SPATIO-TEMPORAL MAMMALIAN COMMUNITY ECOLOGY WITHIN A WILDERNESS NATIONAL PARK

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Fisheries and Wildlife – Doctor of Philosophy

2024

ABSTRACT

Wildlife can alter their behavior in response to increased human activity. As human visitation to protected areas is predicted to increase, wildlife behavioral responses will likely continue to change, influencing ecosystem and inter-species relationships. I investigated how human activity on a national park trail system influenced mammalian spatial patterns and predator-prey relationships during a year with restricted visitation during the COVID-19 pandemic (2020) and a subsequent non-restricted year (2021). I investigated how moose (*Alces alces*), wolves (*Canis lupus*), red fox (*Vulpes vulpes*), and snowshoe hare (*Lepus americanus*) altered space use and diel activity to varying human visitation within and between visitor seasons. I characterized wolf-moose occupancy probabilities at sites ≤50 m from hiking trails across three temporal periods within Isle Royale National Park (IRNP) visitor seasons that reflected varying life history and human visitation patterns. Lastly, I investigated the effects of camera survey duration, timing, density, and on- or off-trail placement on moose detection rates, sex and age ratios, and density estimates to optimize sampling precision in support of management goals. During 2020–2021, moose, wolf, red fox, and snowshoe hare space use decreased as human visitation increased; however, species demonstrated varying seasonal responses to humans within years. On-trail moose, wolf, red fox, and snowshoe hare detections decreased while off-trail detections remained constant. Wildlife altered diel and space use in response to humans on-trails, suggesting that disturbances were localized to trails. Wolves and moose increased their intensity of use at sites with high human site use when visitation peaks (July–August), resulting in higher wolf-moose co-occurrence near humans. However, wolf and moose use of sites near trails remained constant between 2020 and 2021. Wolves and moose increased use intensity at high human use sites during short-term periods of increased human visitation, increasing the potential for interaction between wolves and moose and human-wildlife. Pairing life history events with periods of high detection rates for moose identified optimal survey periods and could be applied to other species. Camera surveys of 25-days during mid-June–mid-July and early December–early January produce consistent and precise calf:cow and bull:cow ratios. More precise density estimates were estimated in early December–early January using ≥4 cameras/km^2 placed on and off-trail in a representative survey area. Even during a year with unparalleled low human visitation due to the COVID-19 pandemic, within

year increases in human use had variable influence on species monitored ≤50 m of trails, suggesting sensitivity to low levels of human recreational use.

This dissertation is dedicated to Mom and Dad.
Thank you for fueling my interest in wildlife and National Parks and teaching me skills that have helped me “navigate” through this process.

ACKNOWLEDGEMENTS

I am deeply indebted to my supervisor, Dr. Jerry Belant, for granting me an opportunity beyond my wildest imaginations, for his extensive support in the form of invaluable advice and insights, for his good-natured and often humorous conversations, and for his unwavering belief in my abilities to successfully complete this dissertation. I would also like to sincerely thank those serving as my committee members: Dr. Kenneth Kellner, Dr. Roland Kays, and Dr. Gary Roloff. They provided various layers of expertise and feedback that helped challenge my thinking, project design, and writing.

This research and funding was made possible by the US National Park Service, Boone and Crockett Program in Wildlife Conservation at Michigan State University, the National Park Foundation, and Edna Baily Sussman Foundation. My sincere thanks to all Isle Royale National Park staff, particularly Mark Romanski and Lynette Potvin, for their time, knowledge, and support throughout this project. Thank you to the postdocs (Elizabeth Orning, David Marneweck, and Adia Sovie), the wolf techs of 2020–2021 (Leah McTigue, Julia Olson, Kelsey Bernard, Dahlia Berns, Adam Mortensen, Katie Pfaff, and Angelica Reed), and data techs (Calee Savu, Mackena Rhadigan, and Sarah Gareau) for your help in various components of this project. I gratefully acknowledge the support I received from my peers, both past and present members of our lab, and other friends I made along the way.

I will be eternally grateful to my family, particularly my parents and brother, for their unconditional love and support throughout this process. Thank you to my mother, who was my writing buddy throughout every chapter of this dissertation, my daily morale booster, and my backyard wildlife reporter. Thank you to my father, who helped me formulate plans every time numerous new obstacles occurred during this journey. I, therefore, dedicate this dissertation to them.

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CHAPTER 1: INTRODUCTION

The goal of this research was to contribute to knowledge on the spatial ecology and relationships of mammals (gray wolves (*Canis lupus*), moose (*Alces alces*), red fox (*Vulpes vulpes*), and snowshoe hare (*Lepus americanus*)) on Isle Royale National Park (IRNP), Michigan, USA. The underlying theme is how human activity on trails influenced mammalian spatial patterns and predator-prey relationships during a year with restricted visitation from the COVID-19 pandemic (2020) and with a subsequent non-restricted year (2021). Human visitation, a potential disturbance to wildlife, is increasing globally in natural recreational areas, including national parks and wilderness areas (Buckley & Foushee, 2012; Welch, 2005). Mammals can alter their behaviors due to increased human presence (Procko et al., 2022; Rogala et al., 2011). Differences in an agency's recreation and wildlife conservation goals could produce complications when collecting information on wildlife or establishing surveys, such as using less optimal survey windows or impediments to the human recreational experience (16 U.S.C. 1131). As such, my research also investigated optimizing remote camera survey design to increase the precision and consistency of moose population demographic estimates (i.e., detection rate, density, sex, and age ratios).

Recreational activities, such as hiking, can be perceived by wildlife as a risk (Suraci et al., 2019). Species can vary in how they perceive increased human activity as a risk (Burton et al., 2024) and subsequently respond, which can alter how species allocate energy toward risk avoidance rather than other behaviors, such as resting and foraging (Lima, 1986), with potential fitness consequences. In chapter 2, I investigated how moose, wolves, red fox, and snowshoe hare alter their space use and diel activity to varying amounts of human visitation in a U.S. national park within and between years using species detections from remote cameras. Due to visitor restrictions from the COVID-19 pandemic, I investigated trends of extreme variation in visitation, where 2021 had 338% greater visitation than 2020. Overall, I predicted that species' space use and activity overlap with humans on trails would decrease with increasing human activity and have stronger responses with increased magnitude of seasonal visitation. I estimated detection rates for all species would decrease within and between years as human visitation increased; however, species demonstrated varying responses to humans within years. From 2020 to 2021, on-trail wildlife detections decreased while off-trail detections remained constant. Wildlife altered diel and space use in response to humans <50m from trails, suggesting disturbances were localized to trails only. Variation in species responses to human visitation could alter predator-prey and community dynamics.

While humans can mediate predator-prey dynamics (Scoyoc et al., 2022), how interacting species alter their behaviors in response to perceived predation risk (Suraci et al., 2019) could influence their response to intensity of human activities. Differences in how predators and prey react to human presence can present multiple scenarios that can lead to predators increasing pressure on certain prey species, switching prey sources, or becoming habituated and increasing the probability of human-wildlife interactions (Scoyoc et al., 2022). In chapter 3, I characterized predator-prey marginal and co-occurrence site use and spatial interaction probabilities within 50 m of hiking trails across three time periods within IRNP visitor seasons that reflected varying human visitation and wolf and moose life history patterns. Based on life history characteristics of wolves and moose, I expected their individual site use and co-occurrence estimates near trails to be constant across the three varying visitation periods. However, if increased human site use and/or periods of high visitation (i.e., peak visitor period and in 2021) influenced wolf and moose spatial relationships, one of the four scenarios would occur at sites near trails: 1. moose would be more likely and wolves less likely to use sites, 2. wolves would be more likely and moose less likely to use sites, 3. wolves and moose be more likely to use sites, or 4. wolves and moose would be less likely to use sites, with scenario 1 being the most probable for IRNP. Counter to my predictions, my results supported scenario 3, that wolves and moose were more likely to use sites with high human site use when visitation peaks, resulting in greater co-occurrence near humans, while there was no effect between years. This suggests that wolves and moose are more likely to use high human use sites during increased human use and periods of higher visitation, increasing the potential for spatial interactions between wolves and moose and human-wildlife conflicts.

Reliable estimates of sex and age ratios, detection rates, and density estimates are fundamental for making management decisions, including establishment hunting quotas (Garel et al., 2010), monitoring long-term population trends (Yoccoz et al., 2001), or influencing decisions to introduce new individuals or species (Van Kleunen et al., 2023). However, life history characteristics and survey timing and duration can influence the precision and accuracy of estimates. In chapter 4, I investigated the effects of camera survey duration, timing, density, and on- or off-trail placement on detection rates, sex and age ratios, and density estimates of moose .

I predicted that variations in detection rates would reflect moose life history patterns, and periods of higher detection would suggest optimal times to estimate demographic ratios and population density. My results showed that camera surveys of 25 days during mid-June–mid-July and early December–early January produced consistent and precise calf:cow and bull:cow ratios. Subsampling camera densities to ≤ 3 cameras/km^2 decreased precision and consistency for density and ratio estimates. Lastly, I recommend estimating moose density during early December–early January and using ≥ 4 cameras/km^2 placed on and off-trail (within 50 m of a trail). Pairing life history events with high moose detection rates identified optimal survey periods and could be applied to other species.

Overall, I highlighted the effects of within and between-year variation in human activity on a mammalian community and the influence of survey design when calculating population demographic parameters within a U.S. national park. Even during a year with unparalleled low visitation due to the COVID-19 pandemic, within year increases in human use had variable influence on species monitored < 50 m of trails, suggesting sensitivity to low levels of human recreational use. In other systems, variation in how species avoid humans has led to disruptions in predator-prey relationships, trophic cascades, or the abundance of certain species (Burton et al., 2024; Dorresteijn et al., 2015). These disruptions can create challenges for conservation in practice and land management agencies or entities whose policy mandates are often to "preserve" and "protect." The U.S. National Park Service has a dual mandate "to conserve the scenery and the natural and historic objects and the wildlife therein, and to provide for the enjoyment of the same in such a manner…as will leave them unimpaired for the enjoyment of future generations" (16 U.S.C. 1131). Mitigating wildlife responses to increased visitation is a management challenge at IRNP and across the National Park system (Dietsch et al., 2016). Reducing visitation during peak seasons or redistributing visitation across a season could reduce wildlife responses to recreational activity while continuing to provide for public enjoyment. Minimizing trail densities and providing refugia for wildlife could further reduce the influence of humans on wildlife and potential human-wildlife conflict. Additionally, altered species' behavior and temporal variation in life history traits can influence precision and consistency when calculating important population demographic parameters. Conducting surveys around periods outside peak visitation and incorporating periods when species' demographics are the most behaviorally similar could meet wildlife conservation and recreation objectives. Whether direct or indirect, impacts of human recreational use likely occur at even low visitation levels, and when land managers consider these impacts in the context of natural perturbations, species' life history, and ecological processes, they will be better positioned to provide stewardship for mammalian communities in their charge.

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CHAPTER 2: DYNAMIC RECREATIONAL TRAIL USE ALTERS MAMMAL DIEL AND SPACE USE DURING AND AFTER COVID-19 IN A U.S. NATIONAL PARK

2.1. Abstract

As human visitation to recreational areas increases, wildlife can alter their space use or activity periods to avoid humans. Short-term or gradual variation in human visitation within and across years makes it challenging to assess species responses. We used data from 156 cameras deployed on and off trails (within 50 m) in Isle Royale National Park (IRNP), Michigan, USA, during 2020–2021 to assess diel activity, temporal overlap, and detection rates for four wildlife species in response to human visitation. While visitation in both years was greatest in June–August, there were 338% more human visitors in 2021 than in 2020 because of COVID-19 pandemic visitor restrictions. Detection rates for all species decreased within and between years as human visitation increased. From 2020 to 2021, on-trail animal detections decreased while off-trail detections remained constant. As visitation declined late season, red fox (*Vulpes vulpes*) and wolf (*Canis lupus*) detection rates increased on trails while snowshoe hare (*Lepus americanus*) and moose (*Alces alces*) remained low or declined further. Moose, snowshoe hare, and red fox diel overlap with humans decreased with increasing visitation as animals became more nocturnal. Red fox and moose overlap with humans, and wolves decreased from 2020 to 2021. Animals altered diel and space use in response to humans <50m from trails, suggesting disturbances occurred mostly on trails. Reducing visitation during the peak visitor season or redistributing the number of visitors across the overall visitor season could reduce mammalian responses to human visitation.

2.2. Introduction

Human visitation, a potential disturbance to wildlife, is increasing globally in natural recreational areas, including National Parks (Buckley & Foushee, 2012; Welch, 2005). For example, annual visitation to lands managed by the U.S. National Park Service increased 22.4% to 325 million individuals from 2002 to 2021 (National Park Service, 2024). Parks and other natural areas are often established for biodiversity conservation (Geldmann et al., 2019; Margules & Pressey, 2000). However, recreational use of these areas by humans can have short- and long-term effects on wildlife behaviors, ranging from increased vigilance and spatio-temporal avoidance to habituation or human shield effects (Procko et al., 2022; Rogala et al., 2011).

Wildlife can perceive recreational activities as a risk (Suraci et al., 2019). The risk-disturbance hypothesis states that responses from disturbed animals will increase when perceived risks from disturbances increase (Frid & Dill, 2002). When species experience increased human disturbances, such as increased trail use by park visitors, behavioral responses should emulate predator avoidance if that risk is perceived to exceed fitness or opportunity costs (Hammitt et al., 2015; Frid & Dill, 2002). Animal risk avoidance behaviors can alter habitat selection, movements, and activity (Gaynor et al., 2019, 2018; Ripple & Beschta, 2004). Species also can vary in how they associate disturbances with perceived risk and subsequently respond, which can alter how species allocate energy toward risk avoidance rather than other behaviors, such as resting and foraging (Lima, 1986), with potential fitness consequences.

Animal responses to humans are not always negative. Although wildlife can avoid humans (Salvatori et al., 2023; Reilly et al., 2022), some species habituate to humans and may use humans as a shield against natural predators (Berger, 2007). Additionally, some species can select for hiking trails, while others may avoid trails (Kays et al., 2016). Given that animals can avoid, be indifferent, or be attracted to areas with increased human activities, detection rates should vary by species and circumstance (Fancourt, 2016; Wilson & Delahay, 2006; Carbone et al., 2001). Diverse responses of wildlife to human disturbances (e.g., Procko et al., 2022; Sytsma et al., 2022; Nickel et al., 2020) can alter community dynamics such as predator-prey relationships (Scoyoc et al., 2023). During the COVID-19 pandemic, mammals have varyingly altered their activity in response to increased human use (e.g., Burton et al., 2024; Anderson et al., 2023). However, these studies were unable to investigate the influence of on and off-trail sites on species' responses to human activity. Additionally, studies typically investigate wild animal-human relationships by combining disturbances across seasons or years (Marion et al., 2020), which may not identify shorter-term response variations (Bateman & Fleming, 2017). Understanding the influence of human trail use and within-season variations in human disturbance is increasingly important as government agencies develop management plans considering seasonal recreational use restrictions to facilitate wildlife conservation (Dertien et al., 2021).

We investigated mammalian community (moose, wolves, red fox, and snowshoe hare) responses to varying amounts of human visitation in a U.S. national park within and between years using species detections from remote cameras. We investigated the influence of visitor restrictions during the COVID-19 pandemic (2020) with a subsequent non-restricted year (2021). We predicted that our focal species' space use via daily detection rates and diel activity overlap with humans would decrease with increasing human detections. We predicted that wolves, the apex predator in this system, would show the greatest decrease in space use and diel overlap with increasing human detections. Furthermore, we expected that moose, red fox, and snowshoe hare would also decrease diel activity overlap with humans when mean daily human detections increased, resulting in increased diel overlap with wolves to avoid the greater perceived threat, humans. Lastly, we predicted that all changes in diel responses, overlap, and space use would be stronger with cameras placed on hiking trails and during a year with greater human visitation. Visitor restrictions by IRNP due to the COVID-19 pandemic, paired with a lack of mammal emigration and immigration, provided a unique quasi-natural experiment to test our predictions.

2.3. Methods

Study Area

Isle Royale National Park (IRNP) is an archipelago comprising 544 km^2 in northwestern Lake Superior, 24 km from the Canadian mainland in the transitional zone of temperature northern hardwoods and boreal forest biomes (Figure 2.1). The park has 20 mammal species, of which 8 weigh ≥ 1.36 kg and 4 are not semi-arboreal or semi-aquatic (moose, gray wolves, red fox, and snowshoe hare). From 1948 to 2018, the wolf population averaged around 22 individuals and fluctuated from 50 individuals in 1980 to 2 related individuals in 2018 (Smith & Peterson, 2023; Romanski et al., 2020; Vucetich et al., 2012). With the decline in wolf abundance, moose abundance increased substantially (Smith & Peterson, 2021), adversely affecting vegetation (De Jager et al., 2020). To restore ecosystem processes, 19 wolves were introduced to IRNP between September 2018–2019 (Romanski et al., 2020). There was a minimum of 12 wolves on IRNP during winter 2019–2020 and 24 wolves during winter 2020–2021 (IRNP unpublished data). Moose abundances in IRNP for 2020 and 2022 were 1876 and 1039 (95% CI = 800–1349), respectively (Sovie et al., 2024; Hoy et al., 2022;). Red fox inhabited IRNP since 1925 (Black et al. 2021). While wolves can kill red fox, particularly near scavenged carcasses (Petroelje et al., 2022), wolves generally only spatially constrain red fox distribution on IRNP (Curras et al., 2024). Snowshoe hare is the primary prey of red fox (Johnson, 1969) and opportunistic prey for wolves (Sovie et al., 2023).

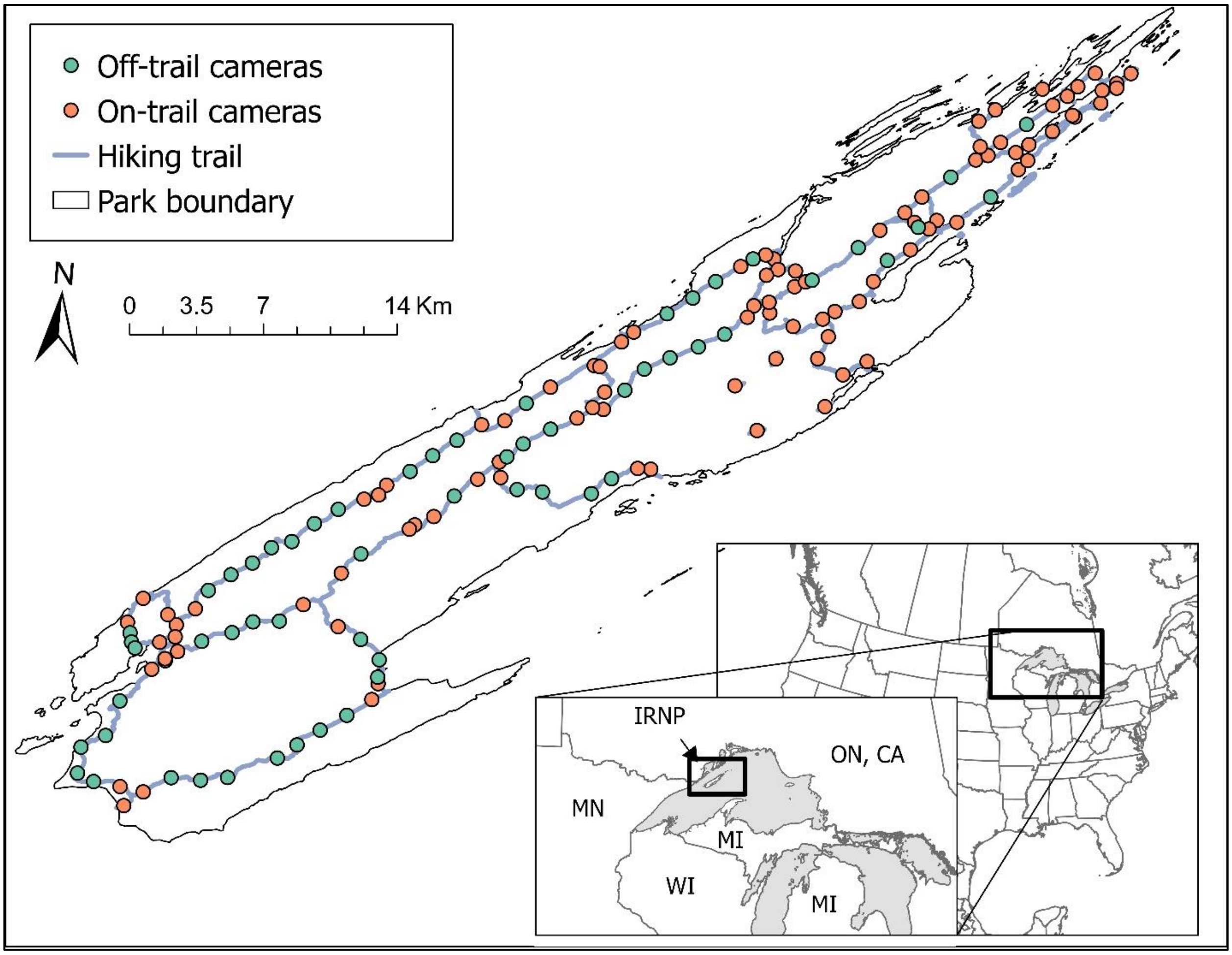

Figure 2.1. Camera locations (n = 156; 98 on-trail, 58 off-trail), Isle Royale National Park, Michigan, USA, April–October 2020–2021.

Typical IRNP visitation dates are 15 April–31 October, depending on weather and Lake Superior ice conditions. Travel within IRNP is limited to boats and hiking on 266 km of trails. There are 36 campgrounds; hunting and trapping on IRNP are prohibited. In 2020, IRNP imposed visitor restrictions in response to the coronavirus pandemic and opened on 26 June, allowing limited access only by private boaters, and seaplanes. The IRNP passenger ferry and commercial vessels did not transport visitors to IRNP in 2020. Further backcountry restrictions in 2020 included that visitor groups could not share campsites or shelters or use part of a main trail, the Minong. The number of visitors increased 338% from 2020 (4,594 visitors) to 2021 (20,109 visitors) (National Park Service, 2024). During 2015–2019, the average annual number of visitors was 16,790, a 45% increase from 2015 to 2019. Since the COVID-19 pandemic in

2020, IRNP visitation has increased annually, with 20,223 visitors in 2022 (National Park Service, 2024).

Camera Deployment and Data Organization

We used images obtained during 15 April–31 October 2020–2021 from 156 infrared cameras (Stealth Cam DS4K; Irving, Texas, USA) positioned along or within 50 m of trails throughout Isle Royale, the main island within IRNP (Figure 2.1). Along each trail segment in Isle Royale, we spaced cameras 350–1600 m apart where cameras nearest trail intersections (100–300 m from an intersection) were placed on-trail (n = 98) and those further, off-trail (n = 58). Camera locations were consistent throughout the study. At each camera location, we placed the cameras to maximize detection area and minimize visual obstruction. To reduce vegetation obstruction that could impair detections (Moll et al., 2020), we cleared 10 m in front of each camera during checks. We assumed that although detection probability is <1, the probability for each species was similar across cameras due to standardized vegetation coverage and placement and regular checks to reduce camera-related issues. We positioned cameras 1.5 m above ground, typically north-facing, and oriented each to detect animals 4–15 m distant. Visitors were rarely detected off-trail so we used only on-trail cameras for estimating human use. We programmed cameras to take five images each detection with a trigger speed ≤0.5 sec and no delay between detections. Species detected were initially identified using Program RECONN.AI (Michigan Aerospace, Ann Arbor, Michigan), which uses regional convolutional neural network models to identify species from images. To ensure accuracy, we manually checked all photos against AI-processed species identification records and grouped images by species taken within a 10-minute interval. We identified potential individuals within a sequence by direction traveled and age and sex classifications. To reflect visitation in a typical visitor year (i.e., 2021), we categorized within-year visitation as early (15 April–9 June), mid (10 June–28 August), and late (29 August–31 October; Figure 2.2). We selected within-year visitation seasons based on shifts in the distribution of human detection rates (number of daily human detections) during 2021 when most park visitation occurred during mid-season and overall distribution reflected a typical visitor year in contrast to 2020.

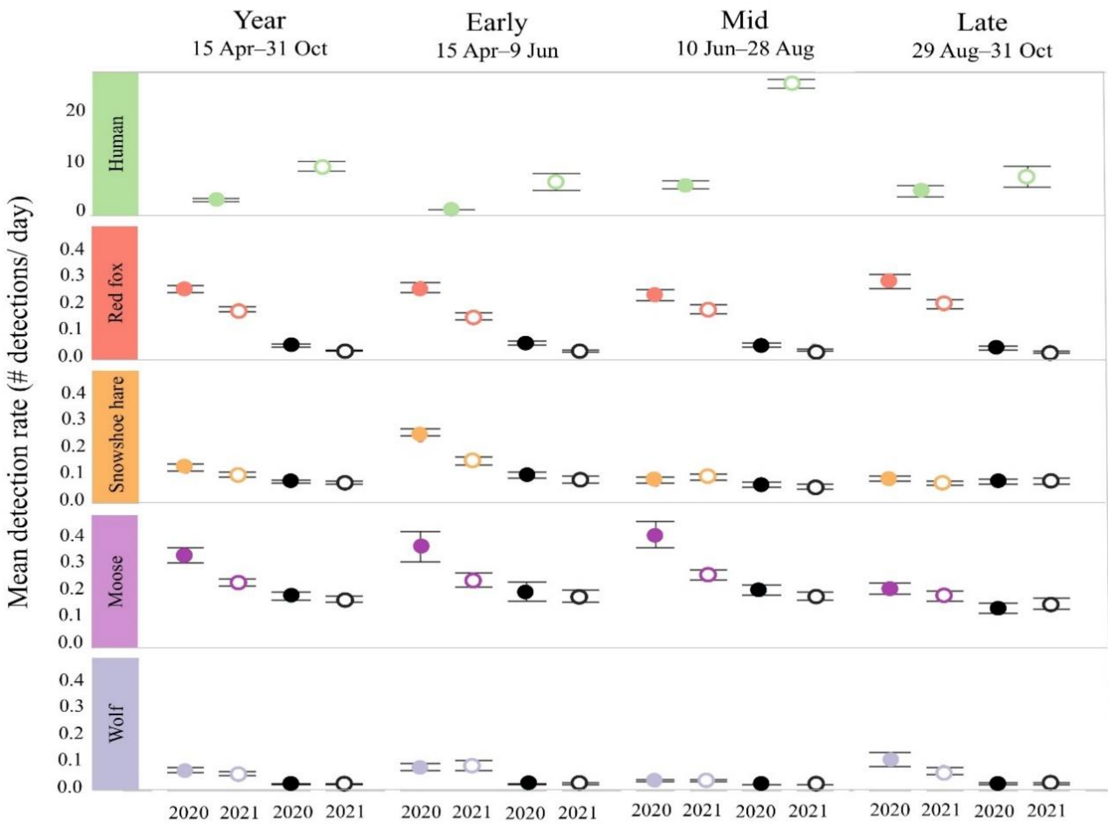

Figure 2.2. Wildlife mean daily detection rates by year, season (early [15 April–9 June], mid [10 June–28 August], and late [29 August–31 October]), and camera grouping (on-trail in color; off-trail in black)), Isle Royale National Park, Michigan, USA, 2020 (solid circles)–2021(open circles). Mean daily detections were derived from daily detections at each camera. Moose detections included unknown age and sex. Error bars represent 95% confidence intervals of detection rate estimates.

For each species, we calculated space use using daily detection rates (number of detections/day) across all sites pooled, on, and off-trail cameras, then calculated overall means and 95% confidence intervals using daily detection rates for each year, season (early, mid, late), and camera grouping (all sites pooled, on- and off-trail cameras). We used overlapping confidence intervals to compare detection rates across years, seasons, and camera grouping.

Diel activity pattern and overlap analysis

We calculated diel patterns for each species for each year, season, and camera grouping using circular kernel density estimators in the *fitact* function in the Activity package (Rowcliffe,

2023) in program R (R Core Team, 2023). We estimated 95% confidence intervals by bootstrapping 1,000 resampling events. We compared variation in species' diel patterns between years, camera groupings, and among seasons using Wald tests in the function '*compareAct'* considering differences statistically significant when $P < 0.05$.

To estimate variation in diel activity in response to humans and wolves, we calculated pairwise diel overlap indexes (Dhat4 [Δ4]) using package overlap (Rowcliffe, 2023; Ridout and Linkie, 2009) for each camera grouping, year, and season. Dhat coefficients represent the difference between species activity distributions and range from 0 (no overlap) to 1 (total overlap) (Ridout and Linkie, 2009). Due to low detections of wolves among-seasons, we only estimated variation of species diel overlap with wolves across all camera sites and not with the on- and off-trail subset datasets. We generated a null distribution of overlap indices using randomly sampled data (25% of total data) from the combined dataset to estimate the probability of the observed overlap occurring by chance using the function overlapEst (Rowcliffe, 2023). We compared the null distribution with bootstrapped (n = 1000) diel overlap estimates, which we generated using *bootCI* to calculate 95% confidence intervals (Ridout and Linkie, 2009) to the percent overlap differences between years and seasons.

2.4. Results

Space use (daily detection rate)

Detections for species decreased with increasing human activity, with 2021 having greater declines in species detection rates for all sites pooled and on-trail sites (Figure 2.1; Table A.2.1). Mean daily human detection rates increased 331% from 2020 (2.0) to 2021 (8.6), whereas mean daily detection rates for wildlife species decreased (-29% wolf, -26% moose, -32% red fox, and -21% snowshoe hare) with increasing human detections (Figure A.2.1; Table A.2.2). All species had higher detection rates on-trail compared to off-trail. Species on-trail detection rates decreased from 2020 to 2021 while off-trail detection rates remained relatively constant between years except for red fox, which exhibited lower off-trail detection rates in 2021 (Figure 2.2). Within a season between years, red fox had consistently lower detection rates in 2021 than 2020 for all seasons (Figure 2.2). During early season 2020, all species except wolves had greater detection rates (-23% wolf, 28% moose, 44% red fox, and 34% snowshoe hare) than during early season 2021 when visitation was restricted, even though human detection rates also were low (Figure 2.2; Table A.2.2). During mid-season, when human detection rates were greatest, moose detection rates were lower in 2021 (Figure 2.2). Snowshoe hare and gray wolf had similar mid-season detection rates between years. As human detection rates declined in late season, wolf detection rates were lower in 2021 (0.03 95%CI: 0.02–0.04) than 2020 (0.06 95%CI: 0.04–0.07), while snowshoe hare and moose had similar detection rates between years (Figure 2.2). Within each year, wolf and snowshoe hare detection rates decreased from early to mid-season when human detection rates increased.

Within-year diel activity and overlap

Moose, snowshoe hare, and red fox on-trail daytime diel activity decreased in 2021 compared to 2020 (Wald tests: moose w = 8.8, p-value = 0.003; snowshoe hare w = 14.7, p-value < 0.001; red fox w = 17.7, p-value < 0.001) (Figure 2.3). Red fox diel overlap with humans decreased from 2020 to 2021 (2020Δ: 0.35, 95% CI = 0.35–0.37; 2021Δ: 0.24, 95% CI = 0.23–0.27) while wolf diel overlap with humans increased (2020Δ: 0.37, 95% CI = 0.37–0.41; 2021Δ: 0.44, 95% CI = 0.42–0.48) (Figure A.2.2). Additionally, red fox diel overlap with humans was lower in 2021 during each season (Figure 2.4). Comparing mid-season between years, wolves had greater overlap with humans in 2021 (Δ: 0.40, 95% CI = 0.33–0.49) than in 2020 (Δ: 0.25, 95% CI = 0.20–0.33). In late-season, moose overlap with humans was lower in 2021 than 2020 whereas wolves and snowshoe hare were similar (Figure 2.4). Wolf, moose, and red fox diel overlap with humans in 2020 decreased from early- to mid-season. During mid-season in both years when humans had the greatest detection rates, wolves were more diurnal off-trail and more nocturnal on-trail (Figure 2.4). In contrast, snowshoe hares were more diurnal on-trail during mid- and late-season both years than off-trail.

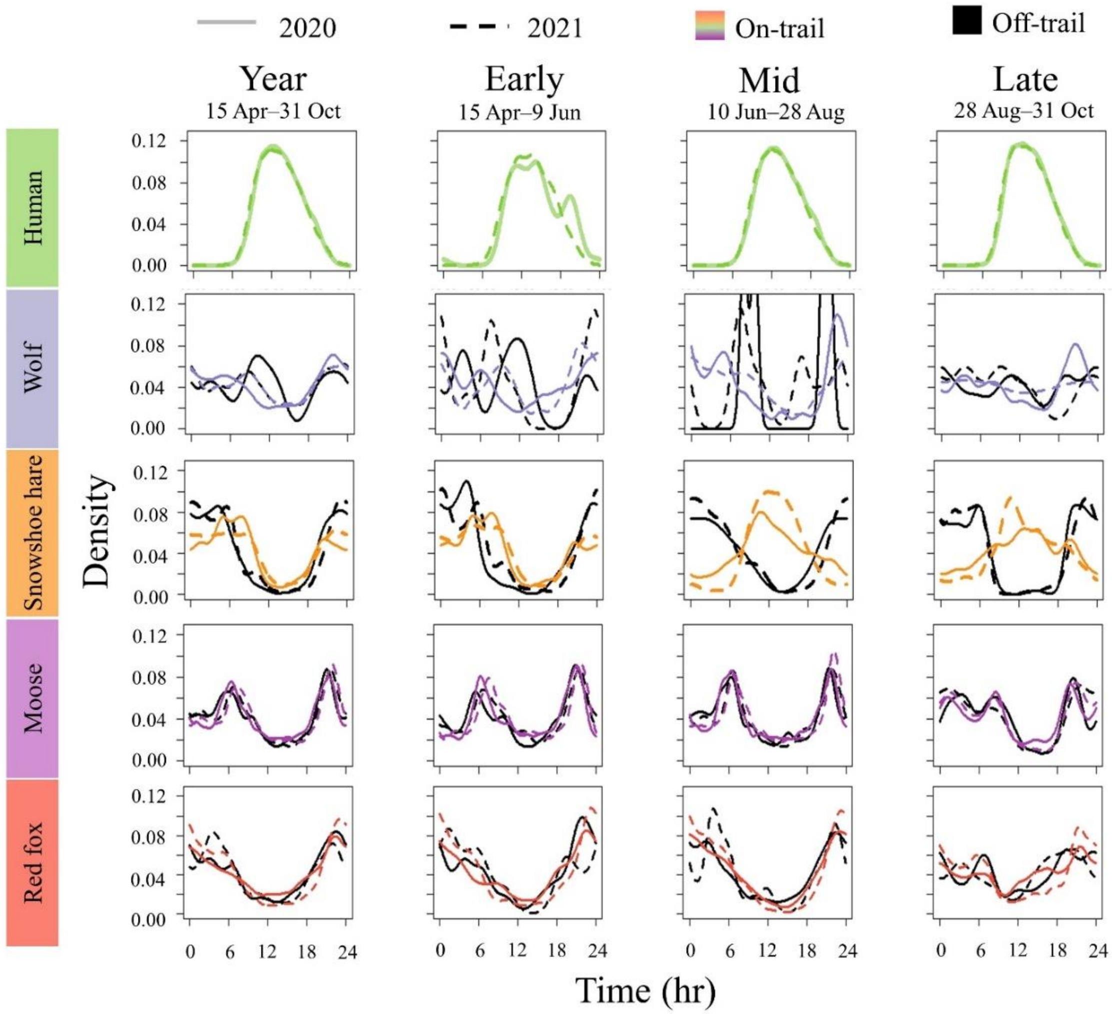

Figure 2.3. Wildlife and human diel activity by year, season (early [15 April–9 June], mid [10 June–28 August], and late [29 August–31 October]), and camera grouping (on trail in color; off trail in black)), Isle Royale National Park, Michigan, USA, 2020 (solid lines)–2021 (dashed lines).

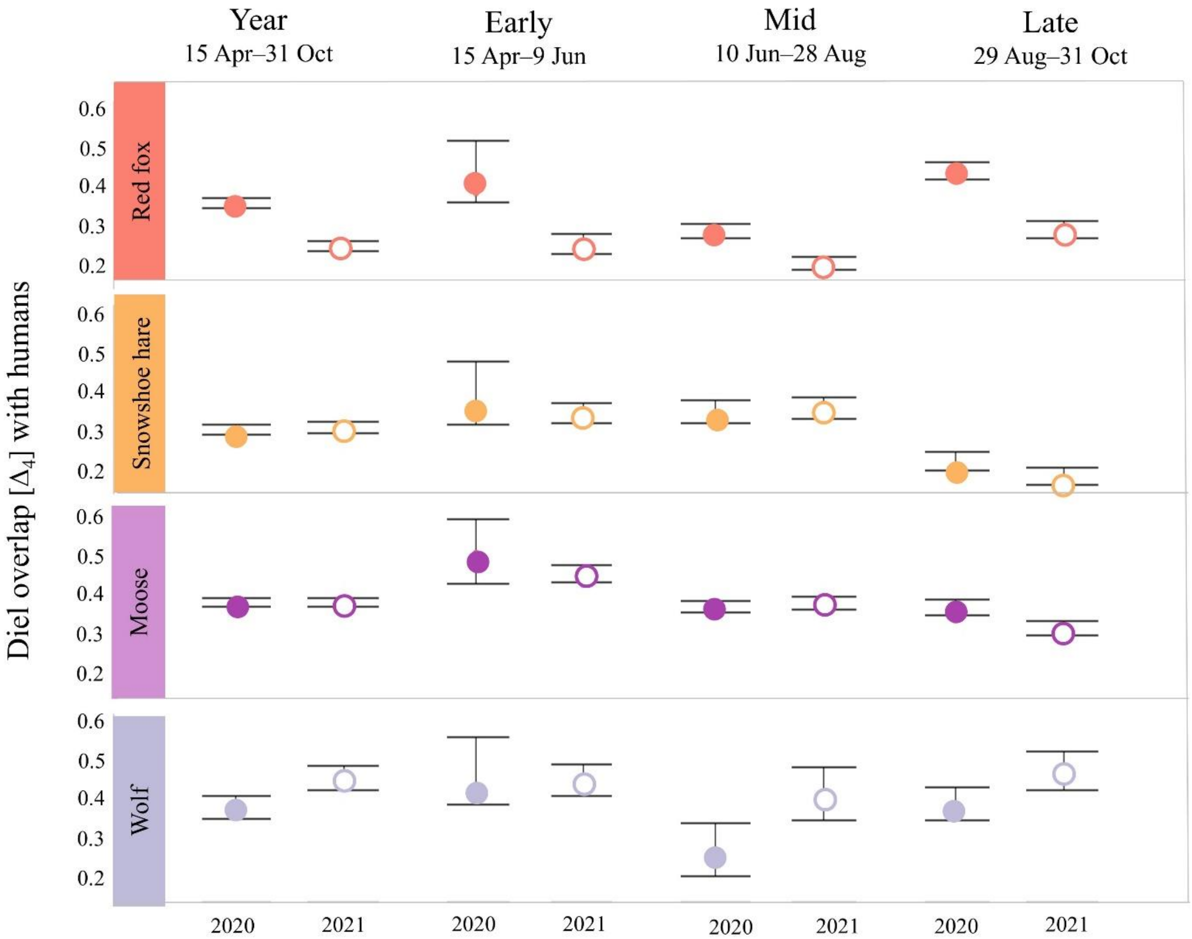

Figure 2.4. Wildlife diel activity overlap (Dhat4 [Δ_4]) with humans by year and season (early [15 April–9 June], mid [10 June–28 August], and late [29 August–31 October]) across all pooled camera sites, Isle Royale National Park, Michigan, USA, 2020 (solid circles)–2021 (open circles). Error bars represent 95% confidence intervals of detection rate estimates.

Wolf overlap with humans increased from 2020 to 2021 while overlap with red fox decreased (2020Δ: 0.35, 95% CI = 0.35–0.37; 2021Δ: 0.24, 95% CI = 0.23–0.27) (Table A.2.2). Yearly diel overlap between wolves and other species in 2020 was lowest with humans (Δ = 0.37) and greatest for red fox (Δ = 0.93) and in 2021 was lowest with humans (Δ = 0.49) and greatest with moose (Δ = 0.88). Across seasons and years, wolves exhibited greater variation in diel overlap with red fox, ranging from Δ = 0.71 in early-season 2020 to Δ = 0.88 in early- and mid-season 2021. Moose and snowshoe hare diel overlap with wolves remained constant between years and across seasons.

2.5. Discussion

We estimated the effects of varying human visitation on space use and activity on and near recreational trails for a U.S. national park's mammal community during the COVID-19 pandemic (2020) when visitation was restricted and a subsequent non-restricted year (2021). We found that seasons and years of higher human use were associated with changes in space use and temporal patterns of wildlife, presumably because the risk from humans exceeded the benefits of site use (Frid & Dill, 2002). Daily detection rates for species decreased with increasing human activity, with 2021 having greater declines in species detection rates for all sites pooled and on-trail sites. We found varied support for our hypothesis that diel activity would change and overlap with humans would decrease with increased human detection rates. Our prediction that if humans were perceived as a risk, wolves would have the greatest decrease in daily detections and overlap with increasing human activity was not supported. Except for red fox, our prediction that species diel activity overlap with wolf activity would increase as human activity increased was not supported. Lastly, we found that while on-trail cameras had greater detections than off-trail, on-trail detections declined when human intensity increased, but off-trail detections remained relatively constant, suggesting human activity influences species' space use occurred mostly on-trails. Overall, we found that for all species, daily mean detections, but not diel overlap with humans, decreased during a year (i.e., 2021) with greater human activity.

Space use (daily detection rate)

While all species' daily detection rates decreased across all pooled and on-trail sites when human detection rates were greater, species exhibited seasonal variation in responses. During both years of this study wolf detections were lowest during mid-season when human trail detections were greatest. However, during late-season when human trail detections declined, wolf detection rates returned to early season levels. Although wolves often use areas with low human disturbance (Ahmadi et al., 2014; Hebblewhite et al., 2005), wolves can also use areas with high human use (Fennell et al., 2023; Shepherd & Whittington, 2006). Wolves alter use across biological seasons, reducing their use of human areas during denning and rendezvous seasons (Anton et al., 2020; Malcolm et al., 2020), even when human activity is low (Sytsma et al., 2022). Alternatively, wolves can increase use near human-occupied areas when human activity decreases (Procko et al., 2022). Seasonal variation in wolf use of the Isle Royale trail network appears influenced by the intensity of human use.

Red foxes can adapt to increased human disturbance (Jahren et al., 2020). In IRNP, we found that red fox detections decreased during a year with increased human visitation, but seasonal variation in detections was not observed. This consistent decrease in red fox detections may be due to IRNP's wolf population doubling from 2020 to 2021 (IRNP unpublished data). On IRNP, red fox can be spatially constrained by wolf occurrence (Curras et al., 2024). However, wolf detection rates demonstrated seasonal variation while red fox did not. Additionally, the consistent decrease in red fox could be due to the overall decline in prey species during the year with increased human disturbance, as decreases in prey can negatively influence red fox abundance when prey diversity is limited (Gomo et al., 2021; Jahren et al., 2020). However, while snowshoe hare detections also decreased in 2021 with increased human visitation, their patterns of declining detection rates within a season and between years (excepting early season) remained relatively constant.

Daily detections of snowshoe hares were lowest mid and late season, while moose were lowest in the late season. Snowshoe hare detections began to decrease mid-season when herbaceous vegetation was greatest. Snowshoe hares select areas with dense understory (Litvaitis et al., 1985) to reduce predation risk (Sievert & Keith, 1985), which could have reduced detections in our study (Moll et al., 2020). However, we removed vegetation 10 m in front of every camera regardless of placement on- or off-trail reducing the impact of vegetation obstruction on snowshoe hare detection. Additionally, our off-trail cameras were positioned to maximize detection probability while limiting the potential for obstruction to influence detection differences between on and off-trail cameras. Moose avoid areas of human disturbance including trails with increased human use (Granados et al., 2023; Naidoo & Burton, 2020), which occurred in our study during the late-season and year with higher visitation.

Diel activity and overlap

Species alter their diel patterns to avoid humans (Green et al., 2022; Gaynor et al., 2018); however, we found only partial support for species decreasing diel overlap with humans and altering their diel activity distributions. Moose had decreased diel overlap with humans during mid-season when human detection rates increased, potentially to avoid perceived human risk (Gaynor et al., 2019). Additionally, moose became less diurnal in 2021 on-trail when human visitation was an order of magnitude greater. During mid- and late-season in both years, snowshoe hares were more diurnal on-trail than off-trail; however, snowshoe hare detection rates on-trail decreased and were similar to off-trail detection rates at the same time. The decreased use of trails could explain the decreasing snowshoe hares diel overlap with humans by late season. However, as snowshoe hares are primarily nocturnal (Procko et al., 2023), this could be a function of decreased daylight hours during late season rather than in response to humans. Red fox was the only species to decrease diel overlap with humans across years and seasons with increased visitation. This result supports other studies that found foxes can mediate their response to increased human activity by decreasing their diel overlap (Green et al., 2023; Gil-Fernández et al., 2020; Díaz-Ruiz et al., 2016). Wolves decreased diel overlap with humans when human intensity peaked in 2020 but not in 2021. This result counters multiple studies that found wolf overlap with humans decreases as human disturbance increases (i.e., Petridou et al., 2023; Haswell et al., 2020). However, we found that wolves were less active during the day on-trail mid-season when human detection rates were greatest. Wolves could alter their temporal patterns on trails to mediate encounters with humans. Red fox was the only species we monitored that decreased their overlap with wolves; however, as red fox diel overlap with humans also decreased during the same seasons, it is unclear whether humans, wolves, both, or neither influenced the reduction in red fox diel overlap.

Our prediction that if humans were perceived as a risk (super-predator [Smith et al., 2017; Clinchy et al., 2016]), wolves would have the greatest decrease in daily mean detections was not supported. Although wolf detections decreased in response to increased human activity, the response was not as strong as the other species monitored. Between 2020 and 2021, IRNP's wolf population doubled in size from a minimum of 12 individuals to 24 (IRNP unpublished data). It is possible that wolves during this population increase had a greater negative response than our estimates indicated as there were more individuals available for detection in 2021. Additionally, as IRNP does not allow hunting and wolves are not harassed, wolf risk perception of humans may be greater in other systems where wolves have more direct, negative interactions with humans. However, variation in how intensely each species negatively responded to humans still can mediate wolf relationships with other species. Spatial mismatch of wolves and moose mid and late seasons due to differences in human avoidance could increase wolves' overall consumption of other prey sources (Dorresteijn et al., 2015). However, we could not assess whether this observed pattern was due to direct or indirect effects of humans (Smith et al., 2017; Clinchy et al., 2016) versus responses to other species (Granados et al., 2023). Delayed response of moose to humans during mid-season could be due to the shield humans produced, as wolf detections decreased as human detections increased (Granados et al., 2023; Berger, 2007). However, during late season when human detections declined, wolf detections increased while moose detections decreased, potentially to avoid humans and wolves. During mid to late summer, wolves generally hunt individually or in smaller groups, and while they can hunt moose individually, the risk is greater than hunting as a pack (Sand et al., 2008). Wolves could also switch to less risky alternative prey, including beaver (*Castor canadensis,* Sovie et al., 2023).

Influence of increased annual visitation and on vs. off-trail

We had varied support that space use and diel overlap responses would increase during a year with greater human visitation compared to COVID-19 visitor restricted year. All species had decreased daily mean detections during 2021 compared to 2020, with greater responses on-trail, indicating greater avoidance when visitation increases. Additionally, while wolves did not have greater decreases in detection rates than other species, wolf response to visitation could be greater than our data suggests as IRNP's wolf population doubled from 2020 to 2021 (IRNP unpublished data). Even with the population size doubled, their annual detection rates still decreased with increased human activity in 2021. Other COVID-19 studies found that multiple species had varied responses to increased human activity (Burton et al., 2024; Procko et al., 2022), while space use of all species in our study decreased with large increases in human activity.

We were able to investigate the influence of on and off-trail sites on species' space use and diel activity patterns. A major finding of our study was that species space use and activity patterns were altered at on-trail sites while remaining constant off-trail within and between years. This suggests that the influence of human activity occurred mostly on-trails, not necessarily at a population level. Additionally, the large fluctuation in species detections on-trail within years suggests that species will adjust their space use to avoid humans as human detections also fluctuation. As our off-trail cameras were placed only 50 m from trails, human activity influence appears constrained to <50 m from trails. While locations of our off-trail cameras remained constant during this study, it is surprising that there were no increases in detection rates at off-trail sites when there were decreases at on-trail sites. Species populations during our study are unable to immigrate or emigrate due to the island's distance from mainland ($\geq$ 22 km from mainland Canada). Consequently, animals could increase their use of areas > 50 m from the trail to avoid humans while reducing use of areas within 50 m of trails. Investigations including more stratified on- and off-trail placements and the influence of trail densities within parks could provide additional insights. Protected areas with lower trail density with similar visitation would be expected to have less impact from human visitation.

We did not find support for diel overlap changing with increasing human visitation; only red fox diel overlap with humans decreased between low and high visitation years. However, some species (moose, red fox, and snowshoe hare) altered their overall diel distributions to be less active during the day with an increased magnitude of human use. COVID-19 presented a rare opportunity to compare the influence of highly varied recreational activities on wildlife populations. However, periods of low visitation such as observed during the COVID-19 restrictions are uncommon and recreational visitation is projected to increase (Buckley & Foushee., 2012; Jones & Scott., 2006), which could further impact short- and long-term recreation effects on wildlife communities.

Conservation implications

We highlight the effects of within and between year variation in human recreational use on a mammalian community within a U.S national park. Even during a year with unparalleled low visitation due to the COVID-19 pandemic, within year increases in human use had variable influence on species monitored < 50 m of trails, suggesting sensitivity to low levels of human recreational use. In other systems, variation in how species avoid humans has led to disruptions in predator-prey relationships, trophic cascades, or the abundance of certain species (Burton et al., 2024; Dorresteijn et al., 2015). These disruptions can create challenges for conservation in practice and land management agencies or entities whose policy mandates are often to "preserve" and "protect." The U.S. National Park Service has a dual mandate "to conserve the scenery and the natural and historic objects the wildlife therein, and to provide for the enjoyment of the same in such a manner…as will leave them unimpaired for the enjoyment of future generations" (16 U.S.C. 1131). Mitigating wildlife responses to increased visitation is a management challenge not only at IRNP but across the National Park system (Dietsch et al., 2016). Reducing visitation during peak seasons or redistributing visitation across a season could reduce mammalian responses to recreational activity while continuing to provide for public enjoyment. Additionally, minimizing trail densities and providing refugia for wildlife could further reduce the influence of humans on wildlife. Whether direct or indirect, impacts of human recreational use are likely present at even low levels of visitation and when land managers consider these impacts in the context of natural perturbations, species' life history, and ecological processes, they will be better positioned to provide stewardship for mammalian communities in their charge.

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APPENDIX

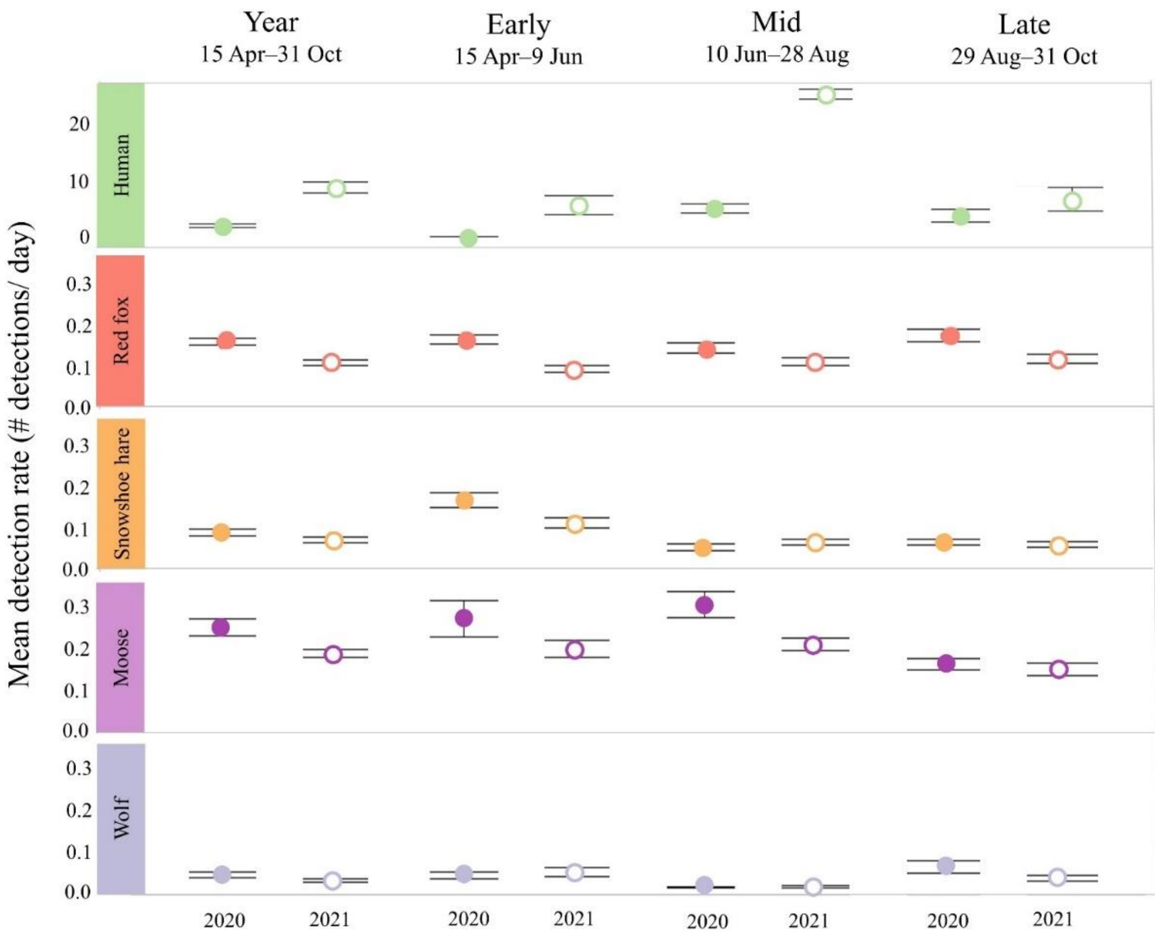

Figure A.2.1. Wildlife mean daily detection rates by year and season (early [15 April–9 June], mid [10 June–28 August], and late [29 August–31 October]), Isle Royale National Park, Michigan, USA, 2020 (solid circles)–2021(open circles) for trail and non-trail cameras combined. Mean daily detections were derived from daily detections at each camera. Moose detections included unknown age and sex. Error bars represent 95% confidence intervals of detection rate estimates.

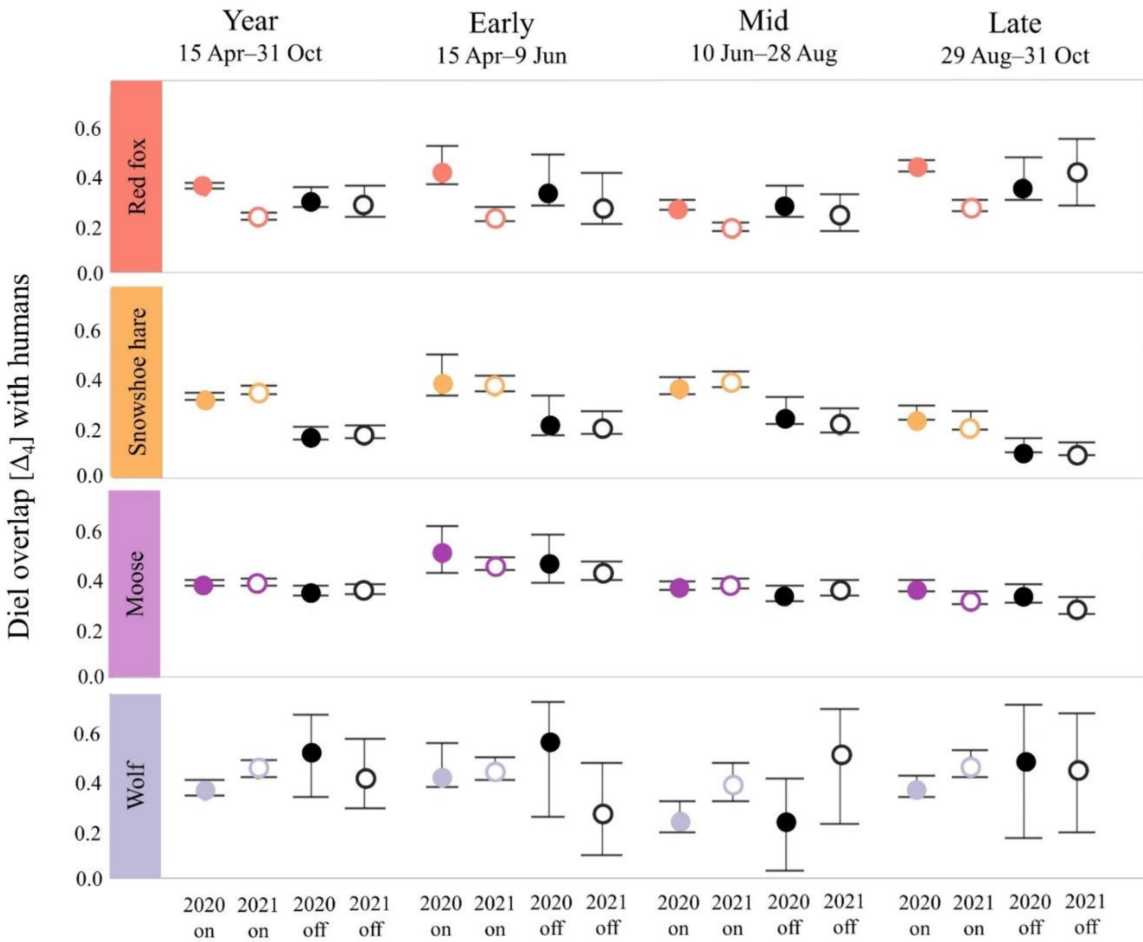

Figure A.2.2. Wildlife diel activity overlap (Dhat4 [Δ_4]) with humans by year and season (early [15 April–9 June], mid [10 June–28 August], and late [29 August–31 October]) across on (color) and off-trail (black) cameras, Isle Royale National Park, Michigan, USA, 2020 (solid circles)–2021 (open circles). Error bars represent 95% confidence intervals of detection rate estimates.

Table A.2.1. Wildlife and human detections by year and season (early [15 April–9 June], mid [10 June–28 August], and late [29 August–31 October]) across all cameras (n = 156), on-trail (n=98), and off-trail (n=58), Isle Royale National Park, Michigan, USA, 2020–2021.

Species	2020											
	Year			Early			Mid			Late		
	Total	On	Off	Total	On	Off	Total	On	Off	Total	On	Off
Human	64102			63			40300			23739		
Wolf	1132	1097	35	382	370	12	132	127	5	618	600	18
Moose	8462	6424	2038	2605	1973	632	4122	3194	928	1735	1257	478
Snowshoe hare	3025	2272	753	1578	1293	285	752	520	232	695	459	236
Red fox	5293	4889	404	1529	1394	142	1926	1756	170	1831	1739	92

Species	2021											
	Year			Early			Mid			Late		
	Total	On	Off	Total	On	Off	Total	On	Off	Total	On	Off
Human	270274			30964			197850			41460		
Wolf	911	863	48	423	408	15	145	132	13	343	323	20
Moose	6286	4359	1927	1857	1285	572	2807	1994	813	1622	1080	542
Snowshoe hare	2419	1738	681	999	765	234	827	622	205	593	351	242
Red fox	3499	3341	158	837	795	42	1440	1355	85	1222	1191	31

Table A.2.2. Wildlife and human mean detection rates (number of detections/day) (95% confidence intervals) by year and season (early [15 April–9 June], mid [10 June–28 August], and late [29 August–31 October]) across all cameras (n = 156), Isle Royale National Park, Michigan, USA, 2020–2021. Mean daily detections were derived from the mean detections of individuals each day across all sites for each year and season.

	2020			
Species	Year	Early	Mid	Late
Human	1.997 (1.555–2.165)	0.0114 (0.002–0.020)	5.007 (4.238–5.776)	3.747 (2.640–4.854)
Wolf	0.041 (0.034–0.047)	0.040 (0.030–0.048)	0.011 (0.008–0.013)	0.059 (0.044–0.075)
Moose	0.250 (0.230–0.271)	0.271 (0.228–0.315)	0.306 (0.274–0.338)	0.160 (0.146–0.174)
Snowshoe hare	0.088 (0.080–0.097)	0.166 (0.149–0.183)	0.056 (0.043–0.060)	0.065 (0.058–0.072)
Red fox	0.159 (0.151–0.167)	0.164 (0.152–0.1760)	0.143 (0.130–0.156)	0.173 (0.158–0.189)
	2021			
Species	Year	Early	Mid	Late
Human	8.615 (7.630–9.599)	5.585 (3.901–7.27)	24.960 (24.073–25.846)	6.544 (4.511–8.57)
Wolf	0.027 (0.022–0.031)	0.048 (0.038–0.059)	0.0120 (0.009–0.015)	0.033 (0.025–0.041)
Moose	0.186 (0.176–0.196)	0.197 (0.177–0.222)	0.209 (0.194–0.224)	0.148 (0.133–0.163)
Snowshoe hare	0.070 (0.064–0.076)	0.110 (0.975–0.123)	0.064 (0.056–0.071)	0.058 (0.051–0.065)
Red fox	0.108 (0.102–0.113)	0.092 (0.083–0.100)	0.111 (0.101–0.120)	0.118 (0.107–0.129)

Table A.2.3. Wildlife diel activity overlap (Dhat4 [Δ_4]) with humans by visitor year and season (early [15 April–9 June], mid [10 June–28 August], and late [29 August–31 October]) across all cameras (n = 156), Isle Royale National Park, Michigan, USA, 2020–2021.

	2020			
Species	Year	Early	Mid	Late
Wolf	0.37 (0.37–0.41)	0.40 (0.37–0.54)	0.25 (0.20–0.33)	0.37 (0.34–0.43)
Moose	0.37 (0.37–0.39)	0.47 (0.41–0.57)	0.36 (0.35–0.38)	0.35 (0.35–0.39)
Snowshoe hare	0.28 (0.28–0.31)	0.33 (0.30–0.46)	0.33 (0.32–0.38)	0.19 (0.19–0.24)
Red fox	0.35 (0.35–0.37)	0.38 (0.34–0.50)	0.27 (0.27–0.30)	0.43 (0.42–0.46)
	2021			
Species	Year	Early	Mid	Late
Wolf	0.44 (0.42–0.48)	0.43 (0.40–0.49)	0.40 (0.33–0.49)	0.46 (0.42–0.52)
Moose	0.37 (0.37–0.39)	0.44 (0.43–0.48)	0.37 (0.36–0.39)	0.30 (0.29–0.33)
Snowshoe hare	0.30 (0.29–0.32)	0.33 (0.31–0.36)	0.34 (0.32–0.38)	0.15 (0.16–0.20)
Red fox	0.24 (0.23–0.27)	0.23 (0.22–0.28)	0.19 (0.19–0.22)	0.28 (0.27–0.31)

Table A.2.4. Wildlife and human diel activity overlap (Dhat4 [Δ_4]) with wolves by visitor year and season (early [15 April–9 June], mid [10 June–28 August], and late [29 August–31 October]) across all cameras (n = 156), Isle Royale National Park, Michigan, USA, 2020–2021.

	2020			
Species	Year	Early	Mid	Late
Human	0.37 (0.35–0.41)	0.42 (0.38–0.56)	0.25 (0.20–0.34)	0.37 (0.34–0.43)
Moose	0.89 (0.86–0.92)	0.80 (0.76–0.86)	0.80 (0.73–0.87)	0.89 (0.85–0.93)
Snowshoe hare	0.85 (0.82–0.89)	0.81 (0.77–0.87)	0.82 (0.74–0.90)	0.81 (0.76–0.86)
Red fox	0.93 (0.90–0.96)	0.88 (0.83–0.93)	0.88 (0.81–0.94)	0.86 (0.82–0.91)
	2021			
Species	Year	Early	Mid	Late
Human	0.44 (0.42–0.48)	0.44 (0.41–0.49)	0.40 (0.34–0.48)	0.46 (0.42–0.52)
Moose	0.88 (0.86–0.92)	0.87 (0.83–0.92)	0.83 (0.77–0.88)	0.81 (0.77–0.87)
Snowshoe hare	0.83 (0.80–0.87)	0.79 (0.74–0.84)	0.92 (0.82–0.95)	0.70 (0.64–0.78)
Red fox	0.76 (0.73–0.80)	0.71 (0.68–0.78)	0.76 (0.68–0.84)	0.81 (0.75–0.85)

CHAPTER 3: WOLVES AND MOOSE INCREASE USE NEAR HUMANS WHEN HUMAN VISITATION PEAKS IN A NATIONAL PARK

3.1. Abstract

Increased human activity in protected areas can alter wildlife space use. Differences in how species respond to increased human activity could mediate predator-prey relationships. However, how predator-prey spatial site use relationships are influenced by varying levels of human activity within-visitor seasons is unclear. We used data from 156 cameras deployed on and off trails in Isle Royale National Park, Michigan, USA to assess the influence of human activity on gray wolf (*Canis lupus*) and moose (*Alces alces*) space use within 50m of trails. Human detections seasonally peaked in July–August, and visitation increased 338% from 2020 to 2021 due to COVID-19 pandemic visitor restrictions. Wolf and moose detections decreased in 2021 compared to 2020 and during wolf rendezvous (peak visitation) and divergence (post-peak) life history periods (LHPs), respectively, while their estimated site occupancy probabilities had no year- or LHP-related influence. Wolves and moose increased site intensity at high human use sites, resulting in higher co-occurrence near humans. When a site human use exceeded 42 detections/day, wolves or moose were less likely to use the site when the other was present. Our results suggest that wolves and moose are more likely to use sites with increased human use during periods of high visitation, increasing the potential for spatial interaction between wolves and moose and human-wildlife conflict. Reducing trails networks, visitor densities, or redistributing peak visitation could reduce human influence on predator-prey relationships and potential human-wolf conflicts.

3.2. Introduction

Protected areas, such as National Parks and wilderness areas, are often created to conserve biodiversity (Geldmann et al., 2019; Margules & Pressey, 2000) but can simultaneously provide other benefits, including recreation that could hinder conservation (Marion et al., 2016). Recreational visitation can disturb wildlife and is increasing globally while habitat quality within corresponding protected areas is declining (Geldmann et al., 2019; Buckley & Foushee, 2012). Recreational visitation to areas managed by the U.S. National Park Service (NPS) increased 18% from 2004 (277M) to 2023 (325M) (National Park Service, 2024). Although increased recreation could achieve some protected areas' objectives, management goals vary among agencies, and increased human activity can alter wildlife behavior (Burton et al., 2024; Sarmento & Berger, 2017). Behavioral changes toward humans can vary within and among species, ranging from avoidance to attraction (Procko et al., 2022; Rogala et al., 2011). Such differences in behavior within mammal communities can influence interspecies interactions, including predator-prey dynamics.

While humans can mediate predator-prey dynamics (Scoyoc et al., 2022), how interacting species alter their behavior in response to perceived predation risk (Suraci et al., 2019) could influence their response to intensity of human activities. The risk allocation hypothesis states that temporal variation in predation risk can affect how animals allocate feeding behavior among situations that differ in risk (Lima & Bednekoff, 1998). Animal behavioral responses to risk could vary seasonally or within minutes of encountering a potential predator or perceived threat (Lima & Bednekoff, 1998). While many animals adjust their behaviors to avoid interacting with large carnivores (Lima, 1986), humans can also be a perceived risk and cause anti-predator behaviors by prey and predator species (Suraci et al., 2019). In contrast, animals can lose their risk perception and be attracted or habituated to increased human activity (e.g., Wheat & Wilmers, 2016). Differences in how predators and prey react to human presence can present multiple scenarios that could lead to predators increasing pressure on certain prey species, switching prey sources, or increasing the probability of human-wildlife interactions (Scoyoc et al., 2022). For example, large herbivores can avoid humans (e.g., Stankowich, 2008) or be attracted to areas with high human activity (Burton et al., 2024), using humans as a shield from predators that are fearful of humans (Berger, 2007). When prey species use areas with higher human activity, predators must assess risk and switch prey (e.g., Muhly et al., 2011) or follow prey into those areas, increasing human-wildlife interaction potential (e.g., Barker et al., 2023). Understanding how predators and prey respond to humans is important for managing individual species within protected areas. However, understanding inter-specific relationships mediated by humans is potentially of greater importance to managing populations and mitigating human-wildlife conflicts.

How animals respond to risk varies temporally based on life history traits and periods, such as body condition and breeding and young-rearing periods (Lima, 1986). For example, gray wolves (*Canis lupus*) predate moose (*Alces alces*) year-round (Messier & Crête, 1985), but time spent hunting moose and kill rates vary based on life history periods and potential risk. When wolves are denning or transitioning to rendezvous sites, wolves hunt individually or in smaller groups and predate calves more than adult moose (Messier & Crête, 1985). However, female moose allocate additional energy to protecting their calves and can injure lone wolves (Sand et al., 2008). Additionally, due to calves' smaller body size compared to adults, wolves must kill more frequently or switch to smaller-bodied prey, like beavers (*Castor canadensis*), during summer to meet nutritional needs (Metz et al., 2011; Sand et al., 2008). During early fall, wolves temporarily diverge with increased dispersion by younger wolves and increased individual hunting and exploration before pack convergence in late fall (Mech & Boitani, 2003). During this divergence period, wolves have similar diets (i.e., smaller-bodied prey or calves) to those during denning and rendezvous periods (Mech & Boitani, 2003).

Similarly, human visitation to recreational areas fluctuates seasonally in predictable patterns. For example, recreational areas managed by the NPS experience high human activity during June–August (National Park Service, 2024). However, how predator-prey relationships are influenced by varying levels of human activity within-visitor seasons is unclear. Most human activity within protected areas occurs on trails or near campgrounds and other developed areas (Wolf et al., 2012). Many studies investigating the influence of human activity on species and interspecies relationships were unable to examine the effect of human activity in proximity to trails and or incorporate within-season temporal variation in species' life history and human activity (e.g., Burton et al., 2024; Scoyoc et al., 2022). Understanding the influence of human activity on predator-prey relationships is increasingly important as government agencies develop management plans considering seasonal recreational use restrictions to facilitate wildlife conservation and ecosystem processes (e.g., predator-prey relations) and mitigate human-wildlife conflicts (Dertien et al., 2021).

We characterized predator-prey marginal and co-occurrence site occupancy and spatial interaction probabilities in Isle Royale National Park (IRNP), Michigan, USA, within and between years using detections from remote cameras within 50 m of hiking trails. Within years, we compared three time 30-day periods (hereafter life history periods, LHPs) that reflected human visitation and wolf and moose life history patterns to investigate the influence of varying visitation patterns within visitor seasons. Between years, we compared overall low (2020, during COVID-19 restrictions) and typical (2021) visitation levels for IRNP. Across the wolf denning LHP (pre-peak visitation), rendezvous LHP (peak visitation), and divergence LHP (post-peak visitation) periods, we expected wolf marginal occupancy (i.e., site use) probabilities to be constant near trails as wolves prioritize rearing young near centralize locations and hunt smaller-bodied prey individually (Messier & Crête, 1985). Across LHPs, we expected moose marginal occupancy probabilities to also be constant as adult female moose rear calves and have limited mobility with calves during these LHPs (Ballard et al., 1981). Therefore, we expected wolf and moose co-occurrence and spatial interaction occupancy probabilities near trails to be constant across LHPs. However, if increased human site use or visitation during the rendezvous LHP (peak visitation) and in 2021 influenced wolf and moose spatial relationships, then one of four scenarios would occur at sites near trails: 1. moose would be more likely and wolves less likely to use sites, 2. wolves would be more likely and moose less likely to use sites, 3. wolves and moose be more likely to use sites, and 4. wolves and moose would be less likely to use sites, with scenario 1 our predicted outcome in IRNP. We defined marginal occupancy probability as the occupancy probability for each species regardless of the occupancy state of another species. We defined the co-occurrence probability as the probability both species used a site. Lastly, we defined the species interaction term as the effect response of a species using a site when the other is present (i.e., if the term is negative, a species is less likely to use a site when the other is present). Due to limited mammal emigration and immigration, our island study provided a unique quasi-natural experiment to test our predictions.

3.3. Methods

Study area

Isle Royale National Park is an archipelago comprising 558 km^{2,} with the main island, Isle Royale, comprising 535 km^2 in northwestern Lake Superior (Figure 3.1). The park is 24 km from the Canadian mainland in the transitional zone of temperate northern hardwoods and boreal forest biomes. About 99% of IRNP is designated wilderness and is open to park visitors annually during 15 April–31 October. Annual mean temperature is 3.9°C and in winter mean high temperature is -3.0°C (Fisichelli et al., 2013).

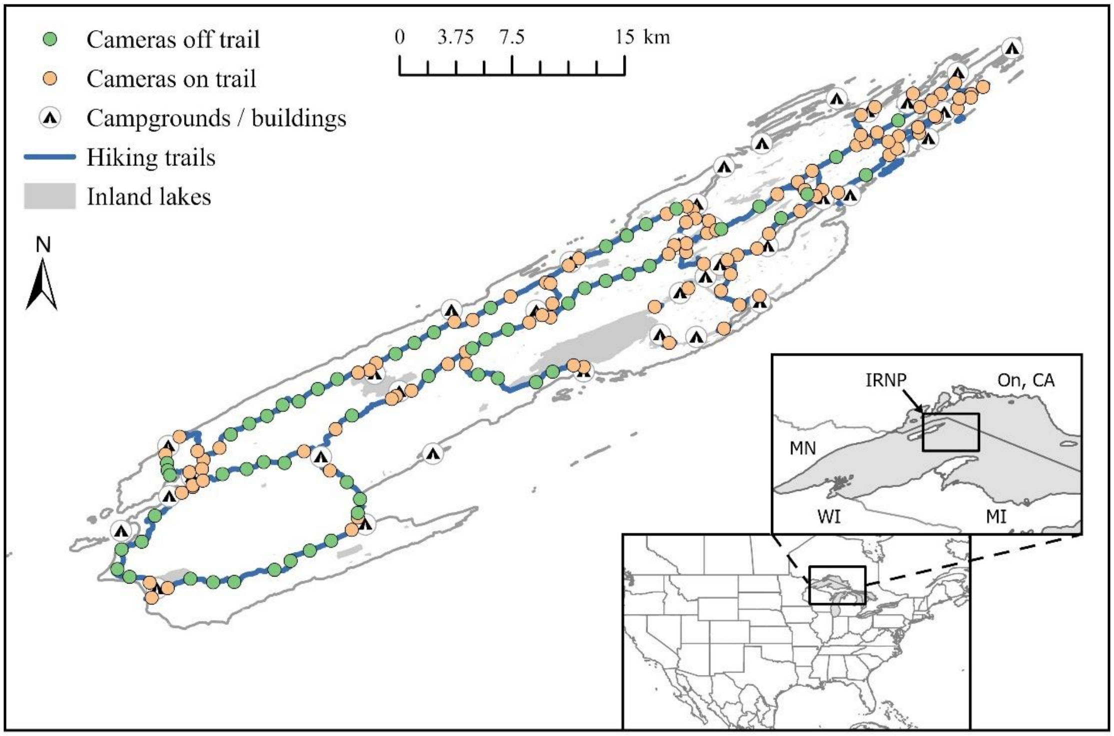

Figure 3.1. Camera locations (*n* = 156), Isle Royale National Park, Michigan, USA, 1 May–8 October 2020–2021.

In the early 1900s, moose colonized IRNP and persisted without major predators until gray wolves colonized in the 1940s (Mech, 1966). From 1948 to 2018, the gray wolf population averaged 22 individuals, ranging from 50 individuals in 1980 to 2 related wolves in 2018 (Smith & Peterson, 2023; Romanski et al., 2020; Vucetich et al., 2012). Low wolf abundance in the last decade facilitated increased moose abundance and associated browsing (Sanders & Kirschbaumm, 2023). To restore ecosystem processes, 19 wolves were introduced to IRNP during September 2018–2019 (Romanski et al., 2020). There were at least 12 wolves on IRNP during winter 2019–2020 and 24 wolves during winter 2020–2021 (Sovie et al., 2024). In December 2020 and 2021, Isle Royale estimated moose density was 2.2 (95% CI = 1.8–2.7) and 1.8 (95% CI = 1.5–2.2) moose/km^2, respectively (Boone et al., 2024b).

Travel within IRNP is limited to boats and hiking on 266 km of trails. There are 36 campgrounds; hunting and trapping on IRNP are prohibited. In 2020, IRNP imposed visitor restrictions in response to the coronavirus pandemic until 26 June, allowing limited access only by private boats and seaplanes. Additional backcountry restrictions in 2020 included that visitor groups could not share campsites or shelters or use part of a main trail (Minong Trail). The number of visitors increased 338% from 2020 (4,594 visitors) to 2021 (20,109 visitors) (National Park Service, 2024). Average annual visitation during 2015–2019 was 16,790, increasing 45% across these years; annual visitation was 20,223 individuals in 2022 (National Park Service, 2024).

Camera Deployment and Data Organization

We used images obtained during 1 May–8 October 2020–2021 from 156 infrared cameras (Stealth Cam DS4K; Irving, Texas, USA) positioned along or within 50 m of trails throughout Isle Royale (Figure 3.1). Along each trail, we located cameras 350–1600 m apart where cameras nearest trail intersections were placed on-trail (n = 98) and those further (>100–300 m) from intersections, 50 m perpendicular from a trail (n = 58; Figure 3.1). Camera locations were consistent throughout the study. We placed cameras at each location to maximize detection area and minimize visual obstruction to reduce differences between on and off-trail cameras. We positioned cameras 1.5 m above ground and oriented each down to detect animals 4–15 m distant while attempting to minimize obstruction from snow and vegetation. At each site, we measured the maximum and minimum distance a camera detected a human. We estimated each camera's viewable area, including camera angle of view (Stealth camera DS4K: $\theta = 43.54$ degrees), using the circular sector area equation $((\theta/360°) * \pi(\text{detection distance})^2)$ where we subtracted the minimum detection distance from the maximum. We programmed cameras to take five images, each detection with a trigger speed of ≤0.5 sec and no delay between detections. To reduce vegetation obstruction that could impair detection (Moll et al., 2020), we cleared 10 m in front of cameras during each check. Species detected were initially identified using Program RECONN.AI (Michigan Aerospace, Ann Arbor, Michigan), which uses regional convolutional neural network models to identify species from images. We manually checked the AI-processed species identification records to ensure accuracy and grouped images by species taken within a 10-minute interval to generate group-size counts.

To investigate the influence of within-season visitation, we defined three 30-day periods (life history periods or LHPs) with varying levels of human visitation that overlapped co-occurring wolf and moose life history periods (Figure 3.2). The periods were denning LHP when wolves and moose rear neonates and human visitation is low (1 May–30 May), rendezvous LHP when wolves rendezvous, moose post-calve, and human visitation peaks (8 July–7 August), and divergence LHP when wolves temporarily disperse, moose breed, and human visitation decreases (8 September–7 October) (Figure 2). By incorporating life history traits when selecting these periods, visitation coincided when moose and wolf spatial patterns were mostly stable.

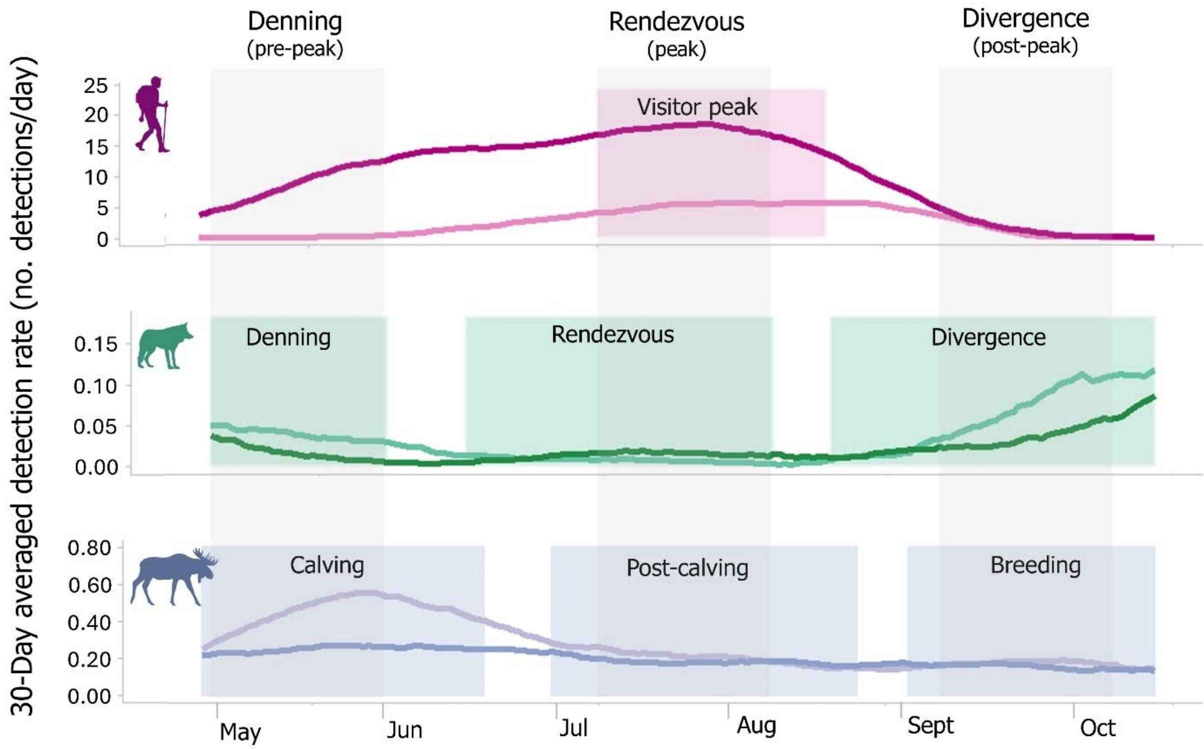

Figure 3.2. Human (pink), wolf (green), and moose (purple) 30-day averaged detection rates (number of detections/day per site) across human visitor (pre-peak, peak, post-peak) and wolf and moose life history periods (denning, rendezvous and divergence), Isle Royale National Park, Michigan, USA, 1 May–14 October 2020 (lighter line) –2021 (darker line). Gray bars represent 30-day periods used for multi-species occupancy models.

To estimate an index of human site use, we calculated 30-day average detection rates (number of human or species detections/day) for each site per LHP. We included year (2020 and 2021) and camera viewable areas as variables. Initially, camera position on or off-trails was a variable; however, because visitors rarely went off trail, our index of human use contained differences between camera positions.

Single-season, two-species occupancy models

We fit single-season, two-species (wolf and moose) occupancy models to our data (Rota et al., 2016). We fit separate models for each LHP, containing data from 2020 and 2021. We interpreted occupancy in these models as species probability of site use within 50 m of trails. In all models, we considered a site as a remote camera location within 50 m of hiking trails in a given year and LHP. We used goodness-of-fit tests (Goldstein et al., 2024; Wright et al., 2016) to determine the optimal length of sampling occasions within each 30-day LHP. Based on these tests, we selected 10 3-day intervals. We modeled occupancy parameters (including first-order parameters and the second-order interaction term) as a function of year and human index of use. Detection for both species was modeled as a function of viewshed area.

We fit all models in program R (V4.2.2, R Core Team, 2024) using package *unmarked* (Kellner et al., 2023; Fiske and Chandler, 2011). During the denning LHP, we had few sites (n = 9) where wolves were detected and few sites with a human use index > 0 during this period; creating separation issues when fitting the multi-species occupancy model (Clipp et al., 2021). We therefore fit the model for this LHP with penalized likelihood using the *optimizePenalty* function in package *unmarked* (Kellner et al., 2023; Clipp et al., 2021). The *optimizePenalty* function selects the optimal penalty values using K-fold cross-validation (Kellner et al., 2023).

For each model, we assessed goodness-of-fit using the calculated sum of squared errors (SSE) from actual data compared to parametric bootstrap SSEs from simulated datasets (n=1000) using the *parboot* function in package unmarked (Kellner et al., 2023). We assumed a good model fit when the SSE from the real dataset fell within the distribution of SSEs from the corresponding simulated dataset. We determined a particular variable to have a statistically significant effect if the parameter's 95% confidence intervals did not overlap zero.

3.4. Results

We obtained 797 wolf detections (435 in 2020; 362 in 2021) and 5,985 moose detections (3,232 in 2020; 2,753 in 2021). Wolf detections were greatest (51% of detections) during denning (May) and lowest (15%) during rendezvous LHP (July–August) (Figure 3.2). Moose detections were similarly highest (37%) during wolf denning and rendezvous LHPs but decreased (26%) during wolf dispersion LHP (September–October, Figure 3.2).

Individual estimates of wolf and moose marginal and co-occurrence occupancy probabilities were constant across LHPs and between years (Figure A.3.1), where wolves had lower naive predicted site use (40%, 95% CI = 31–49%). Moose were predicted to use 85% (95% CI = 78–89%) of sites while wolves and moose were predicted to co-occur at 37% (95% CI = 29–44%) of sites. We found no effect of year for denning (Table A.3.1), rendezvous (Table 3.1), or divergence (Table A.3.2) LHP models on wolf and moose occupancy probabilities and wolf-moose interaction terms. Only the rendezvous LHP model identified a significant effect of human use (Table 3.1), with the wolf and moose occupancy probabilities increasing and the wolf-moose interaction term decreasing with increased human use (Figure 3.3). The wolf-moose spatial interaction was negative when human use exceeded 42 detections/day (Figure 3.3), inferring that when one species used a site with >42 daily human detections, the other species was less likely to be present.

Table 3.1. Peak human visitation (rendezvous LHP) model results for estimating wolf and moose site occupancy probability, spatial interaction, and detection parameter estimates, standard errors (SE), and 95% confidence intervals (CI), Isle Royale National Park, Michigan, USA, 8 July–7 August 2020–2021. Bolded parameters indicate a significant ($p < 0.05$) effect based on confidence intervals not overlapping zero. Spatial interaction can be interpreted as if one species uses a site, the other species' site use probability is lower (negative estimate) or higher (positive estimate).

Occupancy	Parameter	Estimate	SE	CI	
				2.5%	97.5%
Wolf	Intercept	0.27	0.95	-1.60	2.14
	Human use	3.98	1.20	1.62	6.34
	Year: 2021	-0.73	1.02	-2.73	1.27
Moose	**Intercept**	2.94	0.67	1.61	4.26
	Human use	2.81	1.18	0.50	5.11
	Year: 2021	-0.55	0.41	-1.36	0.26
Wolf-moose interaction	Intercept	-0.83	0.99	-2.77	1.11
	Human use	-3.01	1.17	-5.31	-0.71
	Year: 2021	0.87	1.08	-1.24	2.98
Detection	Parameter	Estimate	SE	CI	
				2.5%	97.5%
Wolf	**Intercept**	-2.46	0.17	-2.80	-2.12
	Viewshed area	0.19	0.19	-0.18	0.56
Moose	**Intercept**	-0.43	0.04	-0.51	-0.35
	Viewshed area	-0.03	0.04	-0.11	0.05

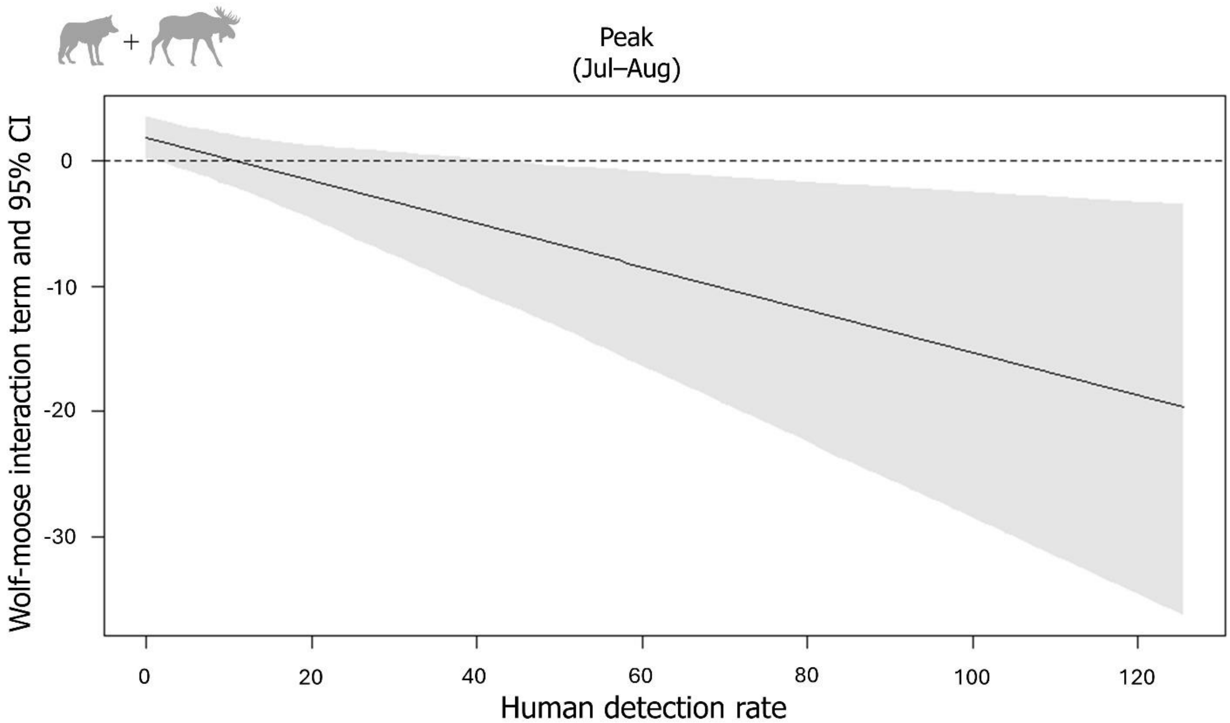

Figure 3.3. Peak human visitation (rendezvous LHP) wolf-moose spatial interaction relationship with 30-day human index of use (95% confidence intervals), Isle Royale National Park. Michigan, USA, 2020–2021. Interaction terms were estimated from the rendezvous (peak visitation) wolf-moose model (8 July–7 August). The interaction term can be interpreted as if one species uses a site, the other species' site use probability is lower (negative estimate) or higher (positive estimate).

Wolf marginal and wolf-moose co-occurrence probabilities, but not moose marginal, increased with increasing human use in the rendezvous and divergence periods (Figure 3.4, Figure 3.5, Figure A.3.2). However, the divergence LHP wolf occupancy model indicated that human use was not a significant influence of wolf overall site use (Table A.3.2). Consequently, wolf-moose co-occurrence had a similar pattern of increase during the rendezvous LHP (Figure 3.5).

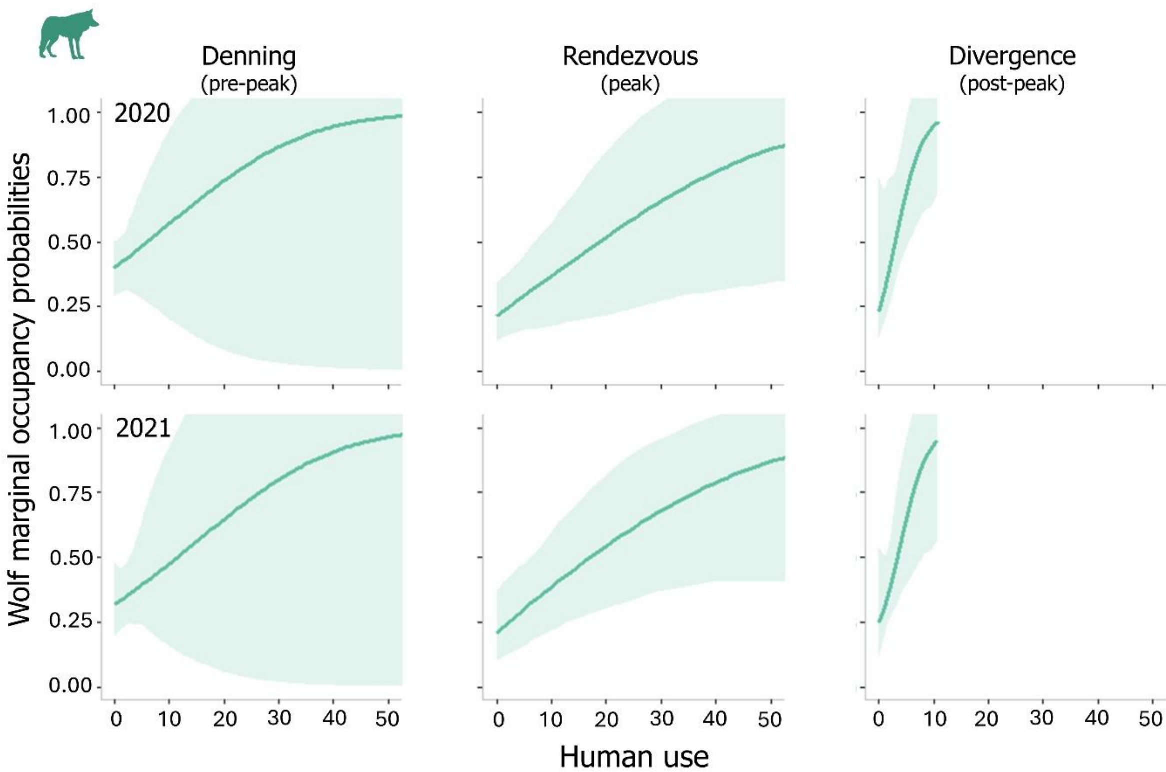

Figure 3.4. Wolf estimated marginal site occupancy probabilities in relation to 30-day human index of use within 50m of trails (95% confidence intervals), Isle Royale National Park. Michigan, USA, May–October, 2020–2021. The wolf marginal probabilities were estimated from the corresponding LHP multi-species occupancy models (denning, rendezvous, divergence). The marginal probability is the probability that a species uses a site regardless of the occupancy state of the other.

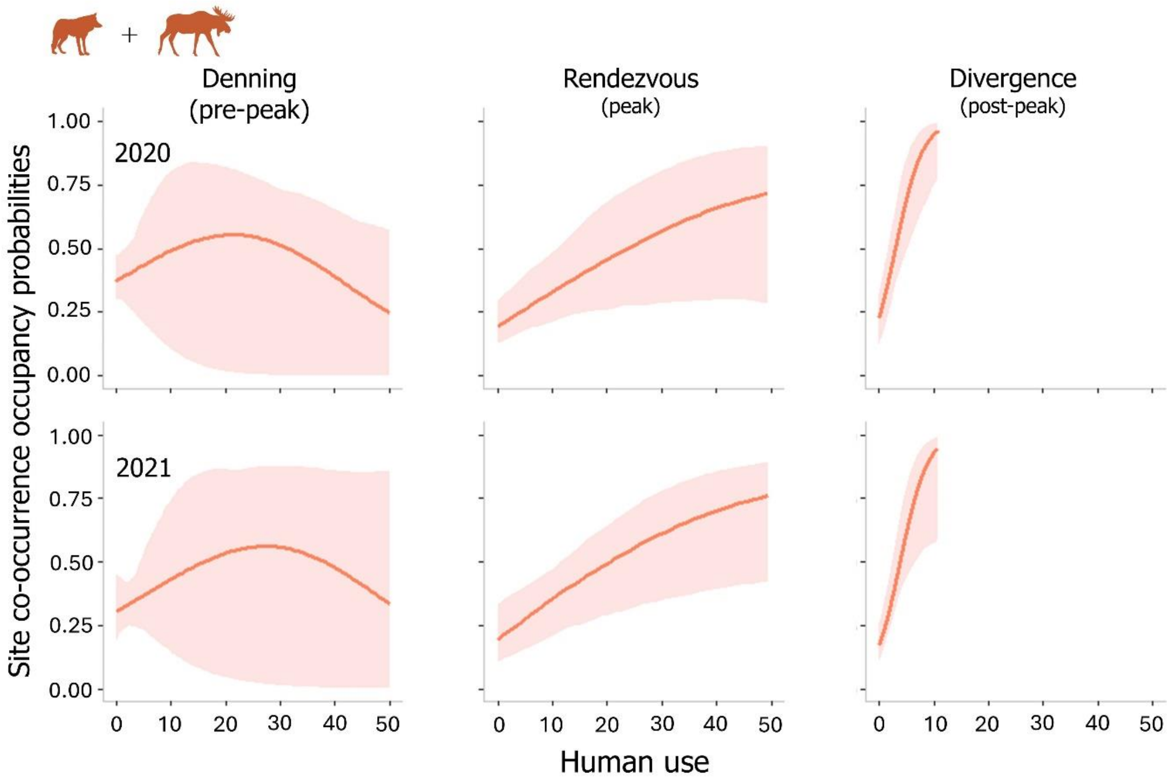

Figure 3.5. Wolf and moose estimated site use co-occurrence probabilities in relation to 30-day human index of use within 50 m of trails (95% confidence intervals), Isle Royale National Park. Michigan, USA, May–October, 2020–2021. The co-occurrence probabilities were estimated from the corresponding wolf LHP multi-species occupancy models (denning, rendezvous, and divergence). The co-occurrence probability is the probability both species use a site.

3.5. Discussion

In the wolf denning (pre-peak visitation), rendezvous (peak visitation), and divergence (post-peak visitation) LHPs, our prediction that wolf and moose marginal and co-occurrence site occupancy and spatial interaction term probabilities near trails would be constant within seasons was supported. We also predicted that when increased human site use occurred during the rendezvous LHP (peak visitation) and in 2021, moose would be more likely and wolves less likely to use these sites. While our results suggest human use influences wolf-moose site use relationships, our expectation that wolves would be less likely and moose would be more likely to use sites with high human use (i.e., human shield; Berger, 2007) was not supported. Instead, we found that wolves and moose were more likely to use sites with high human use; however, if one species was present at a site where human use was >42 detections/day, the other species was less likely to use that site.

Wolves and moose increased their intensity of use at sites with higher human use based on marginal estimates, with wolves having a stronger response in the rendezvous LHP when visitation peaks. The increase in wolf-moose co-occurrence probabilities with increasing human use between LHPs were similar to wolf marginal occupancy trends in relation to human use, suggesting wolves were driving the increase in co-occurrence. Wolves can increase their space use in different habitats used by moose, likely to increase their hunting success (Sand et al., 2021; Kittle et al., 2017). In our study, moose had high occurrence across all sites, including those with high human use. Wolves may increase space use overlap in areas with higher prey abundance and prey-selected habitat (Kittle et al., 2017). Additionally, wolf spatial use of higher human use sites can increase when wolves live proximate to humans (Heilhecker et al., 2007). One wolf pack territory boundary during 2020–2021 overlapped with the more heavily-visited part of IRNP (Sovie et al., 2024), which could have resulted in greater wolf use of high human use sites. However, due to the small sample size of wolves collared and lack of information on wolves outside of the two general packs, pack information could not have been incorporated into our analysis. In Yellowstone National Park, wolf packs that lived near higher human activity had increased tolerance towards humans (Anton et al., 2020).

While wolves, humans, and moose similarly use sites with increased human use, our model results cannot demonstrate direct interactions (Rota et al., 2016). Individual wolves are less likely to predate adult moose, and female moose protect their young during summer (Sand et al., 2008; Messier & Crête, 1985). Wolves can be attracted to human-related foods, or switch to smaller prey that could occur near trails (Mohammadi et al., 2019; Metz et al., 2011; Sand et al., 2008). However, our rendezvous LHP model identified a negative effect of human use on the wolf-moose interaction term during peak visitation. While this interaction term is likely offset by the strong positive wolf and moose site use response to increased human use, it is possible that when human site use exceeds 42 detections/day, one species could be more likely to decrease site use intensity when the other species is present. The multi-species occupancy analysis does not identify which species is responding (Rota et al., 2016); however, as wolf-moose co-occurrence at sites with high human use is similar to marginal patterns observed in wolves and wolves had a stronger response, moose may be less likely to use sites with wolf presence and high human use.

While this contrasted with our prediction of moose potentially using humans a spatial "shield" (i.e., scenario 1, Berger, 2007), moose can alter their use of certain habitat features (e.g., bogs or near roads) to avoid wolves (Loosen et al., 2021; Sand et al., 2021). Moose can also spend less time in areas of higher wolf probability of use (Ditmer et al., 2018).

We demonstrated high moose occurrence, corresponding with a high overall moose density on IRNP (Boone et al., 2024b; Sovie et al., 2024). High observed occurrence could mask some moose responses towards humans and wolves, which may be identified in an abundance or density-related analysis. When species are locally rare, less abundant, or narrowly distributed, occupancy analyses can identify similar trends than abundance analyses (Gaston et al., 2002). In contrast, occupancy analyses are less likely to identify certain intensity effects that abundance analyses can identify (Gaston et al., 2002). Space use of moose on IRNP following peak human visitation (September–October) decreased, whereas wolf local space use increased (Boone et al., 2024a). With increased risk from wolves and humans, moose could be altering their frequency of use at these sites. Responses also could differ by moose sex and age classes to wolf presence as adult moose, especially bulls, are less likely to be predated than calves during summer and early fall (Sovie et al., 2023; Messier & Crête, 1985).

We found no support that increasing yearly visitation's magnitude influenced predator-prey spatial relationships. In contrast, moose site use and intensity of use decreased when visitation increased after partial park closure from COVID-19 in Glacier National Park (Anderson et al., 2023). The differences in results between studies could be that moose had high use across all our sites, and a small portion of sites had only wolves or neither species present. This limited variation can make it difficult to estimate co-occurrence and spatial interactions between species using multi-species models inferred from sites present by all, one, or no species (Clipp et al., 2021). Additionally, as multi-species occupancy models cannot incorporate interactions between variables (Rota et al., 2016), we were unable to test for interactions between year and human use variables directly. Due to data limitations, we were also unable to perform individual annual models for each LHP to test the influence of human use and year. However, as we found that wolves and moose spatial interactions were influenced when human site use exceeded 42 detections/day, it is more likely that human use in 2021 had a stronger influence than in 2020 as >42 detections/day occurred more frequently in 2021 than 2020.

Wolf-human direct interactions increased on IRNP since 2020, including increased encounters and wolves attempting to take human-related items, leading to the establishment of animal-resistant food storage containers at campgrounds in 2024 (IRNP unpublished data). Other protected areas have experienced increased spatial use and habituation at sites with high human activity by wolves (Linnell et al., 2002) and other predators (e.g., grizzly bears (Gunther et al., 2024), black bears (Kirby et al., 2016), coyotes (Baker & Leberg, 2018)). Consequently, multiple protected areas have established protocols to remove, haze, or relocate aggressive animals or actively intervene between animals and visitors while providing education to reduce potential conflicts (e.g., Gunther et al., 2024). As increased spatial overlap with humans can increase conflict potential and alter predator-prey relationships near trails, redistribution of visitors or providing increased areas for wildlife refugia from humans could reduce potential predator tolerance to humans.

Variation in how species spatially respond to increased human activity has led to disruptions in predator-prey relationships, trophic cascades, and the abundance of some species (Burton et al., 2024; Dorresteijn et al., 2015). These disruptions can create challenges for conservation in practice and land management agencies whose policy mandates are to "preserve" and "protect." The U.S. National Park Service has a dual mandate "to conserve the scenery and the natural and historic objects and the wildlife therein, and to provide for the enjoyment of the same in such a manner…as will leave them unimpaired for the enjoyment of future generations" (16 U.S.C. 1131). Mitigating wildlife responses to increased visitation is a management challenge at IRNP and throughout the National Park system (Dietsch et al., 2016). Increasing areas without trails within parks, reducing visitation during peak periods, or redistributing visitation spatially or temporally could mitigate human impacts on wildlife space use and species interactions while continuing to provide for public enjoyment. Whether direct or indirect, impacts of human recreational use likely occur at even low levels of visitation, and when land managers consider these impacts in the context of natural perturbations, species' life history, and ecological processes, they will be better positioned to provide stewardship for mammalian communities in their charge.

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APPENDIX

Table A.3.1. Denning LHP (pre-peak human visitation) model results for estimating wolf and moose site occupancy probability, spatial interaction, and detection parameter estimates, standard errors (SE), and 95% confidence intervals (CI), Isle Royale National Park, Michigan, USA, 1 May–30 May 2020–2021. Bolded parameters indicate a significant ($p < 0.05$) effect based on confidence intervals not overlapping zero. The interaction term can be interpreted as if one species uses a site, the other species' site use probability is lower (negative estimate) or higher (positive estimate).

Occupancy	Parameter	Estimate	SE	CI	
				2.5%	97.5%
Wolf	**Intercept**	-0.96	0.41	-1.76	-0.16
	Human use	1.14	0.94	-0.70	2.97
	Year: 2021	-0.54	0.37	-1.25	0.18
Moose	**Intercept**	1.32	0.29	0.76	1.89
	Human use	0.01	0.47	-0.91	0.93
	Year: 2021	0.30	0.36	-0.39	1.00
Wolf-moose interaction	**Intercept**	0.96	0.35	0.27	1.65
	Human use	-0.63	0.49	-1.59	0.33
	Year: 2021	0.16	0.32	-0.47	0.78
Detection	Parameter	Estimate	SE	CI	
				2.5%	97.5%
Wolf	**Intercept**	-1.48	0.14	-1.75	-1.20
	Viewshed area	-0.15	0.11	-0.37	0.07
Moose	**Intercept**	-0.43	0.06	-0.55	-0.30
	Viewshed area	-0.08	0.07	-0.05	0.02

Table A.3.2. Divergence LHP (post-peak human visitation) model results for estimating wolf and moose site occupancy probability, spatial interaction, and detection parameter estimates, standard errors (SE), and 95% confidence intervals (CI), Isle Royale National Park, Michigan, USA, 8 September–7 October 2020–2021. Bolded parameters indicate a significant ($p < 0.05$) effect based on confidence intervals not overlapping zero. Spatial interaction can be interpreted as if one species uses a site, the other species' site use probability is lower (negative estimate) or higher (positive estimate).

Occupancy	Parameter	Estimate	SE	CI	
				2.5%	97.5%
Wolf	Intercept	-3.41	2.75	-8.80	1.98
	Human use	-0.9	0.76	-1.57	1.40
	Year: 2021	3.26	2.84	-2.31	8.83
Moose	**Intercept**	1.62	0.38	0.89	2.36
	Human use	-0.01	0.41	-0.82	0.79
	Year:2021	0.51	0.59	-0.64	1.66
Wolf-moose interaction	Intercept	3.16	02.79	-2.31	8.62
	Human use	1.01	0.83	-0.61	2.64
	Year: 2021	-3.58	2.90	-9.25	2.10
Detection	Parameter	Estimate	SE	CI	
				2.5%	97.5%
Wolf	**Intercept**	-2.04	0.13	-2.30	-1.78
	Viewshed area	0.31	0.16	-0.01	0.62
Moose	**Intercept**	-0.85	0.04	-0.93	-0.76
	Viewshed area	-0.00	0.04	-0.08	0.09

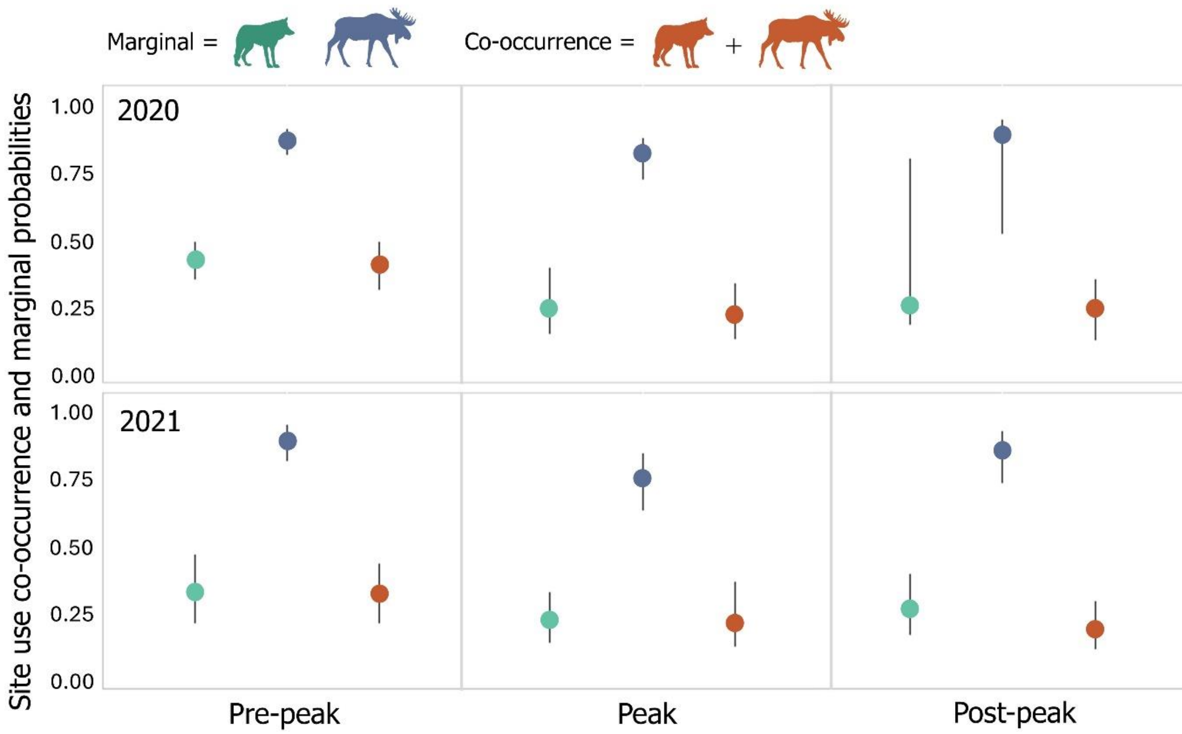

Figure A.3.1. Wolf (green) and moose (purple) site marginal and co-occurrence (orange) occupancy probabilities across visitation periods (pre-peak in May, peak in July–August, and post-peak in September–October) within 60 m of trails (95% confidence intervals), Isle Royale National Park. Michigan, USA, May–October, 2020–2021. Values for each visitation were estimated from the corresponding multi-species occupancy models. The marginal probability is the probability that a species uses a site regardless of the occupancy state of the other. The co-occurrence probability is the probability both species use a site.

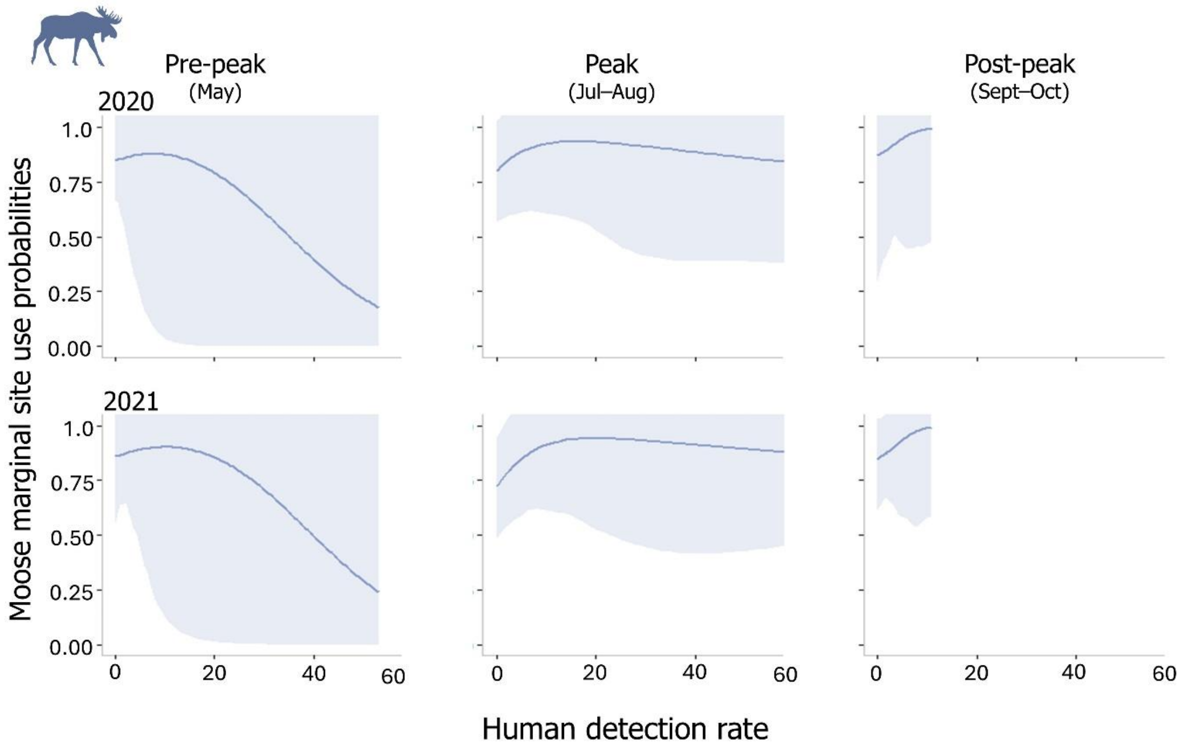

Figure A.3.2. Moose estimated marginal site occupancy probabilities in relation with 30-day human index of use within 50m of trails (95% confidence intervals), Isle Royale National Park. Michigan, USA, May–October, 2020–2021. The moose marginal probabilities were estimated from the corresponding LHP multi-species occupancy models (denning, rendezvous, divergence). The marginal probability is the probability that a species uses a site regardless of the occupancy state of the other.

CHAPTER 4: OPTIMAL TIMING TO ESTIMATE MOOSE *ALCES ACLES* DEMOGRAPHIC PARAMETERS USING REMOTE CAMERAS

4.1. Abstract

Obtaining estimates of demographic parameters are fundamental for managing species. However, survey timing and duration influences the precision and accuracy of estimates. We used motion-activated camera images to investigate the effect of survey duration, timing, camera density and on- or off-trail placement on detection rates, sex and age ratios, and density estimates of moose (*Alces alces*) in Isle Royale National Park (IRNP), Michigan, USA. Variations in detection rates reflected moose life history patterns and suggested the optimal times to estimate demographic ratios and population density. We recommend camera surveys of 25-days during mid-June–mid-July and early December–early January to produce consistent and precise calf:cow and bull:cow ratios. On-trail cameras returned greater detection rates and density estimates, but decreased precision for summer bull:cow and calf:cow ratios than off-trail cameras. Subsampling camera densities to < 4 cameras/km^2 decreased precision and consistency for density and ratio estimates. We recommend estimating moose density during early December–early January, using ≥ 4 cameras/km^2 placed on and off-trail. Pairing life history events with high detection rates can be used to identify optimal survey periods and could be applied to other species.

4.2. Introduction

Reliable estimates of sex and age ratios, and density are fundamental to monitoring wildlife populations and making management decisions (Lindenmayer et al., 2012; Yoccoz et al., 2001). Sex and age ratios such as juvenile:adult female or adult male:adult female are commonly used to infer demographic trends (Harris et al., 2008) and population growth for various ungulate species (e.g., elk *Cervus canadensis* (Harris et al., 2008), caribou *Rangifer tarandus* (DeCesare et al., 2011)). Specifically, summer- and inter-derived juvenile:adult female ratios can index productivity and recruitment, respectively (Van Ballenberghe, 1979). Precise density estimates can be more critical as they are used to establish hunting quotas (Garel et al., 2010), monitor long-term population trends (Yoccoz et al., 2001), or influence the decision to introduce new individuals, predators, or competitors (Van Kleunen et al., 2023).

Estimating demographic parameters can be difficult if the ability to detect or differentiate age or sex classes varies temporally due to animal movements (Keiter et al., 2017) or life history

(Samuel et al., 1987). For example, adult male moose, along with other male cervids, are generally detected more frequently during the breeding season than females or calves due to greater movements by males (Miquelle, 1990; de Vos et al., 1967). These increased movements can result in increased detections, leading to overestimating males during the breeding season (Solberg et al., 2010), inflating density estimates, and skewing population-level sex or age ratios. However, the timing of surveys to estimate ungulate population trends often coincides with factors such as hunting season or preferred weather conditions to reduce survey costs rather than timing based on life history.

We suggest that considering the timing of life history events among sex and age classes could improve detection probability and estimate population characteristics more precisely. Changes in life history events can result in differences in species' sex/age class patterns of mobility, resulting in potential differences and increased variability in detection probabilities (Keiter et al., 2017). For example, moose *Alces alces* adult females (hereafter cows) generally give birth from May to June and restrict their home ranges and mobility to protect their low-mobility young (hereafter calves) (Ballard et al., 1981). Cow and calf mobility increases with calf age, with greatest mobility during late June–October. Adult males (hereafter bulls) undergo rutting and breeding from mid-September to late October (Bowyer et al., 2003) and increase mobility compared to cows. Cow and bull activity and mobility are similar after the breeding season, emphasizing foraging before winter (Borowik et al., 2021; Miquelle, 1990). During late winter, when ambient temperatures are lowest, mobility decreases to conserve energy (Ditmer et al., 2018). Selecting standardized periods where mobility is similar across sex or age classes should improve precision within and across years for population ratios calculations typically used to estimate fecundity (late fall and winter) and productivity (summer).

In addition to mobility, body characteristics change seasonally that can affect the ability to correctly identify sex or age classes, which could lead to decreased precision and consistency when calculating population characteristics. Distinguishing juveniles from adult ungulates becomes more difficult as juveniles mature. While some ungulate species (e.g., white-tailed deer *Odocoileus virginianus*, elk, mule deer *O. hemionus*) offspring have temporary spots, not all juvenile ungulates (e.g., moose, caribou, pronghorn *Antilocapra americana*) have this trait and identification relies on rapidly changing body sizes to differentiate between juveniles and adults which can cause potential misidentification or categorizing as unknown. For example, moose calves weigh 12–20 kg at birth and can increase body mass 1.3–1.6 percent per day (Schwartz et al., 2007). By January–March, calves can weigh 160-225 kg compared to adults weighing 360–600 kg (Schwartz et al., 2007; Solberg et al., 2007). Another common identifiable trait is using antlers to identify adult male cervids; however, shed or undeveloped antlers could lead to misidentification between males and females. For moose, bulls do not grow antlers until mid-April–early May, followed by rapid growth resulting in complete antler development by August or September (Schwartz et al., 2007), and antler loss during late December–late January (Van Ballenberghe, 1979). Misidentification between calves and bulls and a potential increase for unknown identifications can occur in the early winter as calves (<1 year) can produce variable antler characteristics while having closer body mass to adults (Van Ballenberghe, 1979).

To facilitate more precise and consistent population characteristics, survey designs would ideally occur during life history events that increase probability of identifiable body characteristics among target sex and age classes. However, the most common survey method for collecting information on moose populations is aerial surveys during mid to late winter, which coincides when moose are least mobile (Moll et al., 2022; Rönnegård et al., 2008). Behavior differences in summer between sex and age classes can generate biased estimates, limiting the collection of population estimates to occur in winter (Gasaway et al., 1985). Additionally, aerial surveys rely on specific weather and flight conditions, which can further constrain timing and measurement across consecutive days (Gasaway et al., 1986). Hunter observations also have been used to collect moose occurrence data (Crum et al., 2017; Rönnegård et al., 2008); however, this method usually occurs when moose are breeding and there are behavioral differences between sex and age classes (Rolandsen et al., 2003) that can reduce accuracy of detectability, density, and ratio estimates. In contrast, remote cameras could be deployed during more appropriate survey periods to obtain summer and winter population characteristics while being cost-effective and potentially more reliable (Burton et al., 2015). While the influence of survey length on detection rate, species richness, and occupancy has been investigated (Kays et al., 2020), understanding survey timing, duration, and influence of survey design are still needed to optimize precision of detection rates, sex and age ratios, and density.

Federal, state, provincial, and tribal agencies operate under diverse laws, policies, and regulations that influences method selection and execution. For example, the Wilderness Act (1964) prohibits using motorized and mechanized equipment and installations in designated wilderness areas (16 U.S.C. 1131), limiting certain survey methodologies, such as aerial or long-term remote camera surveys. However, the Wilderness Act allows the use of prohibited equipment when their use meets the Act's stated purpose (i.e., to preserve wilderness character) (16 U.S.C. 1131). Many agencies are required to complete a minimum requirements analysis when prohibited methodologies are proposed (16 U.S.C. 1131). Balancing the requirements of laws, policies, and regulations with research objectives often requires evaluating numerous methodologies to assess the most appropriate. While remote cameras do impede the goals of the Wilderness Act, they are non-invasive and adaptable to diverse survey designs and could reduce impacts compared with alternatives like aerial surveys.

We investigated timing, sampling duration, and camera density to estimate moose detection rates, density, and sex and age ratios to identify periods of increased precision using moose detections from remote cameras in a designated wilderness, Isle Royale National Park (IRNP), Michigan, USA. We predicted that seasonal variation in detection rates would reflect moose life history events, as movement influences detection probability (Keiter et al., 2017). We predicted early December–early January would be optimal to estimate density and calf:cow (i.e., recruitment) and bull:cow ratios as bull, calf, and cow movements are similar (Schwartz et al., 2007) and can be differentiated using body size and antlers or pedicels post-shedding of antlers. We expected that bull:cow and calf:cow (i.e., productivity) ratios could also be estimated in late June–late July when calves and cows become more mobile post-calving and bull antlers are more developed. We expected survey durations of 25- to 30-days would produce the most consistent and lowest variation for bull:cow and calf:cow (i.e., productivity) ratios as this interval can increase the probability of detecting (Kays et al., 2020) moose while limiting potential seasonal changes in life history. Lastly, we investigated the effects of camera density and placement on- and off-trail on survey precision and duration.

4.3. Methods

Study area

Isle Royale National Park (IRNP) is an archipelago comprising of 558 km^2 with the main island, Isle Royale, comprising 535 km^2 in northwestern Lake Superior, 24 km from the Canadian mainland in the transitional zone of temperate northern hardwoods and boreal forest biomes (Peterson et al., 1998) (Figure 4.1). Approximately 99% of the IRNP is designated wilderness and is open to park visitors from 15 April– 31 October yearly.

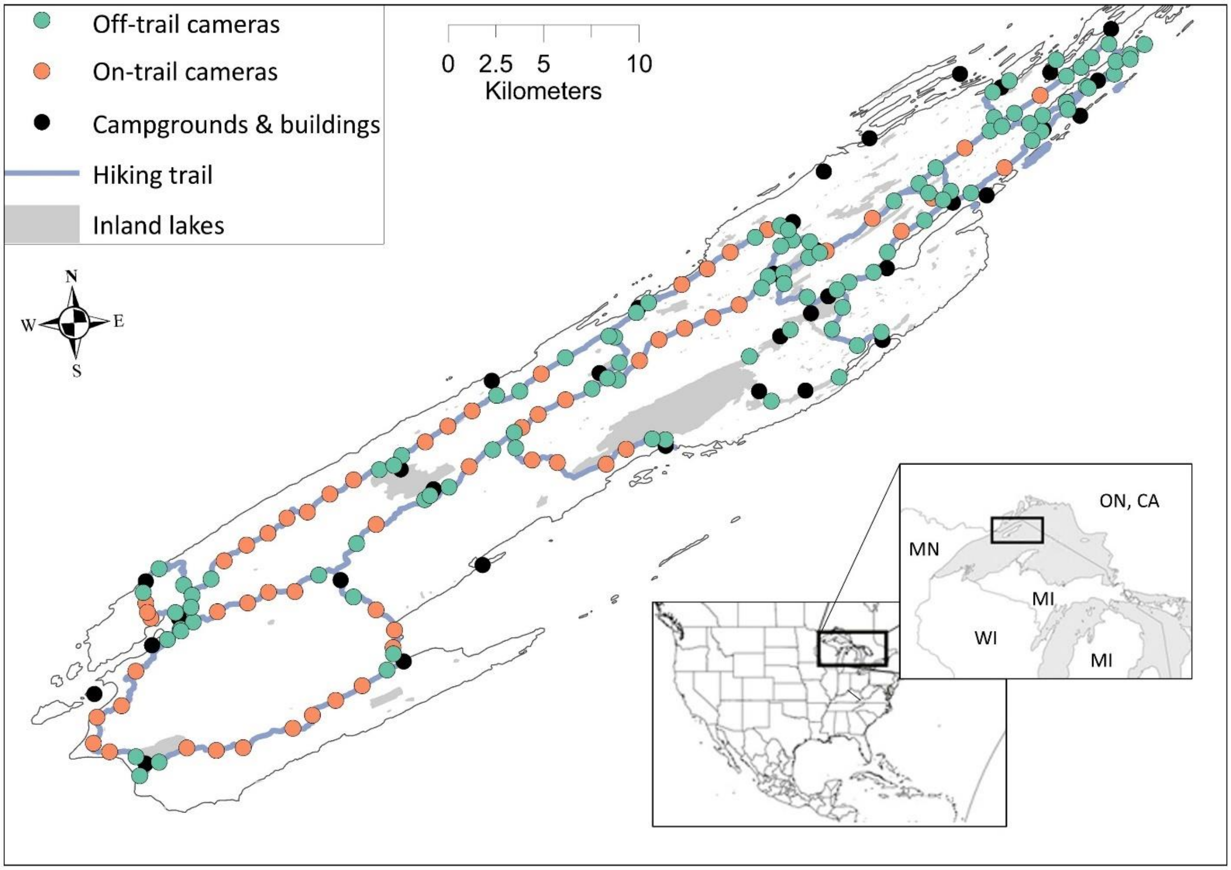

Figure 4.1. Camera locations (*n* = 156), Isle Royale National Park, Michigan, USA, 1 April–31 March 2020–2022.

In the early 1900s, moose colonized IRNP and persisted without major predators until gray wolves colonized in the 1940s (Mech, 1966). The decline of IRNP's wolf population from 50 to 14 individuals, then to two related individuals by 2018 (Romanski et al., 2020; Hedrick et al., 2017; Peterson et al., 1998), assisted in the increase moose abundance, resulting in over-browsed understory conditions, particularly for moose's preferred forage, balsam fir (Sanders & Kirschbaum, 2023). As no hunting occurs in IRNP, wolves were introduced during 2018–2020 to restore ecosystem processes, including wolf predation of moose (Romanski et al., 2020).

Data organization and collection

We used images collected 15 January 2020 to 13 January 2022 from 156 infrared remote cameras (Stealth Cam DS4K; Irving, Texas, USA) positioned along or within 50 m of trails throughout Isle Royale, the main island within IRNP (Figure 4.1). Along each trail segment, we spaced cameras 350–1600 m apart where cameras nearest trail intersections (100–300 m from an intersection) were placed on-trail (n = 98) and those further, 50 m perpendicular from trails (n =

58). Camera locations were consistent throughout the two-year study. At each camera location, we positioned cameras to maximize detection area and minimize visual obstruction to reduce obstruction differences between on and off-trail cameras. To reduce obstruction that could impair detection (Moll et al., 2020), we removed vegetation 10 m in front of each camera during each check. We positioned cameras 1.5 m above ground and oriented each to detect animals 4–15 m distant. We programmed cameras to take five images, each detection with a trigger speed of ≤0.5 sec and no delay between detections. Species detected were initially identified using program RECONN.AI (Michigan Aerospace, Ann Arbor, Michigan), which uses regional convolutional neural network models to identify species from images. We manually checked the AI-processed moose identification records to ensure accuracy and grouped images taken within a 10-minute interval generating group-size counts. We categorized moose as bull, cow, calf (<10.5-months old), and combined (all detections including unknown sex or age). We assigned year ranges as 1 April–31 March to include all calving and late winter seasons and labeled the year to match the start year. To test effects of lower camera densities, we randomly subset the 2020 and 2021 datasets retaining 100% (5 cameras/ km^2), 75% (4), 50% (3), and 25% (1) of cameras to investigate the influence of camera densities on population estimates. Additionally, we ran our estimations across all pooled sites (n = 156), on-trail (n = 98), and off-trail (n = 58) only camera placements.

Gender/Age Ratios, Productivity, and Recruitment Estimates

From 1 April to 31 March 2020–2021, we calculated daily estimates of calf:cow ratios (number of calf detections/number of cow detections) and daily estimates of bull:cow ratios (number of bull detections/number of cow detections). We excluded 2 days when bulls or calves were detected but females were not (i.e., *inf*) and 2 days when no moose were detected across all sites. To identify periods to estimate early season calf:cow ratios (i.e., productivity (Van Ballenberghe, 1979)), late season calf:cow ratios (recruitment), and early- and late-season bull:cow ratios, we initially plotted daily calf:cow and bull:cow ratio estimates across the entire year to identify a period in summer (14 June–17 August) and winter (25 November–29 January) with greater consistency and lower confidence interval differences. We generated daily detection histories for 10- to 50-day periods at 5-day intervals. The start day of each interval was the first day of each period. For example, the 10-day and 50-day 1 April detection histories contained dates 1 April to 10 April and 1 April to 21 May, respectively. We then repeated this step for 2

April, 3 April, etc., until the last day of each period, subset, camera-placement type, and year. We calculated mean demographic ratios across days, standard error, and 95% confidence intervals from each detection history.

To compare mean demographic ratio values within survey intervals (i.e., actual dates) and interval lengths (i.e., 10-day, 15-day, 20-day, and 25-day), we calculated coefficient of variations (CV) and the difference between the upper and lower 95% confidence intervals. We assumed lower differences in confidence intervals, and CVs indicated increased consistency and precision.

Instantaneous Sampling Estimation Modeling

We estimated moose density using on-trail, off-trail, and all cameras using an instantaneous sampling estimation (ISE) model in R package *spaceNtime* (Moeller et al., 2020). The ISE model is a density estimator that incorporates species' count information and the amount of space (viewable area) sampled before a species of interest is detected on cameras. The model uses multiple spatial and temporal replicates to estimate density using the mean count n_{ij} at location $i = 1, 2, \ldots, M$ and occasion $j = 1, 2, \ldots, J$ when divided by a cameras' viewable area (Moeller et al., 2020). During each camera check, we estimated the minimum and maximum distance (m) the camera could detect a person. Camera detection distances at sites varied minimally during the study as cameras were permanently attached to trees and were only moved when the tree or camera was damaged. We then estimated each camera's viewable area, including camera angle of view (Stealth camera DS4K: $\theta = 43.54$ degrees) into the circular sector area equation $((\theta/360°) * \pi(\text{detection distance})^2)$ where we subtracted the minimum detection area from the maximum to get the total area. We assumed detections on and off-trail represented Isle Royale and extrapolated density to the entire island (535 km^2).

We used a 2s window every 30 s to generate a count (group size per sequence) histories using the *build_occ()* and *ise_build_eh()* functions following recommendations to use shorter windows and period lengths when using motion-activated cameras (Ausband et al., 2022; Moeller et al., 2020). As we used 10-minute intervals when classifying moose sequences, we used the initial timestamp of the first detected animal per sequence when running models to reduce overcounting. We estimated density and 95% confidence intervals using 60-day survey windows that started the 1st or 15th of each month during 1 November–31 March each year. We divided the outputs by the surveyed area (535 km^2) to estimate density (number of moose/km^2).

We used 60-days to ensure we had adequate data to estimate density while also ensuring life history events were fully within the survey window as timing of life history events can vary regionally and across years and study sites (Saether et al., 1996).

4.4. Results

Detection rate

Overall, bull, cow, and calf detection rates increased from early-June to mid-July, and mid-November to mid-January (Figure 4.2). Additionally, bulls had increased detections from late September to mid-October. Unknown sex and age detections were greatest from mid-June to early July and late December to late January. All moose sex and age classes had lower detection rates in 2021 than 2020 during early June–mid July and mid-November–early February (Figure 4.2).

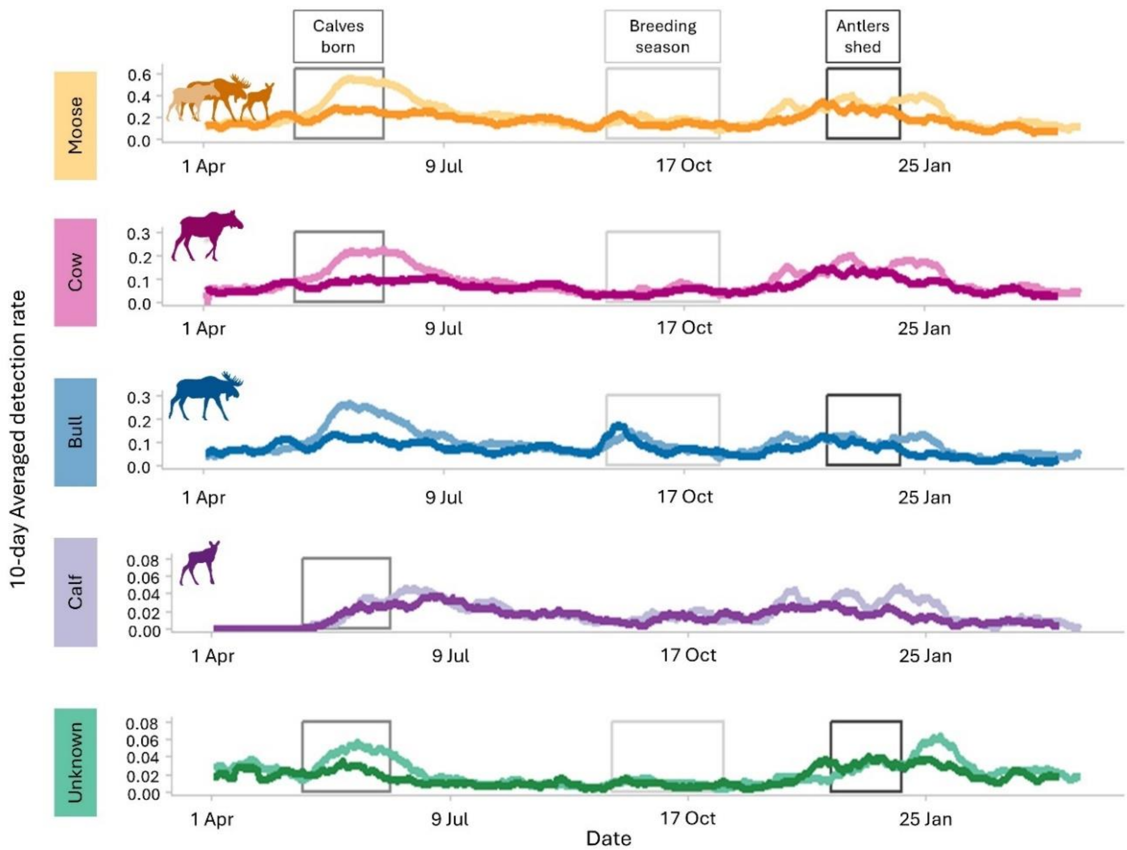

Figure 4.2. Moose mean daily detection rates across 10-days using on- and off-trail cameras (n = 156), Isle Royale National Park, Michigan, USA, 2020 (lighter colors) and 2021 (darker colors). Moose detections included unknown age and sex. Moose neonates are born, breeding season, and

Figure 4.2. (cont'd).

shedding of antlers occur approximately mid-May-early June, mid-September–late October, and mid-December–early January (Bowyer et al., 2003), respectively.

On-trail cameras detected more moose than off-trail cameras (Figure A.4.1). On and off-trail cameras had higher bull, cow, calf, and unknown detections during early June–mid-July and for bulls mid-September–mid-October. Moose detections on-trail were greater in 2020 than in 2021. Only on-trail detection rates increased mid-November–early February. Overall detection rates decreased as camera density per km^2 decreased; however, all camera density subsamples produced similar variation in detection rates across seasons (Figure A.4.2).

Moose density

We found density estimates were most consistent across cameras on- and off-trail, camera density subsamples, and years when 60-day survey windows started in December (Figure 4.3, Figure 4.4). With a start period of 1 December, we estimated 2.2 moose/km^2 in 2020 (95% CI = 1.8–2.7) and 1.8 moose/km^2 (95% CI = 1.5–2.2) in 2021. When extrapolating to Isle Royale area (535 km^2), we estimated 1177 moose (95% CI = 963–1445) in 2020 and 963 moose (95% CI = 803–1177) in 2021. For all models estimating density, 95% confidence intervals overlapped from 1 November to 15 December then diverged after 1 January. On-trail camera derived density estimates were greater and did not overlap with off-trail cameras (Figure 4.3). For camera density subsamples, we found 5 (100%) and 4 (75%) cameras/km^2 had similar estimates and confidence intervals (Figure 4.4), which became increasingly variable at lower camera densities.

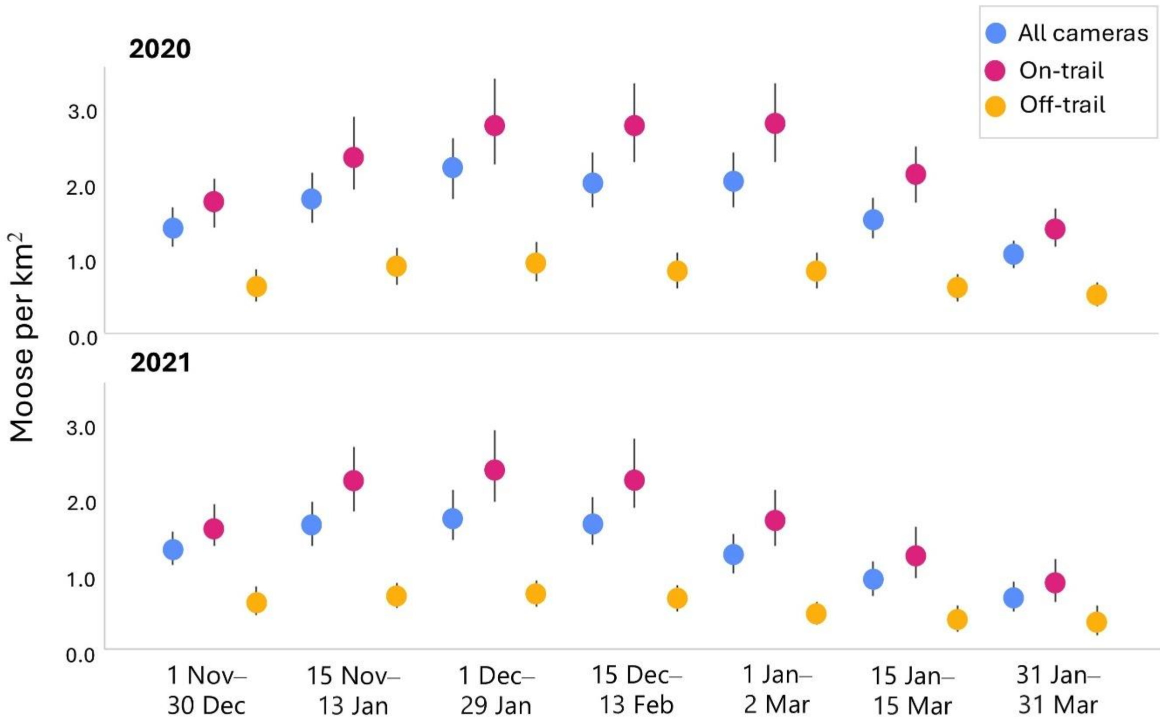

Figure 4.3. Moose density/km^2 estimations (95% confidence intervals) across all pooled (blue; *n* = 156) and on- (pink; *n* = 98) or off-trail (orange; *n* = 58) cameras, Isle Royale National Park (535 km^2), Michigan, USA, 2020 and 2021. Estimations calculated from moose detections within 60-day periods.

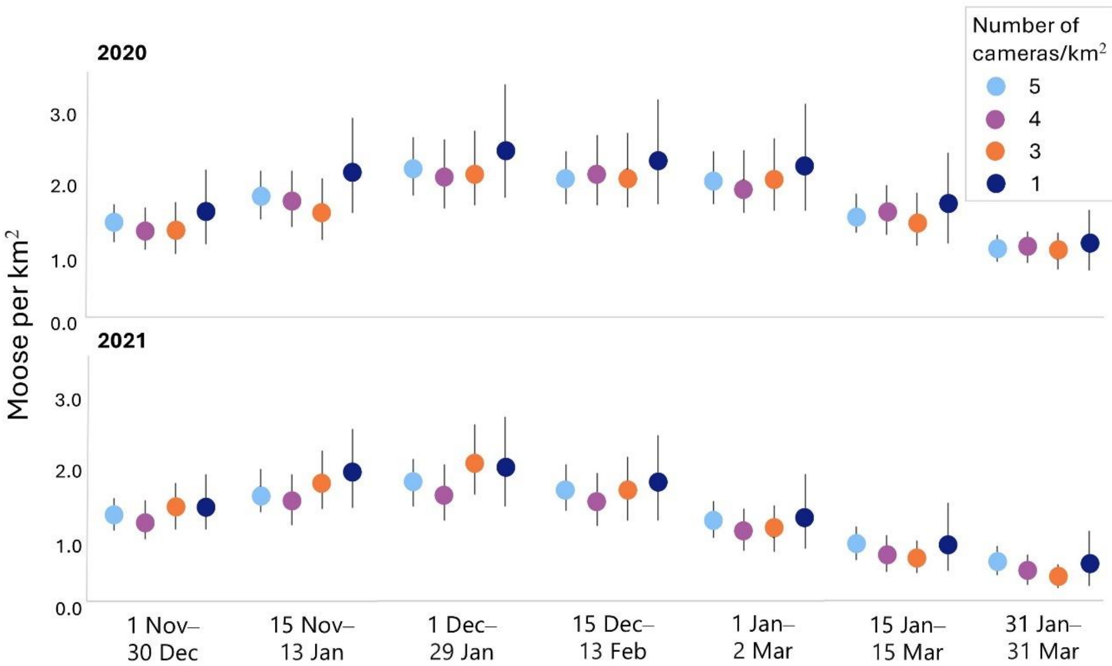

Figure 4.4. Moose density/km^2 estimates (95% confidence intervals) using camera density subsets of 5 (100%), 4 (75%), 3 (50%), and 1 (25%)/km^2, Isle Royale National Park (535 km^2), Michigan, USA, 2020–2021. Estimations calculated from moose detections within 60-day periods. Camera numbers have equal proportions of on- and off-trail cameras and are scaled to 1 km^2.

Age and sex ratios

Calf:cow and bull:cow ratios calculated using 25-day survey periods during mid June–mid July and early December–early January were least variable (Figure 4.5). However, winter derived ratios were more precise than summer ratios. Bull:cow ratios were more variable than calf:cow ratios, especially in summer. Ratios calculated outside mid June–mid July and early December–early January produced large confidence interval differences, and coefficients of variation. For calf:cow and bull:cow ratios, surveys < 20 days had increased variability in mean ratio estimates, and > 30 days had gradual increases in confidence interval differences and coefficient of variation (Figure A.4.3, Figure A.4.4).

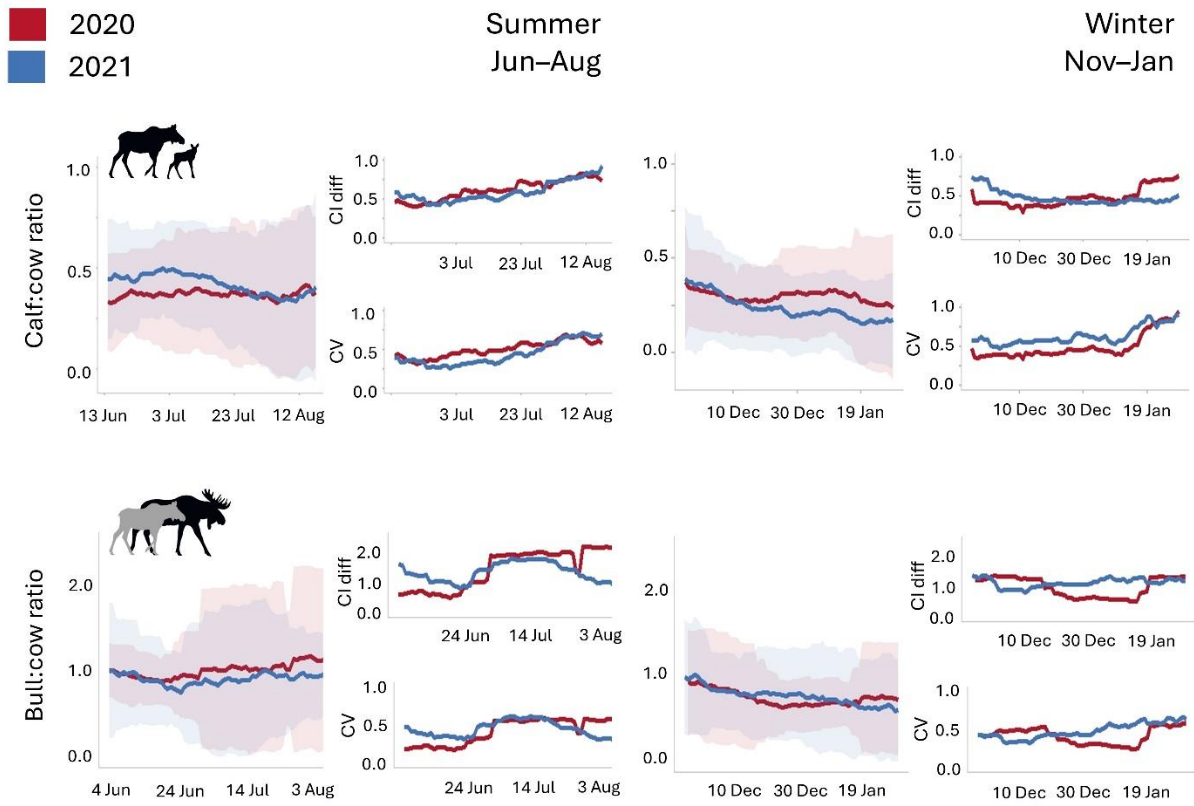

Figure 4.5. Daily mean calf:cow and bull:cow ratios across 25-day moving windows (95% confidence intervals) in summer (June–August) and early winter (November–January), Isle Royale National Park, Michigan, USA, 2020 (red) and 2021 (blue). For each set of ratios, differences in 95% confidence intervals (CI diff – [upper CI – lower CI]) and coefficient of variation (CV) are plotted for 2020–2021. Periods with low CI diff values and CV indicate higher precision.

For summer calf:cow ratios, our most precise estimates were on 21 June 2020 (0.39 95% CI: 0.18–0.60) and 1 July 2021 (0.50 95% CI: 0.28–0.72) and for winter, 11 December 2020 (0.26 95% CI: 0.11–0.42) and 9 January 2021 (0.23 95% CI: 0.03–0.43) (Table A.4.1). The most precise bull:cow ratios occurred on 19 June 2020 (0.87 95% CI: 0.61–1.13) and 1 July 2021 (0.81 95% CI: 0.39–1.23) and for winter, 11 January 2021 (0.64 95% CI: 0.37–0.90) and 11 December 2021 (0.76 95% CI: 0.34–1.18) (Table A.4.2). Except for summer bull:cow ratios, calf:cow and bull:cow ratios calculated using on- and off-trail and cameras densities of 4 and 5/km^2 produced similar ratios with 95% overlapping confidence intervals differences (Figure

A.4.5, Figure A.4.6). Summer off-trail bull:cow ratios had greater confidence interval differences and coefficient of variation than on-trail (Figure A.4.5).

4.5. Discussion

We estimated the effects of survey timing, sampling durations, design, and density on precision and consistency when calculating moose detection rates, density, and sex and age ratios from remote cameras. We found support for our prediction that variation in detection rates reflected moose life history events. Detection rates increased following calving when calves became mobile in late June–July and also increased post-rut when moose increased their mobility for foraging during December–January. Further, we found optimal times to estimate density and sex and age ratios occurred during periods (e.g., mid-June to mid-July and early December to early January) with high but consistent detection rates across age and sex categories. We found support for our prediction that 25-day periods would produce a consistent and low variation in ratios. Windows <25 days had increased daily variability and windows >30 days had increased differences in confidence intervals and coefficient of variations, indicating decreased precision. Our prediction that on-trail placement and low densities of cameras increase variability was supported while also finding camera densities of 4 and 5/km^2 produced similar density, detection rates, and sex and age ratios.

Detection rate

Moose detection rates for sex and age classes varied temporally and our prediction that variation in detections would reflect moose life history events, as movement influences detection probability (Keiter et al., 2017), was supported. Aside from the breeding season, all sex and age classes exhibited similar patterns across seasons and between years. Detection rates for all classes increased in early June, midway through calving season from late May to mid-June. We predicted this delayed increase as calves and cows have limited mobility after birth, and mobility increases within a few weeks (Ballard et al., 1981). Additionally, increase in higher quality-forage and increased foraging could increase mobility in late May (Risenhoover, 1986) and explain why bull and cow detection rates increase during this period compared to late winter. During the breeding season in September–October, only bulls had increased detection rates. Bulls increase mobility and allocate energy to mate with multiple cows rather than other activities such as foraging (Solberg et al., 2010; Miquelle, 1990). In contrast, cows in estrus maintain a breeding area and exhibit lower mobility rates than bulls (DeCesare et al., 2012).

During late November–late January, all classes had increased detection rates with similar variation. During this post-rut period, moose increase foraging to increase body mass before forage quality and quantity further declines (Miquelle, 1990). Mobility and home range size of bulls, cows, and calves are most similar at this time (Borowik et al., 2021; Miquelle, 1990) and likely explain similar detection patterns we observed. After January, all moose detection rates declined, which was expected as moose mobility decreases to conserve energy expenditures in late winter (Ditmer et al., 2018). While overall seasonal variations between years were similar, 2020 had greater overall detections than 2021, particularly during summer. This difference could be related to decreased park visitation in 2020 due to COVID-19 pandemic restrictions; mean detection rates of moose decreased in summer as visitation increased then peaked (Boone et al., 2024a) or from wolf predation as IRNP's wolf population doubled from 2020 to 2021.

Moose density

We found support for our prediction that variability in density estimates reflected variability in detection rates and that early December–early January would be an optimal survey period. Our greatest and most precise density estimates across all pooled sites, camera density subsamples, on- and off-trail, and years occurred during a 60-day survey period beginning in early December. While precision and consistency do not necessarily mean our density estimates reflect true population size, these estimates occurred when bull, cow, and calf mobility and behavior patterns are most similar (Borowik et al., 2021; Miquelle, 1990). When extrapolating our 2021 December density estimate to Isle Royale (535 km^2;1.8 moose/km^2 [95% CI = 1.5–2.2]) or 963 (95% CI = 803–1177) moose, our 2021 extrapolated estimates were similar to the Isle Royale's 2021–2022 moose abundance estimates of 1039 (95% CI = 800–1349) estimated from a winter aerial survey (Sovie et al., 2024). Aerial surveys were not conducted during winter 2020–2021 due to the COVID-19 pandemic; however, similarities between the 2021 estimates provide additional support for conducting surveys in December. Estimates initiated before 15 November or after 1 January generated lower moose density estimates and 95% confidence intervals did not overlap with estimates from surveys starting in December. This difference in density estimates was likely due to fewer detections mid- to post-breeding season from reduced movements caused by increased rest and reduced foraging in late winter (Ditmer et al., 2018). Although we did not estimate moose density during summer, behavioral differences among bulls, cows, and calves during summer and reduced observability can influence estimates from aerial surveys (Gasaway et al., 1985). When extrapolating our density estimates, we assumed that our sampling area was representative of Isle Royale. Further assessments testing representative sampling would further inform potential limitations towards using an instantaneous sampling estimator.

Age and sex ratios

Our predictions that calf:cow and bull:cow ratios could be optimally estimated in early December–early January and late June–late July were supported. Estimates outside these periods exhibited greater detection variability and greater differences in confidence intervals and coefficients of variance. Differences in seasonal behavior across sex and age classes can influence the reliability of sex and age ratios (Solberg et al., 2010). Additionally, we found winter ratios to be more consistent and precise than summer ratios, especially for bull:cow ratios. While all classes forage during summer, cows spend considerable energy protecting and feeding calves (Borowik et al., 2021; Ballard et al., 1981). Consequently, cows and calves have more restricted home ranges than bulls (Schwartz, 2007), which undoubtedly influences detection probability. We found an increase in unknown age- and sex-categorized moose detections starting mid-January and between mid-May–late June, which could have caused increased variability in ratio estimates. During these periods, most unknown classifications occurred even with the moose fully visible in sequences. The increase of unknown classifications coincided with male antler loss after early January and before well-developed antlers in August (Schwartz, 2007).

Survey Design

We found support that camera survey durations of 25 to 30 days would produce consistent and low variation in bull:cow and calf:cow ratios. Moose life history events such as breeding season and calving, are often relatively brief (i.e., 3–4 weeks) (Schwartz, 2007). Pairing the 25-day survey window with life history events and increases in detection rates can reduce variability observed in shorter survey periods (i.e., <20 days) and improve ability for across-year comparisons. While we used unbaited remote cameras to calculate survey duration, we predict ratios derived from baited cameras could produce consistent and less variable estimates sooner than 25 days. However baited cameras need additional maintenance, resulting in additional costs and personnel. Additionally, bait can generate sex and age bias, with greater adult male detections, producing different sex and age ratios than randomly placed cameras regardless of survey duration (Mccoy et al., 2011). The use of bait can also be prohibited in sampling locations, such as IRNP.

In addition to survey length, we found camera placement (i.e., on- and 50 m off-trail) and camera density influenced precision of moose detection rates, sex and age ratios, and density estimates. On and off-trail camera placement can result in differences in detectability for some species, with on-trail placements having often greater detections (Kolowski & Forrester, 2017; Cusack et al., 2015a). Generally, we found that on-trail camera placements had higher detection rates for all moose sex and age classes but only during calving, breeding, and winter foraging seasons. While off-trail camera detections slightly increased detections in calving, breeding and winter foraging seasons, overall detections were consistent each year. However, on- and off-trail camera placements demonstrated temporal variability in detection rates, sex and age ratios, and density. We did not compare off-trail cameras >50 m from trails with on-trail cameras or the effects of cameras on a spatially limited trail network. Our survey design limited our ability to sample within 50 m of trails though variability in detections could differ at distances further from trails. In another study, detection rates were similar for 9 of 12 species (e.g., white-tailed deer and black bear [*Ursus americanus*]) at 0, 25, and 200 m off trail, exclucing coyote (*Canis latrans*), bobcat (Lynx rufus), and chipmunk (*Tamias striatus*) that were detected more frequently on trails with increased human activity (Kays et al., 2016). Further assessments of these camera distributions would further inform potential effects on moose population estimates.

Summer calf:cow ratios and winter calf:cow and bull:cow ratios were similar in estimates and precision. Summer bull:cow ratios were highly variable but greater for off-trail, likely due to mobility differences between bulls and cows. In summer, cows are with calves and have more restricted movements and home ranges than bulls (Ballard et al., 1981). Additionally, unlike bulls, cows allocate considerable energy toward lactation and protecting their young instead of foraging (Bowyer et al., 2003; Ballard et al., 1981). Movement patterns and behavior differences between bulls and cows in summer can lead to overestimating bull:cow ratios due to more detections of bulls than cows (Gasaway et al., 1985). The main difference between on and off-trail estimates occurred when calculating density, as on-trail estimates were greater than off-trail estimates, including when compared to 2021–2022 estimates from aerial winter surveys (Sovie et al., 2024). If management goals are to increase detection probability and obtain age and sex ratios, on-trail-only placements can be effective; however, if using cameras to estimate density, using on and off-trail camera placements or using a refined area based on sampling in the models would likely generate more representative estimates.

We found that 5 and 4 cameras/km^2 produced consistent and similar values of sex and age ratios and density. If obtaining estimates of abundance is a management goal, consideration should be made regarding how abundance is calculated, as some methodology requires denser camera placement to meet assumptions. With 5 or 4 cameras/km^2, instantaneous sample modeling (Moeller & Lukacs, 2022) derived values produced similar estimates as 2021–2022 aerial surveys while attempting to meet the independence assumption. One benefit to using cameras, as demonstrated with our design, is that cameras can be deployed at the same sampling locations, generating a replicable design. However, many methods typically used to survey moose can be difficult to replicate to the same location, time of year, or in relation to moose life history.

Based on our results, we suggest that the timing of typical moose survey methods (e.g., aerial surveys, hunter observations, pellet surveys) has not been optimal in relation to moose life history (Rönnegård et al., 2008). For example, aerial, snow-track and pellet surveys often occur in winter and rely on adequate snow cover (Rönnegård et al., 2008; Samuel et al., 1987; Gasaway et al., 1986). Because of the moose behavior, weather requirements, and winter holidays, these surveys generally occur from late January-early March (Gasaway et al., 1986; Gasaway et al., 1985), which are when moose are least mobile. Hunter observations are less consistent measures and often occur during the moose breeding season, which could result in bias from differences in detections by moose age and sex (Moll et al., 2022; Rolandsen et al., 2003; Ericsson & Wallin, 1999). Additionally, many of these survey methods do not account for imperfect detection (i.e., sightability) (Gasaway et al., 1985). Using remote cameras can allow for better-timed surveys that correspond with moose life history rather than winter or opportunistic samples. Camera placement can be consistent across years, improving comparability for annual trends. Many camera-related analytical approaches to calculate population metrics such as density or occupancy have calibration for imperfect detection.

Placement of cameras within the field is also important to minimize obstruction and imperfection detection. Placement and orientation of cameras should ensure the greatest probability of detecting focal species. We placed our cameras 1.5 m off ground angled 45 degrees towards the ground, north facing, which allowed us to obtain sex and age class information on moose easily while minimizing false triggers that could fill SD cards and deplete battery life. The camera height minimized temporary obstruction from snow and fast-growing vegetation typical in our system. Additionally, maximizing camera detection distances and viewsheds can also minimize imperfect detection and help standardize differences between on and off trail cameras (Moeller et al., 2023). Small changes in a camera's viewshed area can generate error in density estimates that are extrapolated across areas much larger than the collective viewshed areas (Cusack et al., 2015b). Detailed information where moose are in relation to distance from cameras or each camera's area of detection can allow for non-individual derived density estimators, like the instantaneous sampling used in this study and other space to event (TTE and STE) models (Moeller & Lukacs, 2022). Lastly, cameras can be deployed with minimal maintenance while collecting sex and age moose information and other bycatch species detections.

Depending on research or management goals, remote cameras may provide the best "minimum tool" with respect to the minimum requirements obligation of the Wilderness Act (16 U.S.C. 1131). While cameras are a prohibited installation, they can be less noticeable and invasive to wildlife and recreationists compared to aircraft. Survey method selection requires careful evaluation of tradeoffs when considering protected area goals and objectives in the context of law, policy, and regulation. In the case of IRNP, surveying moose using remote cameras could offer an alternative methodology that better preserves wilderness character compared to traditional aerial surveys. Our results suggest cameras can produce similar species abundance and composition ratio estimates to aerial surveys while also being able to be deployed and retrieved during late fall and early spring, avoiding overlap with human visitation. Evaluating methodologies is important to provide options that best meet all management objectives.

Considering that IRNP goals include maximizing human wilderness experiences while maximizing precision of moose demographic estimates, we recommend: 1) deploying remote cameras during the winter, particularly from November–January and ensuring cameras are not placed during peak visitation, 2) using a 25-day survey period to calculate calf:cow and bull:cow ratios and using a 60-day survey period to calculate abundance during early December–early January, 3) the camera array should have an approximately equal ratio of on-and off-trails and ≥4 cameras/km^2 or have representative sampling. Combining life history and detection rate patterns can be used to optimize periods for estimating demographic parameters. Our approach to estimating moose density and sex and age ratios can serve as a framework for monitoring medium- to high-density moose populations and potentially other ungulate species considering life history events.

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APPENDIX

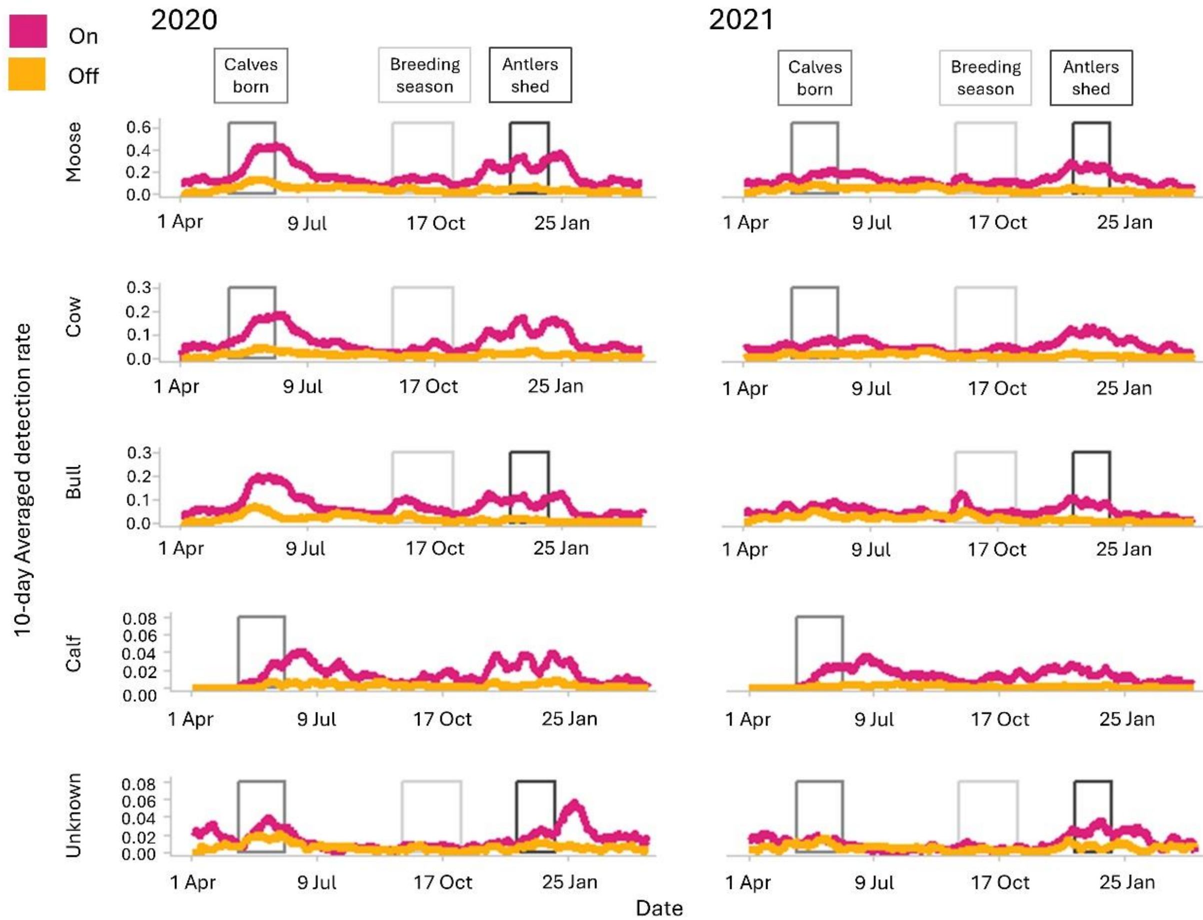

Figure A.4.1. Moose mean daily detection rates across 10-day moving windows using on- (pink; n = 98) and off-trail (orange; n = 58) cameras, Isle Royale National Park, Michigan, USA, 2020–2021. Moose detections included unknown age and sex. Moose neonates are born, breeding season, and antler shed occur approximately mid-May-early June, mid-September–late October, and late November–early January[15], respectively.

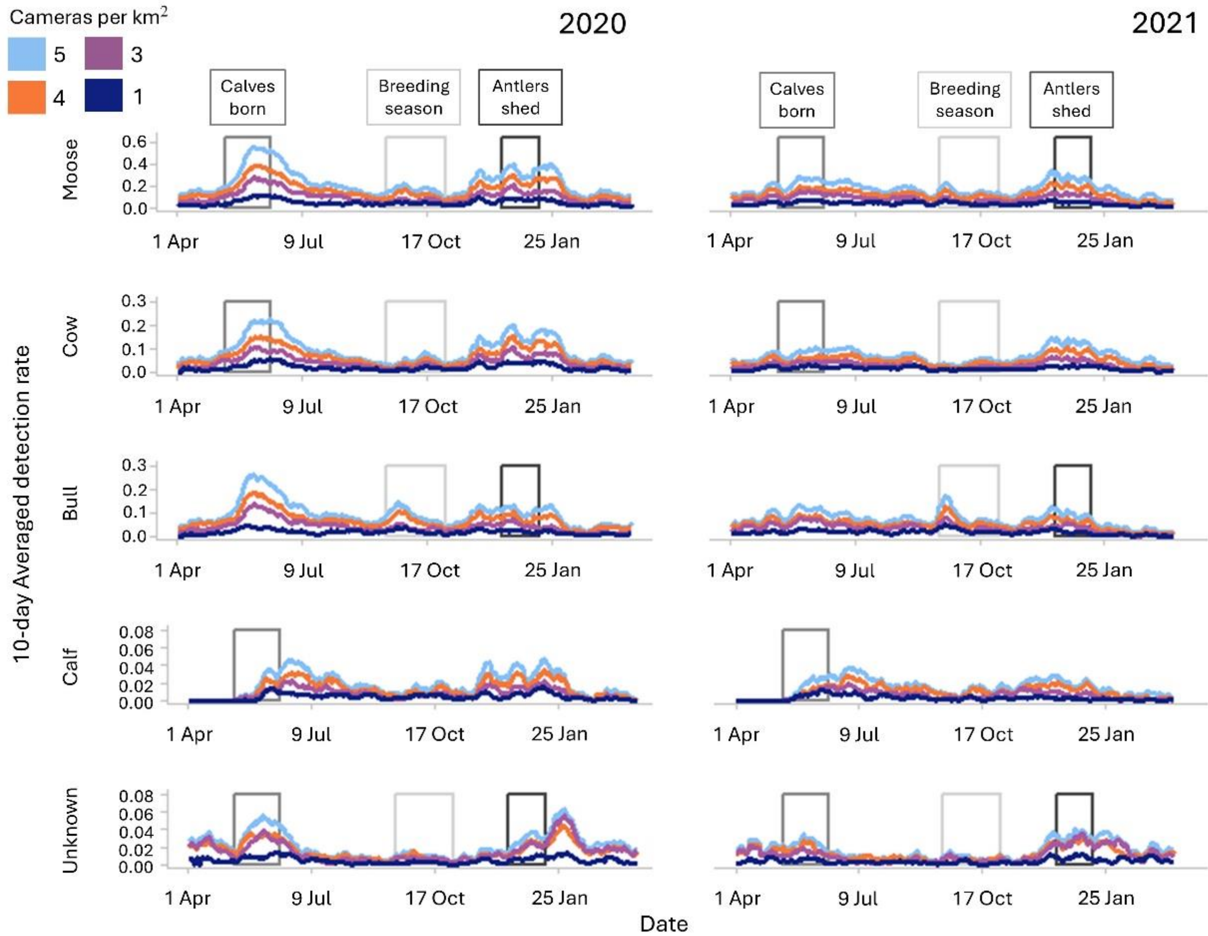

Figure A.4.2. Moose mean daily detection rates across 10-day moving windows using camera densities of 5 (100%), 4 (75%), 3 (50%), and 1 (25%)/km^2, Isle Royale National Park (544 km^2), Michigan, USA, 2020–2021. Moose detections included unknown age and sex. Moose neonates are born, breeding season, and loss of antlers occur approximately mid-May-early June, mid-September–late October, and late November–early January[15], respectively. Camera numbers have equal proportions of on- and off-trail cameras and were scaled to 100 km^2.

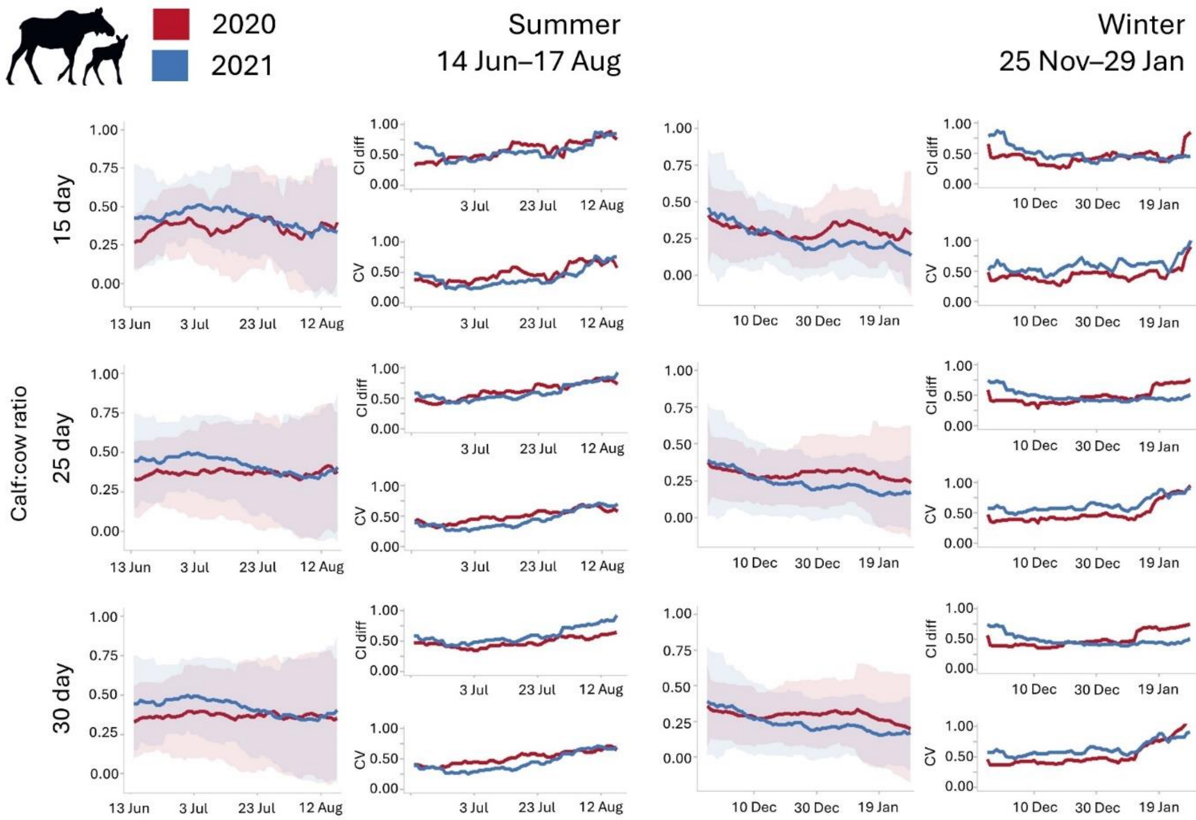

Figure A.4.3. Daily mean calf:cow ratios across 15-, 25-, and 30-day moving windows with 95% confidence intervals across all cameras in summer (14 June–17 August) and early winter (25 November–29 January), Isle Royale National Park, Michigan, USA, 2020 (red) and 2021 (blue). For each set of ratios, differences in 95% confidence intervals (CI diff – [upper CI – lower CI]) and coefficient of variation (CV) are plotted for 2020–2021; periods with low CI diff values and CV indicate higher precision.

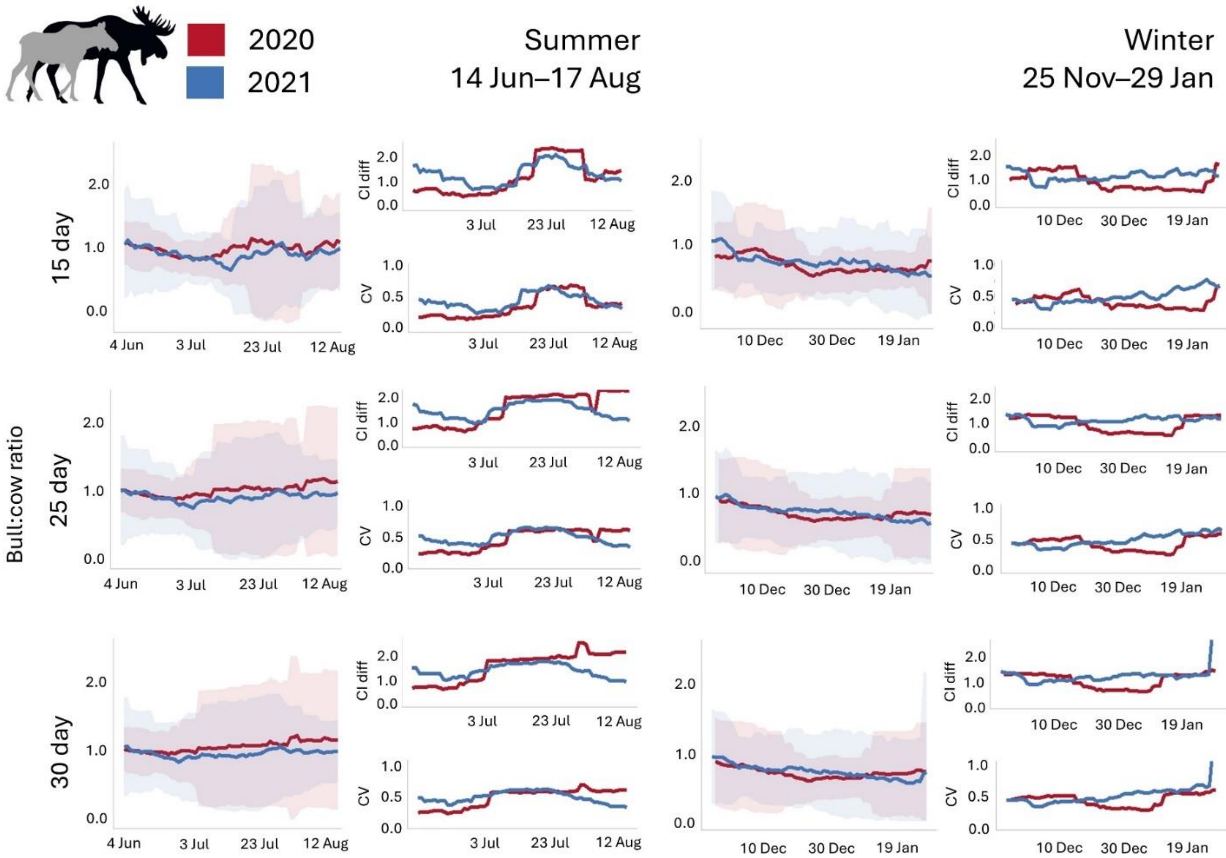

Figure A.4.4. Daily mean bull:cow ratios across 15-, 25-, and 30-day moving windows with 95% confidence intervals across all cameras in summer (14 June–17 August) and early winter (25 November–29 January), Isle Royale National Park, Michigan, USA, 2020 (red) and 2021 (blue). For each set of ratios, difference in 95% confidence intervals (CI diff – [upper CI – lower CI]) and coefficient of variation (CV) are plotted for 2020–2021; periods with low CI diff values and CV indicate higher precision.

Table A.4.1. Calf:cow ratios (number of calf detections/number of cow detections averaged across 25-day survey windows) with the lowest values in 95% confidence intervals differences (CI diff) and coefficient of variation (CV) across all cameras, on-trail, off-trail, and camera density subsets (5 [100%], 4 [75%], 3 [50%], and 1 [25%] cameras/ km^2) in summer (14 June–17 August) and early winter (25 November–29 January), Isle Royale National Park, Michigan, USA, 2020–2021.

Time of year	Subsample	Start date	Mean ratio	95% CI	CI diff	CV
Summer	All cameras (5 cameras/km^2)	21 June 2020	0.39	0.18–0.60	0.41	0.32
	All cameras (5cameras/km^2)	1 July 2021	0.50	0.28–0.72	0.44	0.26
	On-trail	20 June 2020	0.38	0.15–1.61	0.45	0.36
	On-trail	1 July 2021	0.57	0.34–0.80	0.46	0.24
	Off-trail	30 June 2021	0.19	0.00–0.63	0.89	1.43
	Off-trail	21 June 2021	0.25	0.00–0.60	0.82	1.32
	4 cameras/km^2	21 Jun 2020	0.40	0.14–0.66	0.53	0.40
	4cameras/km^2	25 Jun 2021	0.45	0.18–0.71	0.53	0.36
	3cameras/km^2	17 Jun 2020	0.32	0.00–0.67	0.68	0.64
	3cameras/km^2	30 Jun 2021	0.49	0.10–0.89	0.78	0.48
	1 cameras/km^2	14 Jun 2020	0.36	0.00–0.82	0.93	0.80
	1 cameras/km^2	19 Jun 2021	0.45	0.00–1.00	1.06	0.72
Winter	All cameras (5cameras/ km^2)	11 December 2020	0.26	0.11–0.42	0.30	0.35
	All cameras (5cameras/ km^2)	9 January 2022	0.23	0.03–0.43	0.40	0.53
	On-trail	11 December 2020	0.27	0.08–0.46	0.38	0.43
	On-trail	9 January 2022	0.25	0.02–0.47	0.45	0.55
	Off-trail	22 December 2020	0.37	0.00–0.84	0.94	0.78
	Off-trail	13 December 2021	0.18	0.00–0.66	0.96	1.65
	4 cameras/ km^2	5 December 2020	0.31	0.18–0.44	0.27	0.26
	4 cameras/ km^2	24 December 2021	0.24	0.03–0.44	0.41	0.53
	3 cameras/ km^2	11 December 2020	0.23	0.00–0.52	0.58	0.75
	3 cameras/ km^2	7 Jan 2022	0.18	0.00–0.41	0.46	0.79
	1 cameras/ km^2	8 Jan 2021	0.35	0.00–0.75	0.79	0.69
	1 cameras/ km^2	2 Jan 2022	0.12	0.00–0.45	0.66	1.73

Table A.4.2. Bull:cow ratios (number of bull detections/number of cow detections averaged across 25-day survey windows) with the lowest values in 95% confidence intervals differences (CI diff) and coefficient of variation (CV) across all cameras, on-trail, off-trail, and camera density subsets (5, 4, 3, and 1 cameras/km^2) in summer (14 June–17 August) and early winter (25 November–29 January), Isle Royale National Park, Michigan, USA, 2020 and 2021.

Time of year	Subsample	Start Date	Mean ratio	95% CI	CI diff	CV
Summer	All cameras (5 cameras/km^2)	19 June 2020	0.87	0.61–1.13	0.52	0.18
	All cameras (5 cameras/ km^2)	1 July 2021	0.81	0.39–1.23	0.84	0.32
	On-trail	19 June 2020	0.91	0.61–1.21	0.60	0.20
	On-trail	20 June 2020	0.76	0.37–1.14	0.77	0.31
	Off-trail	24 June 2021	0.95	0.10–1.79	1.69	0.54
	Off-trail	30 July 2021	1.17	0.14–2.20	2.06	5.40
	4 cameras/ km^2	11 Jun 2020	1.11	0.60–1.63	1.03	0.28
	4 cameras/ km^2	8 Jun 2021	1.10	0.26–1.93	1.67	0.46
	3 cameras/ km^2	11 Jun 2020	1.24	0.43–2.05	1.62	0.40
	3 cameras/ km^2	20 Jun 2021	0.87	0.11–1.63	1.52	0.53
	1 cameras/ km^2	7 Jun 2020	0.68	0.00–1.45	1.48	0.67
	1 cameras/ km^2	6 Aug 2021	1.00	0.02–1.98	1.96	0.59
Winter	All cameras (5 cameras/km^2)	11 January 2021	0.64	0.37–0.90	0.53	0.26
	All cameras (5 cameras/km^2)	11 December 2021	0.76	0.34–1.18	0.84	0.34
	On-trail	12 January 2021	0.64	0.36–0.92	0.56	0.26
	On-trail	4 December 2021	0.79	0.32–1.27	0.96	0.37
	Off-trail	2 January 2021	0.44	0.00–0.96	1.04	0.72
	Off-trail	11 December 2021	0.84	0.00–1.77	1.86	0.67
	4 cameras/km^2	10 Jan 2021	0.67	0.17–1.17	1.01	0.46
	4 cameras/km^2	30 December 2021	0.67	0.28–1.06	0.78	0.35
	3 cameras/km^2	17 December 2020	0.66	0.22–1.10	0.88	0.40
	3 cameras/km^2	29 November 2021	1.08	0.00–2.21	2.27	0.64
	1 cameras/km^2	8 January 2021	0	0.00–1.08	1.11	0.64
	1 cameras/km^2	24 January 2022	0.54	0.00–1.36	1.64	0.92

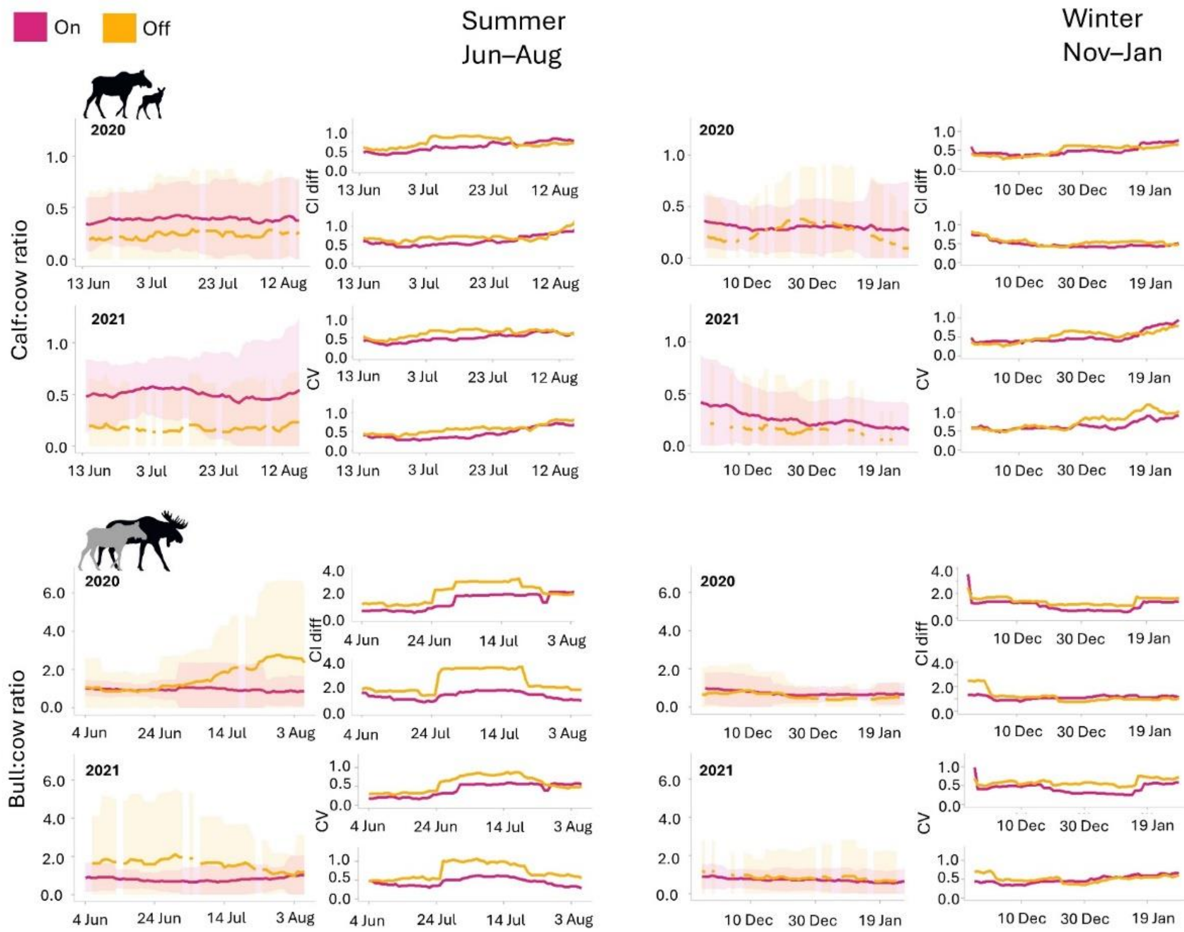

Figure A.4.5. On- and off-trail camera derived daily mean calf:cow and bull:cow ratios across 25-day moving windows (95% confidence intervals) in summer (14 June–17 August) and early winter (25 November–29 January), Isle Royale National Park, Michigan, USA, 2020–2021. For each set of ratios, differences in 95% confidence intervals (CI diff – [upper CI – lower CI]) and coefficient of variation (CV) are plotted for 2020–2021. Periods with low CI diff values and CV indicate higher precision. Missing days indicate no detections of relevant moose occurred on that start day.

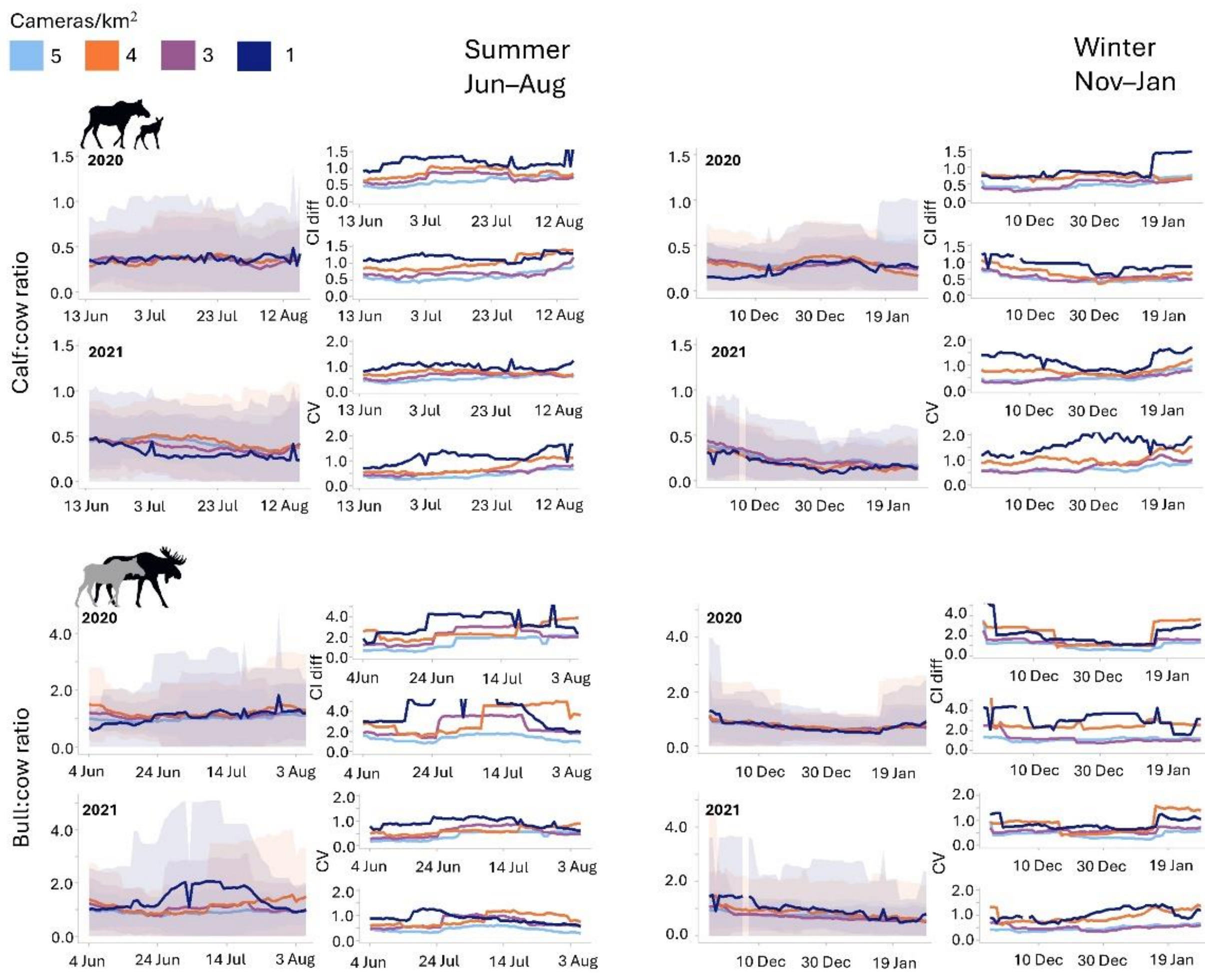

Figure A.4.6. Daily mean calf:cow and bull:cow ratios across 25-day moving windows (95% confidence intervals) using camera densities of 5 (100%), 4 (75%), 3 (50%), and 1 (25%) / km^2 in summer (14 June–17 August) and early winter (25 November–29 January), Isle Royale National Park (544 km^2), Michigan, USA, 2020–2021. For each set of ratios, differences in 95% confidence intervals (CI diff -– [upper CI – lower CI]) and coefficient of variation (CV) are plotted for 2020–2022; periods with low CI diff values and CV indicate higher precision. Camera numbers have equal proportions of on- and off-trail cameras and are scaled to 100 km^2.