behaviour of grizzly bears may still influence temporal behaviour of prey species (Sivertsen et al. 2016). In predator-prey relationships, predation risk can impact prey behaviour even when direct predation is low or zero (Creel et al. 2005, Creel and Christianson 2008). This phenomena of "risk effects" and concept of the "ecology of fear" (Brown et al. 1999) may actually be more important to prey behaviour than direct predation (Kittle et al. 2008, Barnas et al. 2022b).

Grizzly bears, as a well-known predator of Dall's sheep, are a likely suspect of influencing Dall's sheep habitat selection and behaviour. Yet, the temporal partitioning of the two species, which lends clues to their stable (or otherwise) co-existence, has received little research attention (Rachlow and

Bowyer 1998, Corti and Shackleton 2002, Dertien et al. 2017, Lambert Koizumi and Derocher 2019, Van de Kerk et al. 2020). Further, mammal community interactions are complex and difficult to study, especially through non-invasive methods which are often desired by Indigenous community partners (Wong et al. 2017). The use of remote cameras has become an increasingly popular method for investigating temporal ecological niches, as cameras provide high-resolution, temporal data on mammal communities (O'Connell et al. 2011, Burton et al. 2015, Steenweg et al. 2017, Rød-Eriksen et al. 2023, Wolfson et al. 2023). Using remote camera data, time-to-event analysis and activity pattern analysis are two methods that evaluate predation risk by attraction and avoidance over time, and thus provide valuable insights on the coexistence of sympatric species (Frey et al. 2017, Frey et al. 2022, Bell et al. 2023). Remote cameras are additionally beneficial for long-term sampling. For example, long-term data facilitates investigations into how predator-prey relationships may fluctuate throughout any given year in response to biological phenomena (Ikeda et al. 2021), or how the relationships may change over time in response to landscape disturbance (Frey et al. 2022, Khan et al. 2023), and possibly even climate change (Frey et al. 2017, Steenweg et al. 2017).

The objective of this study is to better understand how Grizzly bears and Dall's sheep co-exist temporally in a core habitat area, at different times of the year. Through an Indigenous-led community-based monitoring program, we use remote camera data (Figure 10) from different seasons to derive a time-to-event model investigating if and how grizzly bears are tracking sheep nursery groups and ram bands. We hypothesize that grizzly bears more closely track nursery groups than ram bands, as lambs present a seasonal food source for grizzly bears. We anticipate this relationship is strongest in the early spring and summer when lambs are most vulnerable to predation, and less so in the later summer and early fall as grizzly bears shift behaviour to focus on consuming more plant foods. Through an activity pattern analysis, we also evaluate the differences and similarities in diel activity patterns between the species to estimate temporal niche partitioning. In the activity pattern analysis, we hypothesize that grizzly bears and sheep will share a temporal niche to facilitate this predator-prey relationship.

Figure 10. Left: Image taken of a ewe-like sheep and lamb at 5:27pm on May 8, 2019. Right: Image taken at the same site on the same date, of a mature grizzly bear just 20 minutes later. Note that the bear appears to be smelling the ground that the sheep recently traversed.

3.3 METHODS

3.3.1 Study area

The sampling frame for this study is the Northern Richardson Mountains, along the northern Yukon – Northwest Territories, Canada border. This rugged mountainous terrain is dominated by alpine tundra and exposed rock and is underlaid by continuous permafrost, with a treeline at 300 m (Danks et al. 1997). Located in the high subarctic zone of the tundra cordillera ecological region, the elevation ranges from 400-1200 m (Ecosystem Classification Group 2010). Dall's sheep typically occupy high elevations in rugged alpine areas that offer both refuge from predators and foraging opportunity (Lambert Koizumi et al. 2011, Environment Yukon 2019, Lambert Koizumi and Derocher 2019). These mountains host approximately 4,000 km^2 of Dall's sheep habitat, which has been surveyed aerially since 1984 in 12 stratified survey blocks. Since aerial surveying commenced, this population has fluctuated from max = 1573 in 1997 to min = 496 in 2014 (Davidson et al. 2018). The most recent government survey in 2022 draft estimates a population of 609 sheep (Environment Yukon – in progress). There is limited survey data for grizzly bears in the Northern Richardson Mountains. The latest mark-recapture study estimated a population of approximately 184 grizzly bears (≥ 2 years old) with a density estimate of 19 bears/1000 km^2 in this area (Clarkson et al. 1993). Gwich’in traditional knowledge holders report that grizzly bear numbers in the Northern Richardson Mountains have often fluctuated, but populations are generally noted to be increasing in recent years. Hunting is noted as a main limiting factor for grizzly bears in this area, which is controlled through a management plan and tag system (Benson 2014, Gwich'in Renewable Resources Board 2022). According to Gwich’in traditional knowledge holders, Arctic ground squirrel (*tthaa* in Gwich’in language; *Urocitellus parryii*) along with roots, berries, caribou (*vadzaih* in Gwich’in language; *Rangifer tarandus*), and fish are the most important food sources for grizzly bears, with Dall’s sheep generally playing a smaller dietary role (Benson 2014). Dietary analysis by stable isotopes in this area has found approximately 70% of grizzly diet composed of animal sources, but “mountain mammals” (including Dall’s sheep, caribou, and ground squirrels) were found to comprise less than 30% of overall diet (Lambert Koizumi and Derocher 2019).

In this study, we sampled a portion (approximately 75 km^2) of the ‘Mount Goodenough’ Dall’s sheep survey block, near Black Mountain (*Chigwaazraii* in Gwich’in language). This area was selected for the community-based monitoring program by the Gwich’in Renewable Resources Board (GRRB), in consultation with traditional knowledge holders and Gwich’in Renewable Resource Councils (RRC). Significant traditional knowledge exists of the land and wildlife in the Black Mountain area, which is well-known as productive Dall’s sheep (*divii* in Gwich’in language) habitat year-round (Gwich'in Elders 1997, Benson 2023), and is also identified as good grizzly bear (*shih* (T) or *sheh* (G), in two Gwich’in language dialects) habitat by traditional knowledge holders (Benson 2014). In this area, core areas of Dall’s sheep use overlap with core areas of grizzly bear use (Lambert Koizumi and Derocher 2019, Benson 2023).

3.3.2 Camera image collection and review

We deployed an array of remote wildlife cameras (Reconyx Hyperfire 2 Professional & Reconyx PC900, Holmen, WI, USA) at sites near Black Mountain used by Dall's sheep for forage, travel, lambing, etc., identified by hunters, trappers, and community members during workshops in 2014 and 2018, and by previous research (Lambert Koizumi and Derocher 2019). Subsequently, a team of biologists and community knowledge holders visited the proposed sites and then deployed cameras at snowmobile-accessible sites with high evidence of sheep use. Hence, sites were selected based on known high occurrence of Dall's sheep to sample the population, not to sample the spatial distribution of species on the landscape, as is common in other camera-trap studies (Burton et al. 2015).

Data were collected from 20 sites using 15 cameras between 2018-04-22 and 2022-06-24 (Figure 11). We employed this small number of camera sites to strike a balance between sample size and community capacity for maintenance of this very remote camera array. With a focus on temporal replication over years, not spatial replication, the array is intended to capture variation in fission-fusion dynamics across known sheep locations, not spatial heterogeneity (Goward et al. - in preperation). Cameras were mounted on steel poles embedded in the permafrost, approximately one meter above ground, with a mean spacing between sites of 2,100m ±1,360 m (range: 580 - 4,750 m). Cameras were generally set to a high sensitivity, taking five rapid-fire images when triggered. Images were stored on SD cards, collected and replaced when the cameras were serviced annually in February or March by community members and GRRB staff.

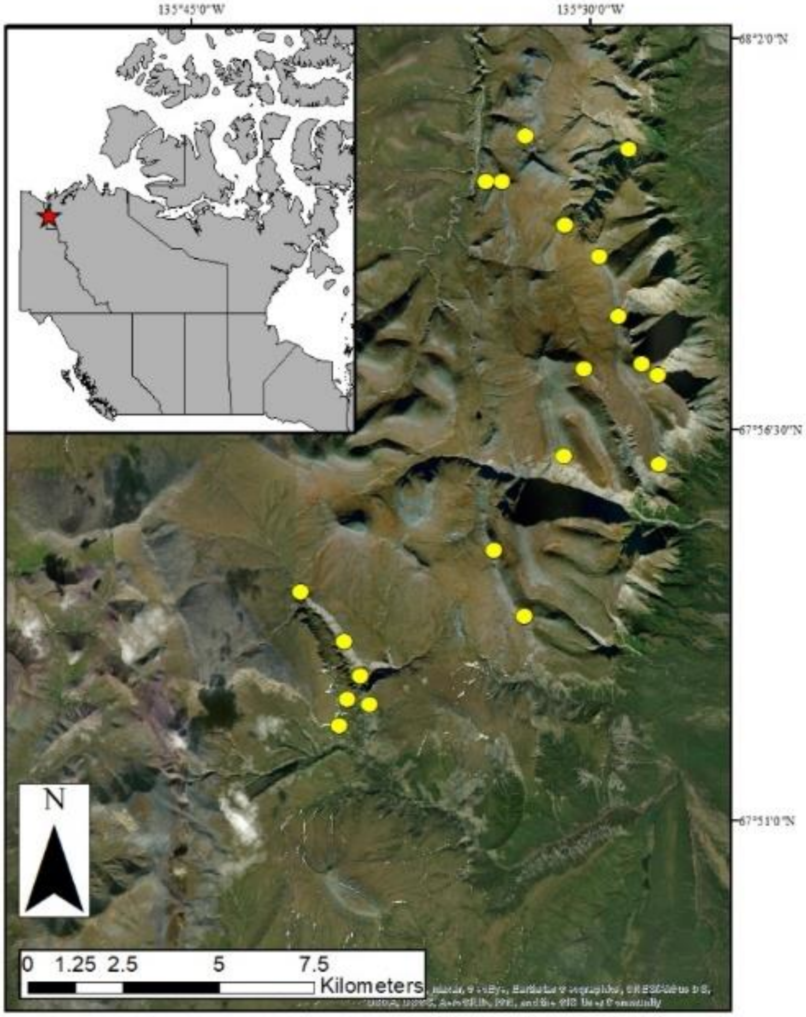

Figure 11. Map of the study location in north-western Northwest Territories, Canada. Locations of remote cameras are represented by the yellow dots (n = 20). The inset map identifies the general location of this area (red star) in reference to Canada. Credit: Canadian provinces and territories layer and base map accessed from ESRI online.

Raw images were initially processed using MegaDetector (MDv4 and MDv5), an artificial intelligence object detection model, to identify empty photos triggered by the sun, snowstorms, and vegetation (Beery et al. 2019, Leorna and Brinkman 2022). Images with a ≥ 0.25 probability of containing animals were then processed manually by a single reviewer using Timelapse 2.0 Image Analyzer software (Greenberg 2022). For each event of an animal detection, we recorded the species, date, time, and a count of individuals in the group. Demography data (sex and age class) was recorded for each individual in the group. Independent detections were defined as starting with the first image taken when the camera is first triggered by the animal, and ending when at least two minutes has passed where the camera was not triggered. We chose this this threshold as activity pattern analysis is strengthened by a low time to independence threshold, which is of particular importance in smaller camera arrays like this (Peral et al. 2022).

“**Nursery groups**” are comprised of ewe-like sheep (ewes, yearlings, and quarter curl rams) and lambs (< one year old), therefore we classified a detection of sheep as a nursery group if there was at least one ewe-like sheep or lamb present in the detection (Figure 12). This definition was important to minimize false absences of lambs or ewe-like sheep in the nursery group when focusing on just individual detections, a challenge noted while reviewing the data of this herding species (Figure 13). We considered a detection part of a “**ram band**” if there was at least one adult male sheep detected (Figure 12). Rams were considered an adult when the horn tip extends at least 180° from the base (i.e., “half curl” or greater). There were 115 detections that met the definition of both nursery group and ram band (i.e., groups with least one ewe-like or lamb, and at least one adult male). In an effort to not restrict true presence data of animal behaviour, these detections were included in analyses for both nursery groups and ram bands. A thorough discussion and data exploration on the effect of these detections is provided in Supplemental information, section 3.7.1.

Figure 12. Left: Example of a Dall’s sheep nursery group with a lamb in the foreground and a ewe-like sheep behind. Right: Example of a ram band of four individuals.

Figure 13. Example of why nursery groups were defined as at least one ewe-like sheep or lamb to minimize false absences in group detections. Both these images were taken of the same group, so we know there are both lambs and ewe-like sheep in this nursery group. However, in the left frame, we only capture lambs and in the right frame, we only capture ewe-like sheep.

3.3.3 Statistical analysis

We evaluated detections of nursery groups, ram bands, and grizzly bears at different time frames within the general period outside grizzly bear torpor (May to October, inclusive) (MacHutchon 2001). During this time period, lamb mortality varies significantly. To capture this variation, we classified two time intervals representing important periods of lamb mortality (Figure 14). "**Peak season**" (May, June, and July) captures the onset of lambing season and the high level of lamb mortality that occurs at this time (Rachlow and Bowyer 1991). "**Stable season**" (August, September, October) captures a period of reduced lamb mortality, when they are less vulnerable to predation and environmental factors (Singer et al. 1991, Lambert Koizumi and Derocher 2019, Van de Kerk et al. 2020). All data manipulation and calculations were done in RStudio v 4.2.2. (RCoreTeam 2017), using the 'lubridate' package for datetime data (Grolemund and Wickham 2011), 'dplyr' and 'tidyr' for general data manipulation (Wickham et al. 2023, Wickham and Vaughan 2023), 'ggplot2' for data visualization (Wickham 2016).

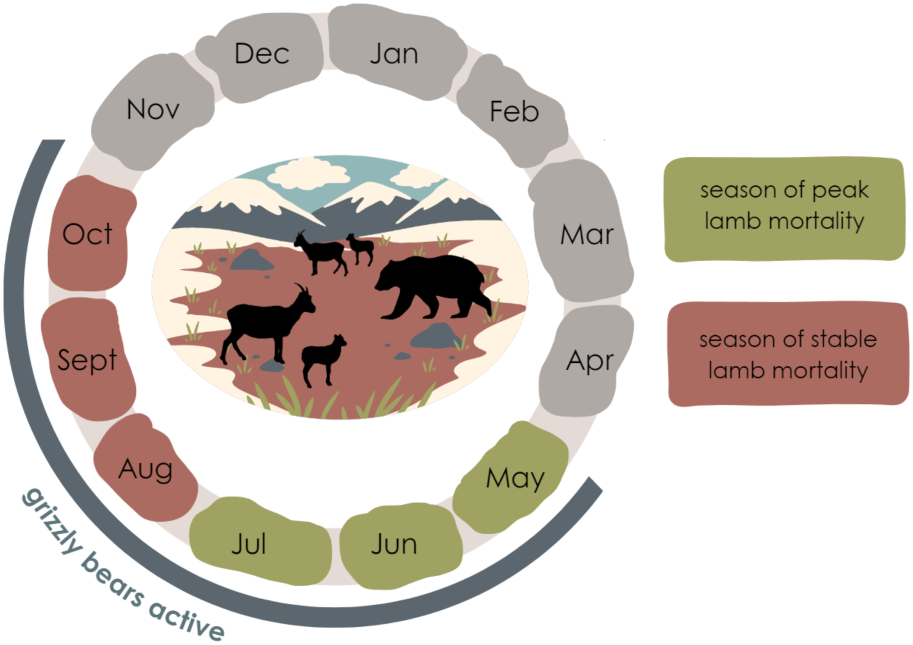

Figure 14. The active period of grizzly bears (May to October, inclusive) described in relation to two time periods relevant to Dall's sheep lamb mortality. Peak lamb mortality season is shown in green and includes May, June, and July, and stable lamb mortality season is shown in brown and includes August, September, and October. The remainder of the months outside the period of grizzly activity, and thus not included in this analysis, are shown in grey.

Time-to-event analysis (TTE)

We evaluated several different event scenarios over different sampling seasons with time-to-event models. We first defined a focal species and lag species; an event was defined to occur when a lag species was detected immediately following a focal species at a single site in a calendar year. The lag time of an event was the difference of hours between the two detections (Figure 15). We then examined the lag times of grizzly bears following nursery groups compared to ram bands throughout the entire season (May to October). To account for random timing of coincident detections, we then examined these lag times of grizzly bears following sheep, compared to sheep following grizzly bears, for both nursery groups and ram bands separately. We then examined the lag times between the peak (May to July) and stable (August to October) seasons for nursery groups and ram bands separately.

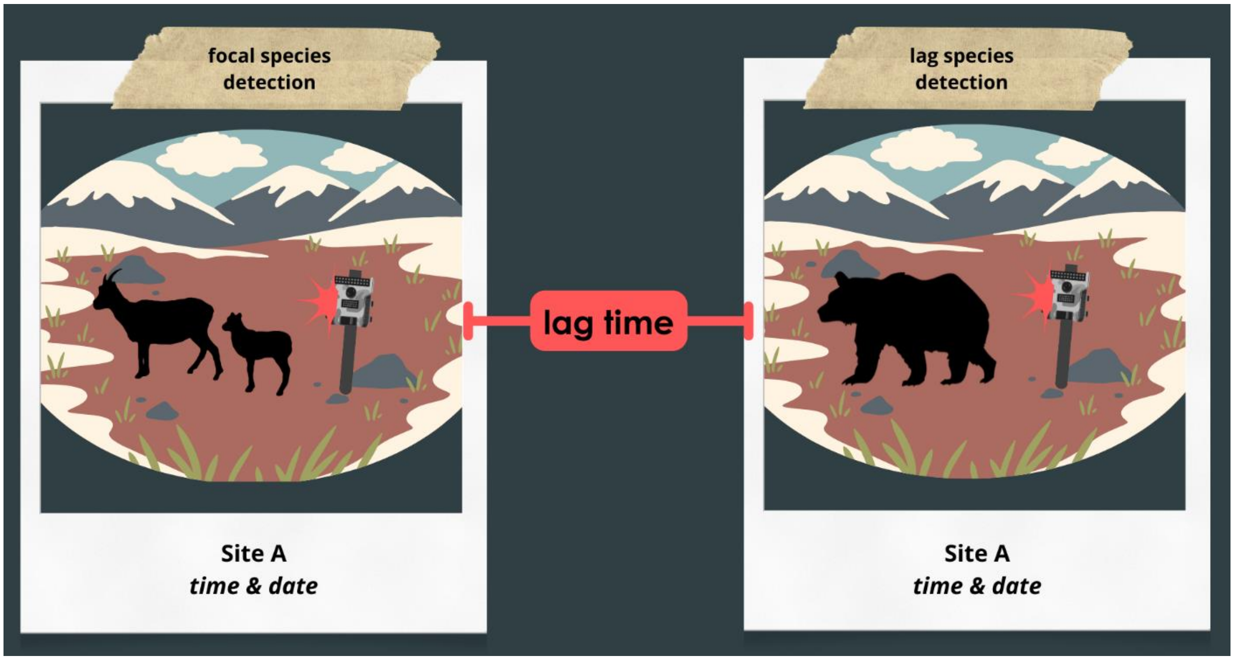

Figure 15. Lag time is the time difference (in hours) between the detection of a focal species (in this example, a nursery group of Dall's sheep) and a lag species (here, a grizzly bear), at the same site.

Of event lag times, we calculated the median, median absolute deviation (MAD), mean (± standard deviation), minimum, and maximum, in hours. To contextualize the magnitude of the difference in lag times in each scenario, we employed a two-sample Mann-Whitney U test (also known as a Wilcox rank-sum test) (Bischof et al. 2014, Loonam et al. 2021, Bell et al. 2023). This test (base r function *wilcox.test*) compares the distribution of lag times to determine if they are similar or different among the two samples (Bauer 1972, Hollander et al. 2013). We examined p-values to understand the degree to which the lag times were similar or differed (Greenland et al. 2016). We considered a threshold of $\alpha = 0.05$ to aid statistical interpretation, where smaller values indicate much different lag times, and larger values indicate less different lag times.

For analyses specific to the peak and stable seasons, we removed events which overlapped the two seasons (e.g., a focal species detection in July and a lag species detection in August). We did not truncate the lag times, as we assumed avoidance or attraction occurring over broad temporal scales is likely to be related to temporal niche partitioning processes, rather than immediate perceived threat that occurs at the shorter intervals (Fisher and Bradbury 2014, Bell et al. 2023), and we do not assume to understand predator-prey dynamics well enough in this system to define the length at which a lag time was no longer relevant to temporal niche partitioning.

In some cases, when examining lags between sheep and grizzly bears, a third-party species, or “species C” occurred between detections of a focal species (i.e., “species A”) and lag species (i.e., “species B”) (Figure 16). The potential for a species C detection increases as the lag time between the focal and lag species increases (Bell et al. 2023). We ignored the presence of any species C in this analysis, as we do not assume to understand predator-prey dynamics well enough in this system to justify when an event/lag time was impacted by a single or multiple species C (i.e., the lag time calculation remains the same regardless of the presence of a species C). There were 21 instances where there was a detection of a single species c between detections of grizzly bears following Dall’s sheep (see Supplemental information, Table 14). We did not explore multi-third-party species detections (i.e., cases where there was more than one detection of a third species). However, in recognition of the complexity of mammal community interactions (Kovarovic et al. 2018, Bell et al. 2023), we also calculated descriptive statistics (mean, median, maximum, minimum, and standard deviation) of lag times of all events with the lag species defined as Grizzly bear, and the focal species defined as either Grizzly bear, Grey wolf (*Canis lupis*), Muskox (*Ovibos moschatus*), Caribou, Lynx (*Lynx canadensis*), Wolverine (*Gulo gulo*), Red fox (*Vulpes vulpes*), and Arctic ground squirrel.

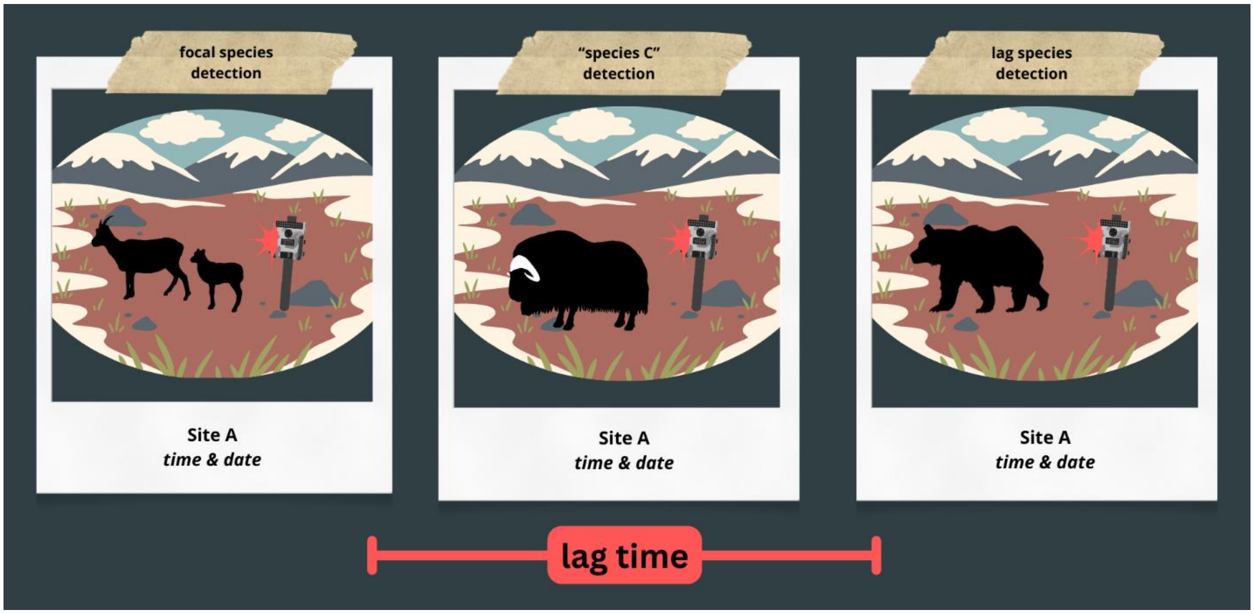

Figure 16. Third party species may occur between detections of sheep and grizzly bears. The lag time calculation remains the same in these situations, i.e., we ignore the presence of potential third-party species in this analysis.

Activity pattern analysis (APA)

We generated overlapping diel activity curves and estimated coefficients of overlap for several different event scenarios over different sampling seasons (Ikeda et al. 2021, Frey et al. 2022, Khan et al. 2023, Wolfson et al. 2023) using the package 'overlap' (Meredith and Ridout 2014). A coefficient of overlap (Δ_4) is a nonparametric estimator of the overlap between kernel densities, between 0 (no overlap) and 1 (complete overlap), which represents the area under the two curves (Meredith and Ridout 2014). We estimated 95% confidence intervals for each activity curve using 10,000 bootstrapped samples (Meredith and Ridout 2014). We then applied the Watson-Wheeler (or Mardia-Watson-Wheeler, or uniform score, MWW) test from the package 'circular' (Lund et al. 2017), which tests for homogeneity of the two samples of circular data (i.e., tests if the two species exhibit statistically different distributions by season, by looking at both circular mean and circular variance, with the assumption of continuous circular observations) (Batschelet 1981, Zar 1999, Frey et al. 2017, Aslam 2022, Frey et al. 2022, Khan et al. 2023). The resulting statistic (w) is the MWW chi-square (χ^2) value, which tests for significant differences among activity curves. We considered a threshold of $\alpha = 0.05$ to aid statistical interpretation, where a low p-value to indicates different activity patterns, and a high p-value indicates similar activity patterns (Frey et al. 2022, Khan et al. 2023).

We ran this activity pattern analysis in four scenarios:

1. Peak season activity compared between grizzly bears and nursery groups
2. Stable season activity compared between grizzly bears and nursery groups
3. Peak season activity compared between grizzly bears and ram bands
4. Stable season activity compared between grizzly bears and ram bands

3.4 RESULTS

Cameras were deployed from 2018-04-22 to 2022-06-24, with an average of 730 days +/- 411 (123 - 1,415), representing 14,604 total camera days total (for camera operability matrix, see Supplement Information, Figure 24). Across the study period, Dall's sheep were detected at 20 of 20 sites (total detection events n = 3498) as expected given our informed stratification for site selection. Grizzly bears were detected at 19 of 20 sites (total detection events n = 257), as early in the year as April 23 and as late as October 19. Additionally, we detected 10 other mammal species (Table 7) and several species of birds.

Table 7. Number of independent detections (based on a two-minute threshold) of all mammal species detected between 2018-04-22 and 2022-06-24, inclusive, in order of n, high to low. The ***key species*** *in this study are shaded and* ***bolded****. Animal names in the Gwich'in language are shown in Gwichya Gwich'in (G) and Teetl'it (T) dialects where specified, and generic where unspecified (Gwich'in Elders 1997, Gwich'in Social & Cultural Institute 2003, Gwich'in Social and Cultural Institute 2009, Aporta et al. 2014).*

Species	**n**	**Gwich'in language**	***Scientific name***
Dall's sheep (total)	3498	divii	*Ovis dalli dalli*
Nursery group (ewe & Lamb)	2370	divii tr'ek (G) & divii gii	*Ovis dalli dalli*
Ram band (medium ram & large ram)	887	datsok (T) & shohzhin' (G)	*Ovis dalli dalli*
Arctic ground squirrel	749	tthaa	*Urocitellus parryii*
Caribou *(only detected in 2020)*	261	vadzaih	*Rangifer tarandus*
Grizzly bear	279	shih (T) or sheh (G)	*Ursus arctos*
Red fox	233	neegoo (T)	*Vulpes vulpes*
Lynx	146	niinjii	*Lynx canadensis*
Wolverine	31	nèhtrùh	*Gulo gulo*
Muskox	39	dachan tat gwi'aak'ii (T)	*Ovibos moschatus*
Porcupine	11	ts'it	*Erethizon dorsatum*
Coyote	10	*see footnote	*Canis latrans*
Grey wolf	27	zhòh	*Canis lupus*
Moose	9	dinjik	*Alces alces*

** There is no word for coyote in Gwich'in language. Coyote natural range has only recently expanded to the Northern Richardson Mountains and occurrences in this area are very rare (Cluff 2006, Mackenzie 2019).*

3.4.1 Time-to-event analysis

From May – October, there were 1613 detections of nursery groups resulting in 89 grizzly bear lag events (i.e., 5.5% of nursery groups were followed directly by a grizzly bear detection), and 352 detections of ram bands resulting in 36 grizzly bear lag events (i.e., 10.2% of ram bands were followed directly by a grizzly bear detection). However, over the entire active grizzly bear season (May to October), lag times of nursery groups followed by grizzly bears were significantly shorter than lag times of ram bands followed by grizzly bears (w = 1031, p < 0.001, Table 8, Figure 17).

Table 8. Results (summary statistics) of time-to-time analysis of grizzly bears following Dall's sheep nursery groups and ram bands, assessed in various time frames. Peak season = May, June, and July. Stable season = August, September, and October. All statistics are lag times, reported in hours. MAD = median absolute deviation.

Sheep (season)	n = detections of sheep	n = detections of grizzly bears	n = events	median	MAD	mean ± SD	min.	max.
Nursery (May-Oct)	1613	276	89	34.54	48.88	89.72 ± 146.08	0.09	945.75
Rams (May-Oct)	352	276	36	120.97	129.87	172.49 ± 191.92	0.09	978.40
Nursery (peak)	1210	152	57	25.47	34.09	69.28 ± 102.00	0.09	436.91
Nursery (stable)	403	124	31	49.07	56.38	99.69 ± 133.62	0.35	668.81
Rams (peak)	232	152	25	120.59	134.14	162.60 ± 201.09	0.09	978.40
Rams (stable)	120	124	9	117.66	117.55	162.33 ± 165.28	24.66	478.08

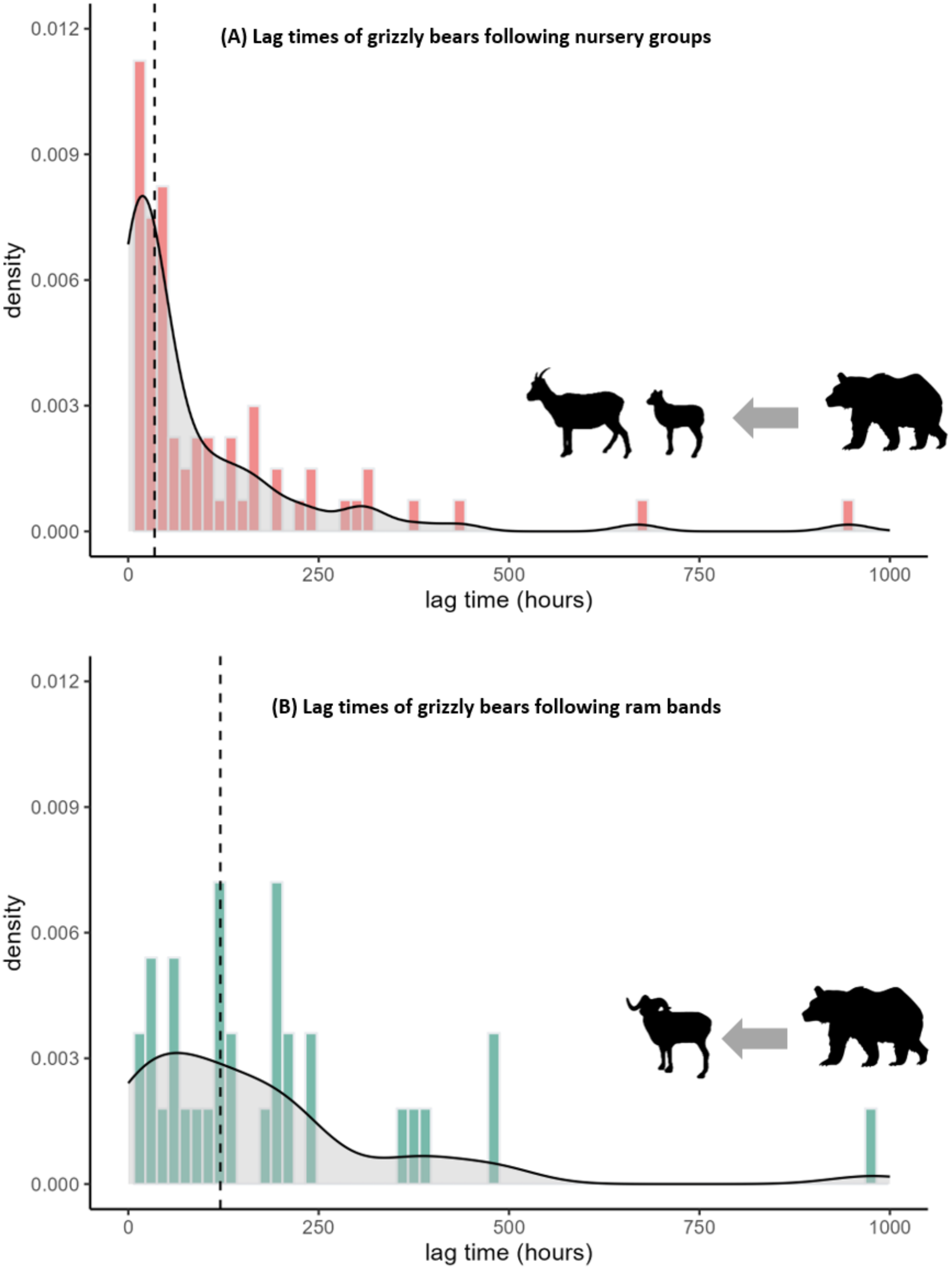

Figure 17. Histograms showing the distribution of the lag times of grizzly bear detections that followed Dall's sheep detections in May-October, inclusive. Top (A): focal species defined as nursery sheep (≥ one ewe-like or young of year detected in group) and lag species defined as grizzly bears. Bottom (B): focal species defined as rams and lag species defined as grizzly bears. A density curve is shown in black and grey. Medians are shown with dashed vertical lines: (A) = 34.54 hours; (B) = 120.97 hours.

Lag times of grizzly bears following nursery groups were significantly shorter than nursery groups following grizzly bears (w = 4992, p-value < 0.004, Figure 18), providing evidence for attractance and avoidance in the predator prey relationship. There was no evidence of a similar relationship between lag times of grizzly bears following ram bands compared to lag times of ram bands following grizzly bears, as lag times were generally similar (w = 700, p-value < 0.301, Figure 18). Descriptive statistics are available in Supplemental information, Table 15.

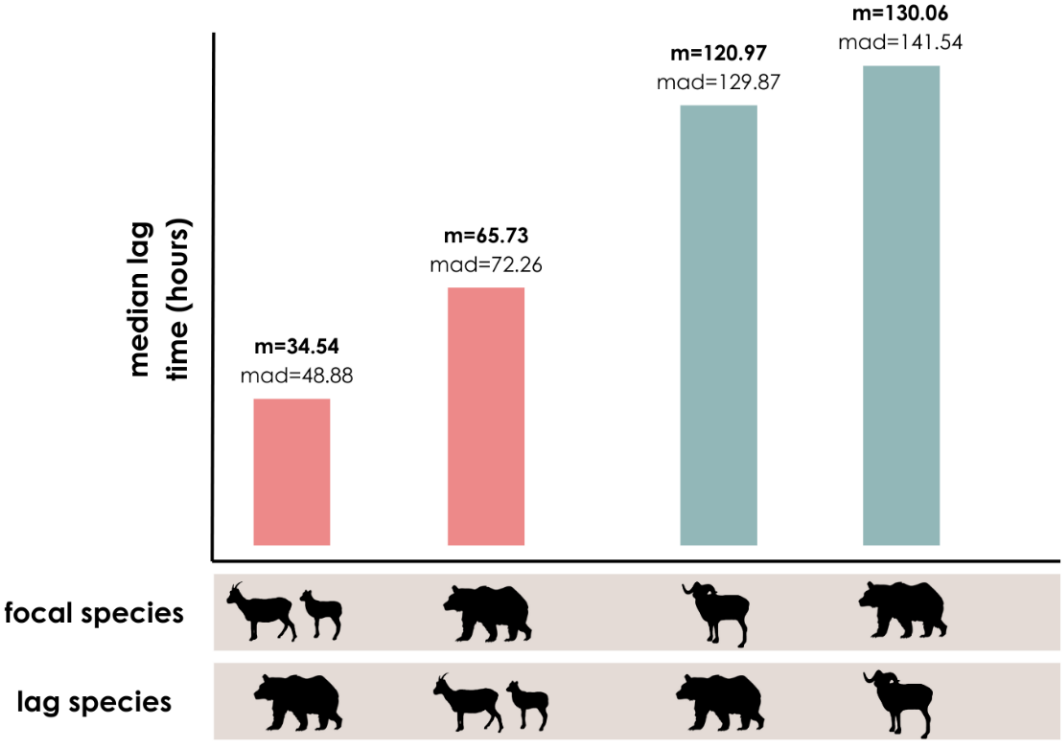

Figure 18. Median lag times of grizzly bears following Dall's sheep compared to lag times of Dall's sheep following grizzly bears. Pink bars are associated with nursery groups and blue bars are associated with ram bands. m = median lag time in hours; mad = median absolute deviation.

In the peak season, lag times of nursery groups followed by grizzly bears were shorter than in the stable season (w = 646, p < 0.019, Table 8, Figure 19) and were the shortest median lag times of all sheep-grizzly events. This seasonal pattern was not seen with ram bands followed by grizzly bears, where the lag times in this case were generally similar (w = 106, p < 0.409, Table 8).

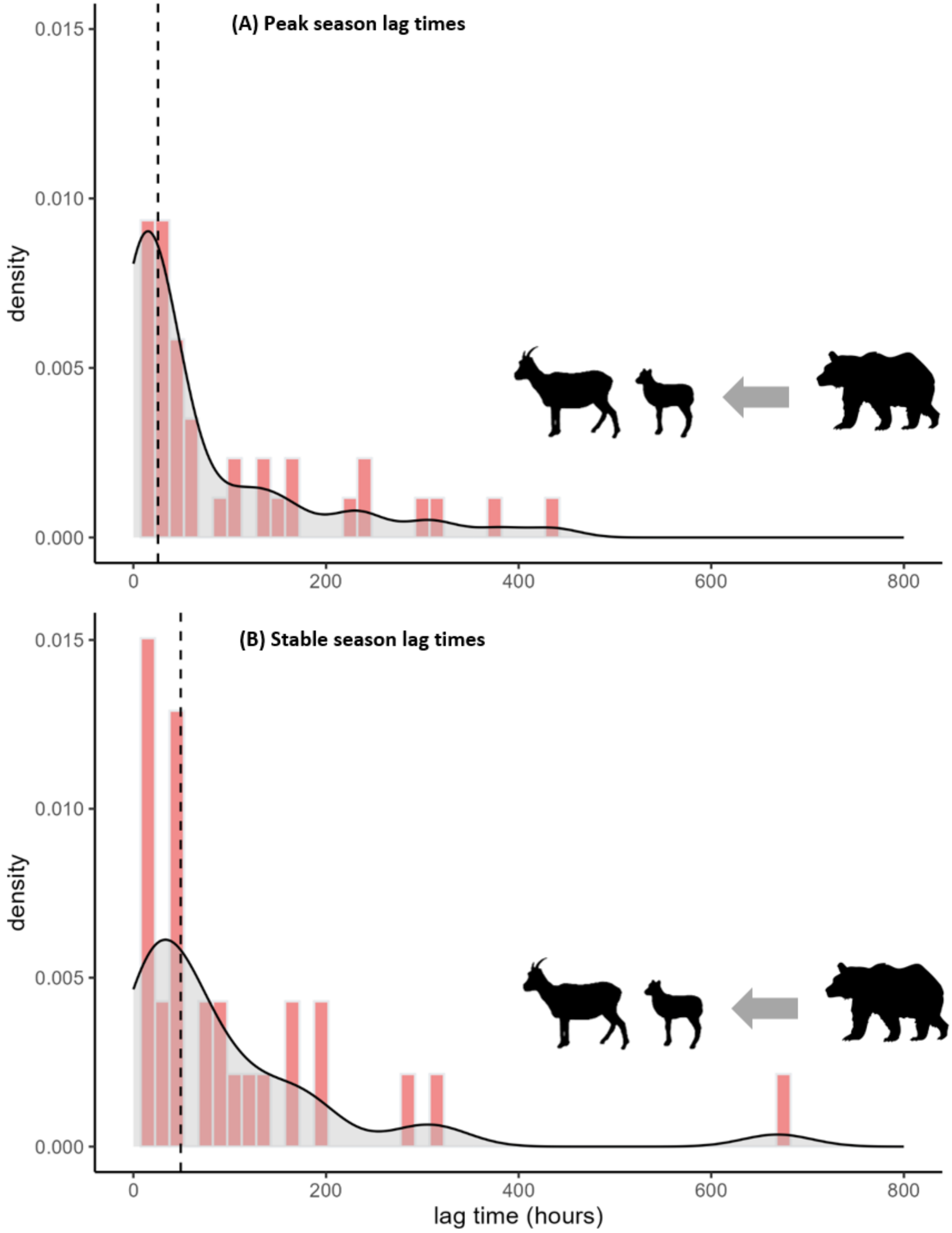

Figure 19. Histograms showing the distribution of lag times of grizzly bears following nursery groups in the peak season and stable season. Top (A) = peak season (May to July) Bottom (B) = stable season (August to October). A density curve is shown in black and grey. Medians are shown with dashed vertical lines: (A) = 25.47 hours for peak season; (B) = 49.07 hours for stable season.

Between May to October, there were 1853 events of a Dall's sheep detection being immediately proceeded by another Dall's sheep detection (based on a two minute threshold). Lag times ranged from 0.004 hours to 824.54 hours, with a median of 2.30 hours and a mean of 26.05 hours (±64.62). This was to be expected, as Dall's sheep are herding animals and we deployed cameras in high use areas.

Sample sizes were limited for other species evaluated. Events of grizzly bears following caribou, other grizzly bears, and muskox had median lag times shorter than the peak nursery lag times. Events of grizzly bears following lynx, Arctic ground squirrel, red fox, wolf, and wolverine all had median lag times longer than peak nursery (Table 9; Supplemental Information, Figure 25).

Table 9. Summary statistics (reported in hours) for events of grizzly bears following various other mammals of interest ordered by shortest to longest median lag times, calculated between May – October. MAD = median absolute deviation. See Supplemental Information, Figure 25 for data visualization.

Focal species	**n = events**	**median**	**MAD**	**mean ± SD**	**minimum**	**maximum**
Caribou	9	17.16	3.93	46.76 ± 99.81	0.51	312.01
Grizzly bear	91	17.35	25.63	78.24 ± 155.84	0.04	961.32
Muskox	5	25.22	23.64	53.03 ± 67.84	2.28	171.84
Lynx	8	26.69	13.44	57.47 ± 72.28	14.10	226.07
Arctic ground squirrel	27	32.68	40.73	72.73 ± 97.43	1.94	384.54
Red fox	11	53.95	60.06	105.66 ± 108.05	6.68	318.16
Grey wolf	2	187.35	229.21	187.35 ± 218.64	32.78	341.95
Wolverine	3	219.24	310.18	232.59 ± 229.53	10.03	468.50

3.4.2 Activity pattern analysis

Coefficients of overlap among both nursery groups (Figure 20) and grizzly bears, and ram bands and grizzly bears (Figure 21) were fairly consistent between seasons. However, there were marked differences in diel activity patterns. Nursery groups appear to temporally segregate from grizzly bears in both the peak season ($w = 22.423$, $p < 0.001$) and stable season ($w = 19.559$, $p < 0.001$), with dissimilar activity patterns (Figure 20). In the peak season, nursery groups are generally active the whole diel cycle, with a peak in the early morning. Grizzly bears generally show a bimodal activity pattern in the afternoon and evening. In the stable season, both nursery groups and grizzly bears display a bimodal activity pattern in the afternoon and evening, but with different peak times of activity in the earlier part of the day. Ram bands appear to temporally segregate from grizzly bears in the peak season only ($w = 10.942$, $p < 0.004$, Figure 21). Like nursery groups, rams are most active in the morning, which is opposite of grizzly bear activity. However, in the stable season, ram band and grizzly bear activity patterns are very similar ($w = 0.074$, $p < 0.964$, Figure 21), both displaying a somewhat bimodal activity pattern in the later part of the day. Activity patterns diverged most from that of grizzly bears for nursery groups in the peak season, and activity patterns were most similar to grizzly bears for ram bands in the stable season.

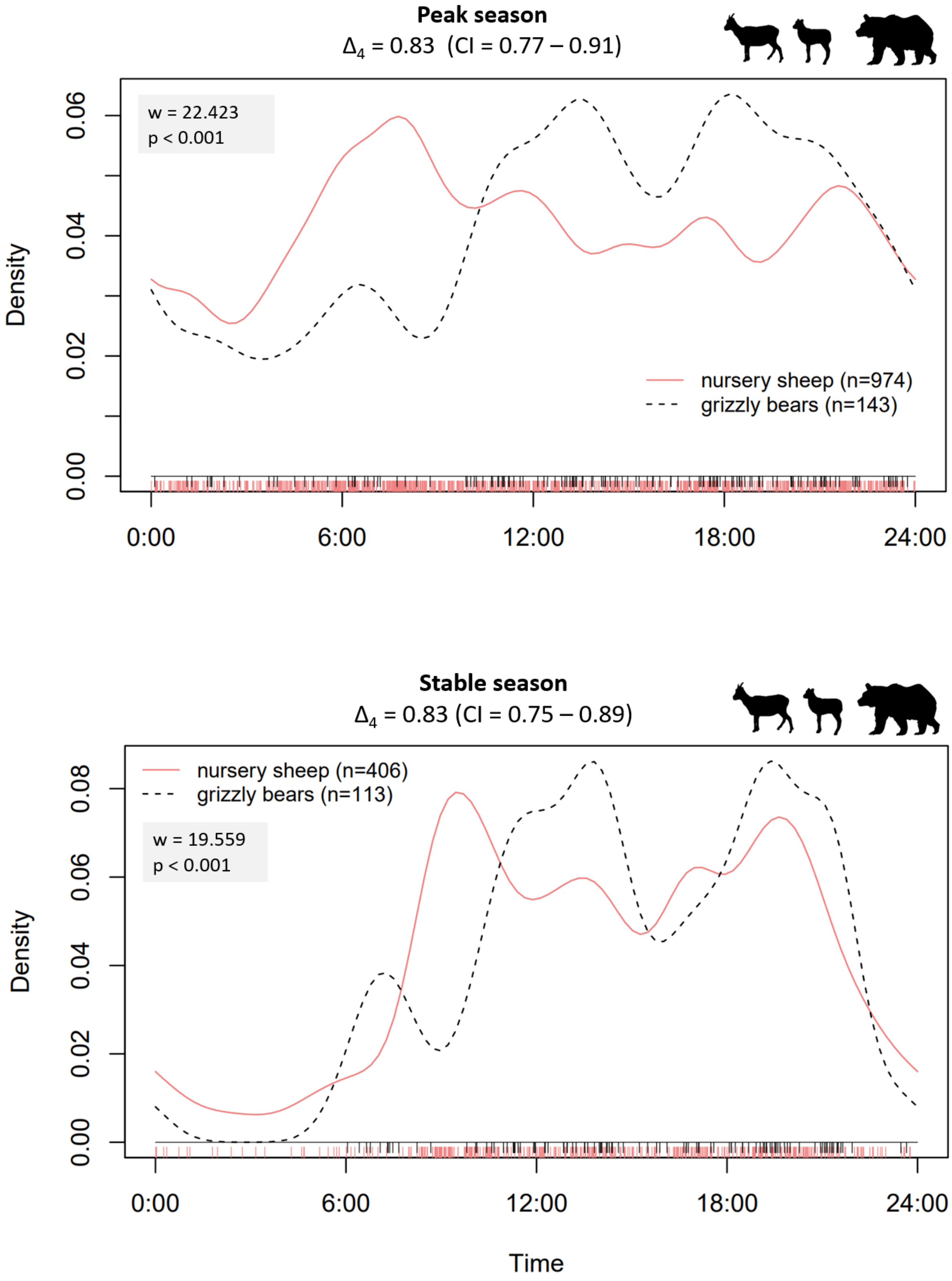

Figure 20. Peak (top) and stable (bottom) season overlapping diel curves for nursery sheep and grizzly bear detections. The rug marks along the x-axis represent activity samples for each species.

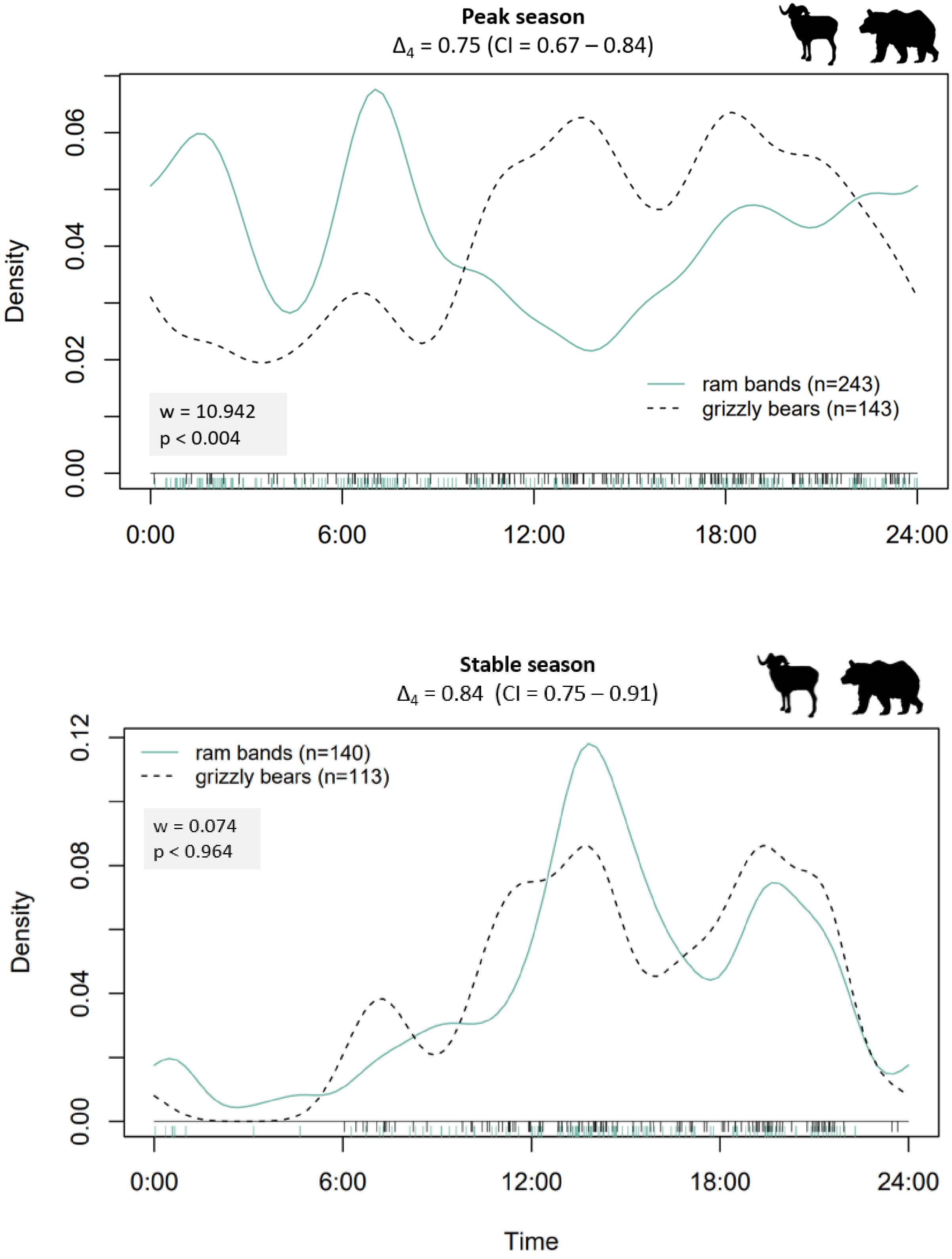

Figure 21. Peak (top) and stable (bottom) season overlapping diel curves for ram bands and grizzly bear detections. The rug marks along the x-axis represent activity samples for each species.

3.5 DISCUSSION

Grizzly bears more closely tracked nursery groups than ram bands, especially in the early season

Grizzly bears more closely track Dall's sheep nursery groups than they track ram bands, a behaviour that is most pronounced during the peak season of lamb mortality. This suggests that bears are preying on lambs during the time of year when lambs are most vulnerable (peak season), but then appear to shift away from this behaviour later in the summer (stable season). This is consistent with research showing that grizzly bears target ungulate neonates in the spring, but generally have behaviour patterns that follow phenological development of plant foods (MacHutchon 2001, Munro et al. 2006, Edwards et al. 2011, Benson 2014, 2023). Our results thus provide support for a plastic behavioural response on the part of the predator (Halle 2000, Frey et al. 2017). In the absence of known sheep mortality rates and causes, a higher probability of temporal encounter with bears may correspond to an estimated higher predation risk (Lambert Koizumi 2012, Lambert Koizumi and Derocher 2019). This possible targeted predation highlights the importance of an optimal foraging framework for nursery groups (Rachlow and Bowyer 1994, 1998, Brown et al. 1999), and points to the importance of escape terrain as a critical component of nursery group habitat especially when young are most vulnerable to predation (Frid 1997, Rachlow and Bowyer 1998, Walker et al. 2007, Dertien et al. 2017, Forshee et al. 2022). Although we did not detect any predation events on the cameras, our results demonstrate that nursery groups are at a higher exposure risk to grizzly bears than rams groups.

Nursery groups consistently occupy a different temporal niche than grizzly bears; ram bands share temporal niche in August through October, but not in May through July

Diel activity analyses show that nursery groups temporally segregate from grizzly bears in both the peak and stable season, which may be a temporal niche predator avoidance strategy. Nursery groups clearly exhibit predator avoidance by spatial segregation and habitat selection (Rachlow and

Bowyer 1998, Hamel and Côté 2007, Lambert Koizumi and Derocher 2019), but this is the first research to evaluate the temporal element of predator avoidance for this dyad. This segregation may be shaped by evolution, but is likely a seasonal response of nursery groups recognizing the inherent risk to their vulnerable young.

This analysis also shows that rams only temporally segregate from grizzly bears in the peak season, but appear to share a temporal niche in the stable season. There are several possible explanations for this pattern. It is possible that rams are an unlikely prey source for grizzly bears. This is consistent with our TTE results showing that ram bands were not being closely followed by grizzly bears, and past research showing that lambs have the highest predation rate compared to adult sheep. However, adult sheep mortality studies are uncommon, and ram mortality is often attributed to age and harsh winter conditions (Hoefs and Bayer 1983, Simmons et al. 1984). In the possible absence of predation, the similar activity patterns may be related to coincidental habitat use (i.e., foraging for similar resources) and circadian rhythms in the long days of Arctic summer. In summer and autumn, forage resources are a key variable in Dall's sheep habitat selection as rams attempt to amass as much growth as possible in preparation for the rut (Lambert Koizumi and Derocher 2019). This pattern of a focus on foraging as the summer progresses is consistent with known grizzly bear foraging habits (MacHutchon 2001, Munro et al. 2006, Edwards et al. 2011, Milakovic et al. 2012) and the fact that spatially, rams in this area are overall exposed to higher predation risk than ewes, with exposure risk peaking in the summer months (Lambert Koizumi and Derocher 2019).

Minimal differences observed in volume of activity overlap between both species and seasons

Our coefficients of overlap (Δ_4) were consistent between seasons for both nursery groups and ram bands in comparison to grizzly bears between seasons, meaning there were minimal shifts in the volume of time that each species was active in the diel cycle. It is unclear what a minimum coefficient of overlap would be required to facilitate direct predation, with no clear benchmarks for describing high or low overlap. For example, previous predator-prey APA research before and after wolf culls in Canada's boreal forest estimated a pre cull Δ_4 of 0.91 (for wolves and moose) and 0.89 (for wolves and deer), but 0.67 and 0.69 post-cull, respectively (Frey et al. 2022), which gives some indication of overlap for predation risk. However, mortality data are needed as evidence that a higher overlap is associated with higher risk of predation of ungulates. More recent research in low disturbance boreal landscapes in Canada estimated Δ_4 for predator-prey relationships among white-tailed deer compared to wolves and grizzly bears to be 0.65 and 0.78 respectively (Khan et al. 2023). Other research on predator prey relationships of eastern cottontail rabbit (*Sylvilagus floridanus*) and mesocarnivores in Mexico described overlaps exceeding 0.70 as "high" (Andrade-Ponce et al. 2022). Finally, single-species research on wild pigs in the United States describes Δ_4 estimates of 0.88 and 0.90 as "average overlap", and estimates <0.90 as "high" (Wolfson et al. 2023). Based on these examples in the literature, our Δ_4 estimates (which ranged from 0.75 – 0.84) appear average or normal for predator-prey relationships. Interpreting these numbers in with the context of traditional knowledge on local grizzly bear and Dall's sheep relationships (Benson 2014, 2023), we conclude our Δ_4 indicates adequate temporal exposure for predation.

Though overlap in diel activity patterns remained fairly consistent between seasons, the timing of activity varied seasonally for all three species (see Supplemental information Figure 26*,* Figure 27*,* Figure 28). This was expected due to factors such as phenological development of plant foods (MacHutchon 2001), the reduced vulnerability of lambs to predation with age, and extreme fluctuations in daylight hours (Bennie et al. 2014). Daylight hours in particular are of notable interest, given the known influence of circadian rhythms on animal behaviour (Schmidt et al. 2016, Arnold et al. 2018, van Beest et al. 2020, Patterson et al. 2022) and the dramatic differences in daylight hours between the seasons in this Arctic environment. Previous studies have shown that in times of 24-hour daylight (i.e., June), grizzly bears tended to be most active in the evening, and with increasing hours of darkness (i.e., September) had peaks of activity in the morning and evening (MacHutchon 2001). More research specifically dedicated to circadian rhythms, activity patterns, and behaviour of Arctic animals would aid in further APA interpretation.

Camera traps can yield fine-resolution insights to interpreting predator-prey relationships

With a small camera array in a community-based monitoring framework, we were able to investigate the temporal relationships between Dall's sheep and grizzly bears, which is an important advance in wildlife monitoring in the face of rapid landscape change (Kokelj et al. 2017, Rantanen et al. 2022, Seider et al. 2022). More, now than ever, it is important to gain a firmer understanding of mammal communities in these environments. These mammal community interactions are complex and difficult to study, yet remote wildlife camera monitoring programs offer an opportunity to explore these complex relationships in a non-invasive way. This community-based monitoring program led by the Gwich'in Renewable Resources Board and Ehdiitat Renewable Resource Council is proving to play a key role in understanding change to community-ecology of Dall's sheep and grizzly bears.

Camera traps offer an alternative to telemetry (Wolfson et al. 2023) that we have demonstrated improves interpretation of predator-prey relationships. Previous research in the Northern Richardson Mountains indicates that rams appear to be at higher predation risk than nursery groups (Lambert Koizumi and Derocher 2019). However, by considering temporal overlap at sites of syntopy – where both species occur at the same place and time – a more complex explanation evolves. Grizzly bears more closely track nursery groups than ram bands; temporal proximity coupled with vulnerability means nursery predation risk is likely higher than rams. Based on these findings, we conclude that temporal modelling, in this case time-to-event and activity pattern analyses, can divulge a deeper understanding of how sympatric species are interacting with each other.

Caveats and limitations

In our TTE analysis, we had a smaller sample size of events where grizzly bears followed rams. The limited sample size of syntopic co-occurrences is not explained by spatial segregation for rams and grizzly bears, as rams have high spatial overlap with grizzly bears in this area (Lambert Koizumi and Derocher 2019). The small sample size may be explained by our evidence that suggests a biological effect, where grizzly bears are simply not following rams as obviously as nursery groups. This pattern may be a function of limited data, and our analysis would be strengthened with more detections of ram bands, which could be improved with more camera data.

In our TTE analysis, it is possible there are “species C” effects on the predatory-prey relationships of Dall’s sheep and grizzly bears that we ignored. For example, according to Gwich’in knowledge holders, the concentration of grizzly bears in core Dall’s sheep habitat may be high due to the area's high abundance of Arctic ground squirrels and plant foods preferred by grizzly bears (Benson, 2014). Arctic ground squirrels have a similar isotopic signature to Dall’s sheep and caribou, and this group of “mountain mammals” are known to compose less than 30% of grizzly bear diet, so it remains unclear how much grizzly bear diet is Arctic ground squirrels compared to Dall’s sheep (Lambert Koizumi and Derocher 2019). In theory, sites with high Arctic ground squirrel use could be attracting grizzly bears in search of squirrels, not Dall’s sheep. However, these relationships can only be explored effectively in a broader community-level analysis. There are essentially unlimited iterations of the order and quantity of species being captured at a site, and it is unclear how other predators (e.g., wolverine, wolf, coyote) in combination with other prey/competitors (e.g., caribou, muskox, Arctic ground squirrel) would impact the relationship of Dall’s sheep and grizzly bears. In this study area, a fulsome exploration of these relationships would require more detection data and a more comprehensive rationale and process for censoring species C detections (Bell et al. 2023).

Interpretation of our results in general may be limited by time scale. Though we evaluated two distinct seasons, a finer resolution approach for defining seasons may reveal different patterns or confirm our results in Dall's sheep and grizzly bear temporal relationships. The three-month long seasonal bins chosen in this study are relatively coarse, considering the rapid changes on the landscape during this time, such phenological development of plants and shifts in daylight hours (MacHutchon 2001). With more detections, we recommend future research investigate temporal relationships at a monthly scale.

Date and time metadata from the cameras in this study was not perfect. There were some issues during deployment with camera settings and deployment procedures where the date and time programing was not always checked during camera deployment and maintenance. This causes some uncertainty regarding specific deployments at specific sites in the accuracy of the dates and times. We mitigated this uncertainty through discussions with field staff to confirm visits to each camera, cross-checking meta data and field GPS tracks, and cross-referencing metadata from other cameras to correct date and times as best as possible.

Future research

Investigating the temporal relationship between Dall's sheep and grizzly bears is a novel application of remote camera trapping, contributing new context to previous telemetry and stable isotope research. We recommend that the current community-based monitoring efforts in Northern Richardson Mountains continue, and ideally be expanded by adding more cameras, with a goal of collecting enough remote camera detections of other mammals to support spatiotemporal analysis on other predators (e.g., wolves, wolverine, coyotes, etc.) and known competitors (e.g., muskox, caribou, etc.). Additionally, we recommend modelling these community relationships in comparison to population trends of Dall's sheep to further understand the factors driving population dynamics.

We also suggest that future research be done to evaluate the impact of group size on temporal and spatial relationships between Dall's sheep and grizzly bears, as nursery group size may affect predation risk (Kasozi and Montgomery 2020). The interactive factors hypothesis predicts that when animals are at a high predation risk due to being far from a refuge, their vigilance should heighten significantly as group size diminishes (Frid 1997). With reduced risk to each individual in a larger group, animals may more willing to venture further away from escape terrain in order to optimize forage (Frid 1997, Rachlow and Bowyer 1998). Conversely, when animals are at a low risk because they are close to a refuge and far from obstructive cover, their vigilance should not increase much, if at all, even as group size decreases, enabling them to take better advantage of feeding opportunities (Frid 1997). A time-to-event model using camera data that evaluated group size as an explanatory variable for differences in lag times between nursery groups being followed by grizzly bears could provide illumination for this ecological question.

3.6 CONCLUSIONS

We describe a grizzly bear – Dall's sheep predator-prey relationship where temporal niche segregation is a likely contributor to co-existence, yet a temporal predation risk signal is still detectable. Our TTE results demonstrate that grizzly bears do target nursery groups on this landscape. We found that both ram bands and nursery groups of Dall's sheep temporally segregate from grizzly bears in May – July. During this time period, nursery groups are at their highest predation risk by grizzly bears. Later in the summer, bears appear to shift behaviour away from targeting vulnerable neonates, possibly in favour of plant foods (MacHutchon 2001, Edwards et al. 2011). In the later summer, ram bands, with less predation pressure than nursery groups and thus less predation fear, do not exhibit temporal avoidance of grizzly bears, possibly prioritize foraging in anticipation of rutting season. Nursery groups, on the other hand, likely have a generally heightened predation risk fear, and thus always maintain temporal avoidance, even as actual predation risk declines, in a balance of safety and nutritional needs

(Frid 1997, Rachlow and Bowyer 1998, Aycrigg et al. 2021). The temporal niche segregation behaviour of nursery groups is likely a mechanism of the ecological theories “ecology of fear” (Brown et al. 1999) and known “risk effects” of predation on prey behaviour (Creel and Christianson 2008). With a small, non-invasive camera array in a community-based monitoring framework, our results have advanced the understanding of how two species use time as a resource, and how they interact with one another, offering valuable insights into the complex dynamics of remote Arctic mammal communities. The Gwich’in Renewable Resources Board Dall’s sheep monitoring project (the divii project) is proving to play a key role in understanding change to community-ecology of Dall’s sheep and Grizzly bears, and thus bolstering our foundational understanding of niche theory within the field of ecology.

3.7 SUPPLEMENTAL INFORMATION

3.7.1 Defining nursery groups and ram bands: variation and challenges in classifying detections of a herding species

Individual detection data is always an imperfect capture of animal presence and absence at any given site and time. It's especially difficult to tag and define groups in herding species, such as Dall's sheep, that exist in loose temporal groups, joining up and dispersing not only at different times in the year, but also throughout the day. Given these fission-fusion dynamics of Dall's sheep, it is a huge challenge to define group identity with strict definitions of ages and sexes to be included, especially over different seasons. Dall's sheep groups within a population are constantly mixing, coming together, and splitting up, and there are many factors that influence how and when they will do that. In animal behaviour studies, a case can be made to never remove true presence data, as every data point is important to assess animal behaviour, and an analysis will be less robust for decreasing samples in either group (Peral et al. 2022).

In this study, there were 115 detections that met the definition of both nursery group and ram band (i.e, groups with least one ewe-like or lamb, and at least one adult male). In an effort to not restrict true presence data of animal behaviour, these detections were included in analyses for both nursery groups and ram bands, a statistically relevant decision (i.e., confirmed presence of a ram is still ram behaviour even if there were females and young with them, and vice-versa). Biologically, there is uncertainty in the accuracy of choosing which events to remove from which group definition. First, our main goal in defining nursery groups was to identify key lamb vulnerability predator-prey signals. We have not seen any evidence in the literature or available traditional knowledge that the presence of a ram will make a lamb less vulnerable to predation, therefore it didn't make sense to remove a nursery group detection if a ram was present. We also didn't want to remove a detection from a ram band if a ewe-like sheep was present, because in some cases, this could have been young ram (i.e., 1/4 curl or less) that was simply classified as "ewe-like", as is standard in Dall's sheep classification given the difficulty of telling the two apart without a direct sighting of genitals (Figure 22). This is a noted challenge in Dall's sheep classification overall, and if removing ewe-like sheep from the definition of ram-band, one could be eliminating detections of a true ram band (i.e., if we remove instances of ewe-like from the ram bands, then we could be losing detections of young rams hanging out with the larger ram band).

However, to test the effect of these 115 replicated data points, we re-ran all analyses, keeping the definition of nursery groups the same (as the original definition was still true), but altering the ram band definition to detections that *only* contained at least one adult male. This meant all 115 data points stayed with the nursery groups and were removed from the ram bands. In the TTE analysis, the 115 detections only resulted in a difference of events of grizzly bears following rams of n = 1 overall, which was an event in the stable season (note: the 115 detections accounted for n = 0 nursery-grizzly events). In the APA analysis, the 115 detections is n = 115 data points. For the both the time-to-event (Table 10, Table 11, Table 12) and activity pattern (Table 13) analyses, we found there was no difference in the interpretation of the statistical results.

Figure 22. Two male Dall's sheep. The animal on the left would normally be classified as a ewe-like sheep, given the horns are 1/4 curl or less. However, this image confirms the male sex based on genitals, which is a fairly rare occurrence. This is an example of where removing ram band data points because they contain ewe-like sheep would remove true presence data related to ram band activity.

*Table 10. Results of the time-to-event Mann-Whitney-U test. Shading and * indicates rows of data that show the effect when the 115 detections that also meet the definition of a nursery group are removed from the ram band data.*

Test group	**TTE result**	**p-value**	**confidence interval**
Are nursery-grizzly lag times < ram-grizzly lag times (May-October)?			
Rams	w = 1126.5	P < 0.001	-inf -34.01
Rams*	w = 1190	P < 0.001	-inf -35.75
Are ram band lag times during peak season < those in the stable season?			
Rams	w = 123	p < 0.479	-inf 80.88
Rams*	w = 106	p < 0.409	-inf 80.88
Is there a difference in lag times of grizzly bears following ram bands compared to ram bands following grizzly bears?			
Rams	w = 1047	p < 0.391	-32.44, 93.55
Rams*	w = 980	p < 0.132	-16.24, 153.46

*Table 11. Results (summary statistics) of time-to-time analysis, for ram bands only. Shading and * indicates rows of data that show the effect when the 115 detections that also meet the definition of a nursery group are removed from the ram band data. Peak season (May to July) and stable season (August to October). All statistics are reported in hours. MAD = median absolute deviation.*

Sheep (season)	**n = detections of sheep**	**n = detections of grizzly bears**	**n = events**	**median**	**MAD**	**mean ± SD**	**min.**	**max.**
Rams (May-Oct)	887	279	42	124.28	129.87	178.29 ± 184.54	0.09	978.40
Rams* (May-Oct)	772	279	41	130.92	137.21	181.71 185.69	0.09	978.40
Rams (peak)	256	152	25	120.59	134.14	162.60 ± 201.09	0.09	978.40
Rams* (peak)	256	152	25	120.59	134.14	162.60 ± 201.09	0.09	978.40
Rams (stable)	147	124	10	89.48	85.89	151.87 ± 169.29	24.66	478.08
Rams* stable	120	124	9	117.66	117.55	117.66	24.66	478.08

*Table 12. Results (summary statistics) of time-to-time analysis of grizzly bears following ram bands compared to ram bands following grizzly bears (May to October), showing the difference of a reduced sample size. Shading and * indicates rows of data that show the effect when the 115 detections that also meet the definition of a nursery group are removed from the ram band data.*

focal spp. – lag spp.	n = events	mean ±SD	median	MAD	minimum	maximum
Ram-Grizzly	42	178.29 ±184.54	124.28	129.87	0.09	978.40
Ram-Grizzly*	41	181.71 185.69	130.92	137.21	0.09	978.40
Grizzly-Ram	45	287.29 ±352.58	139.79	173.87	2.56	1519.42
Grizzly-Ram*	40	353.80 409.67	164.66	178.88	2.56	1754.59

*Table 13. Presentation of activity pattern analyses for the full ram band sample in methods and results, and the reduced ram band sample. Shading and * indicates rows of data that show the effect when the 115 detections that also meet the definition of a nursery group are removed from the ram band data. Peak season (May to July) and stable season (August to October).*

Test group	Coefficient of overlap (confidence interval)	APA test result	p value
Peak season: ram band diel activity pattern compared to grizzly bear diel activity			
Full ram sample	0.75 (0.67 – 0.84)	w = 10.942	p < 0.004
Reduced ram sample*	0.74 (0.65 – 0.83)	w = 13.85	p < 0.001
Stable season: ram band diel activity pattern compared to grizzly bear diel activity			
Full ram sample	0.84 (0.75 – 0.91)	w = 0.074	p < 0.964
Reduced ram sample*	0.83 (0.73 – 0.91)	w = 0.129	p < 0.885

There were also 231 total detections that contained an unclassified sheep. A sheep was considered unclassified when the age and sex could not be estimated with confidence, due to its body position or the clarity of the image (Figure 23). Of those 231 detections, 135 contain only unclassified sheep; these instances do not meet the definition for nursery group or ram band and were therefore not included in any analyses. However, of the 231, there were 10 detections of one or more unclassified sheep as part of a ram band: these events were included in ram band analysis and the overall group met the definition of a ram band. Finally, there were 86 detections of one or more unclassified sheep as part of a nursery group: these events were included in nursery group analyses.

Figure 23. Unclassified sheep indicated by orange arrows. Left: Example of an unclassified sheep in a nursery group. Right: Example of unclassified sheep in a ram band.

3.7.2 "Species C" detections

Table 14. Instances where a third-party species was detected between detections of Dall's sheep and Grizzly bears. The mean, SD (standard deviation), minimum, maximum are between detections of Dall's sheep and Grizzly bears, when the referenced third-party species occurred.

Third-party species	n = events	mean	SD	minimum	maximum
Arctic ground squirrel	7	204.6	284.0	21.8	701.5
Caribou	2	40.27.9	19.0	27.9	53.4
Grey wolf	1	810.3	N/A	N/A	N/A
Lynx	1	42.6	N/A	N/A	N/A
Muskox	1	62.6	N/A	N/A	N/A
Porcupine	1	79.5	N/A	N/A	N/A
Red fox	5	202.2	139.3	29.4	383.6
Wolverine	3	435.0	294.6	216.7	770.1

3.7.3 Camera operability

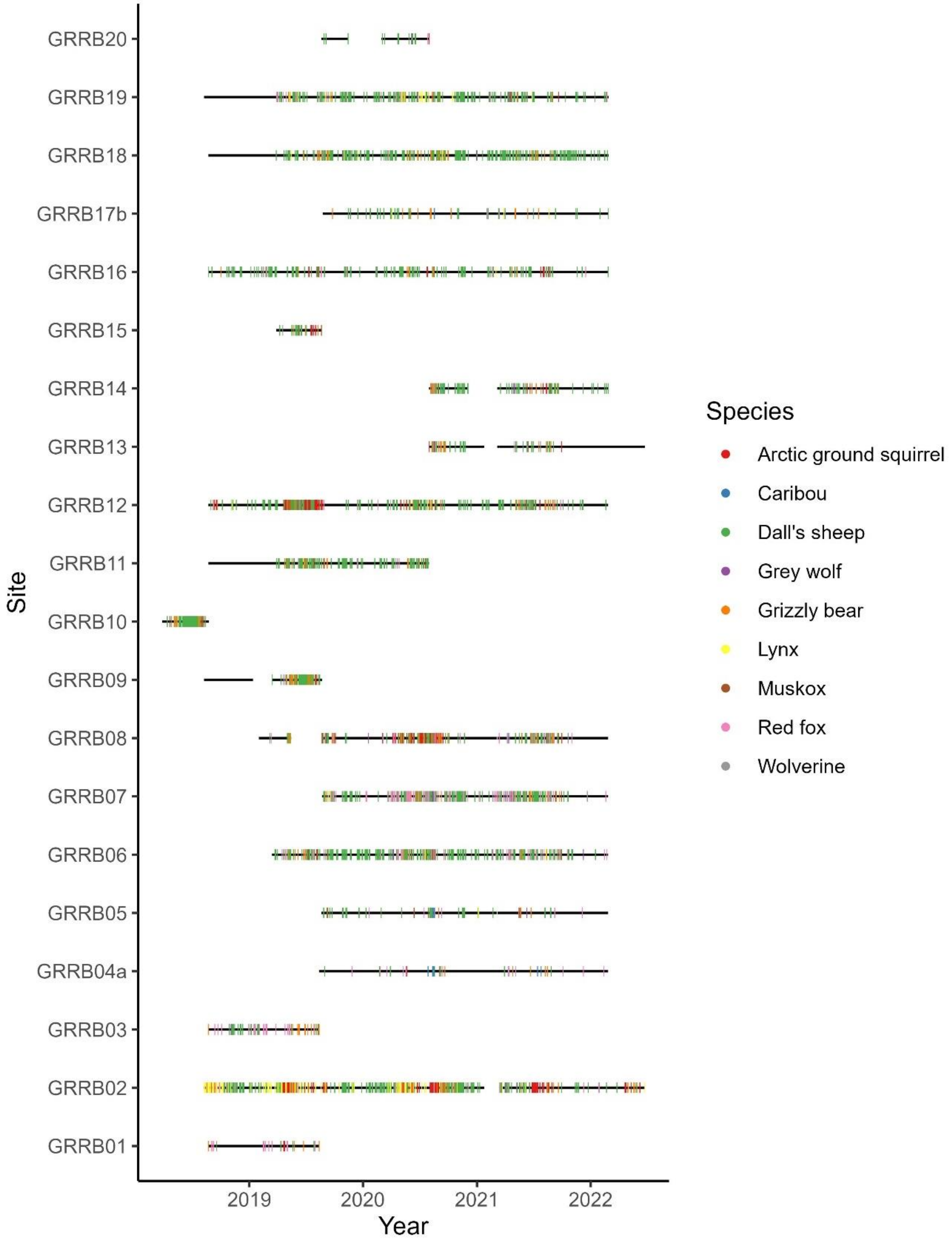

Figure 24. Camera operability matrix, showing a horizontal line representing the camera deployment periods at each site, overlaid with lines that represent wildlife detections, with a unique colour for each species. Data spans 20 sites between 2018 and 2022. Cameras were deployed for an average of 730 days +/- 411 (123 - 1,415), representing 14,604 total camera days total.

3.7.4 Summary statistics of predatory-prey and prey-predator TTE (Figure 18)

Table 15. Results (summary statistics) of time-to-time analysis of grizzly bears following sheep compared to sheep following grizzly bears, using detections from May – October, inclusive, between 2018-2022. Statistics are reported in hours. MAD = median absolute deviation.

focal spp. – lag spp.	n = events	median	MAD	mean ±SD	minimum	maximum
Nursery-Grizzly	89	34.54	48.88	89.72 ± 146.08	0.09	945.75
Grizzly-Nursery	90	65.73	72.26	127.85 ±161.79	0.13	869.14
Ram-Grizzly	36	120.97	129.87	172.49 ± 191.92	0.09	978.40
Grizzly-Ram	34	130.06	141.54	236.08 ±237.31	2.56	915.07

3.7.5 Broader mammal community: grizzly bears following alternate focal species (Table 9)

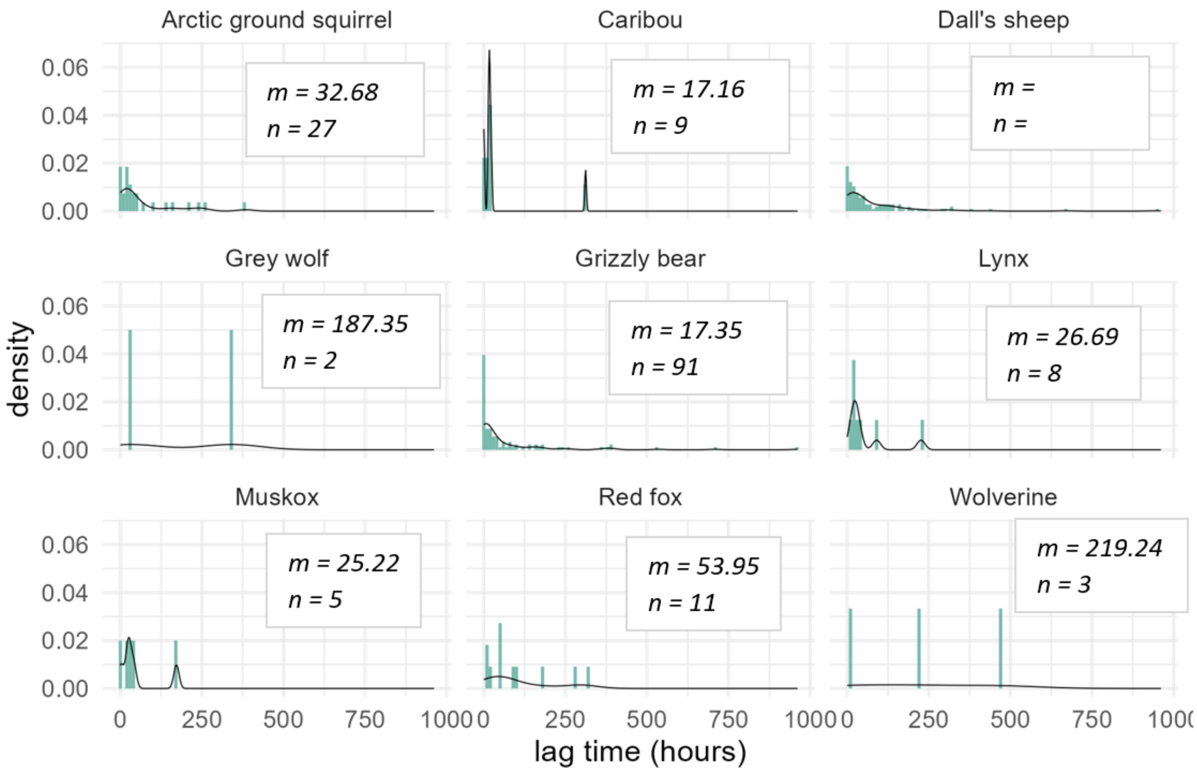

Figure 25. Distribution, shown in blue, of the lag times (hours) of Grizzly bear detected after various focal species detections (time frame May – October, inclusive). Density curves shown in pink. Median lag times, "m", are presented with the number of events, "n".

3.7.6 Activity patterns of singular species, compared between the seasons

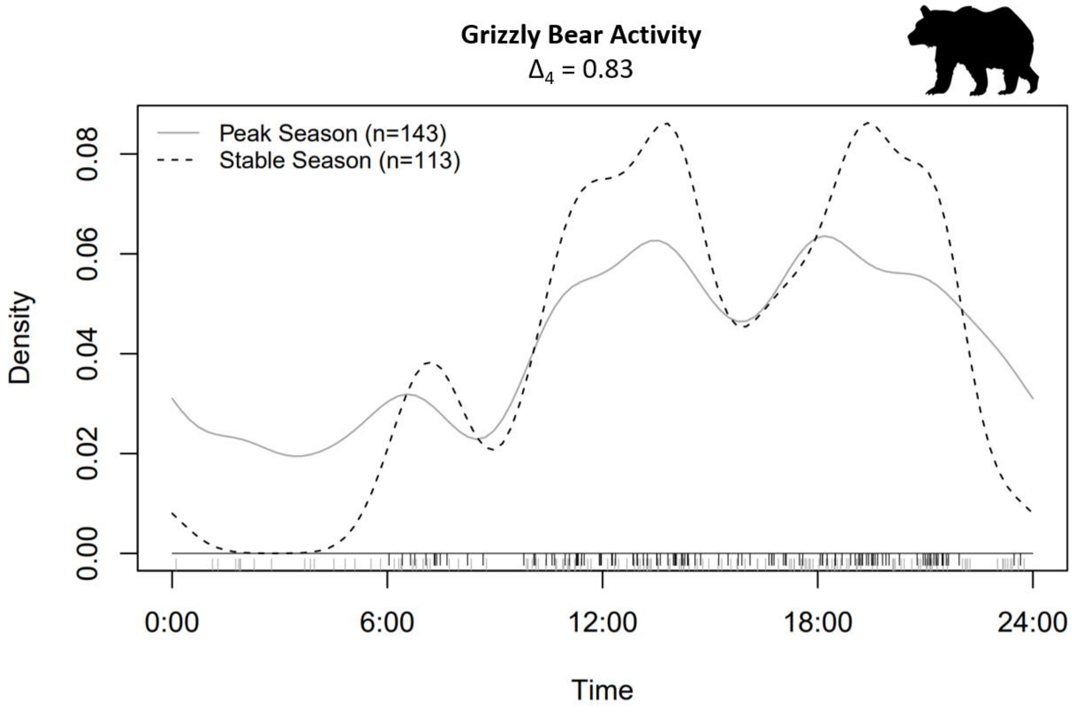

Figure 26. Grizzly bear diel activity patterns in the peak season (May – July) and stable season (August – October) using data from 2018 – 2022, inclusive.

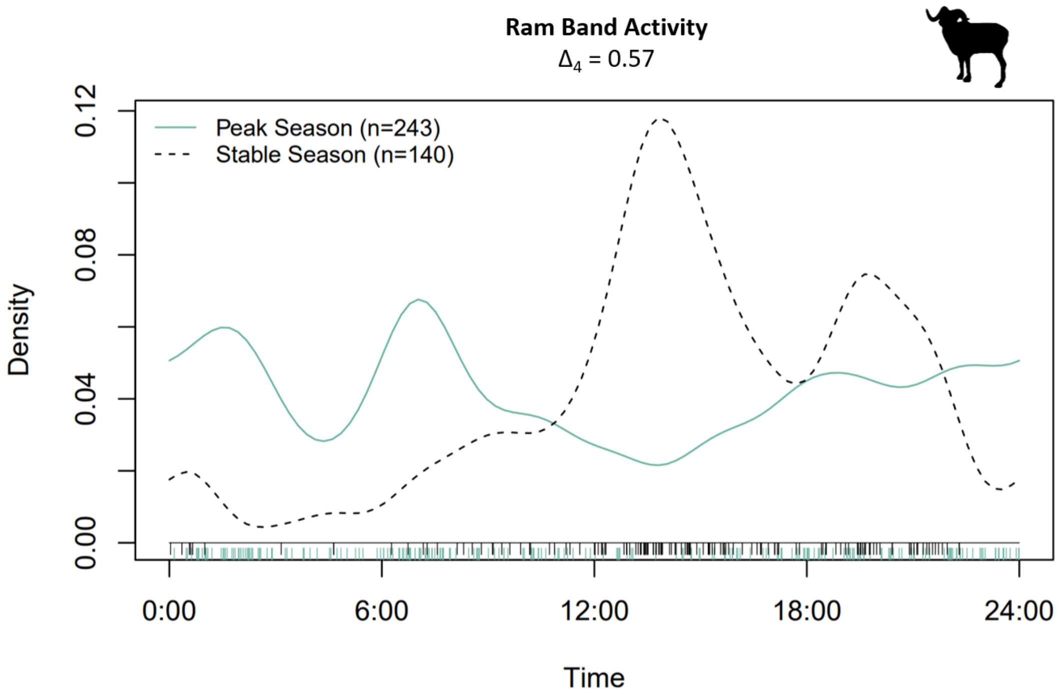

Figure 27. Ram band diel activity patterns in the peak season (May – July) and stable season (August – October) using data from 2018 – 2022, inclusive.

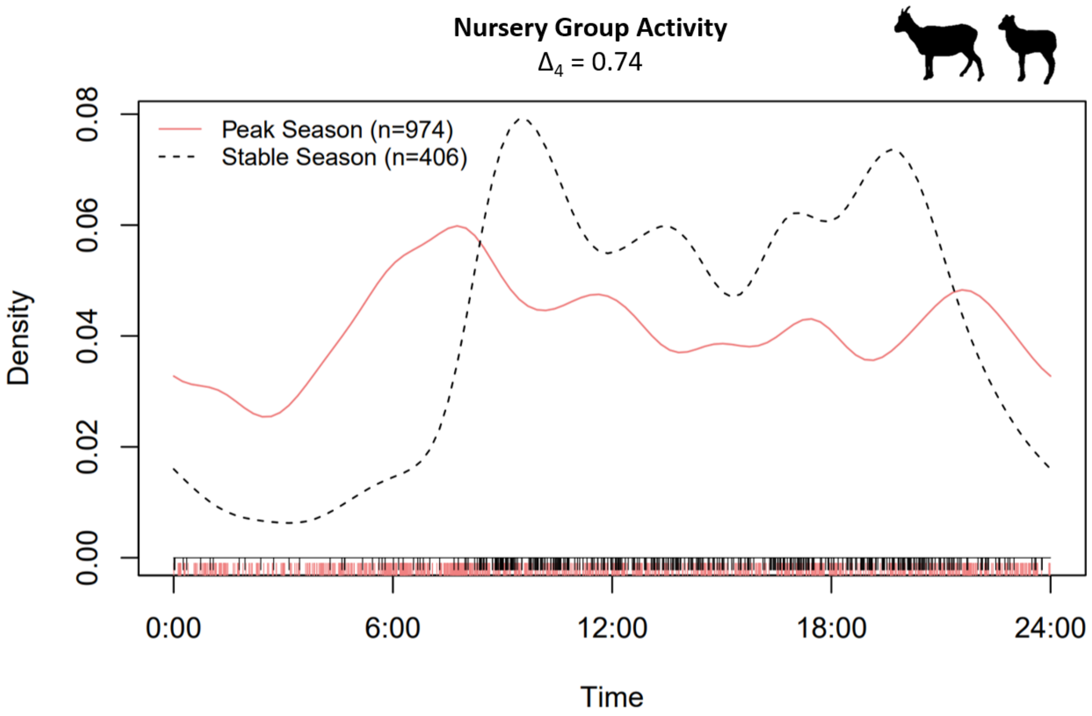

Figure 28. Nursery group diel activity patterns in the peak season (May – July) and stable season (August – October) using data from 2018 – 2022, inclusive.

CHAPTER 4. WHAT DID WE SPY THROUGH THE CAMERA'S EYE?

4.1 STUDY SYNTHESIS

4.1.1 Summary of results

The objective of my thesis was to evaluate the ability of cameras to capture Dall's sheep population demography (Chapter 2) and explore temporal predator-prey relationships among Dall's sheep and grizzly bears (Chapter 3). This study was conducted in partnership with the Gwich'in Renewable Resources Board (GRRB) as part of a broader, community-based monitoring program, with research questions developed in consideration of community interests and research priorities.

In Chapter 2, I explored GRRB Goals 1 and 3[2]. I used three years of data from both the remote cameras and aerial surveys to compare the effectiveness of cameras for estimating key demographic parameters. This study compared two methods of acquiring Dall's sheep population demography: remote cameras and aerial surveys. I estimated specific parameters of lamb:nursery ratio, ram:nursery ratio, and ram classification. I found that camera data collected in appropriate seasons produced reliable lamb:nursery, ram:nursery, and ram classification proportions, as compared to aerial surveys, ultimately indicating similar population status trends between the two methods. However, the ram:nursery ratio was more challenging to determine, given the fission-fusion dynamics of Dall's sheep. Moreover, this study highlights the importance of considering the temporal nature of sampling wildlife populations (Frey et al. 2017, Kemna et al. 2020, Wiskirchen et al. 2022). The camera's continuous sampling provided an opportunity to calculate demographic parameters for multiple sample periods, unlike aerial data,

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[2] The GRRB developed the objectives for this camera trap program, which were based on input from the RRCs and community members:
1. Determine annual and seasonal population demographics of divii using cameras
2. Model annual changes to these demographic parameters
3. Compare the camera demographics to those obtained from aerial surveys
4. Examine habitat changes, predation, or other variables that are known to affect populations
5. Provide recommendations that will inform the community-based monitoring program

which provided a single sample. Obtaining reliable demographic ratios was heavily reliant on multiple samples, as variations were drastically reduced with accumulation (Fischer 2011, Burton et al. 2015, Lebreton and Gaillard 2016), which we achieved through the application of traditional knowledge in the study design. High seasonal variation demonstrates the value of selecting appropriate samples for ecological survey methods - the sample that best reflects true populations state should be selected based on knowledge of behaviour and movement, the two factors affecting fission-fusion dynamics and the sample variation it imparts (Cross et al. 2005).

This study is important because wildlife demography is a crucial parameter in monitoring and modelling a population's persistence through time. Currently, aerial surveys are the most common method for obtaining demographic data for large mammals, but they come with limitations such as sample size, temporal constraints, and costs, whiling causing significant disturbance to wildlife and limiting local community participation. Routine aerial surveys are still important in determining large mammals' population sizes and identifying trends over time. However, incorporating a remote camera system into a monitoring process allows for a more comprehensive and consistent examination of demography, while fostering an opportunity to explore further questions related to the broader mammal community. In summary, this study highlights remote cameras a useful wildlife monitoring tool, providing continuous longitudinal and repeated sampling of population demography, particularly useful for species that aggregate in fission-fusion dynamics, such as Dall's sheep.

In Chapter 3, I explored GRRB goal 4[1]. I used data from the cameras to evaluate the temporal partitioning of Dall's sheep and grizzly bears through a time-to-event analysis (TTE) and activity pattern analysis (APA), and thus better understand temporal predator-prey attractance (how grizzly bears follow Dall's sheep), and avoidance (how Dall's sheep escape grizzly bears). I found that grizzly bears are more closely tracking nursery groups than ram bands, a relationship that is most profound during the early spring, when lambs are most vulnerable to predation. These results show that nursery groups consistently occupy a different temporal niche than grizzly bears. Though ram bands and grizzly bears occupy a different temporal niche in the spring and early summer, they share a temporal niche in the later summer and early fall. This research on the temporal relationship between Dall's sheep and grizzly bears using remote camera trapping provides nuance and context to other wildlife monitoring tools, such as GPS collars and stable isotope analysis. With a small camera array in a community-based monitoring framework, I was able to investigate fine-scale temporal relationships between Dall's sheep and grizzly bears, which is an important advance in wildlife monitoring in the face of unprecedented landscape change.

4.1.2 Implications

While this study has far-reaching significance to researchers in the field of wildlife ecology, I will start by prioritizing discussion of localized implications. This study provides Gwich'in communities and land managers with new, community-valued scientific knowledge on population demography (Chapter 2) and temporal predator-prey co-occurrence (Chapter 3). In combination with local and traditional knowledge (Benson 2023), this information will support local stewardship decisions about harvesting and land-use in the immediate term, while also providing more robust base-line data for monitoring the future. In the Black Mountain area and Northern Richardson Mountains more broadly, there is on-going monitoring but limited direct management, likely due to a lack of anthropogenic pressure. However, given the declining status of this population of immense cultural, social, and ecological value, a fulsome understanding of the status of this population and the factors influencing it will be key to an effective management plan for Dall's sheep in the Northern Richardson Mountains. The drafting of this plan commenced in 2008, and will incorporate scientific studies such as this one, in combination with traditional/local knowledge (Working Group for Northern Richardson Mountains Dall's Sheep 2008).

Overall, my thesis provides support for community-based monitoring of Dall's sheep, and offers new methods in remote camera trapping for the scientific community at-large. Chapter 2 provides supporting evidence that camera traps can be used as an alternative to aerial surveys for capturing demography of social mountain ungulates such as Dall's sheep, while providing fine-resolution data for other aspects of population monitoring, as illustrated in Chapter 3. Chapter 3 advances the field of ecological niche theory and community ecology, by exploring temporal relationships between Dall's sheep and grizzly bears, in ways previously never studied. Further, the array has been able to document and report incidences of disease, horn deformities, and the rare presence of species (i.e., coyote) expanding their natural range, as outlined below in section 4.2. Overall, the use of remote wildlife cameras to estimate population demographics and examine species interactions, as applied in this study, could revolutionize wild sheep research and management more broadly by providing a non-invasive, cost-effective tool that produces far more data than infrequent helicopter surveys.

4.1.3 Caveats & limitations

Caveats and limitations specific to my two studies have been laid out in Chapter 2 and Chapter 3. However, in this section I present several additional limitations and caveats related to the camera array design as a whole and my overall conclusions.

Given the nature of the community-based monitoring program with limited maintenance and data management capacity, this is an exceptionally small array compared to more typical array designs for scientific analysis (Rovero et al. 2013, Burton et al. 2015, Caravaggi et al. 2020, Kays et al. 2020). Through the application of traditional and local knowledge in study design, the cameras were able to generate enough detections for the analyses conducted in this thesis, but sampling is still limited. For example, camera locations were targeted to capture as many detections of Dall's sheep as possible, focusing only on high-use areas and prominent trails. There was no systematic sampling grid employed or formal stratification of the cameras based on typical factors such as known seasonal habitat use/types, landscape features, existing Habitat Suitability Indices, etc. This array is thus best suited to examining questions that are temporal in nature, and limits our ability to extrapolate our conclusions to a broader area and other populations. A probabilistic design capturing representative heterogeneity in the landscape and the species' distribution would be needed to investigate additional questions. Another challenge with the array design is that the sites with the highest use characteristic are more likely to be associated with nursery groups and not ram bands, based on known habitat use and movement ecology of different classes of sheep (Rachlow and Bowyer 1998, Corti and Shackleton 2002, Nagy et al. 2013, Dertien et al. 2017, Lambert Koizumi and Derocher 2019, Aycrigg et al. 2021, Benson 2023). It is possible that the low ram:nursery ratio derived in Chapter 2 is possibly a result of this possible sampling bias; however, the ratio was also low as estimated by aerial surveys which are not necessarily prone to the sampling issue discussed. The overall low ram:nursery ratio, however, may provide some explanation for the lag-time results in Chapter 3, where temporal patterns between ram groups and grizzly bears were more difficult to disentangle than patterns between nursery groups and grizzly bears.

There were some issues with camera settings and deployment procedures to be aware of. First, not every camera in the array was the exact same model. It is notable that different camera models may have different sensitivity and image quality, possible impacting the overall detections of each camera type (Palencia et al. 2022, Recoynx 2024). Second, the use of "timelapse" settings varied, which limited the ability for a full camera operability analysis. This will be a critical issue to fix moving forward, given the necessity of camera operability in other spatial analyses (Burton et al. 2015, Caravaggi et al. 2020, Palencia et al. 2022, Taylor et al. 2022). Third, as a field error, the date and time programing was not always confirmed during camera deployment and maintenance. This causes some uncertainty during specific deployments at specific sites in the accuracy of the dates and times, which is an issue particular salient to Chapter 3 analysis. I did my best to correct issues through discussions with field staff, cross-checking GPS tracks, and cross-referencing other cameras, as described in Chapter 3, but it should be noted our date-time data is not perfect.

Working in an extreme environment such as the Northern Richardson Mountains presents additional challenges for camera operability and thus detection rates (Palencia et al. 2022). This is a minor concern for this study given because most of our analysis was focused on non-winter months. However, the primary concerns are still worth discussing.

The first concern is the effect of temperature on camera operability. Remote wildlife cameras are built to function in outdoor environments, but are tested to one end of their extreme limits in Arctic environments, leading to questions on the actual cold-weather functionality of the cameras (Palencia et al. 2022). Camera performance in cold temperatures will vary depending on brand, model, and battery type. The most prominent model used in this array, the Reconyx Hyperfire 2 Professional, is weather rated to -40°C, when using high-quality lithium batteries (Recoynx 2024). Our camera metadata included an estimate of the temperature when the image was taken, though the accuracy of this data is unconfirmed. The coldest temperature we recorded on the camera metadata was -39°C, but it is likely the temperatures in the field were occasionally colder than this. It is difficult to determine how well cameras preformed over varying winter temperatures, as “timelapse” settings were not consistently utilized, thus limiting a detailed camera operability analysis.

Two additional concerns, related to detection rates and camera operability, are camera icing (Figure 29) and snow coverage (Figure 30). In this area, the snow depths appear to change drastically over relatively short periods of time, likely from the wind. Cameras at some sites were occasionally snowed in, which risks partially or fully obscured detections temporarily (Figure 30).

The final concern was the prevalence of false detections; I estimate approximately 50% of a camera’s annual images at some sites were triggered by blowing snow (Figure 31). This is unavoidable in a mountainous, arctic environment. The use of MegaDetector, an artificial intelligence object detection model (Beery et al. 2019), during data processing allowed efficient sorting through images like this, thus false detections from blowing snow did not drastically increase processing time overall. However, it should be noted that these models have the potential to generate false negatives, thus missing some true detections (Beery et al. 2019, Greenberg 2020). I mitigated this risk by testing different probability thresholds with the data, prior to implementing the model in my workflow. The use of a conservative threshold was important to mitigate false detections without a high risk of false absences.

Figure 29. Camera covered in frost and ice. Operability of this camera at this time is unknown due to inconsistent timelapse settings.

Figure 30. Snow partially or fully obscuring detections.

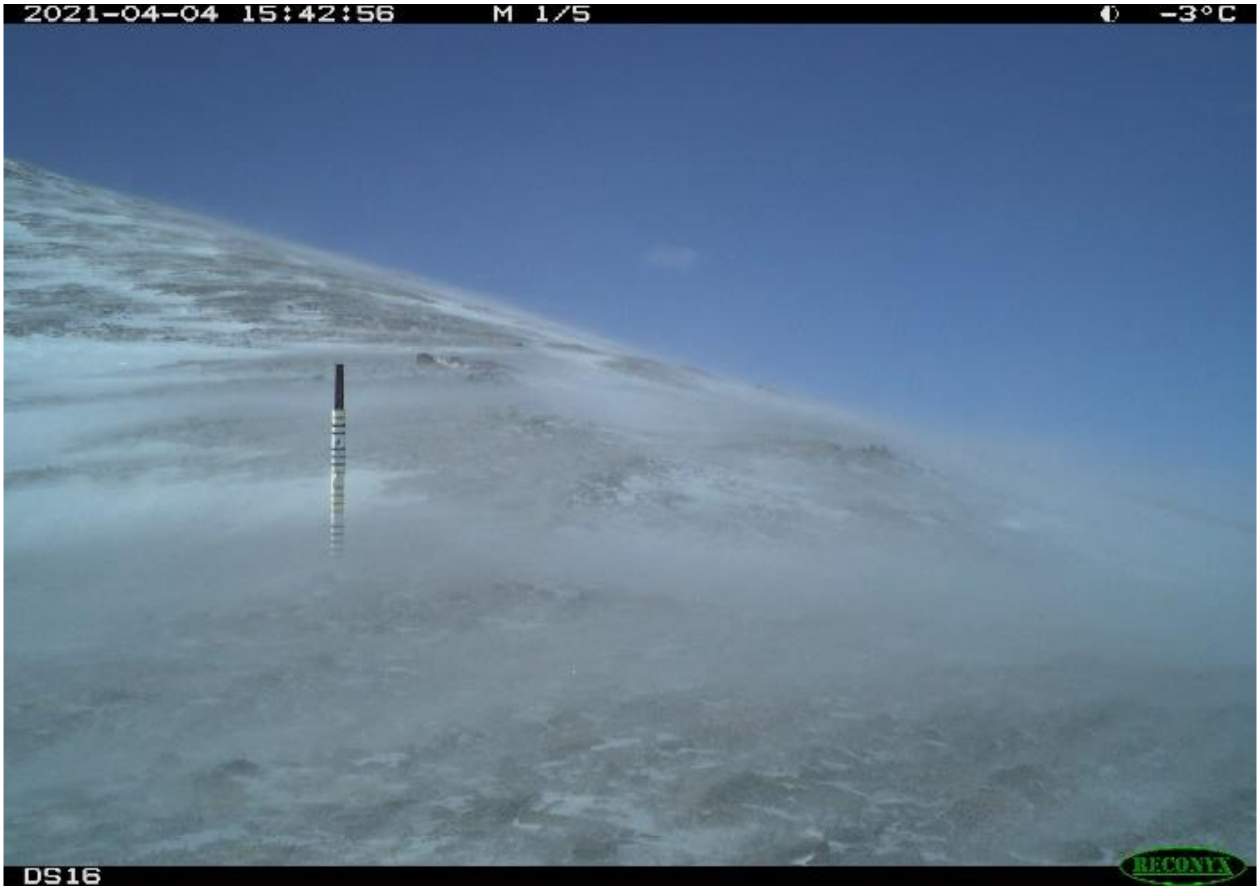


Figure 31. Movement of blowing snow triggering the camera, resulting in a false detection.

4.1.4 Future research considerations

Future research considerations specific to each of the two studies have been laid out in Chapter 2 and Chapter 3. In consideration of the thesis overall, identified gaps in related literature, and in respect of GRRB goal 5[1] and community interest, I offer the following additional research recommendations.

In reflection of the thesis overall, future research should focus on understanding the connections between population demography (Chapter 2) and species co-occurrence (Chapter 3), as demography may influence diel activity patterns (Wolfson et al. 2023) and time-to-event modelling could help to tease out predator-prey dynamics which ultimately may drive population demography (Bonsall and Hastings 2004). Both demography and species co-occurrence could also be further modelled in relation to climate change impacts, such as changes to extreme weather events, spring green-up periods, and plant community phenology, to further understand factors driving the population (Bjorkman et al. 2020, Aycrigg et al. 2021, Seider et al. 2022). In particular, the spring, summer, and autumn lamb:nursery ratio modelled in comparison to fine scale weather data (temperature, snowfall, icing events) would be useful in understanding the impact of weather on recruitment of this population. Previous lamb survival studies in the Northwest Territories and Yukon (Simmons et al. 1984) have attributed the majority of mortality to unfavourable weather during the lambing season, which can account for 40-60% of mortality (Scotton 1998).

Given the limited geographical sampling frame in this study and relatively small number of cameras deployed, repetition and expansion of this study is recommended to understand the applicability of the results to other ungulate species and study areas. With a larger array, the opportunity to stratify cameras based on habitat types and features would open the possibly of adding occupancy modelling for a variety of species, particularly predators and mesocarnivores that can not be enumerated during period surveys. A larger array may also increase detections of species enough to preform spatiotemporal spacing analysis and occupancy modelling, and allow researchers to obtain a more fulsome understanding of broader community ecology and its impacts on Dall's sheep.

There are a few areas of interest to expand on demography modelling as related to Chapter 2. First, a routine government aerial survey was conducted in June 2022. It would be worthwhile to repeat the Chapter 2 analysis using that June flight and compare it to the spring 2022 camera data, which was not available at the time of this study. Second, with more time to dedicate to tagging, it would be useful to re-review the ram detections and estimate their ages. From the new ram age estimates and current horn curl classification data, an estimation of ram productivity (i.e., on average, how old is a ram when they reach a certain curl class) could be obtained. This information is useful for harvest management recommendations and understanding range health (i.e., forage quality) and genetics in a population (Hemming 1969, Bunnell 1978, Singer and Zeigenfuss 2002, Eamer 2014, Monteith et al. 2018, Environment Yukon 2019). Third, demographic ratios provide valuable information, but may be best paired with population abundance data for truly understanding the status of a population (Thinhorn Sheep Indigenous Perspectives and Thinhorn Sheep Management Teams 2022). This could be achieved with a more robust camera array for population density and/or more regular aerial surveys. Further, with an expanded array, there may be opportunity for exploring integrated population modelling (Johnson et al. 2010, Schaub and Abadi 2011, Moeller et al. 2021).

4.2 CAMERAS FOR SCIENCE AND STORY

Through collaboration with the GRRB and in communication with RRCs, community members, and youth, a key underpinning of this this work was to conduct the study in a community-valued way. These cameras essentially function as additional eyes on the land. With their continuous sampling, the cameras contain much more than just data – they contain stories. These observations and stories contribute to local knowledge, a sentiment expressed to me while listening to a traditional knowledge interview with an Gwich'in elder. These stories are for science, too. They not only provide valuable context to interpreting scientific results, but also seed ideas for future scientific inquiry. It is important to acknowledge that science forms just one block of concrete in the foundation of understanding wildlife and determining stewardship actions. Other forms of knowledge and experiences, as well as relationships and values, are a part of building a robust foundation (McGregor 2004, Smith 2005, Johnson et al. 2015, Thompson et al. 2020).

What I've learned through this research and conversations in community is that many of the questions of value to communities don't necessarily come from a formal scientific analysis of the camera data: each and every photograph is of value for the information it holds. As the sole observer of every single image in the divii project dataset, I feel it is my responsibility to share the stories that have been shared with me by the animals and land. Through community open houses (Figure 32), school engagement sessions (Figure 33), and Q&As at GRRB meetings, I was able to get a better understanding of what information from this project, outside the two data chapters, is of high interest and value to people. The following is an opportunity to document these stories.

Figure 32. Presenting a project update at a community open house in Aklavik, 2022. At this open house, I was able to connect with community members directly to hear what matters most to them with the camera data.

Figure 33. School engagement sessions in the Gwich'in Settlement Area in the fall of 2022.

General observations:

- 12 species of mammals and at least 9 species of birds (some I could not identify with certainty due to blurry images)
- No animals with GPS collars or identifying ear tags were detected
- No people, off-road vehicles, or aircraft were detected, other than when the cameras were being serviced by GRRB staff and community members

4.2.1 A story about Coyote

The Coyote (*Canis latrans*) is rapidly expanding its natural range across North America (Jensen et al. 2022). Coyotes have had a known presence in the NT for decades, but have only been documented north of Great Slave Lake since the 1960’s (Cluff 2006). Documented sightings of coyote in the Beaufort Delta are rare (Mackenzie 2019) and there is little known about how their increasing presence on the land may impact the mammal community (Benson 2023). To my knowledge, there is no Gwich’in word for coyote, another testament to the general absence of these canines on this landscape.

However, in the face of rapid climate change and resulting habitat changes in this area, mammal community structure is expected to change alongside the vegetation and weather (Lantz et al. 2022, Rantanen et al. 2022, Seider et al. 2022), and expanding coyote presence is no exception. Coyotes are a known predator of wild sheep in other jurisdictions of North America. In some populations of Dall’s sheep in central Alaska, coyotes have accounted for the highest levels of predation on Dall’s sheep lambs (Scotton 1998, Arthur and Prugh 2010). Like most predator encounters, lambs are far more vulnerable to predation by coyotes than an adult sheep are (Bleich 1999). As coyote range expands into


An individual coyote detection in May 2020

core areas of Dall's sheep habitat in the Northern Richardson Mountains (as documented by the divii project), this monitoring program may provide important information for stewardship decisions in this ecosystem. Remote cameras can be used to understand species movements over time, and species occurrence data can serve as important baseline data in monitoring coyote range expansion and investigating the impact of their increasing presence on the broader mammal community (Steenweg et al. 2017). As a result, there is high community interest in detections of coyote.

We observed ten detections of coyote from April 2018 – February 2021 (Table 16). The detections do not indicate how many individuals were observed, or how many coyotes are currently located in the area.

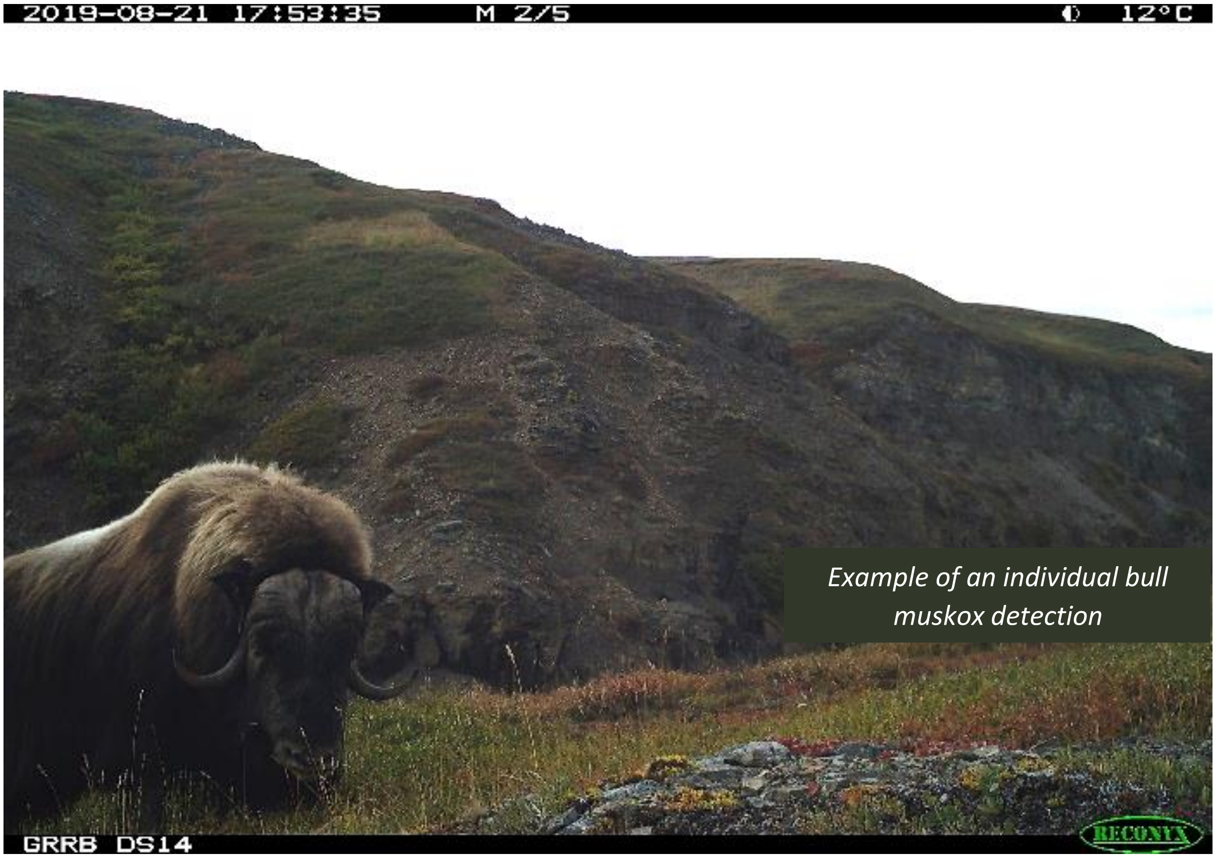
Table 16. Summary of all coyote detections observed during tagging.

Site	Date (dd/mm/yyyy)
GRRB02	04-01-2019
GRRB02	01-02-2019
GRRB07	08-04-2020
GRRB07	09-04-2020
GRRB12	12-09-2018
GRRB12	11-10-2018
GRRB12	31-20-2018
GRRB12	05-02-2021
GRRB14	19-08-2020
GRRB20	04-05-2020
GRRB02	04-01-2019

4.2.2 Muskox (dachan tat aak'ii)

The history of Muskox (*Ovibos moschatus*) presence in the Northern Richardson Mountains and around Black Mountain is complex and often debated among locals (Wishart 2004). The current population is descendant from translocation projects in Alaska, which have been considered a successful conservation story by some, where populations were extirpated in the mid 1800's (Reynolds 1998, Cuyler et al. 2020, Carter 2021). However, the extent of the population's expansion into the mountainous areas of the GSA is a concern to local communities like Teetł'it Zheh (Fort McPherson, NT), where there is minimal evidence of Muskox presence or harvest in oral history (Wishart 2004). The presence of Muskox in the Northern Richardson Mountains is of concern to community members, as there is uncertainty on how muskox may impact highly valued species like Dall's sheep and caribou (Benson 2023). There is community interest in what the cameras can tell us about muskox in the Black Mountain Area, and there are on-going traditional knowledge studies and scientific inquiries into the topic of species co-existence and muskox impacts on the land.

I observed 39 detections of muskox (2018 = 3 detections; 2019 = 8; 2020 = 15; 2021 = 13). The detections do not indicate how many individuals were observed, or how many muskoxen are currently located in the area. Single muskoxen were observed 22 times, and groups of ≥2 individuals were observed 17 times. The largest group size was seven animals. I did not collect age and sex data on all muskox observed, however anecdotally, the solitary animals were often bulls. There was one calf observed. There are muskox bulls collared in this region(Mike Suitor, *pers comms.*); however, I did not observe any collared animals on the cameras. I did observe one individual in a group with a suspected skin infection (see section 4.2.3).



Example of an individual bull muskox detection

One of the larger herds of muskox observed

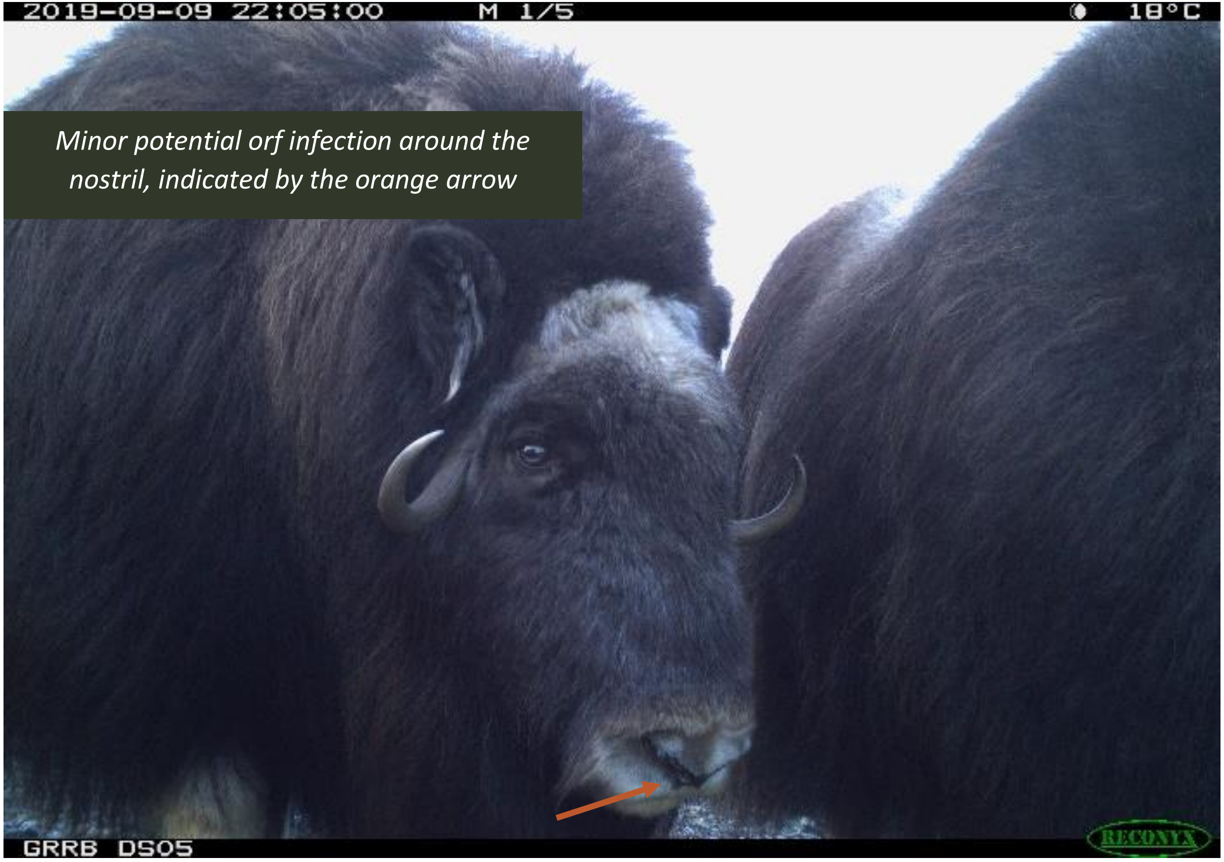
4.2.3 Disease observations and the presence of Orf

Orf virus is a type of *Parapoxvirus*, or skin herpes, causing a contagious ecthyma known as "Orf". The infection is not uncommon in sheep and goats, and also occurs in other wildlife such as muskox and caribou. It can be found on any skin but, on sheep, is most often observed around the soft skin of eyes, lips, teats, nares, and genitals. Infections are both more common and more severe in young animals, and though usually not fatal, it can lead to death by restricting the animal's ability to feed properly (Spyrou and Valiakos 2015). Transmission of orf occurs most often through contact with damaged skin, where the virus can enter epidermal cells. It can remain viable on contaminated materials for significant periods, even up to 17 years in dry climates. Orf is also a zoonotic disease, meaning it is transmissible to human from animals (Spyrou and Valiakos 2015). The Government of the Northwest Territories recommends hunters wear gloves when handling sheep with any signs of orf, and states that meat from infected animals can be safe to eat, with precautions such as proper trimming and knife disinfection (Government of Northwest Territories 2017).

There were 19 detections of suspected orf infections in sheep, meaning approximately 0.6% of sheep detections contained a sheep with visible infection. This does not mean there were 19 individuals – it is possible the same infected individual was detected more than once. Infection severity ranged. Only one individual muskox was noted to have a suspected minor orf infection around the nose, however, the disease may have been more difficult to detect in muskox via cameras. In addition to a limited sample of Muskox on the cameras, they also do not investigate the cameras as closely as sheep, and the colour of their fur and skin may aid in concealing an infection. Though this infection is noted in Dall's sheep populations across other jurisdictions (Tryland et al. 2018), I did not find any documentation of orf in the Northern Richardson Mountain sheep in previous research. Therefore, this community-based monitoring program is the first known documentation of orf infections in this population. These observations have been reported to the appropriate community leaders and Government officials.

Less severe example of suspected orf

More severe example of suspected orf



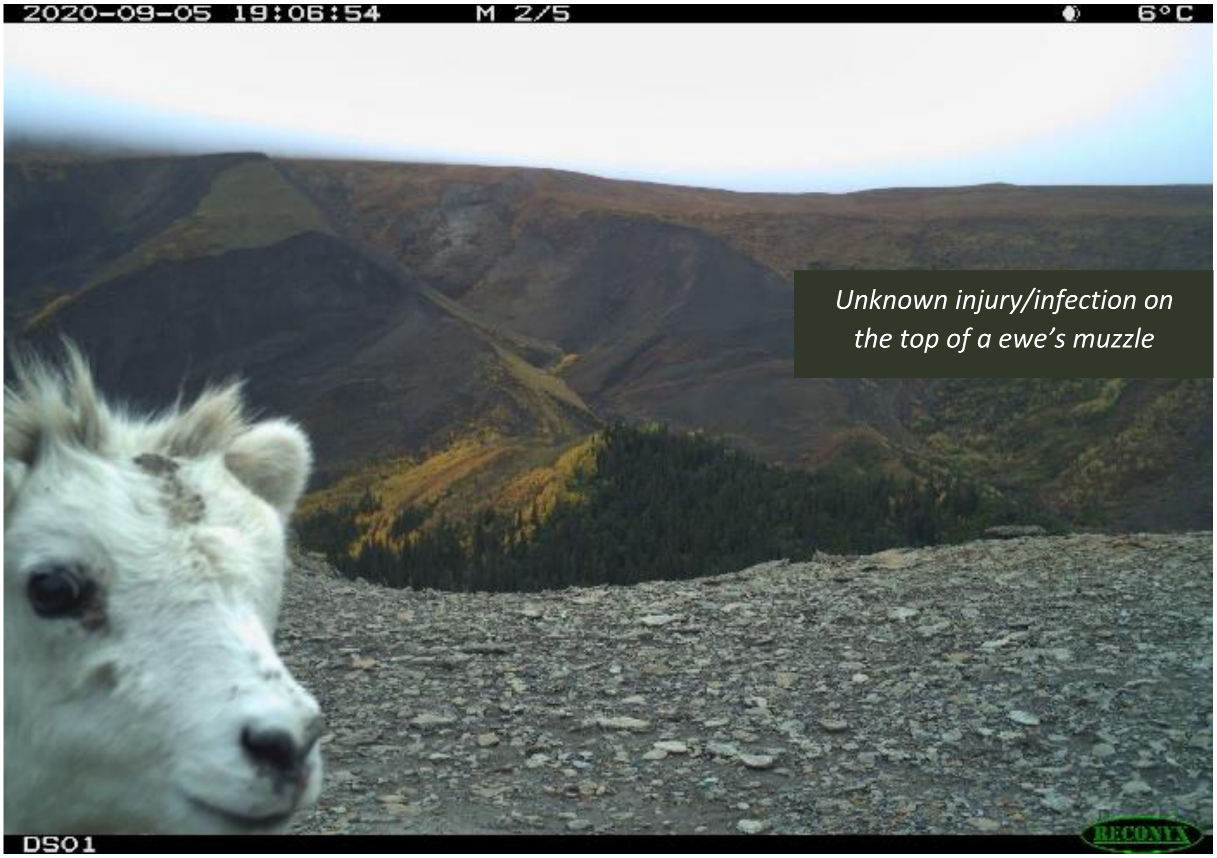
Minor potential orf infection around the nostril, indicated by the orange arrow

4.2.4 Other health concerns and injuries

There were a few rare observations of other health concerns or injuries noted on the sheep. I have not included the common occurrences of damage to ram horns and noses that I suspect were inflected during normal rutting behaviour. The below images and inset descriptions cover the main abnormalities observed in the camera data.


A ewe that appears to have a badly damaged or missing right eye


Unknown injury/infection at the base of the neck/upper left shoulder on a young ram



Unknown injury/infection on the top of a ewe's muzzle

Unknown injury/infection on lamb's face, particularly around eyes and nostrils

4.2.5 Divii horn growth and abnormalities

Dall’s sheep have true horns: living tissue surrounded by an outer bone-like keratin sheath (Bunch et al. 1984, Eamer 2014). Horns amass the majority of their growth during the summer months when foraging resources are plentiful. Horn growth slows to a standstill over the winter, creating a visible annulus in the outer horn every year, which can be counted to estimate the age of a sheep (Geist 1966). Annuli are most obvious in rams, as their horns are much larger than ewe’s. Due to time constraints, few rams were aged during the tagging process, however aging the rams was possible. High quality images from cameras, usually at multiple angles, made confidentially aging the rams relatively easy, but only when the rams were close enough to the camera.

Horn growth patterns are highly influenced by nutrition and age, and to a lesser extent, though highly debated, genetics (Monteith et al. 2018). Physical damage of the horns (e.g., extreme cold) can cause necrosis of the horn core, causing abnormalities (Hoefs et al. 1982, Bunch et al. 1984). Short conical protuberances and extreme twisting are two commonly described abnormalities documented in the Yukon (Hoefs et al. 1982). The prevalence of horn abnormalities is important to be aware of. For example, these abnormalities in some cases could be a symptom of poor nutrition, potentially indicating an issue with range quality that could be impacting population in a bigger way (Bunnell 1978, Monteith et al. 2018).

I noted several difference types of horn abnormalities during tagging (see below images). Anecdotally, the most common abnormality was one stunted or broken horn on an adult sheep. Less commonly, I also observed drooping horns and cases of rams with “twisters”. The Gwich’in Renewable Resources Board shared this finding on Facebook in May 2022, asking if anyone had seen horns like this before or knew what caused them, but we did not receive any comments from community members. The Divii Traditional Knowledge Report did not note anything relating to unique or abnormal horns .


2020-05-20 06:26:26 M 5/5 2°C
GRRB DS01
RECONYX
2019-06-21 14:57:49 M 5/5 21°C
GRRB DS02
RECONYX
2020-07-15 00:35:35 M 4/5 8°C
GRRB DS07
RECONYX
2021-04-29 11:19:32 M 4/5 9°C
DS03
RECONYX
2020-02-15 11:00:41 M 2/5 -31°C
GRRB DS08
RECONYX
2019-06-01 08:15:18 M 1/5 10°C
GRRB DS03
RECONYX

4.2.6 Lynx (niinjii)

Lynx (*Lynx canadensis*) span most of Alaska and Canada (Poole 2003) and populations are currently considered secure in the NT (Government of Northwest Territories 2024). Lynx detections were most common as individuals, but there were a few instances of groups. It is likely that these are family groups or breeding pairs (Mowat and Slough 1998, O'Donoghue et al. 2010).

Three lynxes in one frame; the two in the background are circled in orange

As discussed in Chapter 3, mammal community interactions are complex. Recent research in the Yukon has found that climate variables can explain nearly 70% of variation in lamb recruitment. However, hare population cycles and resulting cycles of predators such as lynx and coyote may also be driving recruitment of Dall's sheep (Wong et al. 2023). The relationship between lynx and Dall's sheep is complex (Wilmshurst et al. 2006, Arthur and Prugh 2010), but future research with cameras such as a spatiotemporal spacing analysis similar to that conducted in Chapter 3, may be able help untangle such complexities.

Though I did not observe any hares on the cameras, lynx detections were common (n = 146). In one special event, I was tagging a common occurrence of a couple ewes walking past this camera and the next images were of a lynx, but the ewes were still in the background, grazing, not far away. The sheep looked up at the lynx but didn't run, and the lynx appeared to be walking normally along the trail, aware of the sheep. This was the last image the camera captured of the occurrence.

A lynx in the foreground with two Dall's sheep ewes in the background, circled in orange

4.2.7 Divii and birds

Unexpected to me, the cameras documented many birds, including Golden eagle, Raven, American robin, Golden Plover, American Kestrel, Ptarmigan, Peregrine Flacon, Owls, Canada Jay, and other species of raptors I was not able to identify to species. It is well documented that large raptors like Golden eagles will prey on lambs, especially in the spring when they migrate North to this area for their breeding season (Arthur and Prugh 2010, Benson 2023). However, I have not heard stories of other birds interacting with the sheep, until on one occasion, I witnessed what appears to be several ravens harassing at least three ewes. This event is difficult to see in a selection of still photos, and is best visualized with clicking through a series of images in full screen, as the ravens are very small in the background and the white snow does not contrast well with the sheep coats for visibility. One can speculate that animals are constantly interacting on the land, but it is interesting to actually see these occurrences on camera, and it is important to document the stories for the future.


2019-10-12 14:26:07 M 5/5 -6°C
GRRB DS13
RECONYX


2019-10-12 14:25:10 M 5/5 -6°C
GRRB DS13
RECONYX


2019-10-12 14:26:05 M 1/5 -6°C
GRRB DS13
RECONYX

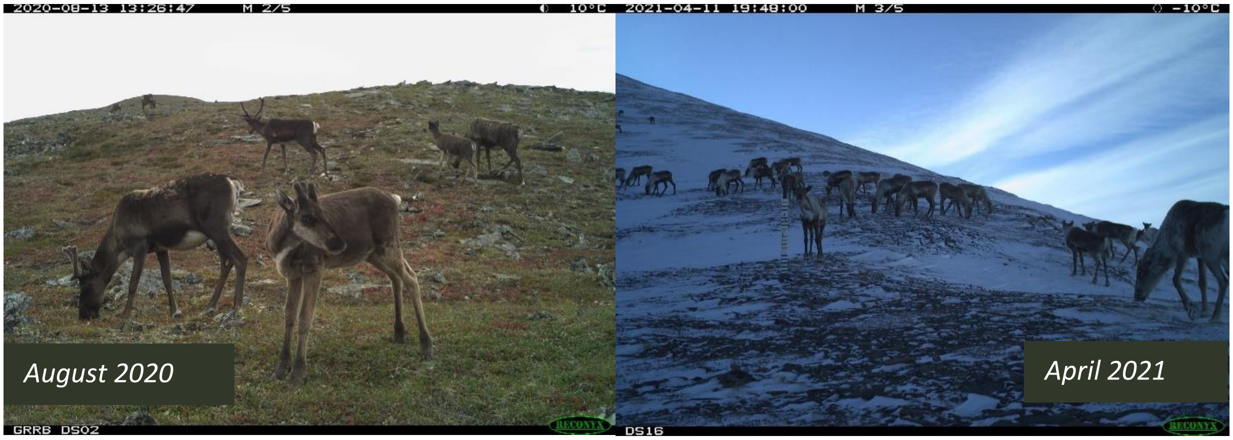

2019-10-12 14:26:06 M 2/5 -6°C
GRRB DS13
RECONYX


2019-10-12 14:26:06 M 3/5 -6°C
GRRB DS13
RECONYX


2019-10-12 14:26:07 M 4/5 -6°C
GRRB DS13
RECONYX

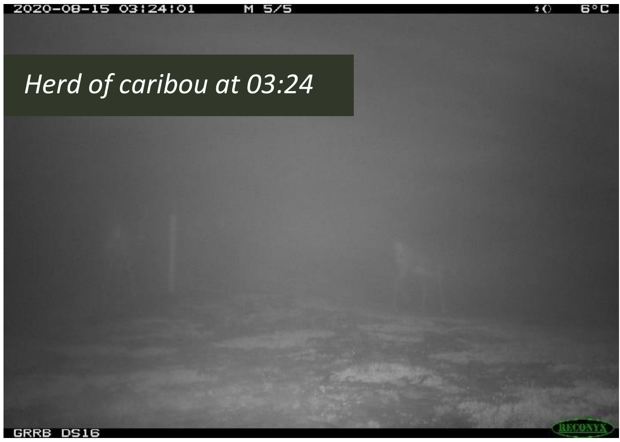
4.2.8 Caribou (vàdzaih)

Caribou have been a key food source for Gwich'in people for tens of thousands of years, but the relationship between the people and animals is beyond that of a food source, and is special and deeply rooted (Benson 2019). The Black Mountain area is sometimes part of the Porcupine caribou migration route, and the positive impact of caribou being available to harvest locally is significant to communities during these times. The areas between Black Mountain and Rat River have been favourite hunting areas in the fall (Benson 2019). Caribou migrated through the camera array in August 2020; there were also a few images taken in April 2021. Group sizes and demography were difficult to capture, given the large herd size and movement patterns as well as the landscape and viewshed of the cameras. The other animals seemed to key in on their presence. There were a few instances of this where we see caribou and then grizzly bears or wolves shortly after. Expanding Chapter 3 methods, with an increase in detections (either by increasing the number of cameras or expanding the number of years included in analysis), future research could investigate predator-prey interactions of caribou, and competition interactions between caribou and sheep.



Herd of caribou fleeing

Grizzly bear less than 2 minutes later

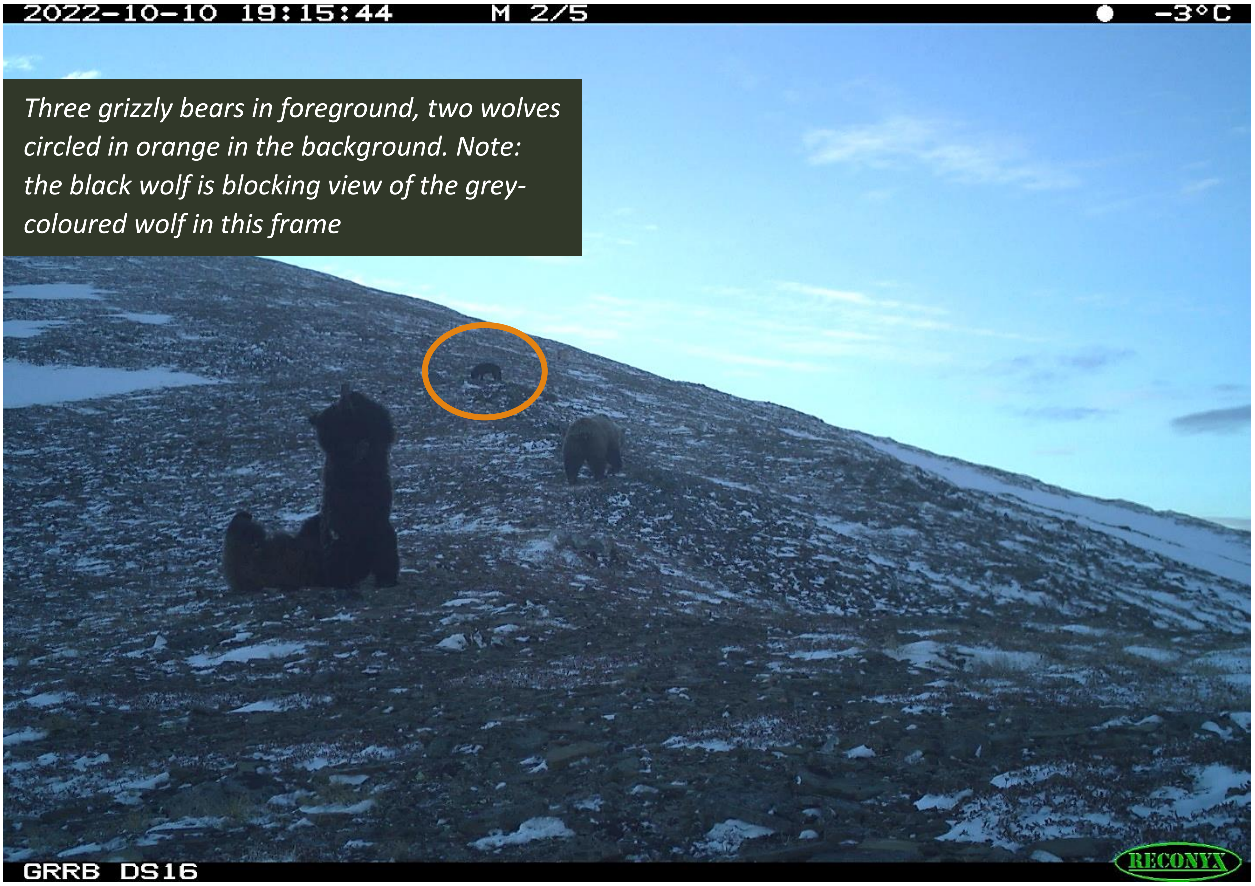


Herd of caribou at 03:24

Wolf at 03:27

4.2.9 A sighting of grizzly bears (shih) and wolves (zhòh)

I witnessed a family of grizzly bears (mom and 2 cubs I suspect are 1-2 years old) in the foreground of the picture, triggering the camera. In the background you can identify two wolves not too far away (one black and one grey).



Three grizzly bears in foreground, two wolves circled in orange in the background. Note: the black wolf is blocking view of the grey-coloured wolf in this frame

Three grizzly bears in foreground, two wolves circled in orange in the background

4.2.10 Interesting observations of fox (neegoo)

One of the only times I saw two foxes together, both circled in

I did not often see foxes this colour, almost black

It wasn’t very common to see multiple species in the same image, but the cameras allow us to observe these interactions, without our presence influencing behaviour. In this case, a fox walked into the frame and then laid down, all curled up, for few a few moments before a young ram entered the frame. The ram approached the fox and the commences grazing beside it. The fox stood up and watched the ram for a moment before casually sauntering off.

4.2.11 A note on wolverine (nèhtrùh)

Most wolverine detections (n = 31) were of individuals, but there were a few instances of two adult wolverines travelling together, likely a breeding pair.

4.2.12 Moose (dinjik) around Black Mountain

Moose usually spend their time around forage and cover at lower elevations in the delta and river-banks, and therefore moose don’t usually spend as much time in sheep habitat around Black Mountain (Benson 2023), however some moose are known to migrate through mountain drainages (Smits 1991). According to local and traditional knowledge, moose and caribou are unlikely to be competing with sheep for resources, and they likely just ignore or avoid each other on the land when they occasionally are in the same area (Benson 2023). I saw moose on the cameras nine times at three different sites. Group size ranges from one to three individuals.

4.3 CONCLUDING REMARKS

I conducted this research in partnership with the Gwich’in Renewable Resources Board to answer community-driven questions that will eventually inform local policy and stewardship decisions. The lessons learned from participating in the natural resource co-management structure of the Gwich’in Settlement Area apply to many areas of natural resource management across many jurisdictions, as more and more emphasis is being placed on collaborative stewardship, where western science and local knowledge are the cornerstones of decision-making. Policy and stewardship decisions that are based on collaborative work will combine these uniquely different but valuable knowledges, however it is doing our work in respectful and meaningful collaboration that is so critical.

As we talk about advancing science-informed decision-making and policy development, we must check-in with our core values in how we conduct science. This thesis provided me an opportunity to begin exploring these principles in my research through developing meaningful partnerships, cultivating a community-informed and engaged process, and letting community interests guide the development of my research. As a non-Gwich’in researcher, I have a responsibility to ensure that I am doing my work in a way that respects Gwich’in people, culture, and processes. However, as researchers and professionals, we also need to recognize and respect what our role and responsibility is. At its core, my research is an application of scientific methods, and is separate from elements such as the traditional knowledge study component of the divii project, but that doesn’t mean it cannot be conducted in a meaningful way by integrating community values, such as reciprocity, transparency, and relationships into the research process. Developing research questions and interpreting results in the context of local and traditional knowledge is also of chief importance. Continual relationship building with Gwich’in organizations and community members has been key in directing this study, and I have found meaning in this work, by credit to the many aspects of community-valued processes that extend beyond the bounds of the requirements of a thesis. For example, taking time to find additional funding and travel to the local schools to interact with youth and hosting community open houses, all in the spirit of reciprocity and transparency, was a major highlight in my research experience overall. Further, I hope that by doing this type of work, grad students and researchers in the natural sciences find inspiration for creative ways of connecting back to communities, and putting science in the hands of the people who are most impacted by the outcomes, while inspiring the next generation of scientists and land stewards.

This community-based effort is the first of its kind to study Dall's sheep demography and predator-prey relationships using remote cameras. As such, this project can serve as a model for other communities with similar research and monitoring objectives. Rooted in community values and knowledge, this scientific inquiry takes a step back from immediate management goals to explore community-based monitoring, new methods in wild sheep population demography, and the core foundations of ecological niche theory. It is my sincere ambition that through this work, I have been a good listener to the people, land, and animals, offering divii a chance to tell their story, and sharing that story in a meaningful way.

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