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Moose Movement in an Urbanizing Landscape

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MOOSE MOVEMENT IN AN URBANIZING LANDSCAPE

by

Lucian R. McDonald

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

of

DOCTOR OF PHILOSOPHY

in

Wildlife Biology

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ABSTRACT

Moose Movement in an Urbanizing Landscape

by

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Utah State University, 2024

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Department: Wildland Resources

As urban development reshapes landscapes, wildlife, like moose (*Alces alces*), must navigate fragmented landscapes with changing predation and disturbance risks. The risk-disturbance hypothesis asserts that wildlife respond similarly to these risks, minimizing risk and maximizing forage availability. The risks vary in space-time, creating a dynamic landscape of fear that may impact subpopulations differently based on life-history. This research explores the impact of anthropogenic landscape change on moose behavior and the implications of these responses for moose-vehicle collision (MVC) mitigation. First, I review literature on adaptations to anthropogenic landscape change. In Chapters II–IV, I quantify selection based on these disturbances using integrated step selection analysis. In Chapter II, I compare moose selection to the gradient of human modification (gHM) to evaluate the risk-predation and risk-disturbance hypotheses. Moose behavior reflects predictions by both hypotheses, avoiding high disturbance and predation risk, a phenomenon I refer to as urban refugia. Further, resident and cow moose avoidance of both extremes leads them towards intermediate levels of gHM, which overlaps corridors of high MVC risk. In Chapter III, I compare cow moose selection to gHM to evaluate hypotheses based on life history differences between subgroups of cow moose based on age and calving behavior. Like the population response, cow-calf pairs avoided both extremes, while lone cows did not. This may explain why most MVCs involve young moose, as selection by cows may create an ecological trap for their calves. In Chapter IV, I compare winter road avoidance and road-crossing behavior to traffic levels to evaluate the risk-disturbance and predator-shield hypotheses. Moose avoided crossing and being near roads as traffic levels increased but may select to be near roads at night when traffic is not considered. Unlike other studies, vegetation did not impact road selection or road crossings and moose moved slower near roads than they would on average. In Chapter V, I conclude with a synthesis of results. This dissertation combines behavioral and spatial ecology concepts to further our understanding of how plasticity in animal behavior due to dynamically changing ecological pressures can be used to explain the distribution of wildlife in urban spaces.

(170 pages)

PUBLIC ABSTRACT

Moose Movement in an Urbanizing Landscape

Lucian R. McDonald

Humans disturb the environment in specific places and at specific times. As wildlife learn to navigate these disturbances, they react as they would to the risk of predation. Wildlife biologists can identify where and when these disturbances will lead wildlife to congregate by comparing geospatial data, such as metrics that represent vegetation, topography, or other environmental conditions, to known locations of the animal(s) in question. In Chapter I, I discuss the impact of human disturbances, like urbanization and roads, on wildlife behavior. In Chapter II, I compare the risk of moose-vehicle collisions (MVCs) to moose selection of urbanized landscapes to determine which demographics of moose are most likely to be found in targeted hunting areas. Moose captured near roads avoided both natural and urban landscapes, leading them towards intermediately disturbed areas where vehicle collisions with wildlife are common. Targeted hunting for moose along high MVC risk corridors may indeed reduce MVCs, but the effect may only be temporary. In Chapter III, I conduct a similar study to the previous chapter but focus on cow moose and their calving behavior to determine if both cows and calves benefit from the cow's movement away from natural and urban landscapes. Cows exhibiting calving behaviors were more likely to avoid both extremes than other cows, suggesting the high number of MVCs that involve young moose could be due to cow refuge-seeking. In Chapter IV, I compare moose road avoidance and road crossing behavior to traffic and account for the potential effects of time of day and vegetation on these behaviors. Moose rarely crossed roads and avoided being within 220 m of any road. Moose movement towards roads was more likely at night on average, but crossings were equally likely at all times of day. Vegetation didn’t impact moose movement in relation to roads, but moose did move slower near roads than on average. The final chapter summarizes the research findings and provides management and research recommendations. Findings from this research informs our understanding of the distribution of wildlife in urban spaces and the dynamically changing conditions that lead wildlife to take up residence near humans.

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CHAPTER I

INTRODUCTION & LITERATURE REVIEW

Urbanization and intensification of resource use cause spatiotemporally heterogeneous impacts on ecosystems, humans, and wildlife. About 43% of the Earth's surface has been transformed for agriculture or human residence, and the remaining areas are dissected by transportation networks (Barnosky et al. 2012). This anthropogenic change to the landscape already exceeds the physical changes induced following the last glacial-interglacial transition when 30% of Earth's ice-covered surface became ice-free (Barnosky et al. 2012). More than 75% of Earth's ice-free land shows evidence of anthropogenic alteration (Ellis and Ramankutty 2008). Nearly 1/3 of global forest cover has been deforested since the mid-1800s and 70% of the remaining forest is within a kilometer of the forest edge, subject to the edge effects of fragmentation (Haddad et al. 2015). Ever-increasing disturbance, degradation, and fragmentation of the landscape reduces ecosystem services essential for the maintenance of wild and urban spaces (Foley et al. 2005). As human activity and infrastructure continue to degrade, fragment, or replace habitat, the richness and diversity of species that can thrive along the continuum between natural and urban landscapes may be permanently altered (McKinney 2002, Gonzalez et al. 2016).

In response to this increase in anthropogenic activity, wildlife typically change their behavior. Many species respond with avoidance, the magnitude and duration of which reflects the life history of the impacted species. Songbirds (*Passeriformes spp.)* avoid the noise of human traffic even when a road does not exist (Ware et al. 2015). White-tailed deer (*Odocoileus virginianus*) occurrence has been negatively related to human recreation levels (George and Crooks 2006). Pronghorn (*Antilocapra americana*) avoid anthropogenic features, like fencing, at multiple spatial scales (Jones et al. 2019). Migrating mule deer (*O. hemionus*) altogether avoid or speed up their migration near oil and gas development sites (Lendrum et al. 2012, Lendrum et al. 2013). Mesopredators, like coyotes (*Canis latrans*) and bobcats (*Lynx rufus*), shift their space use to areas away from and at times without human activity (George and Crooks 2006). Globally, and across taxa, species have become more nocturnal to avoid human disturbance (Gaynor et al. 2018). Alternatively, anthropogenic resource subsidies, disturbance-related vegetation changes, or relaxed predation risk may cause wildlife populations to take up residence within urban landscapes and potentially forgo long-held migratory traditions (Brown and Hall 2018). These changes in behavior may have a cascading effect on species interactions, community structure, or ecosystem function. Identifying which behavioral changes have deleterious effects on wildlife is a pressing concern for wildlife managers (Wilson et al. 2020).

Anthropogenic climate change may further disrupt behavioral cycles and migratory pathways, forcing wildlife to adapt to local resource constraints. For example, in many areas, changes in climatic conditions and the predictability of seasonal resources threaten migratory behavior by homogenizing environmental conditions (Robinson et al. 2009, Martin et al. 2018). Changing snow conditions are known to impact moose migration and ultimately may cause the species distribution to shift (Singh et al. 2012). For example, warming temperatures and decreased snowpack along the boundary between moose (*Alces alces*) and white-tailed deer range favors the expansion of deer northwards (Weiskopf et al. 2019). Phenological changes, like shifts in the peak of green-up, may cause ecological mismatches that further degrade the benefits of migratory behavior (Mysterud et al. 2013, Middleton et al. 2018). Additionally, the politically manufactured uncertainty around climate change has seeped into wildlife conservation discourse in Canada, threatening caribou (*Rangifer tarandus*; Boan et al. 2018). Altogether, climate change exacerbates problems in wildlife management and conservation (Abrahms 2021).

The above problems are made even worse as the human population loses their connection to wild spaces and wildlife. The vast majority (>80%) of the global population lives in cities, and this is only expected to increase (Ellis and Ramankutty 2008). Increasing urbanization decreases the number of human-nature experiences for most of the population. This may negatively impact human health and wellness, and ultimately may result in disaffection toward nature (Soga and Gaston 2016, Cox and Gaston 2018).

At the wildland-urban interface and within urban refugia, increased human-wildlife interactions can affect the cultural perception of the species (Messmer 2000, Soulsbury and White 2015). If these interactions with nature and wildlife are not net-positive, it may become difficult to conserve the species (Nyhus 2016). In Argentina, 92% of surveyed farmers perceived scavenger birds as predators of newborn livestock, while actual depredation events were rare (Ballejo et al. 2020). In New York, exurban landowners without a history of positive wildlife interactions indicated less support for land and wildlife conservation (Kretser et al. 2009). In more urban areas, preferences for deer population levels were lower among drivers who perceived a higher risk of deer-vehicle collisions (DVCs; Stout et al. 1993, Marcoux and Riley 2010). As land use intensifies outward from urban centers, human and wildlife communities require active management to ensure coexistence (Messmer 2000).

INDIVIDUAL RESPONSES TO URBANIZATION

The outcome of a human-wildlife interaction depends both on the human's perception of the species and the animal's perception of humans (Messmer 2000, Messmer 2009, Nyhus 2016). Human perception is dependent on shared and individual experiences related to the species involved. When deciding how to interact with an animal, a human will weigh benefits and costs based on any given action's risk (Conover 1997). Under the risk-perception attitude framework (Rimal and Real 2003), people who understand the risk of danger and know how to effectively manage that danger are more likely to engage in self-protective behavior. Similarly, the animal perceives some amount of risk that determines whether the interaction with a human is dangerous enough to illicit anti-predator behavior. Based on the predation-risk allocation hypothesis (Lima and Bednekoff 1999), animals that perceive more risk are more likely to allocate time and energy to anti-predator behavior. This concept has been extended to include non-consumptive interactions that may illicit anti-predator behavior via the risk-disturbance hypothesis (Frid and Dill 2002). This hypothesis considers stimuli like noise and light pollution, human infrastructure, and human activity as disturbances that may be avoided by wildlife. Since human perception changes with species and different taxa react to predators in a variety of ways, the risk of taking up residence within an urban area will vary with species (Ditmer et al. 2021).

Despite the challenges brought on by urban expansion, some large predator species manage to benefit from urban features when human density is low. Predator species often avoid areas with humans due to a history of predator control, but where human development is low, predators may take advantage of habitat near, though concealed from, humans (Ordiz et al. 2011). Wolves (*C. lupus*) adaptively respond to increasing human activity levels by first increasing their use of an area at low levels of human activity, then decreasing their use at high levels of human activity (Hebblewhite and Merrill 2008). Some predators may use anthropogenic linear features, like roads, to facilitate movement and increase hunting efficiency where human activity is low (Dickie et al. 2020). While most predators avoid high levels of human presence and activity temporally, smaller predators may spatially select for more developed areas (Nickel et al. 2020, Ditmer et al. 2021).

Alternatively, generalist species at lower trophic levels, like herbivores and mesopredators, may thrive closer to human settlements (Bridge and Harris 2020, Brooks et al. 2020). Prey species are driven to minimize spatial overlap between themselves and their predators, making urban refugia out of human-disturbed habitat most large predators avoid (Muhly et al. 2011). Urban green spaces and anthropogenic resource subsidies can provide forage opportunities to generalists (Gallo et al. 2017, Brown and Hall 2018). In the short-term, this lack of predators and wealth of forage can cause populations to thrive (Hansen et al. 2007), but eventually, something will limit the population – either resources or humans. For example, urban white-tailed deer thrive near human settlements in the eastern US (Curtis 2020). Eventually, they become habituated to human disturbances or reach densities that push them too close to highly trafficked roadways, threatening human safety and thus eliciting lethal management (Messmer et al. 1997, Sullivan and Messmer 2003).

Benefits and costs within species may also change due to individual differences. Hunted male game species may avoid non-protected areas with good forage that non-hunted females will use (Kucera 1992). Individual differences in risk-taking behavior can also inhibit wildlife from residing in urban spaces (Found and St. Clair 2019). Bolder, more exploratory individuals may find their way into urban spaces faster, and due to the same trait, may be more likely to interact with humans (Honda et al. 2018). Managers require a better understanding of a species' life history and behavioral trade-offs to understand why some individuals of the same species choose to live within urban areas and others do not and how those that do might be impacted by or impact humans.

URBAN REFUGIA

Without human interference, most ungulate population growth is constrained by the top-down impact of predation and the bottom-up limitation of forage conditions (Fryxell and Sinclair 1988). Furthermore, their space use is constrained to areas where foraging can occur in relative safety from predation (Fryxell and Sinclair 1988). Animals most wary of predators, especially those with young, may adopt a migratory strategy that seasonally limits their time in an area (Ouellet et al. 1996, White et al. 2014). Migration can also develop as a response to temporally or spatially changing forage conditions (Avgar et al. 2014, Borowik et al. 2020) or as a response to interspecific competition (Sawyer et al. 2016, Barker et al. 2019). Differences in resident and migrant behavior may be based on the scale at which each individual selects for forage and avoids predation. For example, resident bighorn sheep (*Ovis canadensis*) coarsely selected for predator avoidance and finely selected for forage, while migrant bighorn sheep did the opposite (Spitz et al. 2020). Ultimately, the changes associated with urban expansion tamper with the trade-offs influencing ungulate behaviors and population dynamics.

In developing areas of Alaska, moose face changes to their behavioral trade-offs and population constraints. Harvest of moose is often paired with harvest of predators to maintain populations of both groups on the landscape, while maximizing moose available for human harvest (Regelin et al. 2005). Humans harvest older individuals than wolves and bears, but both humans and predators impact the moose population’s growth (Boertje et al. 2020). Predators have largely been removed from areas near human settlements in Alaska (Regelin et al. 2005, Boertje et al. 2010). Additionally, hunting is mostly focused on males unless managers specifically allow calf or antlerless moose permits, which may be needed to meet stakeholder’s population objectives (Fulton and Hundertmark 2004, Young and Boertje 2004, Young et al. 2006). These spatiotemporal differences in harvest and predation place different pressures on moose in different sex and age classes.

Alongside this, forage conditions may be increasingly unpredictable spatiotemporally. Through winter, the survival of moose is largely regulated by previous summer food intake (Shively et al. 2019). Changing seasonality has influenced snow-depths, which normally impede the movement and forage of moose during winter, leading them to lower elevations, where most human development also occurs (Ballard et al. 1991). Agricultural expansion, suburban gardens, and disturbance-related growth have led to an abundance of forage near boreal human settlements, even in winter (Maier et al. 2005, Brown et al. 2018). Potentially year-round forage near urban areas paired with unpredictable conditions in natural areas may lead moose, especially female moose attempting to avoid calf predation, toward urban refugia during winter and encourage them to stay year-round.

Ultimately the management of urban moose will depend upon the traits of the individuals that choose to reside year-round within urban spaces. Individuals that do not perceive humans as a threat can be detrimental to human-wildlife coexistence. Human-sensitized and risk-averse individuals are likely to avoid human-dominated landscapes and avoid interaction with humans (Lowry et al. 2013, Honda et al. 2019). Bold individuals are more likely to take up residence near human settlements and may cause more negative interactions due to their eventual habituation to human activity (Honda et al. 2018, Found and St. Clair 2019). If the collective interactions or perceptions between a species and humans become net negative, local communities may become less tolerant of the species and cultural carrying capacity may lower (Ellingwood and Spignesi 1986, Zinn et al. 2008).

Female moose and their calves are more likely to benefit from urban refugia than males or nonmaternal females. Female moose with calves exhibit more anti-predator behavior than moose without calves (Ouellet et al. 1996, White et al. 2014, Droghini et al. 2024). Increased anti-predator behavior with versus without young is also documented among other ungulates, such as mountain sheep (*O. canadensis*; Bleich 1999) and Japanese serow (*Capricornis crispus*; Takada et al. 2019). Unlike their male conspecifics, females may have no reason to avoid humans within urban refugia. If urban areas become successful areas to birth and raise calves, selection pressure or learned behavior may further encourage the use of urban areas for sex and age classes of moose that do not face harvest pressure or otherwise have a reason to see humans as a threat.

Calf development within an urban context may be detrimental to their long-term survival. The longer and earlier an animal is subjected to human disturbance, the more easily the animal is habituated (Bejder et al. 2009, Geffroy et al. 2015). Urban-raised individuals may be more likely to become problem individuals in need of removal due to decreased wariness of humans and subsequently increased human-wildlife interactions (Honda et al. 2018). Furthermore, animals raised without the threat of predation may be less prepared for life outside the urban boundary, either leading them to reside forever near humans or be easily depredated once they leave; bolder individuals often have a higher risk of mortality due to their exploratory behavior (Sih et al. 2012). If females specifically raise calves in urban areas with the intention of increasing their survival, they may be falling into an ecological trap due to the long-term fitness consequences of their risk-prone calves' lowered ability to react to predators once they disperse into more natural areas. If females are simply prioritizing their own survival, seeking human shielding or forage in urban areas, the long-term consequences for their calves may not impact the female's behavior. Altogether, an animal's misplaced perception of safety within urban areas may spell disaster for moose in rapidly growing areas of Alaska.

MITIGATING HUMAN-MOOSE CONFLICTS

DVCs have become a common threat wherever deer and humans overlap spatially (Conover et al. 1995, Romin and Bissonette 1996, Sullivan and Messmer 2004). A complex social-ecological system has developed around the issue of DVC management as the public has become more concerned with this threat to their property and safety (Sullivan and Messmer 2004). Cultural carrying capacities among stakeholder groups will differ depending on their beliefs and attitudes towards the deer species of interest

(Zinn et al. 2000). Commuters may demand decreased population levels, while groups that harvest deer call for the opposite. Some stakeholders may find lethal management unacceptable, while others may volunteer to harvest urban deer (Messmer et al. 1997). Managers even differ in their preferred solution. While wildlife managers focus on ways to maximize wildlife resources and habitat, transportation engineers focus on efficiency and safety, creating competing ideas for how to reduce DVCs (Sullivan and Messmer 2004). Cervids living near urban areas trade the potential increase in forage and decrease in predation risk with disturbance and potential negative human interactions, such as a DVC. Meanwhile, motorists have little to no control over the density and placement of roads they travel, or the times at which they need to use them. However, their potential involvement in a DVC is relatively predictable spatially and temporally (Niemi et al. 2017, McDonald et al. 2019). This is due to the occurrence of 'hotspots' where deer densities and traffic densities are high (Sullivan et al. 2004).

Using the risk-perception framework (Rimal and Real 2003), we can expect hazardous events, such as DVCs, to elicit self-protective behavior from motorists only if the events are common and the behavior is efficacious. When DVC issues are just beginning, motorists may not be able to recognize the patterns of DVC hotspots, especially when the events are rare for any given motorist. As DVCs become more common, individuals may initiate their own self-protective behaviors, but educating motorists on the most effective ways to avoid a DVC can help them be more proactive when driving (Sullivan et al. 2004). Ultimately, deer and humans become habituated without constant feedback, so encouraging deer to avoid roads may be more effective than educating motorists depending upon the extent of the local DVC problem.

As more moose and humans co-locate, the threats to the moose population are far-ranging, but the threats to the human population are extremely specific (McDonald et al. 2019). McDonald et al. (2012) surveyed residents of Prince George, British Columbia to determine public perceptions of potential conflicts with moose and compared those perceptions with available local data. Their respondents tended to underestimate both the presence of moose and moose-human conflicts, and outdoor enthusiasts were no more knowledgeable about the management of moose-human conflicts than other respondents.

The Matanuska-Susitna Borough has been cited as 'the fastest growing [area] in the state of Alaska' with an average human population growth of 3.4% per year since 1991 (Hunsinger et al. 2012, Sandberg 2016). The frequency and severity of moose-vehicle collisions (MVCs) in this borough is a major concern with such a large-bodied ungulate living at high densities in such a rapidly growing area (Niemi et al. 2017). The borough estimates 34% of the roughly 100,000 residents commute to Anchorage for work. Collisions here are clustered in time, with the majority occurring during rush hours in winter (McDonald et al. 2019). However, per our understanding of risk-perception, the ability of the public to initiate self-protective driving behaviors is likely low due to the rarity of occurrences per capita (Rimal and Real 2003). Additionally, visibility, which is already hindered by the short period of daylight during winter days and lack of artificial lighting, is likely low due to harsh Alaskan winter conditions and low year-round due to high speeds (McDonald et al. 2019). Nevertheless, a strategy for helping the local community avoid collisions is warranted alongside management of the moose population. McDonald et al. (2012) suggested that broader public education and awareness programs that were designed to mitigate MVC risks would be needed to reduce conflicts related to increased urbanization.

DISSERTATION FORMAT

The goal of this dissertation is to combine behavioral and spatial ecology concepts to better understand what drives moose and other wildlife to live near humans given the various costs and benefits faced by urban wildlife. The diagram in Figure 1-1 represents the major differences between each chapter, and the additional diagrams, Figures 1-2, 1-3, and 1-4, expand these differences to explain the models and identify the subgroupings and variables used to assess the hypotheses in each chapter. These diagrams are based on the general conceptual framework for movement ecology (Nathan et al. 2008). In Chapter II, I focus on the costs and benefits that lead different moose demographic and migration strategy groups to select or avoid urban spaces (Figure 1-2). Understanding what costs and benefits could lead moose to stay near urban spaces will be beneficial in mitigating moose-human conflicts, but also provides further insight into the plasticity of animal behavior in a rapidly changing landscape. In Chapter III, I focus on the costs and benefits that may lead female moose to live near urban spaces to understand whether potential long-term consequences of refuge seeking behavior, such as the likelihood of losing a calf to an MVC, influences female moose behavior (Figure 1-3). If female moose are unresponsive to such long-term threats to reproductive output, population gains from increased predator safety in urban areas may eventually be outpaced by losses from MVCs as the number of MVCs continues to increase over time. Understanding adaptation and maladaptation to anthropogenically altered landscapes will help us better manage wildlife, but also provides insight into how animal behavior changes over time to reflect the costs and benefits of the current conditions of the landscape. The first two chapters focus on general human disturbances and their impact on coarse scale selection, while in Chapter IV, I focus on moose movement in relation to roads to better understand how moose respond to direct impacts of human development (Figure 1-4). Roads have various impacts explained throughout this review, so understanding which impacts influence moose in this system will benefit mitigation of human-moose conflicts while also validating previously assumed hypotheses about animal behavior in relation to predation risk and other disturbances.

One management strategy used by the Alaska Department of Fish and Game to better manage MVCs in Alaska is targeted antlerless moose hunting (Young and Boertje 2011). Because these permits are only scheduled in winter when migrant and resident moose are both overwintering in urban areas, it is important for managers to know whether the resident moose can be spatially differentiated from migrant individuals. Removal of migrant moose may be less useful, as these moose should be more wary of human disturbance than habituated resident moose. In Chapter II, I quantify moose summer and winter selection in relation to anthropogenic landscape change to determine how moose with varying migration behavior and demographic characteristics navigate urbanizing landscapes. By understanding the drivers behind urban selection by moose, we may be able to discourage the behavior and reduce the number of adverse human-wildlife interactions that occur in the area.

Among reported MVCs, most impacted moose are in younger age classes (calves and yearlings). As neonate survival is likely a driver of residency within predator-free urban refugia, in Chapter III, I will discuss the potential for moose-vehicle collision mortalities to convert urban refuges for cows into ecological traps for calves by quantifying selection in relation to anthropogenic landscape change for subgroups of cow moose with different life-history constraints. Identifying factors contributing to the majority of MVCs will be useful for managers considering mitigation options.

Similarly, it is important to understand how moose perceive the road system specifically. Based on the risk-disturbance hypothesis, moose should respond to the human disturbance of traffic as they and other ungulates would typically respond to predation risk, by fleeing (Frid and Dill 2002, Jacobson et al. 2016). However, based on the predator-shield hypothesis, if predators avoid traffic, moose may select to be near these disturbances (Berger 2007). In Chapter IV, I quantify moose winter selection based on road proximity and road-crossing behavior to determine how moose navigate around roads. Understanding how moose perceive and react to the road system will be crucial for modeling landscape use and informing the public of how to avoid MVCs.

REFERENCES

Abrahms, B. 2021. Human-wildlife conflict under climate change. Science. 373:484–485.

Avgar, T., G. Street, and J. M. Fryxell. 2014. On the adaptive benefits of mammal migration. Canadian Journal of Zoology 92:481–490.

Ballard, W. B., J. S. Whitman, and D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildlife Monographs 114:3–49.

Ballejo, F., P. I. Plaza, and S. A. Lambertucci. 2020. The conflict between scavenging birds and farmers: field observations do not support people's perceptions. Biological Conservation 248:108627.

Barber-Meyer, S. M., and L. D. Mech. 2008. Factors influencing predation on juvenile ungulates and natural selection implications. Wildlife Biology in Practice 4:8–29.

Barker, K. J., M. S. Mitchell, K. M. Proffitt, and J. D. DeVoe. 2019. Land management alters traditional nutritional benefits of migration for elk. Journal of Wildlife Management 83:167–174.

Barnosky, A. D., E. A. Hadley, J. Bascompte, E. L. Berlow, J. H. Brown, M. Fortelius, W. M. Getz, J. Harte, A. Hastings, P. A. Marquet et al. 2012. Approaching a state shift in Earth's biosphere. Nature 486:52–58.

Bartlam-Brooks, H. L. A., M. C. Bonyongo, and S. Harris. 2011. Will reconnecting ecosystems allow long-distance mammal migrations to resume? A case study of a zebra *Equus burchelli* migration in Botswana. Oryx 45:210–216.

Bejder, L., A. Samuels, H. Whitehead, H. Finn, and S. Allen. 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Marine Ecology Progress Series 395:177–185.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.

Bleich, V. C. 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. Journal of Mammalogy 80:283–289.

Boan, J. J., J. R. Malcolm, M. D. Vanier, D. L. Euler, and F. M. Moola. 2018. From climate to caribou: how manufactured uncertainty is affecting wildlife management. Wildlife Society Bulletin 42:366–381.

Boertje, R. D., M. A. Keech, and T. F. Paragi. 2010. Science and values influencing predator control for Alaska moose management. Journal of Wildlife Management 74:917–928.

Boertje, R. D., G. G. Frye, and D. D. Young. 2020. Lifetime sex-specific moose mortality during an intentional population reduction. Journal of Wildlife Management 84:6–19.

Borowik, T., M. Ratkiewicz, W. Maslanko, N. Duda, and R. Kowalczyk. 2020. The level of habitat patchiness influences movement strategy of moose in eastern Poland. PLoS ONE 15:e0230521.

Bridge, B., and S. Harris. 2020. Do urban red foxes attack people? An exploratory study and review of incidents in Britain. Human–Wildlife Interactions 14:151–165.

Brooks, J., R. Kays, and B. Hare. 2020. Coyotes living near cities are bolder: implications for dog evolution and human-wildlife conflict. Behaviour 157: 289–313.

Brown, C. L., K. Kielland, E. S. Euskirchen, T. J. Brinkman, R. W. Ruess, and K. A. Kellie. 2018. Fire-mediated patterns of habitat use by male moose (*Alces alces*) in Alaska. Canadian Journal of Zoology 96:183–192.

Brown, L. M., and R. J. Hall. 2018. Consequences of resource supplementation for disease risk in a partially migratory population. Philosophical Transactions of the Royal Society B: Biological Sciences 373:20170095.

Conover, M. R. 1997. Wildlife management by metropolitan residents in the United States: practices, perceptions, costs, and values. Wildlife Society Bulletin 25:

306–311.

Cox, D. T. C., and K. J. Gaston. 2018. Human–nature interactions and the consequences and drivers of provisioning wildlife. Philosophical Transactions of the Royal Society B 373:20170092.

Curtis, P. D. 2020. After decades of suburban deer research and management in the eastern United States: where do we go from here? Human–Wildlife Interactions 14:111–128.

Dickie, M., S. R. McNay, G. D. Sutherland, M. Cody, and T. Avgar. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. Journal of Animal Ecology 89:623–634.

Ditmer, M. A., D. C. Stoner, C. D. Francis, J. R. Barber, J. D. Forester, D. M. Choate, K. E. Ironside, K. M. Longshore, K. R. Hersey, R. T. Larsen, et al. 2021. Artificial nightlight alters the predator–prey dynamics of an apex carnivore. Ecography 44:149–161.

Droghini, A., T. W. Nawrocki, J. B. Stetz, P. A. Schuette, A. R. Aderman, and K. E. Colson. 2024. Variation among individual female moose in habitat selection suggests different responses to risk-forage trade-offs. Ecosphere. In Press.

Ellingwood, M. R., and J. V. Spignesi. 1986. Management of an urban deer herd and the concept of cultural carrying capacity. Transactions of the Northeast Deer Technical Committee 22:42–45.

Ellis, E.C. and N. Ramankutty. 2008. Putting people in the map: anthropogenic biomes of the world. Frontiers in Ecology and the Environment 6:439–447.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S.

Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, et al. 2005. Global consequences of land use. Science 309:570–574.

Found, R., and C. C. St. Clair. 2019. Influences of personality on ungulate migration and management. Frontiers in Ecology and Evolution 7:438.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Ecology and Society 6:11.

Fryxell, J. M., and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution 3:237–241.

Fulton, D. C., and K. Hundertmark. 2004. Assessing the effects of a selective harvest system on moose hunters' behaviors, beliefs, and satisfaction. Human Dimensions of Wildlife 9:1–16.

Gallo, T., M. Fidino, E. W. Lehrer, and S. B. Magle. 2017. Mammal diversity and metacommunity dynamics in urban green spaces: implications for urban wildlife conservation. Ecological Applications 27:2330–2341.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science 360:1232–1235.

Geffroy, B., D. S. M. Samia, E. Bessa, and D. T. Blumstein. 2015. How nature-based tourism might increase prey vulnerability to predators. Trends in Ecology and Evolution 30:755–765.

George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. Biological Conservation 133:107–117.

Gonzalez, A., B. J. Cardinale, G. R. Allington, J. Byrnes, K. A. Endsley, D. G. Brown,

D. U. Hooper, F. Isbell, M. I. O'Connor, and M. Loreau. 2016. Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. Ecology 97:1949–1960.

Haddad, N.M., L.A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:1500052.

Hansen, B. B., S. Henriksen, R. Aanes, and B. E. Sæther. 2007. Ungulate impact on vegetation in a two-level trophic system. Polar Biology 30:549–558.

Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45:834–844.

Honda, T, H. Iijima, J. Tsuboi, and K. Uchida. 2018. A review of urban wildlife management from the animal personality perspective: the case of urban deer. Science of the Total Environment 644:576–582.

Honda, T., N. Yamabata, H. Iijima, and K. Uchida. 2019. Sensitization to human decreases human–wildlife conflict: empirical and simulation study. European Journal of Wildlife Research 65:71.

Hunsinger, B. E., D. Howell, and E. Sandberg. 2012. Alaska's highly migratory population: annual moves to, from, and across the state. Alaska Economic Trends 32:4–13.

Jacobson, S. L., L. L. Bliss-Ketchum, C. E. de Rivera, and W. P. Smith. 2016. A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. Ecosphere 7:e01345.

Jones, P. F., A. F. Jakes, A. C. Telander, H. Sawyer, B. H. Martin, and M. Hebblewhite. 2019. Fences reduce habitat for a partially migratory ungulate in the northern sagebrush steppe. Ecosphere 10:e02782.

Kretser, H. E., P. D. Curtis, J. D. Francis, R. J. Pendall, and B. A. Knuth. 2009. Factors affecting perceptions of human-wildlife interactions in residential areas of northern New York and implications for conservation. Human Dimensions of Wildlife 14:102–118.

Kucera, T. E. 1992. Influences of sex and weather on migration of mule deer in Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52:122–130.

Lendrum, P. E., C. R. Anderson, R. A. Long, J. G. Kie, and A. R. T. Bowyer. 2012. Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. Ecosphere 3:1–19.

Lendrum, P. E., Anderson Jr, C. R., Monteith, K. L., Jenks, J. A., and Bowyer, R. T. 2013. Migrating mule deer: effects of anthropogenically altered landscapes. PLoS One 8:e64548.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist 153:649–659.

Lowry, H., A. Lill, and B. B. M. Wong. 2013. Behavioural responses of wildlife to urban environments. Biological Reviews 88:537–549.

Maier, J. A. K., J. M. V. Hoef, A. D. McGuire, R. T. Bowyer, L. Saperstein, and H. A. Maier. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. Canadian Journal of Forest Research 35: 2233–2243.

Martin, J., V. Tolon, N. Morellet, H. Santin-Janin, A. Licoppe, C. Fischer, J. Bombois, P. Patthey, E. Pesenti, D. Chenesseau, et al. 2018. Common drivers of seasonal movements on the migration - residency behavior continuum in a large herbivore. Scientific Reports 8:7631.

Marcoux, A., and S. J. Riley. 2010. Driver knowledge, beliefs, and attitudes about deer–vehicle collisions in southern Michigan. Human–Wildlife Interactions 4:47–55.

McDonald, A. M., V. Rea, and G. Hesse. 2012. Perceptions of moose-human conflicts in an urban environment. Alces 48:123–130.

McDonald, L. R., T. A. Messmer, and M. R. Guttery. 2019. Temporal variation of moose-vehicle collisions in Alaska. Human–Wildlife Interactions 13:8.

McKinney, M.L. 2002. Urbanization, biodiversity, and conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. Bioscience 52:883–890.

Messmer, T. A., Cornicelli, L., Decker, D. J., and Hewitt, D. G. 1997. Stakeholder acceptance of urban deer management techniques. Wildlife Society Bulletin 25:360–366.

Messmer, T.A. 2000. The emergence of human–wildlife conflict management: turning challenges into opportunities. International Biodeterioration and Biodegradation 45:97–102.

Messmer, T.A. 2009. Human–wildlife conflicts: emerging challenges and opportunities. Human–Wildlife Conflicts 3:10–17.

Middleton, A. D., J. A. Merkle, D. E. McWhirter, J. G. Cook, R. C. Cook, P. J. White, and M. J. Kauffman. 2018. Green-wave surfing increases fat gain in a migratory ungulate. Oikos 127:1060–1068.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani. 2011. Human activity helps prey win the predator-prey space race. PLoS One 6: e17050.

Mysterud, A. 2013. Ungulate migration, plant phenology, and large carnivores: the times they are a-changin'. Ecology 94:1257–1261.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, D. and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences 105:19052–19059.

Nickel, B. A., J. P. Suraci, M. L. Allen, and C. C. Wilmers. 2020. Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. Biological Conservation 241:108383.

Niemi, M., C. M. Rolandsen, W. Neumann, T. Kukko, R. Tiilikainen, J. Pusenius, E. J. Solberg, and G. Ericsson. 2017. Temporal patterns of moose-vehicle collisions with and without personal injuries. Accident Analysis and Prevention 98:167–173.

Nyhus, P. J. 2016. Human–wildlife conflict and coexistence. Annual Review of Environment and Resources 41:143–171.

Ordiz, A., O. G. Støen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia 166:59–67.

Ouellet, J.-P., J. Ferron, and L. Sirois. 1996. Space and habitat use by the threatened Gaspe caribou in southeastern Quebec. Canadian Journal of Zoology 74:1922–1933.

Regelin, W. L., V. P, and R. D. Boertje. 2005. Management of large predators in Alaska. Wildlife Biology in Practice 1:77–85.

Rimal, R. N., and K. Real. 2003. Perceived risk and efficacy beliefs as motivators of change use of the risk perception attitude (RPA) framework to understand health behaviors. Human Communication Research 29:370–399.

Robinson, R. A., H. Q. P. Crick, J. A. Learmonth, I. M. D. Maclean, C. D. Thomas, F. Bairlein, M. C. Forchhammer, C. M. Francis, J. A. Gill, B. J. Godley, et al. 2009. Travelling through a warming world: climate change and migratory species. Endangered Species Research 7:87–99.

Romin, L. A., and J. A. Bissonette. 1996. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. Wildlife Society Bulletin 24:276–283.

Sandberg, E. 2016. Settlement of the Mat-Su: how Alaska’s fastest growing borough came to be. Alaska Department of Labor and Workforce Development, Alaska Economic Trends 36:12–17.

Sawyer, H., A. D. Middleton, M. M. Hayes, M. J. Kauffman, and K. L. Monteith. 2016. The extra mile: ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk. Ecosphere 7:e01534.

Severud, W. J., T. R. Obermoller, G. D. Delgiudice, and J. R. Fieberg. 2019. Survival and cause-specific mortality of moose calves in northeastern Minnesota. Journal of Wildlife Management 83:1131–1142.

Shively, R. D., J. A. Crouse, D. P. Thompson, and P. S. Barboza. 2019. Is summer food intake a limiting factor for boreal browsers? Diet, temperature, and reproduction as drivers of consumption in female moose. PLoS One 14:e0223617.

Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioural syndromes. Ecology Letters 15:278–289.

Singh, N. J., L. Borger, B. Borger, H. Dettki, N. Bunnefeld, G. Go, and G. Ericsson. 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. Ecological Applications 22:2007–2020.

Soga, M., and K. J. Gaston. 2016. Extinction of experience: the loss of human–nature interactions. Frontiers in Ecology and the Environment 14:94–101.

Soulsbury, C. D., and P. C. L. White. 2015. Human–wildlife interactions in urban areas: a review of conflicts, benefits, and opportunities. Wildlife Research 42:541–553.

Spitz, D. B., M. Hebblewhite, and T. R. Stephenson. 2020. Habitat predicts local prevalence of migratory behaviour in an alpine ungulate. Journal of Animal Ecology 89:1032–1044.

Stout, R. J., R. C. Stedman, D. J. Decker, and B. A. Knuth. 1993. Perceptions of risk from deer-related vehicle accidents: implications for public preferences for deer herd size. Wildlife Society Bulletin 21:237–249.

Sullivan, T. L., and T. A. Messmer. 2003. Perceptions of deer-vehicle collision management by state wildlife agency and department of transportation administrators. Wildlife Society Bulletin 31:163–173.

Sullivan, T. L., A.F. Williams, T.A. Messmer, L.A. Hellinga, and S.Y. Kyrychenko 2004. Effectiveness of temporary warning signs in reducing deer-vehicle collisions during mule deer migrations. Wildlife Society Bulletin 32:907–915.

Takada, H., Nakamura, K., and Minami, M. 2019. Effects of the physical and social environment on flight response and habitat use in a solitary ungulate, the Japanese serow (*Capricornis crispus*). Behavioural Processes 158:228–233.

Ware, H. E., C. J. W. McClure, J. D. Carlisle, J. R. Barber, and G. C. Daily. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. Proceedings of the National Academy of Sciences of the United States of America 112:12105–12109.

Weiskopf, S. R., O. E. Ledee, and L. M. Thompson. 2019. Climate change effects on deer and moose in the Midwest. The Journal of Wildlife Management 83:769–781.

White, K. S., N. L. Barten, S. Crouse, and J. Crouse. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology 95:225–237.

Wilson, D. S., A. B. Clarke, K. Coleman, and T. Dearstyne. 1994. Shyness and boldness in humans and other animals. Trends in Ecology and Evolution 9:442–445.

Wilson, M. W., A. D. Ridlon, K. M. Gaynor, S. D. Gaines, A. C. Stier, and B. S. Halpern. 2020. Ecological impacts of human-induced animal behaviour change. Ecology Letters 23:1522–1536.

Young, D. D., and R. D. Boertje. 2004. Initial use of moose calf hunts to increase yield, Alaska. Alces 40:1–6.

Young, D. D., R. D. Boertje, C. T. Seaton, and K. A. Kellie. 2006. Intensive management of moose at high density: impediments, achievements, and recommendations. Alces 42:41–48.

Young, D. D., and R. D. Boertje. 2011. Prudent and imprudent use of antlerless moose harvests in interior Alaska. Alces 47:91–100.

Zinn, H. C., M. J. Manfredo, and J. J. Vaske. 2000. Social psychological bases for stakeholder acceptance capacity. Human Dimensions of Wildlife 5:20–33.

TABLES AND FIGURES

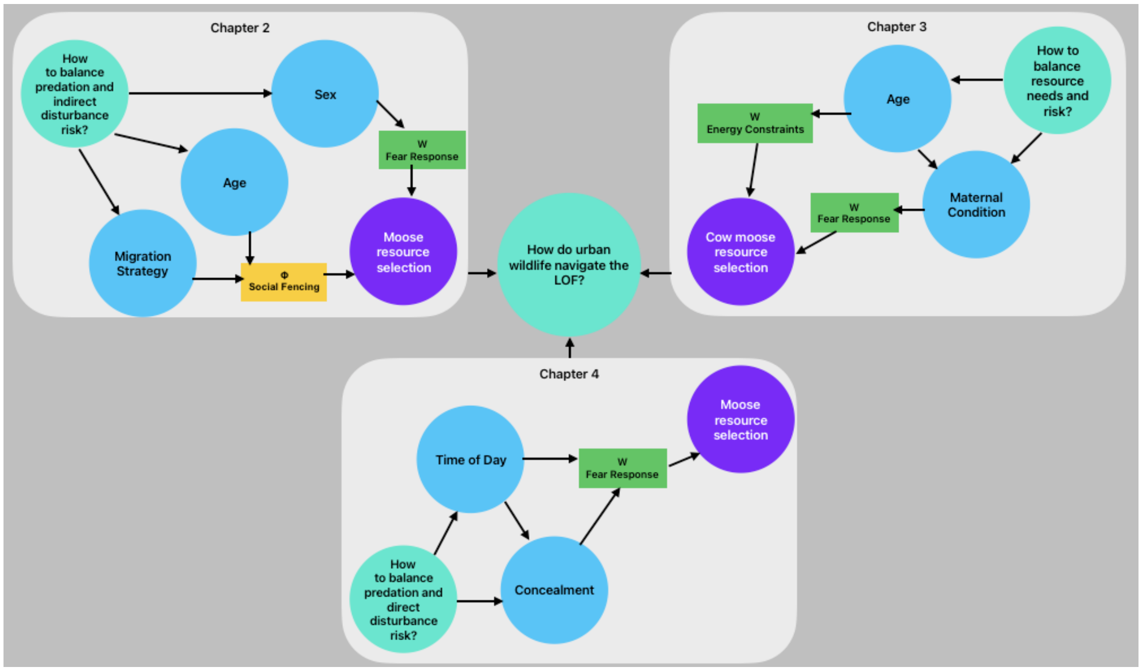


Figure 1-1. A diagram depicting the major differences between the questions (light blue circles) presented in each chapter of the dissertation. The blue circles and green boxes represent the most important factors used to explain hypotheses related to moose resource selection in the additional diagrams in Figures 1-2, 1-3, and 1-4.

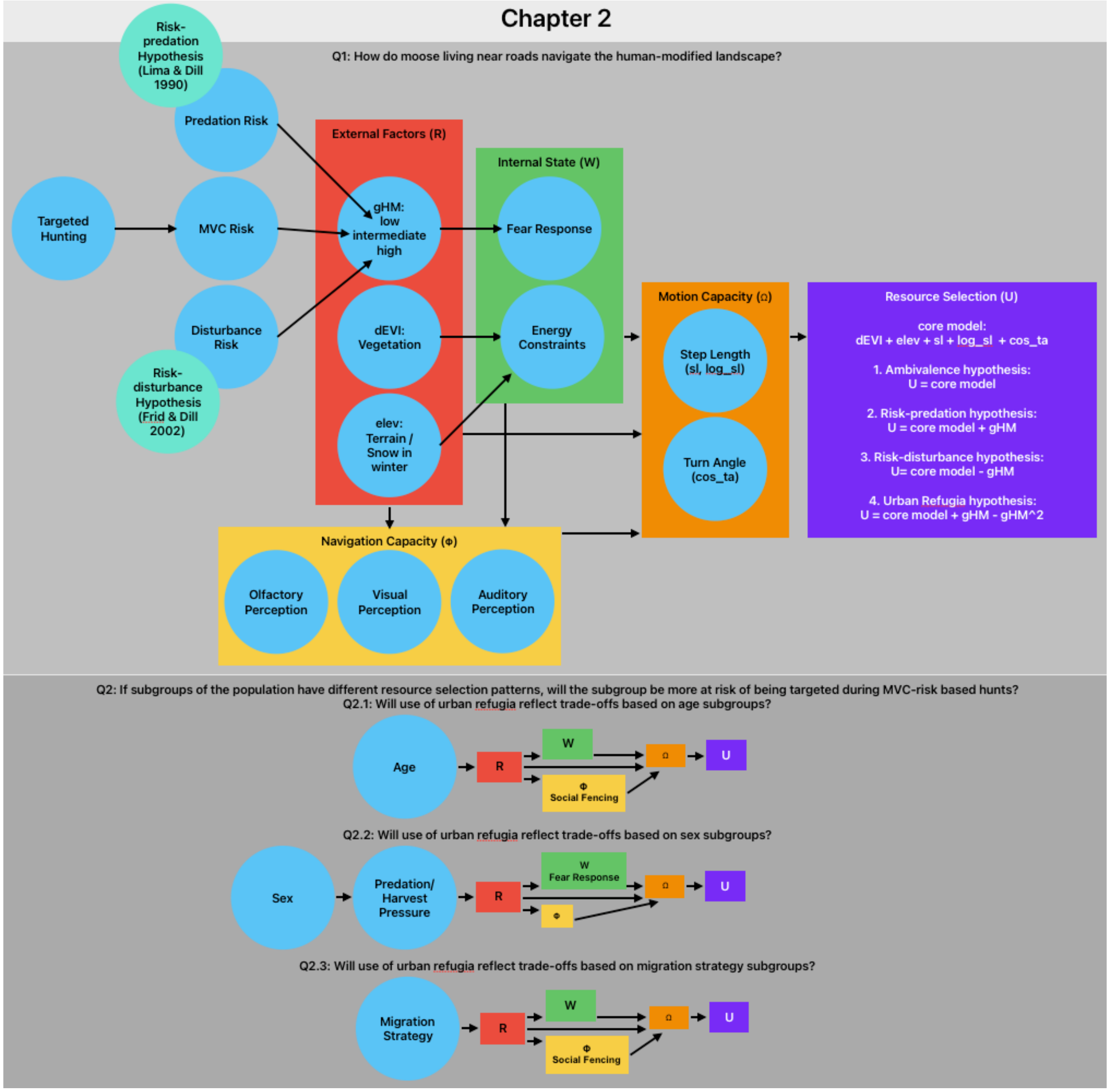


Figure 1-2. A diagram depicting the models, subgroupings, and covariates used to inform the hypotheses in Chapter II based on the general conceptual framework for movement ecology (Nathan et al. 2008).

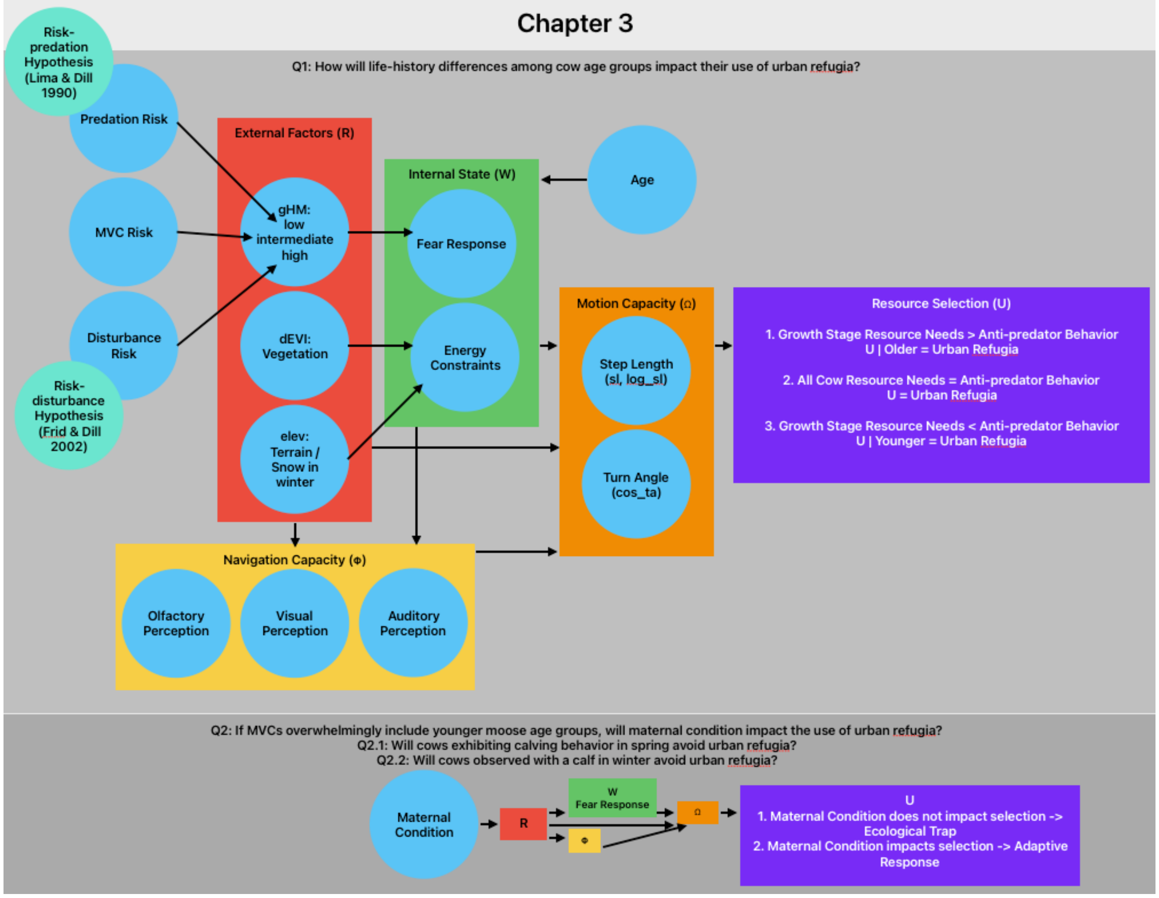
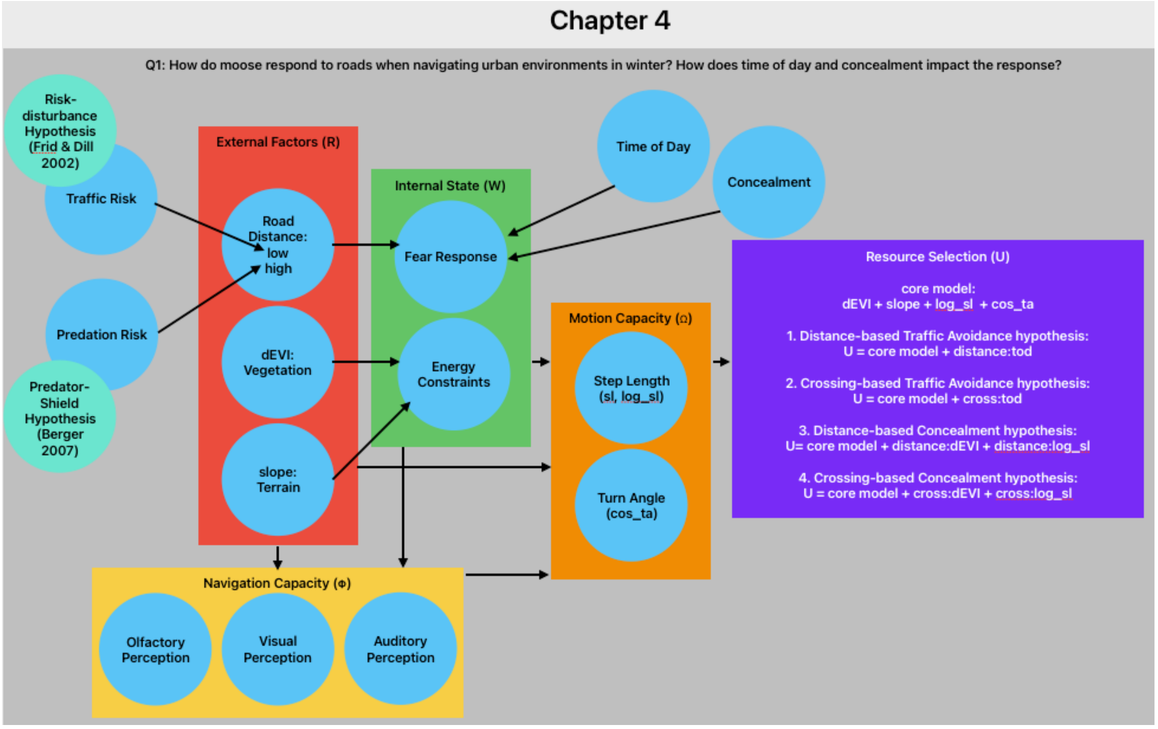


Figure 1-3. A diagram depicting the models, subgroupings, and covariates used to inform the hypotheses in Chapter III based on the general conceptual framework for movement ecology (Nathan et al. 2008).



Chapter 4

Q1: How do moose respond to roads when navigating urban environments in winter? How does time of day and concealment impact the response?

Resource Selection (U)

core model:
dEVI + slope + log_sl + cos_ta

1. Distance-based Traffic Avoidance hypothesis:
U = core model + distance:tod

2. Crossing-based Traffic Avoidance hypothesis:
U = core model + cross:tod

3. Distance-based Concealment hypothesis:
U= core model + distance:dEVI + distance:log_sl

4. Crossing-based Concealment hypothesis:
U = core model + cross:dEVI + cross:log_sl

Figure 1-4. A diagram depicting the models, subgroupings, and covariates used to inform the hypotheses in Chapter IV based on the general conceptual framework for movement ecology (Nathan et al. 2008).

CHAPTER II

ALASKAN MOOSE WINTER SELECTION FAVORS DISPERSAL TOWARDS URBAN SETTLEMENTS IN THE MATANUSKA-SUSITNA BOROUGH, ALASKA, USA.

ABSTRACT

Localized deer (Family *Cervidae*) abundance in urban areas may result in density-dependent effects, such as an increased risk of deer-vehicle collisions. Although wildlife tend to avoid areas of increased human disturbance and predation risks, in dynamic landscapes characterized by seasonal variation in weather and human use, certain individuals may benefit from seasonal dispersal and occupation of human-influenced landscapes.

In these high human-use areas, deer population reduction is a common practice used to alleviate human-wildlife conflicts. From 2017-2020 in the Matanuska-Susitna Borough of Alaska, USA, I studied the movement of moose (*Alces alces*), marked with global positioning system transmitters, to assess resource selection by moose subgroups and its relation to human disturbance using the gradient of human modification (gHM) – a measure of anthropogenic-based change to the landscape. I compare this resource selection to areas where the level of human landscape modification matches the level of MVC risk, to better understand which subgroups of moose are most likely to be affected by targeted hunting intended to reduce moose-vehicle collision (MVC) risk in winter.

Using integrated step selection, I quantified moose summer and winter selection in relation to gHM. At the population level, moose avoided areas with high or low gHM and selected for intermediate gHM, a phenomenon I refer to as urban refugia. In winter, MVC incidents peaked at the same gHM that was selected for by resident and migrant cow moose. Targeted winter removal of moose in areas where MVC risk is high should reduce MVCs, but the effect may only be temporary.

KEYWORDS

Alces alces, Alaska, Alaskan moose, human-wildlife conflict, moose-vehicle collisions, risk-disturbance hypothesis, targeted hunting, ungulates

As wildlife continue to follow instinctive patterns established to enhance their fitness, changes in predation pressure over space and time result in a dynamic alteration in the landscape of fear, which may further impact animal behavior and space use (Messmer et al. 1997, Palmer et al. 2022). Wildlife management agencies in the U.S. often establish population management objectives to maximize the number of animals available for humans to harvest, minimize the number of non-human competitors, and mitigate human-wildlife conflicts (Conover 2001). However, increasing urbanization has reduced public interest in hunting as a wildlife management strategy as attitudes toward wildlife orient away from utilitarianism (Riley et al. 2003, Cerri et al. 2021).

In Alaska, when conflicts occur between moose (*Alces alces*) and humans, the Alaska Department of Fish and Game (ADFG) has the authority to target hunts in specific areas where high densities of moose occur to mitigate the conflicts. For example, in past efforts to reduce the risk of moose-vehicle collisions (MVCs), ADFG has permitted hunters to cull moose congregating near road corridors with a high risk of MVCs. However, little is known about which subgroups of moose are most likely to be in these areas or whether moose selection will lead to the recolonization of these locations as moose densities decrease.

Moose, like other large ungulates, exhibit partial migration, wherein some portion of the population stays in the same home range year-round while the others shift their home range between seasons (Ball et al. 2001, Singh et al. 2012). The shift in selection of various landscape elements between seasons is the result of differential costs and benefits faced by individuals in different local environments (Nicholson et al. 1997). Differences in selection between subgroups should reflect the tradeoffs faced by the group (Fryxell and Sinclair 1988). By comparing relative selection between subgroups, managers may delineate which subgroups of moose will be most impacted by targeted hunts and conclude whether the practice has the potential to meet their objective.

In this study, I ask two questions to delineate which subgroups of moose will be most impacted by targeted hunts. Wildlife vehicle collisions are typically clustered in intermediately disturbed areas where motorists can reach higher speeds and dispersed housing allows for higher densities of wildlife than in urban centers. First, I ask how moose navigate the human modified landscape based on the level of development, which requires quantifying moose population level response to the gradient of human modification (gHM). The gHM index combines multiple anthropogenic stressors, which include the physical extent of human settlements, infrastructure, and natural resource extraction sites, to account for the spatial extent, intensity, and co-occurrence of human activities in terrestrial ecosystems (Kennedy et al. 2018).

Based on previous research, moose response should follow one of four strategies. The first is ambivalence: moose neither select nor avoid new locations based on gHM.

Second, moose could follow the risk-predation hypothesis: moose selection favors new locations with higher gHM to avoid predators (Lima and Dill 1990, Nicholson et al. 2014). A third strategy follows the risk-disturbance hypothesis, whereby moose selection favors new locations with lower gHM to avoid human disturbance (Frid and Dill 2002). Finally, moose selection could strategize the use of urban refugia; moose selection favors new locations with intermediate gHM to both avoid predators and human disturbance.

Second, I ask how group-based differences within the population, such as age, sex, and migration strategy, change the selection of gHM based on the following hypotheses. For the age-based benefit, I predict selection of gHM by older moose to favor urban refugia, as older moose will have had more time to select for the preferred level of development and subsequently displace younger moose from these areas. For the sex-based benefit, I expect selection of low or high gHM by male moose to be more prevalent than for female moose. Harvest pressure is likely to be lowest in the most developed areas but may also be low where no development occurs and where road access is limited. Similarly, adult female moose with calves will face more predation pressure, which may lead to avoidance of low gHM. For the migration strategy-based benefit, I expect selection of gHM by residents to be more aligned with selection by the population, as resident moose should be able to adjust to local human disturbance year-round, unlike migrants. If so, migrants may be fenced from otherwise preferred locations. Using these hypotheses, I determined if age-, sex-, or strategy-based incentives explained the selection of their respective subgroups and provided MVC mitigation considerations for targeted hunts based on the relationship between moose step selection and the level of development associated with high MVC rates.

STUDY AREA

My study was completed within the southern central portion of the Matanuska-Susitna Borough of Alaska between 149.7-151.1°N longitude and 61.2-62.5°W latitude, where most of the borough's human population resides. The area has experienced the fastest population growth in Alaska in recent years and the borough had a human population of approximately 108,317 in 2019 (U.S. Census Bureau 2019). The level of human disturbance to the landscape ranged from 0 to 0.67 based on the gHM index (Figure 2-1). The area's topography ranges between sea level and a peak of 4443 m above sea level (Figure 2-1).

For the years of the study, 2017–2020, the average annual temperature was 4.1 °C, with the lowest daily temperature falling to -18.9 °C and the highest daily temperature rising to 32.2 °C. During this time, average rainfall varied between 37.0 and 46.8 cm per year, and average snowfall varied between 147.6 and 237.0 cm annually (Western Regional Climate Center 2020). Forest vegetation typically consisted of alders (*Alnus* spp.), cottonwoods (*Populus* spp.), willows (*Salix* spp.), or spruces (*Picea* spp.).

The Alaska Department of Fish and Game (ADFG) managed the moose population in this area (Game Management Unit 14A; GMU), which had an estimated population of 8756 moose (0.0128 moose/hectare) in 2018 (T. C. Peltier, ADFG, personal communication). Between 2017 and 2020, 954.5 moose were harvested in the GMU each year on average. Moose were the only ungulate species within the valley. Human harvest and MVCs accounted for most mortality in the developed areas, which were concentrated within a small portion of the GMU. Less disturbed areas contained predators that cause high calf mortality during the summer. The ADFG calculated moose population demographics in this GMU using aerial surveys, harvest reporting, and MVC reporting data.

METHODS

Moose captures and monitoring

Beginning in March of 2017, the ADFG deployed 60 necklace-style global positioning system (GPS) transmitters (30 Iridium GPS Vertex Plus Collars, 30 Iridium GPS Vertex Lite Collars, VECTRONIC Aerospace GmbH, Berlin, Germany) on wintering moose within the study area using a mixture of ground- and helicopter-based darting methods (IACUC Protocol No. 0032-2018-42). The GPS transmitters provided hourly data on moose movements in the study area. I downloaded radio-collared moose location data via satellite link (VECTRONIC Aerospace GmbH, Berlin, Germany). As radio-marked moose mortalities were detected, the ADFG redeployed the retrieved GPS transmitters.

Integrated step selection analysis

Integrated step selection analysis (iSSA) simultaneously quantifies resource selection and step selection via conditional logistic regression, wherein the dependent variable represents whether consecutive pairs of GPS locations (steps) were used or available to the animal and the independent variables represent the resources at either the start or end of the step and the step characteristics (Avgar et al. 2016). The consecutive series of locations where the animal was observed were the used steps, while the available steps were randomly generated using statistical distributions related to the movement characteristics of the individual animal. Using a series of GPS locations recorded for each animal every 5 hours, I computed the gamma distribution of the step lengths using the distance between consecutive steps and the von Mises distribution of the turn angles using directional persistence between consecutive steps. I used a temporal resolution of 5 hours to get adequate sampling of each hour of the day while reducing autocorrelation. I computed these movement measurements and their distributions using the *amt* package in R (R Core Team 2022, Signer et al. 2011). Then, I used the resulting distributions to sample 15 available steps the animal could have taken for each location at the start of each step.

I extracted the covariates deciduousness, elevation, and gHM (described below), to each used and available step and paired the series of steps with the same start location to stratify the inputs to the conditional logistic regression model. Using the *stan_clogit* function from the *rstan* package (Stan Development Team 2022) in R, I computed individual conditional logistic regression models for each moose during each year's summer (July 1 to August 31) and winter (December 1 to March 31) life-history period (Ballard and Whitman 1988). I sampled coefficient estimates using 4 Markov chains, 2000 iterations per chain, and 1000 warmup iterations per chain resulting in 4000 posterior samples per moose-season-year combination. Available steps and used steps beginning at the same starting location were set to the same strata identifier in the conditional logistic regression model, which is a grouping mechanism used in analyses where there is only 1 success (the used step) contrasted against multiple failures (the available steps). The resulting effect sizes of each resource-based covariate are considered free of the bias of movement while the resulting effect sizes of each movement-based covariate are considered resource-independent (Avgar et al. 2016).

Covariates

Using the *rgee* package implemented in R, I extracted covariates representing deciduousness, elevation, and gHM to each used and available location from Google Earth Engine (Gorelick et al. 2017, Aybar et al. 2020). The deciduousness covariate is represented by the change in phenological measurements across the growing season (Street et al. 2015). First, I considered using the Normalized Difference Vegetation Index (NDVI), as done in previous studies (e.g., Street et al. 2015, Prokopenko et al. 2017, Jakes et al. 2020, Salganek et al. 2024), but due to persistent cloud cover in the region, I opted for the Enhanced Vegetation Index (EVI), which removes smoke and cloud cover. I extracted EVI values from the Terra Moderate Resolution Imaging Spectroradiometer 16-day 250 m vegetation index dataset (MOD13Q1.061) for each year of the study (Land Processes Distributed Active Archive Center 2021). I calculated the change in EVI (ΔEVI) value using the EVI values for July and October for each year to represent summer and fall phenology. Then, I calculated the difference between the seasonal measurements for each year and extracted the resulting ΔEVI value to each used and available step endpoint. High values of ΔEVI indicate a significant change in productivity across seasons, making ΔEVI a helpful index ranging from no cover (low ΔEVI), where EVI does not change between seasons, to deciduous cover (high ΔEVI), where EVI changes the most between seasons (Street et al. 2015). To each used and available step endpoint, I also extracted the elevation covariate using the 3D Elevation Program 10 m Digital Elevation Model (US Geological Survey 2021).

Then, I extracted the gHM value represented by each position as my measure of anthropogenic landscape disturbance, which is computed at a resolution of 1 sq km

(Kennedy et al. 2018). High values of gHM represent highly modified urban landscapes, while low values of gHM represent less modified landscapes. The gHM index is scaled between 0 and 1 and covers the entire globe during the year 2016; low values are those near 0 and high values are near 1. In this study area, the maximum value of gHM was near 0.67. For my study, I equated gHM with the level of risk perceived by the moose, as the amount of human modification to the environment should approximate the amount of anthropogenic sensory cues experienced by the animal. Other studies of WVCs have opted to use road density to provide similar inferences (e.g., Neumann et al. 2012, Ha & Shilling 2018). However, the road system in this area was highly concentrated, making most values of road density zero when using lower resolutions. The coarser scale of gHM provided a more continuous gradient, while capturing a similar phenomenon, as WVC risk is often high where road densities are intermediate to high. Deciduousness, elevation, and gHM covariate values were scaled and centered at zero for analysis.

From my iSSA, I included the movement-based covariates step length, ln-transformed step length, and cosine-transformed turn angle. The effect size of the step length and ln-transformed step length represent the difference between the shape and scale of the gamma distribution used to compute the available step lengths, and the shape and scale of the gamma distribution used to model the step lengths in the resource-independent movement kernel (Avgar et al. 2016). The effect size of the cosine-transformed turn angle represents the difference between the mean of the von Mises distribution used to compute the available turn angles, and the mean of the von Mises distribution used to model the turn angles in the resource-independent movement kernel (Avgar et al. 2016).

Moose-vehicle collision monitoring

From August 2016 to August 2020, I located MVCs reported to local law enforcement and recorded their GPS locations. I extracted gHM values from Google Earth Engine to these locations to get an estimate of MVC density in relation to the gHM index for the seasonal moose life history periods: spring (migration/calving), summer, fall (rut/migration), and winter (Ballard and Whitman 1988; Figure 2-2).

Classification of movement strategy

I classified moose movements into three categories based on the overlap between their summer and winter home range. I used locations from December 1 to March 31 to compute winter home ranges and locations from July 1 to August 31 to compute summer home ranges based on the typical timing of these life history periods for moose in south-central Alaska (Ballard and Whitman 1988). I calculated home ranges using the local convex hull method (k=10) provided by the *amt* package in R (Signer et al. 2011). Any moose with 168 or less relocations for a seasonal period was removed to ensure seasons were represented by a minimum of once weekly relocations. Then, I classified individual moose-years as either resident or migrant based on the overlap between their summer and winter home range. I classified individuals that exhibited both behaviors across years as partial migrants.

Hypothesis testing

To identify the selection strategy used by the moose population, I tested my four hypotheses, ambivalence, risk-predation, risk-disturbance, and urban refugia, using the mean effect size of the gHM covariates within three distinct conditional logistic regression models, and then I compared the difference in fit among the three models using leave-one-out cross validation (LOO-CV). For the ambivalence hypothesis, I used the core model [deciduousness + elevation + step length + ln(step length) + cos(turn angle)], which omits gHM as a covariate. For the risk-predation hypothesis, I used the core model with the addition of gHM. If there was a positive relationship between selection and gHM, this would indicate selection for gHM. For the risk-disturbance hypothesis, I used the same model [core model + gHM]. If there was a negative relationship between selection and gHM, this would indicate avoidance of gHM. For the urban refugia hypothesis, I used the core model and a quadratic form of gHM. If there was a positive relationship between selection and gHM at low levels of gHM and the opposite relationship at high levels of gHM, the resulting parabolic relationship would indicate avoidance at both extremes.

I evaluated model fit via LOO-CV using the *loo* package in R (Vehtari et al. 2022). I compared the LOO-CV results by season to choose the hypothesis that performed best on average, based on the minimization of the change in expected log-pointwise predictive density (ΔELPD, aka *diff_elpd*) between each individual's set of models. The model with the highest ELPD should yield predictions that are the closest to representing the data generating process. ΔELPD is the between-individual difference in ELPD, where all values are subtracted from the highest value. I averaged ΔELPD values by individual before comparing among seasons.

To measure effect size, I used ln-relative selection strength (lnRSS) as described by Avgar and colleagues (2017). The lnRSS for a given covariate represents the difference in selection between two possible locations, x1 over x2, holding all other covariates equal. For log-relative selection strength (lnRSS) comparisons, posterior estimates from each moose-season model were averaged by year to avoid biasing towards any one individual.

To evaluate whether group-based cost-benefit differences change selection of gHM, I used the lnRSS results of the urban refugia model to compare relative selection strength between seasons and within demographic groups including age, sex, and movement strategy. I recalculated the average coefficient values based on these groupings to compute the group-based lnRSS results. For the age-benefit hypothesis, I predicted that older moose selection will favor intermediate gHM, while younger moose, fenced from these otherwise preferred areas by older moose, will not favor intermediate gHM. For the sex-benefit hypothesis, I predicted that selection by females will favor intermediate gHM, while males may favor more remote low gHM or more urban high gHM. For the migration strategy-based hypothesis, I predicted that selection by resident moose will favor intermediate gHM. If so, migrant moose may be fenced from these otherwise preferred areas, leading to selection for high or low gHM.

RESULTS

Between 2016 and 2020, I tracked the movements of 101 moose (29 bulls, 72 cows) resulting in a total of 159,617 summer and winter used steps. The ADFG captured a total of 10 yearling, 9 two-year-old, and 10 adult bulls and 5 yearling, 16 two-year-old, and 51 adult cows. Of this sample, bulls account for 48 summer and 62 winter subsamples and cows account for 138 summer and 184 winter subsamples. In the summer, there was an average of 358 used steps per bull-season and 358 used steps per cow-season. In the winter, there was an average of 361 used steps per bull-season and

384 used steps per cow-season. Of the 73 moose observed across consecutive summer and winter periods, I classified 19 as migrants, 9 as mixed migrants, and 45 as residents.

Moose-vehicle collision monitoring

The density of MVCs peaked between 0.4-0.5 gHM in every season except summer, where the density is consistent regardless of gHM (Figure 2-2). Winter road conditions as well as increasing densities of moose in lower elevations increase the likelihood of MVCs during the winter months. In fall and spring, moose that decide to migrate or that are searching for mates during the rut or calving sites during late spring are more mobile, also increasing the likelihood of road crossings.

Population-level selection

The coefficients of covariates at the population-level varied considerably among the 101 radio-marked moose. In both seasons and for all selection covariates, the 80% uncertainty interval of the posterior coefficient estimates overlapped zero (Table 2-1). The average response to deciduousness ($\beta_{\Delta EVI}$ = [summer: 0.18, winter: 0.07]) and elevation ($\beta_{elevation}$ = [summer: 0.34, winter: 2.84]) was positive in both seasons. Most of the posterior estimates (>60%) for deciduousness were positive in both seasons. Most of the posterior estimates (>60%) for elevation were positive in winter, but 58% of estimates were negative in summer. The average response to gHM was negative in summer and positive in winter (β_{gHM} = [summer: -3.14, winter: 1.30]), but posterior estimates were not overwhelmingly positive or negative. The average response to the quadratic form of gHM was negative in both seasons ($\beta_{gHM}{}^2$= [summer: -7.89, winter: -1.55]), and most posterior estimates (>64%) were negative.

Posterior estimates for the linear and quadratic human modification coefficients (β_{gHM}, $\beta_{gHM}{}^2$) covaried at low levels of human modification in both seasons, but more so in summer than winter (Figure 2-3). For moose that were observed at the lowest levels of human modification (0-0.1 gHM), estimates for the linear and quadratic terms were positively correlated. At this low level of human development, the relationship reflected by the average estimates above (parabolic) would be linear, with more consistent avoidance or selection of human developement as gHM increases.

Model selection

For the LOO-CV results of each individual moose-season, the urban refugia model had the lowest mean ΔELPD in both summer and winter (Table 2-2). On average, the urban refugia model performed as expected with low and high gHM avoided and intermediate gHM selected. In both seasons, average selection for gHM (β_{gHM} = [summer: -3.14, winter: 1.30]) was higher than the associated quadratic term ($\beta_{gHM}{}^2$= [summer: -7.89, winter: -1.55]) suggesting selection for intermediate levels of gHM and avoidance of both high and low levels of gHM (Figure 2-4).

Age benefit hypothesis

When stratified by age, groups with more than 10 individuals showed a response similar to the population-level response for each selection covariate. Ages ranged from 1 to 14 years old, but only 3 age groups had more than 10 individuals (2 [n = 27], 4 [n = 32], and 6 [n = 12] years old), so I could not infer a clear trend in selection with age (Appendix A, Table 1). Unused age groups had seven or fewer individuals.

Sex benefit hypothesis

I inferred selection from 27 bulls and 67 cows in summer and 29 bulls and 72 cows in winter. When stratified by sex, the distribution of positive and negative posterior estimates for selection by both sexes was congruent with population-level estimates for all covariates (Appendix A, Table 2). During summer, bull and cow selection were similar, with both groups avoiding high and low gHM (Figure 2-4). During winter, bull selection favored high gHM while the peak in selection for cows shifted to slightly higher but still intermediate gHM (Figure 2-5). When starting from a point with the mean value of gHM (0.34), bulls selected for intermediate gHM (0.26-0.33) in summer and high gHM (0.34-0.67) in winter. Cows selected for higher gHM at the lower bound (0.31-0.33) than bulls in summer but a slightly lower range of gHM values at the higher bound (0.34-0.41 gHM) than bulls in winter. Unlike bulls, cows continued to avoid high gHM in winter.

Strategy benefit hypothesis

I inferred selection from 19 migrant, 9 mixed migrant, and 45 resident moose to quantify the difference in selection of gHM by moose using these different migration strategies. When I pooled data from individual moose grouped by movement strategy, the distribution of positive and negative posterior estimates for selection by each group was congruent with population-level estimates for all covariates (Appendix A, Table 3). Resident moose selection favored intermediate to high levels of gHM year-round, while migrant and mixed migrant moose avoided both extremes of gHM during summer and selected for extremes in the winter (Figure 2-6). During summer, resident moose selected for higher values of gHM (0.34-0.42) than the combined population (0.28-0.33) of residents and migrants. During summer, the migrant group selected higher levels of gHM (0.34-0.67) compared to residents, while the mixed migrant group selected for lower levels of gHM (0-0.34) compared to residents.

DISCUSSION

I studied behavioral responses to human development and disturbance by Alaskan moose to provide management recommendations to mitigate moose-vehicle collision risks. On average, moose in my study area avoided extremely urban and remote landscapes and selected for intermediate levels of gHM, providing support for the urban refugia hypothesis. Seiler (2005) also found that MVCs were most prevalent at intermediate levels of traffic, which is expected to repel wildlife at more intense levels. Similarly, deer-vehicle collision risk is often highest in suburban areas (Hothorn et al. 2012).

Relative avoidance of high gHM relaxed during winter, when densities of moose typically increase near human settlements. However, I found that, while avoidance decreased overall, selection increased for specific subgroups within the population. Selection of gHM increased for both cows and bulls, but cows continued to avoid extreme levels of gHM. Neonate and calf survival are high priorities to female cervids, which often opt for predator free birthing sites and home ranges (Barten et al. 2001, Bjorneras et al. 2012, Droghini et al. 2024). Moose, especially cow-calf pairs, have shown consistent avoidance of predation risk (Ouellet et al. 1996, Ditmer et al. 2018). Moose avoided areas of lower human disturbance (low gHM), which I assumed had higher potential for predation, as expected by the risk-predation hypothesis and areas of higher human disturbance (high gHM) as expected by the risk-disturbance hypothesis.

Combining the two, the urban refugia model is best supported for moose familiar with urban areas.

Most of the radio-marked moose exhibited a resident strategy for the duration of observation. Resident moose selected gHM levels that also correlated to high MVC occurrence in winter. Between summer and winter, selection of gHM decreased for migratory individuals, even as it increased for resident individuals. Dissimilar from other studies (e.g., Nicholson et al. 1997, Found and St. Clair 2019), individuals that migrated consistently throughout the study period selected for high levels of gHM in summer. This suggests that either predation-risk avoidance is higher than disturbance-risk avoidance for these individuals or that these individuals have no choice but to move closer to human settlements as residents take up the otherwise preferred intermediate gHM areas. As observed with other ungulates (e.g., Nicholson et al. 1997), mixed migrants selected for lower levels of gHM in summer than residents. Moose-vehicle collision threats are highest in winter, but the range of the population shifts to a smaller area during this season due to high snow depths at high elevations (McDonald et al. 2019); thus, it is not surprising that the migrants and mixed-migrants don’t show as strong of a response to the extremes of gHM as residents, which should be more familiar with the areas they inhabit year-round. As MVC risk increases from summer to winter, mixed-migrants may be moving farther away from human settlements to avoid this risk until it decreases again the next summer or may be taking advantage of potentially less competitive tracts of available browse during the snow free periods, while migrants may be returning from their less disturbed summer ranges to avoid predation risk and high snow depths.

Because the values of gHM are scaled coarsely and reflect a gradient, large jumps from low to high values would be unlikely given that available steps are calculated relative to previous steps and moose home ranges only covered a few independent cells due to the low resolution of the gHM data. This scaling may account for the high amount of variation in my population-pooled estimates. Combination of multiple posterior estimates from animals subjected to different landscape conditions may lead to diminution of the peak in selection when using a quadratic model. Finer-scale data on landscape characteristics may strengthen posterior estimation. Additionally, my core model covariates are merely indices of vegetation (ΔEVI) and snow depth (elevation), which are understood to impact moose selection (Dussault et al. 2005). Quality remotely sensed imagery is still difficult to acquire in Alaska, partially due to consistent cloud cover, so investments in climate and vegetation monitoring would be beneficial for better estimation of dynamic responses to available browse and the landscape of fear.

While there were no clear trends in selection for human development among the age classes used in this analysis, there may be some evidence for age-dependent decline in selection for deciduousness (Appendix A, Table 1). As moose are more likely to stay in their defined home ranges as they age, selection for deciduousness may decrease with age as moose learn where local browse is available and decrease their need to search for new sources of vegetation. For moose that survive to old age in urban areas, selection for deciduousness may also be less important than avoidance of human development and predation risk, but a more comprehensive analysis of different adult age classes and their selection for both vegetation and human development may be needed to identify the specific costs and benefits older moose prioritize when maintaining a home range in an urban area.

My study demonstrated that dynamic pressures faced by wildlife can explain their selection patterns. By reducing the benefits of living near human settlements, we will be better at reducing urban wildlife overabundance and human-wildlife conflicts (Blumstein 2016, Honda et al. 2018). As deer overabundance issues are likely to increase with time, effective ways to manage urban cervid populations will always be needed. Additionally, as the public's dominant attitudes about the value of wildlife change, we must be ready to adapt our management strategies to ensure wildlife do not become considered nuisances. Understanding the causes and consequences of the proliferation of specific demographics and behaviors is necessary to appropriately manage complex wildlife issues.

The moose in my study were mostly residents. Additionally, the proportion of cows in the population, and thus also the sample of captured moose selected for the study, was higher than that of bulls. Sex-based and migration-based subgroups selected for levels of gHM associated with high MVC occurrence, which is expected, as most moose should be in these areas. In that context, removal of individuals from areas where MVC risk is high should reduce population-wide selection for gHM as resident and cow moose abundance decline. Providing information to stakeholders about the consequences of high moose densities may encourage participation in removals (Boertje et al. 2019). However, hunting activity may not affect movement rates, so any reduction in MVCs will likely be due to decreased density, which may not last if selection causes additional moose to fill in the new gaps (Neumann et al. 2009, Neumann and Ericsson 2018).

While migrants and mixed migrants did not select for gHM levels most closely related to MVCs in winter, moose behavioral strategies can change as conditions change. As these individuals continue to avoid extreme levels of gHM, reduction of population densities may allow migratory individuals to inhabit local environments where the need to migrate is diminished. Hazing strategies designed to disturb moose near human settlements may be helpful for reducing the benefits provided by urban environments (Bonnell and Breck 2017, Found and St. Clair 2018). As the cultural value of moose is extremely high, the public may be averse to such actions without proper communication on their necessity. Field experimentation to quantify the reduction of MVCs and local moose densities following implementation of targeted hunts or other hazing activities should be used to evaluate their efficacy.

MANAGEMENT CONSIDERATIONS

At the population level, the moose population I studied selected for areas with intermediate gHM while avoiding high and low levels. Intermediate gHM is typified by suburban mixtures of developed and undeveloped land. In these areas, MVC rates and moose selection peaked. Predators and humans should both be less common here than in remote or highly urban areas, respectively, while forage is also likely to be abundant between low density human residences. This mixture provides a potential refuge for ungulates seeking large amounts of forage and low amounts of disturbance or predation risks, but this refugia comes at the cost of endangerment from motorists traveling at higher speeds.

To adequately reduce MVC rates, selection of these areas should be discouraged. While using targeted winter moose hunting in areas where MVC risk is high could reduce

MVC rates, the effect may only be temporary if the number of removed animals can be quickly replaced through annual recruitment and migration. Removal paired with hazing or other measures designed to reduce selection, such as removal of roadside forage, may reduce the possibility of yearly recolonization by winter migrant moose and nearby resident moose. Similarly, concentration of urban development may instigate more avoidance, as most of the moose studied here did avoid the most developed areas. Concentrating human activity into a smaller extent would increase the intensity of sensory cues moose may be already learning to avoid.

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REFERENCES

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

Avgar, T., S. R. Lele, J. L. Keim, and M. S. Boyce. 2017. Relative selection strength:

quantifying effect size in habitat- and step-selection inference. Ecology and Evolution 7:5322–5330.

Aybar, C., Q. Wu, L. Bautista, R. Yali, and A. Barja. 2020. rgee: An R package for interacting with Google Earth Engine. Journal of Open Source Software 5:2271.

Ball, J. P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose, *Alces alces*, ranges in northern Sweden. Wildlife Biology 7:39–47.

Ballard, W. B., and J. S. Whitman. 1988. Susitna hydroelectric project, final report, big game studies, Vol. II-Moose Upstream. Alaska Department of Fish and Game https://www.arlis.org/docs/vol1/Susitna/41/APA4128.pdf

Barten, N. L., R. T. Bowyer, and K. J. Jenkins. 2001. Habitat use by female caribou: tradeoffs associated with parturition. The Journal of Wildlife Management 65:77–92.

Bjorneraas, K, I. Herfindal, E. J. Solberg, B. Saether, B. van Moorter, and C. M. Rolandsen. 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. Oecologia 168:231–243.

Blumstein, D. T. 2016. Habituation and sensitization: new thoughts about old ideas. Animal Behavior 120:255–262.

Boertje, R. D., G. G. Frye, and D. D. Young. 2019. Lifetime, known-age moose reproduction in a nutritionally stressed population. Journal of Wildlife Management 83:610–626.

Bonnell, M. A., and S. W. Breck. 2017. Using resident-based hazing programs to reduce human-coyote conflicts in urban environments. Human–Wildlife Interactions 11: 146–155.

Caughley G. 1981. Overpopulation. Pages 7-20 *in* P. A. Jewell and S. Hold, editor. Problems in management of locally abundant wild mammals. Academic Press, New York, NY, USA.

Cerri, J., E. L. Procaccio, M. Ferretti, and E. Mori. 2021. Modernization-induced socio-economic changes and their effect over the spatial distribution of recreational hunting and volunteering with animals. Human Dimensions of Wildlife 26:401–410.

Conover, M. R. 2001. Effect of hunting and trapping on wildlife damage. Wildlife Society Bulletin 29:521–532.

Conover, M. R., and D. O. Conover. 2022. Human–wildlife interactions: From conflict to coexistence. Second edition. CRC Press, Boca Raton, Florida, USA.

Ditmer, M. A., J. R. Fieberg, R. A. Moen, S. K. Windels, S. P. Stapleton, and T. R. Harris. 2018. Moose movement rates are altered by wolf presence in two ecosystems. Ecology and Evolution 8:9017–9033.

Droghini, A., T. W. Nawrocki, J. B. Stetz, P. A. Schuette, A. R. Aderman, and K. E. Colson. 2024. Variation among individual female moose in habitat selection suggests different responses to risk-forage trade-offs. Ecosphere. In Press.

Dussault, C., J. P. Ouellet, R. Courtois, J. Huot, L. Breton, and H. Jolicoeur. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619–628.

Found, R., and C. C. St. Clair. 2019. Influences of personality on ungulate migration and management. Frontiers in Ecology and Evolution 7:438.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Ecology and Society 6:11.

Fryxell, J. M., and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution 3:237–241.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. Google Earth Engine: planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18–27.

Ha, H. and F. Shilling. 2018. Modelling potential wildlife-vehicle collisions (WVC) locations using environmental factors and human population density: A case-study from 3 state highways in Central California. Ecological Informatics 43:212–221.

Healy, W. M., D. S. deCalesta, and S. L. Stout. 2022. A research perspective on white-tailed deer overabundance in the northeastern United States. Wildlife Society Bulletin 25:259–263.

Honda, T., H. Iijima, J. Tsuboi, and K. Uchida. 2018. A review of urban wildlife management from the animal personality perspective: the case of urban deer. Science of the Total Environment 644:576–582.

Hothorn, T., R. Brandl, and J. Müller. 2012. Large-scale model-based assessment of deer-vehicle collision risk. PLoS One 7:e29510.

Jakes, A. F., N. J. DeCesare, P. F. Jones, P.F., C. C. Gates, S. J. Story, S. K. Olimb, K. E. Kunkel, and M. Hebblewhite. 2020. Multi-scale habitat assessment of pronghorn migration routes. PLoS One 15:e0241042.

Kennedy, C. M., J. R. Oakleaf, D. M. Theobald, S. Baruch-Mordo, and J. Kiesecker.

2019. Managing the middle: a shift in conservation priorities based on the global human modification gradient. Global Change Biology 25:811–826.

Kilpatrick, H. J., A. M. Labonte, and J. S. Barclay. 2007. Acceptance of deer management strategies by suburban homeowners and bowhunters. Journal of Wildlife Management 71:2095–2101.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

McDonald, L. R., T. A. Messmer, and M. R. Guttery. 2019. Temporal variation of moose-vehicle collisions in Alaska. Human–Wildlife Interactions 13:8.

Messmer, T. A, L. Cornicelli, D. J. Decker, and D. G. Hewitt. 1997. Stakeholder acceptance of urban deer management techniques. Wildlife Society Bulletin 25:360–366.

Messmer, T. A. 2000. The emergence of human-wildlife conflict management: turning challenges into opportunities. International Biodeterioration and Biodegradation 45:97–102.

Neumann, W., G. Ericsson, and H. Dettki. 2009. The non-impact of hunting on moose Alces alces movement, diurnal activity, and activity range. European Journal of Wildlife Research 55:255–265.

Neumann, W., G. Ericsson, H. Dettki, N. Bunnefeld, N. S. Keuler, D. P. Helmers, and V. C. Radeloff. 2012. Difference in spatiotemporal patterns of wildlife road-crossings and wildlife-vehicle collisions. Biological Conservation 145:70–78.

Neumann, W., and G. Ericsson. 2018. Influence of hunting on movements of moose near roads: Hunting and rutting effects on moose movement. Journal of Wildlife Management 82:918–928.

Nicholson, K. L., C. Milleret, J. Månsson, and H. Sand. 2014. Testing the risk of predation hypothesis: the influence of recolonizing wolves on habitat use by moose. Oecologia 176:69–80.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

Ouellet, J. P., J. Ferron, and L. Sirois. 1996. Space and habitat use by the threatened Gaspe caribou in southeastern Quebec. Canadian Journal of Zoology 74:1922–1933.

Palmer, M. S., K. M. Gaynor, J. A. Becker, J. O. Abraham, M. A. Mumma, and R. M. Pringle. 2022. Dynamic landscapes of fear: understanding spatiotemporal risk. Trends in Ecology and Evolution 37:911–925.

Prokopenko, C. M., M. S. Boyce, and T. Avgar. 2017. Characterizing wildlife behavioural responses to roads using integrated step selection analysis. Journal of Applied Ecology 54:470-479.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riley, S. J., D. J. Decker, J. W. Enck, P. D. Curtis, T. B. Lauber, and T. L. Brown. 2003. Deer populations up, hunter populations down: Implications of interdependence of deer and hunter population dynamics on management. Ecoscience 10:455–461.

Salganek, S., K. A. Schoenecker, and M. L. N. Terwilliger. 2024. Using integrated step selection to determine effects of predation risk on bison habitat selection and movement. Ecosphere 15:e4909.

Seiler, A. 2005. Predicting the locations of moose– vehicle collisions in Sweden. Journal of Applied Ecology 42:371–382.

Signer, J., J. Fieberg, and T. Avgar. 2011. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution 2019:880–890.

Singh, N. J., L. Borger, H. Dettki, N. Bunnefeld, and G. Ericsson. 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. Ecological Applications 22:2007–2020.

Stan Development Team. 2022. RStan: the R interface to Stan. R package version 2.21.5.

Street, G. M., L. M. Vander Vennen, T. Avgar, A. Mosser, M. L. Anderson, A. R. Rodgers, and J. M. Fryxell. 2015. Habitat selection following recent disturbance: model transferability with implications for management and conservation of moose (*Alces alces*). Canadian Journal of Zoology 93:813–821.

Sullivan, T. L., and T. A. Messmer 2003. Perceptions of deer-vehicle collision management by state wildlife agency and department of transportation administrators. Wildlife Society Bulletin 31:167–173.

Vehtari A., J. Gabry, M. Magnusson, Y. Yao, P. Bürkner, T. Paananen, A. Gelman. 2022. “loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models.” R package version 2.5.1

TABLES AND FIGURES

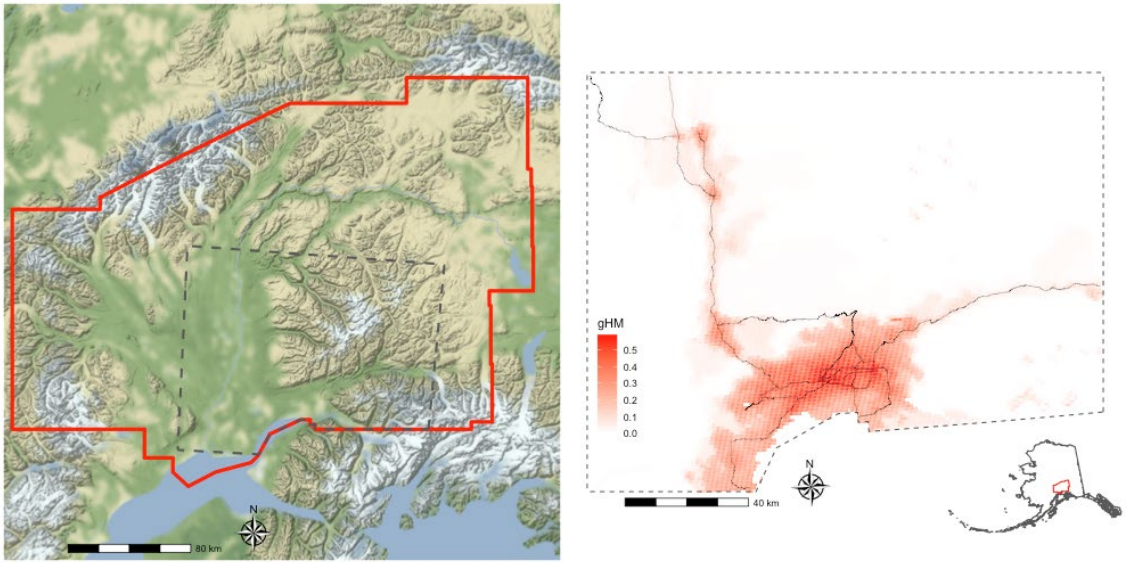

Figure 2-1. A gradient of human modification index (gHM) denoting the level of human modification to the landscape in the moose (*Alces alces*)-vehicle collision abatement study area, Matanuska-Susitna Borough, Alaska, USA, 2017-2022. In the right map, the lines represent major roads and highways in the study area. The left map shows a dashed outline of the study area and a red outline of the borough atop a stamen terrain map.

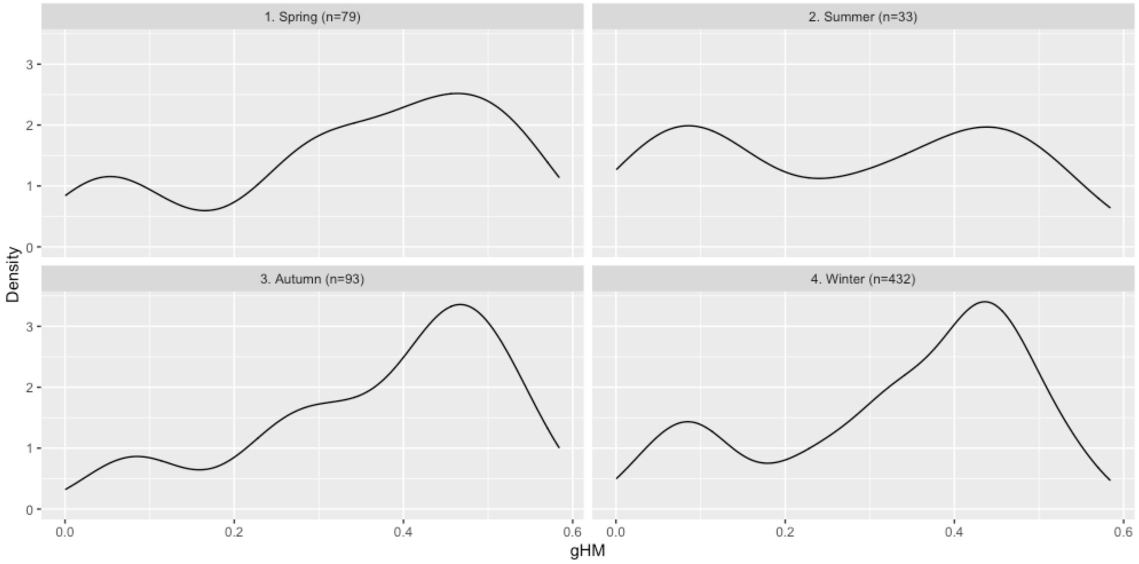

Figure 2-2. Gradient of human modification (gHM) indices at moose (*Alces alces*)-vehicle collision locations in the Matanuska-Susitna Borough, Alaska, USA study area, 2016-2020.

Table 2-1. Population summary of seasonal moose (*Alces alces*) selection coefficient values for the urban refugia model based on the 80% uncertainty interval (UI) of each variable's posterior estimates, Matanuska-Susitna Borough, Alaska, USA study area, 2017-2020. The % Positive value represents the percentage of samples that were above zero. Covariates include deciduousness (ΔEVI), elevation, and the gradient of human modification index (gHM).

	Summer				Winter			
Coefficient	10% UI	Mean	90%UI	% Positive	10% UI	Mean	90%UI	% Positive
ΔEVI	-0.17	0.18	0.58	0.72	-0.42	0.07	0.57	0.60
elevation	-8.59	0.34	4.60	0.42	-3.58	2.84	10.43	0.64
gHM	-25.80	-3.14	22.76	0.57	-6.72	1.30	9.90	0.59
gHM^2	-18.8	-7.89	3.49	0.24	-7.18	-1.55	3.80	0.36

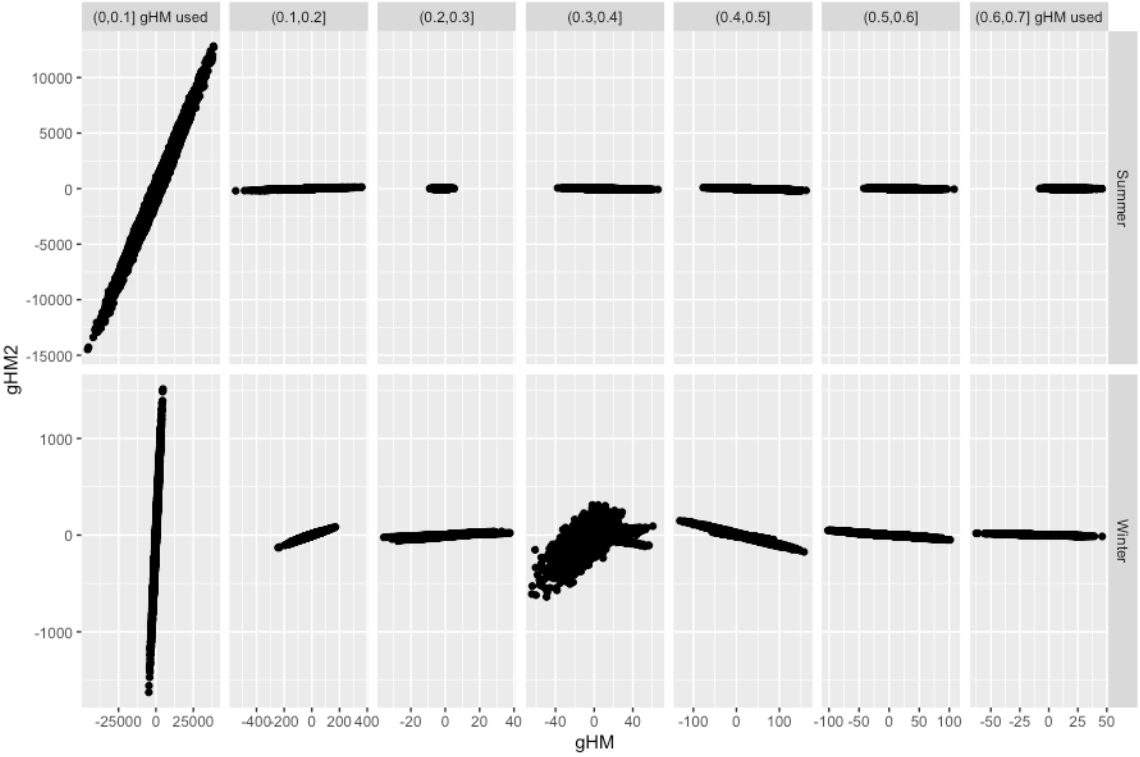

Figure 2-3. Covariation between coefficient estimates in each posterior sample for the gradient of human modification linear (gHM) and quadratic (gHM2) covariates, Matanuska-Susitna Borough, Alaska, USA study area, 2017-2020. Estimates are compared across samples for each individual moose-season and binned based on the average level of human modification for the individual moose-season’s used steps.

Table 2-2. Leave-one-out cross validation results for the three models used to compute integrated step selection effect sizes for moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA study area, 2017-2020. The associated hypotheses are ordered by minimum change in expected log-pointwise predictive density (ΔELPD).

	Mean ΔELPD	
Model	Summer	Winter
Urban Refugia	-0.707	-0.683
Risk-Predation/Disturbance	-1.32	-1.33
Ambivalence	-1.87	-1.81

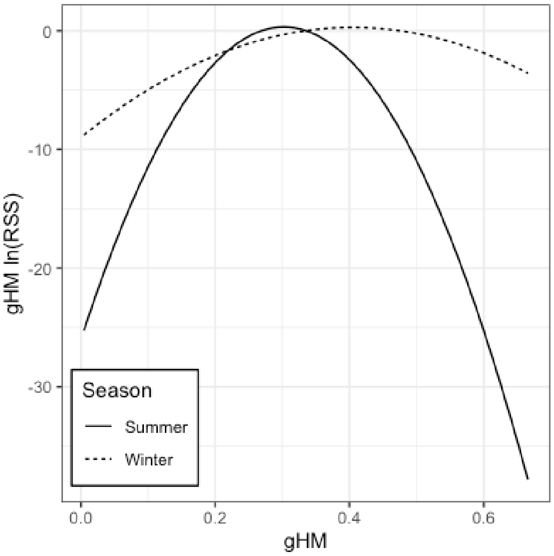

Figure 2-4. Seasonal log-relative selection strength (lnRSS) for selecting a step (x1) with any value of gHM compared to a step (x2) with the average value of gHM for moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA study area, 2017-2020. gHM represents the gradient of human modification index value at x1. lnRSS values were calculated using the average of the coefficients from the urban refugia models' posterior samples.

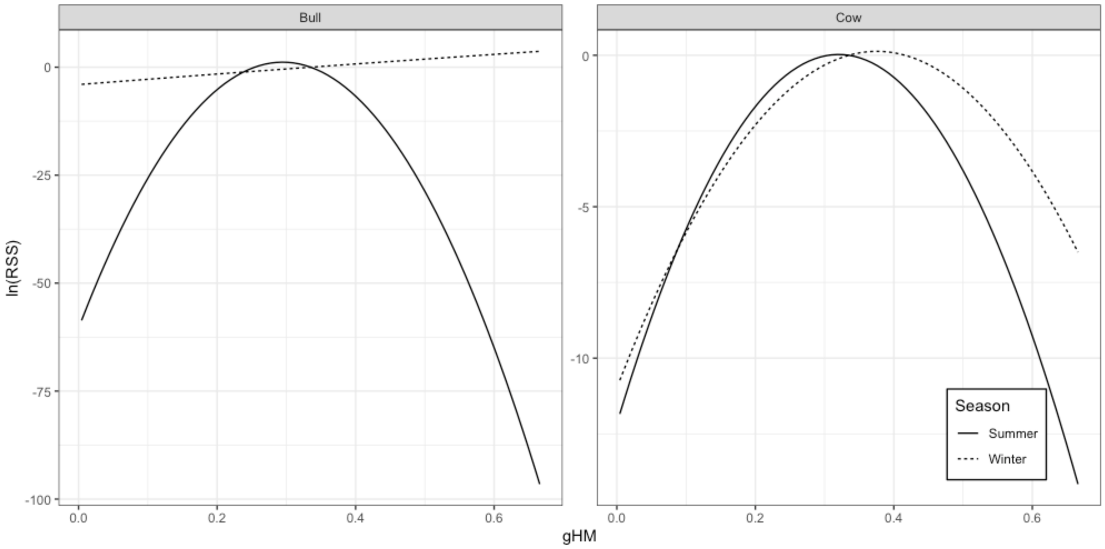

Figure 2-5. Seasonal log-relative selection strength (lnRSS) for selecting a step (x1) with any value of gHM compared to a step (x2) with the average value of gHM for moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA study area, 2017-2020. gHM represents the gradient of human modification index value at x1. lnRSS values were calculated using the average of the coefficients from the urban refugia models' posterior samples grouped by season (Summer, Winter) and sex (Bull, Cow).

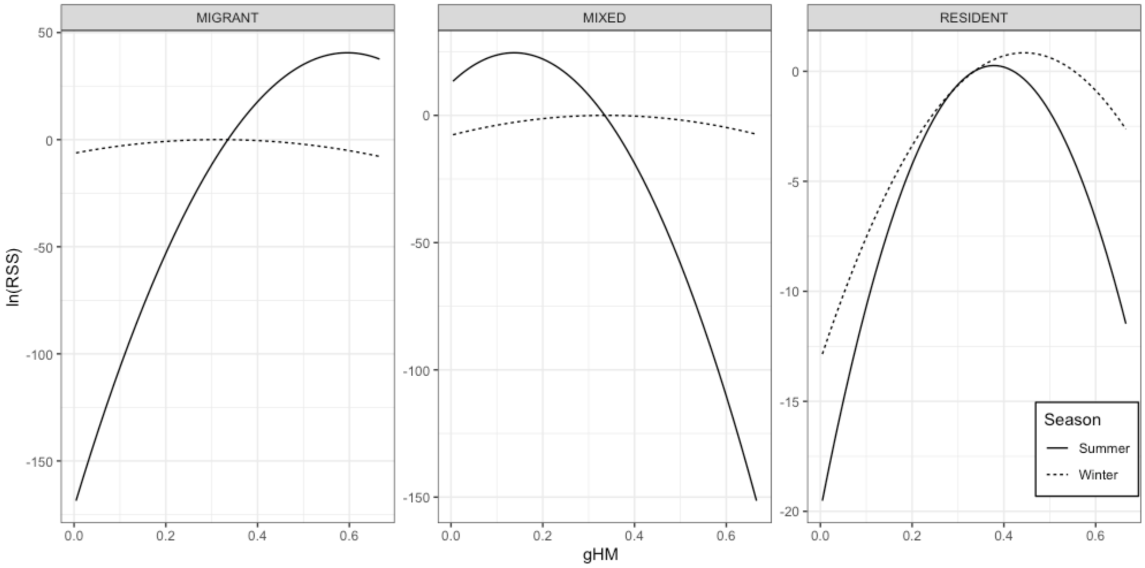

Figure 2-6. Seasonal log-relative selection strength (lnRSS) for selecting a step (x1) with any value of gHM compared to a step (x2) with the average value of gHM for moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA study area, 2017-2020. gHM represents the gradient of human modification index value at x1. lnRSS values were calculated using the average of the coefficients from the urban refugia models' posterior samples grouped by season (Summer, Winter) and movement strategy (Migrant, Mixed, Resident).

APPENDIX A. COEFFICIENT SUMMARIES

Table 1. Age-stratified summary of coefficient values for the urban refugia model based on the 80% uncertainty interval (UI) of each variable's posterior estimates. The % Positive value represents the percentage of samples that were above zero. Covariates include deciduousness (ΔEVI), elevation, and the gradient of human modification index (gHM).

		Summer					Winter				
Age	Coefficient	10% UI	Mean	90% UI	% Positive	N	10% UI	Mean	90% UI	% Positive	N
1	ΔEVI					0	0.42	1.55	2.78	0.97	1
2	ΔEVI	-0.13	0.27	0.78	0.73	24	-0.46	0.10	0.72	0.62	27
3	ΔEVI	0.01	0.15	0.31	0.91	2	-0.02	0.14	0.33	0.86	2
4	ΔEVI	-0.20	0.11	0.44	0.69	32	-0.20	0.16	0.55	0.67	32
5	ΔEVI	-0.19	0.04	0.24	0.61	5	-0.09	0.13	0.46	0.66	5
6	ΔEVI	-0.07	0.23	0.57	0.81	12	-0.41	0.03	0.37	0.62	12
8	ΔEVI	-0.23	0.17	0.45	0.74	6	-1.07	-0.11	0.47	0.52	7
9	ΔEVI	-0.35	-0.18	0.00	0.10	1	-1.19	-0.46	0.16	0.22	2
10	ΔEVI	-0.04	0.39	0.96	0.86	3	-0.49	-0.15	0.12	0.28	3
12	ΔEVI					0	-1.63	-1.14	-0.67	0.00	1
14	ΔEVI	0.11	0.38	0.65	0.97	1	-0.25	0.16	0.57	0.69	1
1	elevation					0	15.50	20.99	26.52	1.00	1
2	elevation	-10.59	-1.74	3.94	0.37	24	-3.60	1.94	10.28	0.58	27
3	elevation	-3.51	-0.53	2.03	0.46	2	-0.49	2.62	5.04	0.87	2
4	elevation	-4.56	-0.16	4.32	0.46	32	-1.38	2.82	6.99	0.72	32
5	elevation	-6.43	-1.04	1.99	0.31	5	-1.90	0.30	3.17	0.46	5
6	elevation	-10.93	-3.34	4.01	0.35	12	-5.65	2.04	11.69	0.59	12

8	elevation	-7.43	23.90	127.84	0.56	6	-3.20	18.10	55.00	0.79	7
9	elevation	2.72	3.97	5.22	1.00	1	-1.55	2.27	7.07	0.68	2
10	elevation	-0.67	0.68	2.67	0.66	3	-18.54	-4.37	2.87	0.51	3
12	elevation					0	8.41	13.59	18.63	1.00	1
14	elevation	-9.23	-7.13	-5.08	0.00	1	-10.33	-5.03	0.19	0.11	1
1	gHM					0	-7.86	2.05	11.13	0.63	1
2	gHM	-55.62	-53.26	42.02	0.58	24	-10.47	0.57	14.04	0.53	27
3	gHM	-3309.30	196.31	4173.09	0.45	2	-5.64	-1.29	1.93	0.40	2
4	gHM	-53.55	17.03	35.33	0.46	32	-7.33	0.52	7.58	0.50	32
5	gHM	-13.91	-0.49	6.04	0.78	5	-0.50	4.59	9.10	0.89	5
6	gHM	-3.87	2.91	12.99	0.59	12	-1.15	3.15	10.87	0.73	12
8	gHM	-7.90	-1.74	8.69	0.53	6	-8.04	-1.69	2.64	0.39	7
9	gHM	-16.81	1.56	19.39	0.55	1	-4.35	3.82	11.82	0.74	2
10	gHM	-1.89	0.80	2.85	0.78	3	-0.01	3.53	8.62	0.90	3
12	gHM					0	2.53	7.06	11.76	0.98	1
14	gHM	-332.00	-25.99	282.38	0.45	1	-17.57	3.52	24.51	0.59	1
1	gHM^2					0	-23.17	-7.35	6.92	0.29	1
2	gHM^2	-26.07	-5.79	15.67	0.31	24	-8.36	-0.78	5.40	0.38	27
3	gHM^2	-1141.98	23.87	1272.99	0.42	2	0.04	2.03	4.07	0.90	2
4	gHM^2	-26.29	-16.50	4.65	0.24	32	-7.03	-1.57	2.35	0.38	32
5	gHM^2	-7.73	-3.31	-0.01	0.10	5	-5.74	-2.67	0.50	0.13	5
6	gHM^2	-5.91	-2.01	1.14	0.26	12	-4.46	-1.37	0.98	0.28	12
8	gHM^2	-20.83	-5.19	0.28	0.11	6	-6.34	-1.87	7.98	0.59	7
9	gHM^2	-10.71	-1.99	6.59	0.39	1	-7.11	2.06	10.99	0.75	2
10	gHM^2	-2.37	-0.96	0.53	0.16	3	-4.31	-1.79	0.04	0.10	3
12	gHM^2					0	-9.69	-5.91	-2.40	0.01	1
14	gHM^2	-110.84	-10.95	90.30	0.44	1	-11.00	-0.67	9.74	0.97	1

Table 2. Sex-stratified summary of coefficient values for the urban refugia model based on the 80% uncertainty interval (UI) of each variable's posterior estimates. The % Positive value represents the percentage of samples that were above zero. Covariates include deciduousness (ΔEVI), elevation, and the gradient of human modification index (gHM).

		Summer					Winter				
Sex	Coefficient	10% UI	Mean	90% UI	% Positive	N	10% UI	Mean	90% UI	% Positive	N
Bull	ΔEVI	-0.13	0.21	0.65	0.75	27	-0.40	0.14	0.67	0.65	29
Cow	ΔEVI	-0.18	0.17	0.55	0.71	67	-0.43	0.05	0.54	0.59	72
Bull	elevation	-7.61	-1.06	5.24	0.45	27	-3.09	3.44	13.54	0.68	29
Cow	elevation	-8.83	0.91	4.35	0.41	67	-3.88	2.60	9.55	0.62	72
Bull	gHM	-783.63	-9.48	765.26	0.56	27	-7.74	1.91	12.23	0.48	29
Cow	gHM	-10.45	-0.58	14.89	0.58	67	-6.12	1.06	9.37	0.64	72
Bull	gHM^2	-301.37	-19.40	206.17	0.30	27	-6.01	-0.04	5.07	0.46	29
Cow	gHM^2	-12.77	-3.25	1.28	0.22	67	-7.65	-2.15	3.40	0.32	72

Table 3. Strategy-stratified summary of coefficient values for the urban refugia model based on the 80% uncertainty interval (UI) of each variable's posterior estimates. The % Positive value represents the percentage of samples that were above zero. Covariates include deciduousness (ΔEVI), elevation, and the gradient of human modification index (gHM).

		Summer				Winter				
Strategy	Coefficient	10% UI	Mean	90% UI	% Positive	10% UI	Mean	90% UI	% Positive	N
Migrant	ΔEVI	0.06	0.37	0.73	0.94	-0.25	0.12	0.48	0.70	19
Mixed	ΔEVI	-0.21	0.05	0.37	0.58	-0.16	0.16	0.61	0.69	9
Resident	ΔEVI	-0.16	0.15	0.51	0.71	-0.29	0.06	0.45	0.58	45
Migrant	elevation	-6.72	8.45	12.72	0.62	-12.28	6.10	18.39	0.72	19
Mixed	elevation	-6.88	-1.33	1.80	0.34	-7.12	0.45	7.11	0.67	9
Resident	elevation	-8.47	-1.17	4.19	0.42	-2.65	1.45	7.43	0.57	45
Migrant	gHM	-438.07	51.55	736.21	0.48	-7.46	-0.41	6.77	0.44	19
Mixed	gHM	-1021.18	-41.21	820.84	0.55	-10.19	0.05	3.14	0.49	9
Resident	gHM	-6.58	2.01	12.76	0.60	-3.97	2.55	9.93	0.71	45
Migrant	gHM^2	-211.72	-16.37	145.52	0.33	-6.94	-1.75	5.39	0.55	19
Mixed	gHM^2	-337.91	-17.25	261.54	0.30	-11.43	-1.88	2.38	0.34	9
Resident	gHM^2	-10.25	-3.87	0.68	0.16	-6.33	-1.94	1.61	0.25	45

CHAPTER III

ALASKAN MOOSE IN SUBURBIA: ECOLOGICAL TRAP OR URBAN REFUGIA?

ABSTRACT

As the anthropogenic footprint increases on the landscape, some wildlife species have adapted to the accompanying changes in land-uses by dwelling in urban environments. This adaption however is not without cost. Some Alaskan moose (*Alces alces*), like other cervids, have selected to live near human settlements. Concomitantly, moose, especially young moose, are increasingly involved in moose-vehicle collisions (MVCs). From 2017-2020, I studied the movements of female moose marked with global positioning system transmitters to determine if female moose selection for urban refugia was influenced by maternal condition.

Using integrated step selection analysis, I quantified summer and winter selection by female moose in relation to the gradient of human modification (gHM). Year-round, reproductive-age moose selected for intermediate levels of gHM associated with high numbers of reported MVCs. In summer, younger cow moose selected for low gHM, but selection favored intermediate gHM in winter. I found higher selection for high gHM in cow moose that did not exhibit calving behavior than cows that did exhibit calving behavior. Moose observed with a calf in 2020 selected for similar levels of intermediate to high gHM, while moose not observed with a calf in 2020 avoided intermediate gHM in winter. As human development and disturbances continue to sprawl away from urban centers, roads in areas of intermediate disturbance could become ecological traps for young moose, or other cervids, that have not learned how to navigate increasing traffic volumes if the females they learn from continue to seek urban refugia.

KEYWORDS

Alces alces, Alaska, Alaskan moose, ecological trap, human-wildlife conflict, moose-vehicle collisions, urban refugia, ungulates

Urbanization of the landscape alters the sensory cues on which wildlife base their behavior, and the ability of wildlife to adapt to such change is reduced as the change becomes more rapid (Sih et al. 2011, Gaynor et al. 2018, Guiden et al. 2019, Ditmer et al. 2021). Increased human activity and anthropogenic landscape change redistributes predators, which are often urban avoiders, and forage, which initially decreases due to land conversion and subsequently increases due to agricultural and horticultural practices. This redistribution favors the dispersal of herbivorous prey species, which often become urban utilizers or dwellers, towards human settlements (Muhly et al. 2011, Fischer et al. 2015, Boucher et al. 2022). Densities of such prey species can become elevated enough for conflicts to arise with humans, and the effective long-term mitigation of such conflicts requires removing the incentives urban areas provide (Messmer 2000, Blumstein 2016, Honda et al. 2019).

For Alaskan moose (*Alces alces*), large mammalian predators can limit population growth by reducing calf survival (Boertje et al. 2010). Cow moose in favorable conditions will begin to reproduce at three years old (Keech et al. 2000). Once parturient, cow moose localize their movements to suitable (i.e., predator-free, forage-abundant) birthing sites by May, and the resultant calf pairs with the cow until the next spring (Keech et al. 2000, Severud et al. 2015). But ultimately, lifelong female fitness outweighs short-term neonate mortality (Duquette et al. 2014). Thus, long-term cow behavior may be more reflective of their survival needs than that of their offspring.

Encounters with predators occur in semi-consistent diel and seasonal patterns, which may only influence prey behavior at coarser scales (Kohl et al. 2018, French et al. 2022). In contrast, disturbances due to humans are consistently centralized around urban areas and transportation networks. Moose hunter effort is clustered in time and space due to harvest management policy and recreational access, which can encourage movement of moose into areas where hunting is less likely or prohibited (Brown et al. 2018, Sergeyev et al. 2021). Similarly, moose encounter consistent diel, seasonal, and spatial traffic patterns as they move towards human settlements. This is reflected in patterns of MVC risk, which are elevated when traffic volumes and speeds increase (Conover et al. 1995, McDonald et al. 2019). In the Matanuska-Susitna Borough of Alaska, most of the urban dwelling moose I studied selected to move towards suburban areas, which is where moose-vehicle collisions (MVCs) are reported most (see Chapter 1). This observation is attributed to a balancing of disturbance-, competitor-, and predator-related avoidance within the demographically variable and dynamically changing landscape of fear (LOF; Laundre et al. 2001, Palmer et al. 2017, Kohl et al. 2018).

Navigating the LOF requires balancing risk mitigation against other needs (Searle et al. 2008, Wevers et al. 2020, Palmer et al. 2022). The relative importance of each need may depend upon the individual's life history; for example, female moose selected areas closer to roads in the Yellowstone ecosystem during the calving season, which shielded offspring from traffic-averse brown bears (*Ursus arctos*; Berger 2007). In south-central Alaska, cows unsuccessful at rearing their calf the previous year were more likely to calve further from that calving location the next year (Testa et al. 2000). Demographic characteristics or physical condition may also influence this balance. Among females, age and body mass are positively related to fecundity, with the youngest cows requiring the most resource gain to successfully produce calves (Sand 1996, Keech et al. 2000). But as moose age, they must give birth to heavier offspring to be as fecund as younger moose (Ericsson et al. 2001). Cows also reduce their movements with age as they optimize their range, potentially reducing resource requirements (Hundertmark 1998). Ultimately, these differences may impact moose population density and space-use in areas where forage can be found without the influence of predation, such as in urban greenspaces.

The objective of this study is to determine the role of demographics in female moose space-use patterns that elevate MVC risk. Based on the life history differences between younger and older cows, I developed the following hypotheses and expectations: 1) cows in their growth stage (<4 years old) will have resource needs that are a greater priority than antipredator behavior; thus, cow moose should increasingly seek urban refugia with age, 2) all cows' resource needs and antipredator behavior are equal due to increasing reproductive costs with age, resulting in similar refugia seeking behavior regardless of age, and 3) resource needs are a greater priority than antipredator behavior for older than younger cows due to increasing reproductive costs with age, which may lead cows to reduce refuge-seeking behavior with age.

Additionally, reported MVCs overwhelmingly include young moose, but it is unclear whether the use of suburban environments during the first year of the calf's life constitutes an ecological trap due to refuge seeking by the cow. I hypothesized if urban areas act as refugia for cow-calf pairs, cows exhibiting calving behavior in spring and cows observed with a calf in winter should select for levels of gHM associated with lower MVC risk than other cows. Alternatively, if urban areas are a potential ecological trap for calves, cows with calves will select for levels of gHM associated with higher MVC risk. To test these hypotheses, I compared resource selection of gHM to the level of human modification that included the most MVC reports between cows that exhibited calving behavior and those that did not and between cows that were observed with a calf and those that were not. If cows that exhibited calving behavior or that were observed with a calf did not adjust their selection to areas where MVC reports were most common, then the refuge seeking behavior of the cow is unlikely to benefit the calf's survival.

STUDY AREA

I conducted my study within the southern central portion of the Matanuska-Susitna Borough of Alaska between 149.7-151.1°N longitude and 61.2-62.5°W latitude, where most of the borough's human population resides. The area has experienced the fastest population growth in Alaska in recent years and had a human population of approximately 101,135 in 2017 and 107,360 in 2020 (U.S. Census Bureau 2020). The level of human disturbance to the landscape ranged from 0 to 0.67 based on the gHM index (Figure 3-1). The area's topography ranges between sea level and a peak of 4443 m above sea level (Figure 3-1).

For the years of the study, 2017–2020, the average annual temperature was 4.1 °C, with the lowest daily temperature falling to -18.9 °C and the highest daily temperature rising to 32.2 °C. During this time, average rainfall varied between 37.0 and 46.8 cm per year, and average snowfall varied between 147.6 and 237.0 cm annually (Western Regional Climate Center 2020). Forest vegetation typically consists of alders (*Alnus* spp.), cottonwoods (*Populus* spp.), willows (*Salix* spp.), or spruces (*Picea* spp.). The Alaska Department of Fish and Game (ADFG) manages the moose population in this area (Game Management Unit 14A), which had an estimated population of 8756 moose in 2018 (T. C. Peltier, ADFG, personal communication). Approximately 330 MVCs occur each year in the most urbanized portions of the borough (Figure 3-1, Figure 3-2).

METHODS

Moose captures and monitoring

Beginning in March of 2017, the ADFG deployed 45 necklace-style GPS transmitters (30 Iridium GPS Vertex Plus Collars, 30 Iridium GPS Vertex Lite Collars, VECTRONIC Aerospace GmbH, Berlin, Germany) on moose wintering within the study area using a mixture of ground- and helicopter-based darting methods (IACUC Protocol No. 0032-2018-42). The GPS transmitters provided hourly data on moose movements in the study area, and I downloaded radio-collared moose location data via satellite link (VECTRONIC Aerospace GmbH, Berlin, Germany). As radio-marked moose mortalities were detected, the ADFG redeployed the retrieved GPS transmitters.

Integrated step selection analysis

Integrated step selection analysis (iSSA) simultaneously quantifies resource selection and step selection via conditional logistic regression, wherein the dependent variable represents whether consecutive pairs of GPS locations (steps) were used or available to the animal and the independent variables represent the resources at either the start or end of the step and the step characteristics (Avgar et al. 2016). Using a series of GPS locations recorded for each animal every 5 hours, I computed the gamma distribution of the step lengths using the distance between consecutive steps and the von Mises distribution of the turn angles using directional persistence between consecutive steps. I used a temporal resolution of 5 hours to get adequate sampling of each hour of the day while reducing autocorrelation and computation effort. I computed these movement measurements and their distributions using the *amt* package in R (R Core Team 2022, Signer et al. 2011). Then, I used the resulting distributions to sample 15 available steps the animal could have taken for each location at the start of each step.

I extracted the covariates, deciduousness, elevation, and gHM, to each used and available step and paired the series of steps with the same start location to stratify the inputs to the conditional logistic regression model. Using the *stan_clogit* function from the *rstan* package in R, I computed individual conditional logistic regression models for each moose during each year's summer (July 1 to August 31) and winter (December 1 to March 31) life-history period (Ballard and Whitman 1988, Stan Development Team 2022). I sampled coefficient estimates using 4 Markov chains, 2000 iterations per chain, and 1000 warmup iterations per chain resulting in 4000 posterior samples per moose-season-year combination. Available steps and used steps beginning at the same starting location were set to the same strata identifier in the conditional logistic regression model, which is a grouping mechanism used in analyses where there is only 1 success (the used step) contrasted against multiple failures (the available steps). The resulting effect sizes of each resource-based covariate are considered free of the bias of movement while the resulting effect sizes of each movement-based covariate are considered resource-independent (Avgar et al. 2016).

Covariates

Using the *rgee* package implemented in R, I extracted covariates representing deciduousness, elevation, and gHM to each available step and used step from Google Earth Engine (Gorelick et al. 2017, Aybar et al. 2020). The deciduousness covariate is represented by the change in phenological measurements across the growing season (Street et al. 2015). I first considered using the Normalized Difference Vegetation Index (NDVI) as done in previous studies, but due to persistent cloud cover in the region, I opted for the Enhanced Vegetation Index (EVI), which removes smoke and cloud cover. I extracted EVI values from the Terra Moderate Resolution Imaging Spectroradiometer 16-day 250 m vegetation index dataset (MOD13Q1.061; Land Processes Distributed Active Archive Center 2021) for each year of the study. I calculated the change in EVI (ΔEVI) value using the EVI values for July and October for each year and extracted the resulting ΔEVI value to each used and available step endpoint. High values of ΔEVI indicate a significant change in productivity across seasons, making ΔEVI a helpful index ranging from no cover (low ΔEVI) to deciduous cover (high ΔEVI). To each used and available step endpoint, I also extracted the elevation covariate using the 3D Elevation Program 10 m Digital Elevation Model (US Geological Survey 2021).

Then, I extracted the gHM value represented by each position as my measure of anthropogenic landscape disturbance (Kennedy et al. 2018). High values of gHM represent highly modified urban landscapes, while low values of gHM represent less modified landscapes. As the gHM index is scaled between 0 and 1 and covers the entire globe, low values are those near 0 and high values are near 1. In this study area, which is relatively less urban than other areas of the globe, the maximum value of gHM was near 0.67. For my study, I equated gHM with the level of risk perceived by the moose, as the amount of human modification to the environment which should approximate the amount of anthropogenic sensory cues experienced by the animal. Deciduousness, elevation, and gHM covariate values were scaled and centered at zero for analysis.

From my iSSA, I included the movement-based covariates: step length, ln-transformed step length, and cosine-transformed turn angle. The effect size of the step length and ln-transformed step length represent the difference between the shape and scale of the gamma distribution used to compute the available step lengths, and the shape and scale of the gamma distribution used to model the step lengths in the resource-independent movement kernel (Avgar et al. 2016). The effect size of the cosine-transformed turn angle represents the difference between the mean of the von Mises distribution used to compute the available turn angles, and the mean of the von Mises distribution used to model the turn angles in the resource-independent movement kernel (Avgar et al. 2016).

Moose-vehicle collision monitoring

From August 2016 to August 2020, I located MVCs reported to local law enforcement and recorded their GPS locations. I extracted gHM values from Google Earth Engine to these locations to get an estimate of MVC density in relation to the gHM index for the seasonal moose life history periods: spring (migration/calving), summer, fall (rut/migration), and winter (Ballard and Whitman 1988; Figure 3-2).

Classification of calving behavior

I classified cow moose based on the existence of calving behavior during May and June between 2017 and 2020. Following the assignment criteria of Nicholson et al. (2019), I considered a moose to exhibit calving behavior if the moose had an initial spike in movement followed by a localization of movement to within 100 m for > 3 days. This behavior has been reported for calving moose in previous studies (Welch et al. 2000, Severud et al. 2015). I calculated and plotted the distance between each consecutive hourly relocation to visually classify each moose-year of data. In Figure 3-3, I provide an example of each movement behavior.

On December 30, 2020, ADFG aerial surveyed the radio-marked cow moose for the presence of calves. I used this survey to compare expected calving behavior to confirmed calving behavior.

Hypothesis testing

To evaluate my hypotheses, I compared effect sizes using log-relative selection strength (lnRSS; Avgar et al. 2017). The lnRSS for a given covariate represents the difference in selection between two possible locations, x1 over x2, holding all other covariates equal. For lnRSS comparisons between age groups and parturition groups, posterior estimates were not averaged, as the behavior has the potential to change across years. To evaluate the first set of hypotheses, I compare seasonal lnRSS of gHM by age groups. To evaluate the second set of hypotheses, I compare seasonal lnRSS of gHM between moose that did or did not exhibit calving behavior and moose that were or were not observed with a calf during a calving survey on December 30, 2020.

RESULTS

Between 2016 and 2020, I tracked the movements of 72 cow moose resulting in a total of 120,048 summer and winter used steps. The ADFG captured a total of five yearling, 16 two-year-old, 11 three-year-old, and 40 four-year-old or older cow moose. Cows in the <4-year-old age group account for 20 summer subsamples and 48 winter subsamples. Cows in the 4+ year-old age group account for 101 summer subsamples and 116 winter subsamples. Within the 4+ year-old age group, 94 moose-years exhibited calving behavior in spring. Of these, 92 cows were tracked in summer, and 77 cows were tracked in winter. A total of nine moose-years did not exhibit calving behavior in spring when the cow was 4+ years-old. Of these, eight cows were tracked in summer and seven cows were tracked in winter. In the winter of 2020, nine cows were observed with a calf and seven cows were observed without a calf.

Population-level selection

Among the 73 radio-marked cow moose, selection coefficients were variable with 80% uncertainty intervals overlapping zero in both seasons (Table 3-1). The average response to deciduousness ($\beta_{\Delta EVI}$ = [summer: 0.16, winter: 0.06]) and elevation ($\beta_{elevation}$ = [summer: 0.37, winter: 1.82]) was positive in both seasons. Most of the posterior estimates (67%) for deciduousness were positive in summer. The posterior estimates for deciduousness in summer and elevation in both seasons were within 10% of having 50:50 positive to negative values. Average response to gHM was near zero in summer but increased in winter (β_{gHM} = [summer: 0.18, winter: 1.71]). The posterior estimates for gHM were mostly positive in winter (64%). The average response to the quadratic form of gHM was mostly negative (summer: 73%, winter: 63%) in both seasons ($\beta_{gHM}{}^2$= [summer: -3.69, winter: -1.96]).

Growth vs. reproduction hypotheses

For moose aged one to three years old, I inferred selection for 20 cows in summer and 48 cows in winter. For moose older than three years old, I inferred selection for 101 cows in summer and 115 cows in winter. When I stratified the cow moose based on these age groups, most younger moose posterior samples (62%) had a negative response to elevation unlike the broader population in summer ($\beta_{elevation}$ = [young: -2.75, old: 1.05, population: 0.37]), which was dominated by older cows that positively responded to elevation. But I found that on average both groups responded positively to elevation in winter and responses to deciduousness were similar among groups in both seasons (Appendix A, Table 1).

In summer, younger cows responded negatively to gHM on average, but the distribution of posterior samples was not very skewed (41% positive). In winter, values were similarly skewed (57% positive) but near zero. In both seasons, I found that most posterior samples from the younger cows (68-69%) were negative for the quadratic form of gHM ($\beta_{gHM}{}^2$= [summer: -5.33, winter: -2.7]). Alternatively, older cows showed positive responses to gHM, though the skew was more positive (66%) in winter (β_{gHM}= [summer: 1.86, winter: 2.03]) than summer (56%). I found that older cows also mostly responded negatively to the quadratic form of gHM (summer: 73%, winter: 60%; $\beta_{gHM}{}^2$= [summer: -2.91, winter: -1.41]).

When starting from a point with the mean value of gHM (0.34), younger cows selected for low gHM (0-0.33) in summer and avoided all values of gHM in winter when compared to the mean (Figure 3-4). Given the same conditions, older cows selected for intermediate to high levels of gHM in summer (0.34-0.43) and winter (0.34-0.57).

Parturition status hypotheses

Within the pool of reproductive-aged moose (4+ years old), most of the radio-marked moose exhibited calving behavior. I found that responses to each covariate were similar to those observed for the 4+ age group as a whole (Appendix A, Table 2). However, moose that did not exhibit calving behavior selected for higher values of gHM than moose that did exhibit calving behavior (Figure 3-5). When starting from a point with the mean value of gHM (0.34), cows that did not exhibit calving behavior selected for a broader range of high gHM values in summer (0.34-0.61) and winter (0.34-0.67) than cows that did exhibit calving behavior. Given the same conditions, cows that did exhibit calving behavior selected for a slightly lower range of gHM in summer (0.34-0.41) than winter (0.34-0.55).

In 2020, I inferred selection from nine cows observed with a calf and seven cows that were not observed with a calf in both summer and winter. Of the seven moose observed without a calf in winter, six exhibited calving behavior the previous spring. All nine moose that were observed with a calf also exhibited calving behavior the previous spring. Within this year of data, I found responses to gHM that were not congruent with estimates pooled across years (Appendix A, Table 3). While moose observed with calves responded similarly to gHM as those exhibiting calving behavior, I found that single cows avoided the mean level of gHM in winter and selected for more extreme values compared to the mean (Figure 3-6). When starting from a point with the mean value of gHM (0.34), cows observed with calves selected for intermediate to high levels of gHM in summer (0.34-0.57) and expanded the upper bound of their selection to a higher level of gHM in winter (0.34-0.67). Cows that were not observed with calves selected for intermediate to high levels of gHM in summer (0.34-0.67), but then selected for extreme values of gHM in winter (0-0.34; 0.34-0.67). The inversion of the dashed winter parabola indicates avoidance of the mean and selection for the extremes, which is in opposition to the parabola graphed for the summer.

DISCUSSION

To determine the role of demographics in moose space-use patterns that elevate MVC risk, I studied the behavioral responses of female moose to various levels of human development and disturbance in the Matanuska-Susitna Borough of Alaska. Anthropogenic disturbances and alteration of the landscape cause a redistribution of forage, prey, and predators that often encourages prey species to utilize or dwell in more developed environments (Fischer et al. 2015). To successfully mitigate MVC risk, we must decipher the trade-offs that lead moose to select for potentially hazardous aspects of their environment (Blackwell et al. 2016). While the inferences here are limited to averages, as most uncertainty intervals overlapped zero, each reproductively aged cohort displays a consistent selection for urban areas in winter. While cow moose did avoid urban areas in some cases, the level of development associated with the most MVC reports overlaps the level of development selected for by moose in each group. This suggests that calf survival in relation to MVCs may not be the primary driver of resource selection by cow moose living near human settlements.

For moose populations in south-central Alaska, the geographic range seasonally contracts as snow depths increase at higher elevations, likely due to the locomotory cost of traversing deep snow (Ball et al. 2001). As the cow moose in this study formed their winter ranges, avoidance of human settlements decreased for all groups. As human settlements in the area are at lower elevations, this decrease is likely attributable to lower snow depths.

For reproductive-aged cows, this decrease in avoidance was minimal, and avoidance of natural and urban environments were relatively similar in both seasons, consistent with other studies in urban environments that provide shielding from predators (Berger 2007). However, cows in the younger age group selected to be farther from human settlements in summer, which may provide support for the hypothesis that growth stage resource needs outweigh anti-predator behavior. Other studies have found similar results wherein younger moose typically travel farther than older moose, ostensibly in search of better-quality forage, while older moose sustain their home ranges (Hundertmark 1998). Other hypotheses could also explain this difference in selection between age groups, as older moose may simply have been more likely to survive due to their initial choice of selection, which could be due to learned predator avoidance behavior when they were calves or from exploratory movements as they aged that led them to human shielded areas. Younger moose could also be fenced from urban refugia by more dominant individuals depending on the density of moose in the area and the availability of browse.

Regarding the parturition-based hypotheses, all reproductively aged cows' peaks in selection continued to overlap areas of high MVC risk in winter. In summer, selection for the level of development by cows that did not exhibit calving behavior remained similar to selection in winter. Cows that did exhibit calving behavior were more likely to avoid the more urban areas in both seasons than cows that did not. As cows with calves are more sensitive to predation risk, they may also be more sensitive to disturbance, leading them to avoid developed areas more than cows without calves. In summer, the relaxation of urban selection by cows that exhibited calving behavior may also be due to the snow depth change. As MVC risk is lower and less clustered, it is unlikely that the disturbances related to MVC risk would deter moose from these areas in summer if they do not impact selection in winter, when MVC risk is high and clustered near urban areas.

In future studies, uncertainty in parturition assignment should be calculated and incorporated into the model. I completed a simple visual check, but a more comprehensive version would algorithmically assign calving behavior status using the same criteria used by Nicholson et al. (2019). In their evaluation, using a visual method, a rolling window minimum convex polygon (rMCP) method, and a behavioral change point analysis (BCPA) method, all methods resulted in similar results, but the rMCP and BCPA methods allowed for uncertainty estimates to be assigned based on how well each moose fit the defined parameters. Additionally, calving surveys, like the one conducted in 2020 in this study, could be performed to identify which moose had surviving calves and to identify potential false positives in parturition assignments. However, moose are less detectable during spring surveys than during winter surveys when snow is present, so detection is less likely directly following parturition.

Consequently, using a visual only method and having only winter surveys to check for false positives, I chose not to directly incorporate uncertainty into the models. The number of moose that are considered to exhibit calving behavior may be overestimated if they were unusually slow for a period during the spring, and any moose that moved unusually quickly following parturition will not have been classified as exhibiting calving.

Moose observed with a calf in the winter of 2020 selected to be closer to urban areas in both seasons, and avoidance increased in summer within this cohort. This provides additional support for the ecological trap hypothesis, as cow behavior did not change with the addition of a calf, but due to a lack of calf survival data, inferences here are limited and based on observed cow behavior. Cows observed alone, all but one of which exhibited calving behavior, avoided both extremes of human developement in summer, yet selected to be near both extremes in winter. Reproductively aged cows selecting more natural areas was relatively uncommon in this study and could be due to the low sample size for this cohort. However, cows that lose calves change their movement patterns, so this could also be evidence of calves lost before winter (Obermoller et al. 2019).

Most reported MVCs involve young moose, and this phenomenon is likely to continue if reproductively aged moose continue to be driven to urban areas by high snow depths in higher elevations and the potential for predation in low-lying non-urban areas. The relative synchronicity and spatial clustering of human disturbances in developed environments may be easier to adapt to than the potentially asynchronous and spatially disparate predator encounters in more natural environments (Palmer et al. 2022). As moose are exposed to human disturbances each winter, desensitization may also occur over time, reducing fear with age and encouraging urban dwelling (Honda et al. 2019). These influences could explain the selection for intermediately disturbed urban areas, but mainly, the results support avoidance of both extremes in most cases.

Past studies of antipredator behavior and predator-shielding have shown that predators avoid human disturbance leading to a perception of safety by prey species living near human settlements and infrastructure (Berger 2007, Muhly et al. 2011, Shannon et al. 2014), but few discuss the potential for this perception of safety to be maladaptive. If MVC rates and urban moose population densities continue to increase, a ‘hunting for fear’ tactic, wherein harvest pressure is applied to reduce use of targeted areas, could be useful for reducing female moose selection of high MVC risk road corridors (Cromsigt et al. 2013). Landscape-level hunter access impacts the space-use of male ungulates, but female ungulates are less impacted by harvest pressure (Kucera 1992, Brown et al. 2018). In this study, cow moose are available for harvest during antlerless winter hunts only, while bull moose are sought during both winter and fall hunts. Similarly, human disturbance, such as targeted hazing, has the potential to change moose behavior but will need to be asynchronous to avoid temporary displacement (Kohl et al. 2018). Whatever course of action is taken, the perception of safety near human settlements will need to decrease if female moose are expected to reduce their use of urban areas long term (Neumann et al. 2011, Honda et al. 2019).

MANAGEMENT CONSIDERATIONS

The female moose I studied had variable selection patterns in summer, with younger cows opting for less developed areas, where they are more likely to find quality forage, predators, and less human disturbance. Ultimately, the young and old cow moose tended to congregate toward human settlements in winter, where most reproductively aged moose selected to stay year-round. With young moose being the main demographic involved in MVCs, the perception of safety for cows may constitute an ecological trap for their calves. Perceptions of safety near human settlements, and especially near heavily trafficked road corridors, should be discouraged if we aim to reduce population density and subsequently MVC risk.

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REFERENCES

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

Avgar, T., S. R. Lele, J. L. Keim, and M. S. Boyce. 2017. Relative selection strength: quantifying effect size in habitat- and step-selection inference. Ecology and Evolution 7:5322–5330.

Aybar, C., Q. Wu, L. Bautista, R. Yali, and A. Barja. 2020. rgee: An R package for interacting with Google Earth Engine. Journal of Open Source Software 5:2271.

Ball, J. P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. Wildlife Biology 7:39–47.

Ballard, W. B., and J. S. Whitman. 1988. Susitna hydroelectric project, final report, big game studies, Vol. II-Moose Upstream. Alaska Department of Fish and Game. https://www.arlis.org/docs/vol1/Susitna/41/APA4128.pdf

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.

Blackwell, B. F., T. L. DeVault, E. Fernández-Juricic, E. M. Gese, L. Gilbert-Norton, and S. W. Breck. 2016. No single solution: application of behavioural principles in mitigating human–wildlife conflict. Animal Behaviour 120:245–254.

Blumstein, D. T. 2016. Habituation and sensitization: new thoughts about old ideas. Animal Behavior 120:255–262.

Boertje, R. D., M. A. Keech, and T. F. Paragi. 2010. Science and values influencing predator control for Alaska moose management. Journal of Wildlife Management 74:917–928.

Boucher, N. P., M. Anderson, A. Ladle, C. Procter, S. Marshall, G. Kuzyk, B. M. Starzomski, and J. T. Fisher. 2022. Cumulative effects of widespread landscape change alter predator–prey dynamics. Scientific Reports 12:11692.

Brown, C. L., K. Kielland, T. J. Brinkman, S. L. Gilbert, and E. S. Euskirchen. 2018. Resource selection and movement of male moose in response to varying levels of off-road vehicle access. Ecosphere 9:e02405.

Conover, M. R., W. C. Pitt, K. K. Kessler, T. J. DuBow, and W. A. Sanborn. 1995. Review of human injuries, illnesses, and economic losses caused by wildlife in the United States. Wildlife Society Bulletin 23:407–414.

Cromsigt, J. P. G. M., D. P. J. Kuijper, M. Adam, R. L. Beschta, M. Churski, A. Eycott, G. I. H. Kerley, A. Mysterud, K. Schmidt, and K. West. 2013. Hunting for fear: innovating management of human–wildlife conflicts. Journal of Applied Ecology 50:544–549.

Ditmer, M.A., D. C. Stoner, C. D. Francis, J. R. Barber, J. D. Forester, D. M. Choate, K. E. Ironside, K. M. Longshore, K. R. Hersey, R. T. Larsen, et al. 2021. Artificial nightlight alters the predator–prey dynamics of an apex carnivore. Ecography 44: 149–161. https://doi.org/10.1111/ecog.05251

Duquette, J. F., J. L. Belant, N. J. Svoboda, D. E. B. Jr, and P. E. Lederle. 2014. Effects of maternal nutrition, resource use and multi-predator risk on neonatal white-tailed deer survival. PLOS One 9:e100841.

Ericsson, G., K. Wallin, J. P. Ball, and M. Broberg. 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. Ecology 82:1613–1620.

Fischer, J. D., S. C. Schneider, A. A. Ahlers, and J. R. Miller. 2015. Categorizing wildlife responses to urbanization and conservation implications of terminology. Conservation Biology 29:1246–1248.

French, J. T., N. J. Silvy, T. A. Campbell, and J. M. Tomeček. 2022. Divergent predator activity muddies the dynamic landscape of fear. Ecosphere 13:e3927.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science 360:1232–1235.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. Google Earth Engine: planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18–27.

Guiden, P. W., S. L. Bartel, N. W. Byer, A. A. Shipley, and J. L. Orrock. 2019. Predator–prey interactions in the Anthropocene: reconciling multiple aspects of novelty. Trends in Ecology and Evolution 34:616–627.

Honda, T., N. Yamabata, H. Iijima, and K. Uchida. 2019. Sensitization to human decreases human-wildlife conflict: empirical and simulation study. European Journal of Wildlife Research 65:71.

Hundertmark, K. J. 1998. Home range, dispersal and migration. Pages 303–335 *in* A. W.

Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution Press, Washington, DC, USA.

Keech, M. A., R. T. Bowyer, J. M. V. Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. The Journal of Wildlife Management 64:450–462.

Kennedy, C. M., J. R. Oakleaf, D. M. Theobald, S. Baruch-Mordo, and J. Kiesecker. 2019. Managing the middle: a shift in conservation priorities based on the global human modification gradient. Global Change Biology 25:811–826.

Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. Ecological Monographs 88:638–652.

Kucera, T. E. 1992. Influences of sex and weather on migration of mule deer in Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52:122–130.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. Canadian Journal of Zoology 79:1401–1409.

McDonald, L. R., T. A. Messmer, and M. R. Guttery. 2019. Temporal variation of moose-vehicle collisions in Alaska. Human–Wildlife Interactions 13:8.

Messmer, T. A. 2000. The emergence of human-wildlife conflict management: turning challenges into opportunities. International Biodeterioration and Biodegradation 45:97–102.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani. 2011. Human activity helps prey win the predator-prey space race. PLoS One 6:e17050.

Neumann, W., G. Ericsson, and H. Dettki. 2011. The impact of human recreational activities: moose as a case study. Alces 47:17–25.

Nicholson, K., M. Warren, C. Rostan, J. Månsson, T. Paragi, and H. Sand. 2019. Using fine-scale movement patterns to infer ungulate parturition. Ecological Indicators 101:22–30.

Obermoller, T. R., G. D. Delgiudice, and W. J. Severud. 2019. Maternal behavior indicates survival and cause-specific mortality of moose calves. The Journal of Wildlife Management 83:790–800.

Palmer, M. S., J. Fieberg, A. Swanson, M. Kosmala, and C. Packer. 2017. A 'dynamic' landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. Ecology Letters 20:1364–1373.

Palmer, M. S., K. M. Gaynor, J. A. Becker, J. O. Abraham, M. A. Mumma, and R. M. Pringle. 2022. Dynamic landscapes of fear: understanding spatiotemporal risk. Trends in Ecology and Evolution 37: 911–925.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Sand, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. Oecologia 106:212–220.

Searle, K. R., C. J. Stokes, and I. J. Gordon. 2008. When foraging and fear meet: using foraging hierarchies to inform assessments of landscapes of fear. Behavioral Ecology 19:475–482.

Sergeyev, M., B. R. McMillan, L. K. Hall, K. R. Hersey, C. D. Jones, and R. T. Larsen. 2022. Reducing the refuge effect: using private-land hunting to mitigate issues with hunter access. Journal of Wildlife Management 86:e22148.

Severud, W. J., G. D. Giudice, T. R. Obermoller, T. A. Enright, R. G. Wright, and J. D. Forester. 2015. Using GPS collars to determine parturition and cause-specific mortality of moose calves. Wildlife Society Bulletin 39:616–625.

Shannon, G., L. S. Cordes, A. R. Hardy, L. M. Angeloni, and K. R. Crooks. 2014. Behavioral responses associated with a human-mediated predator shelter. PLOS One 9:e94630.

Signer, J., J. Fieberg, and T. Avgar. 2011. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution 2019:880–890.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications 4:367–387.

Stan Development Team. 2022. RStan: the R interface to Stan. R package version 2.21.5.

Street, G. M., L. M. Vander Vennen, T. Avgar, A. Mosser, M. L. Anderson, A. R. Rodgers, and J. M. Fryxell. 2015. Habitat selection following recent disturbance: model transferability with implications for management and conservation of moose (*Alces alces*). Canadian Journal of Zoology 93:813–821.

Testa, W., E. F. Becker, and G. R. Lee. 2000. Movements of female moose in relation to birth and death of calves. Alces 36:8.

Welch, I. D., Rodgers, A. R., and McKinley, R. S. 2000. Timber harvest and calving site fidelity of moose in northwestern Ontario. Alces 36:93-103.

Wevers, J., J. Fattebert, J. Casaer, T. Artois, and N. Beenaerts. 2020. Trading fear for food in the Anthropocene: how ungulates cope with human disturbance in a multi-use, suburban ecosystem. Science of the Total Environment 741:140369.

TABLES AND FIGURES

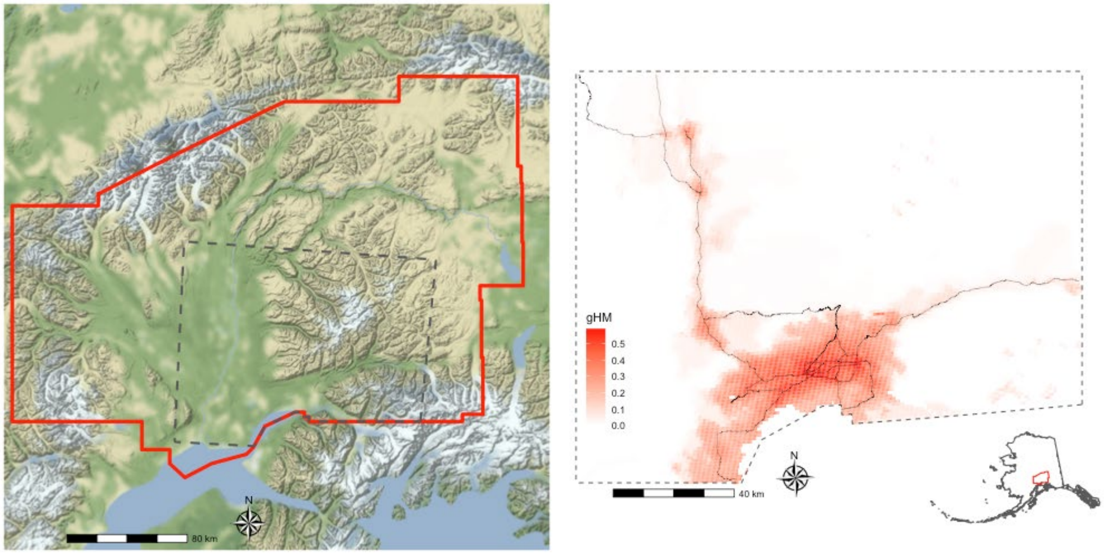

Figure 3-1. A gradient of human modification index (gHM) denoting the level of human modification to the landscape in the moose (*Alces alces*)-vehicle collision abatement study area, Matanuska-Susitna Borough, Alaska, USA, 2017-2022. In the main map, the lines represent major roads and highways in the study area. The left map shows a dashed outline of the study area and a red outline of the borough atop a stamen terrain map.

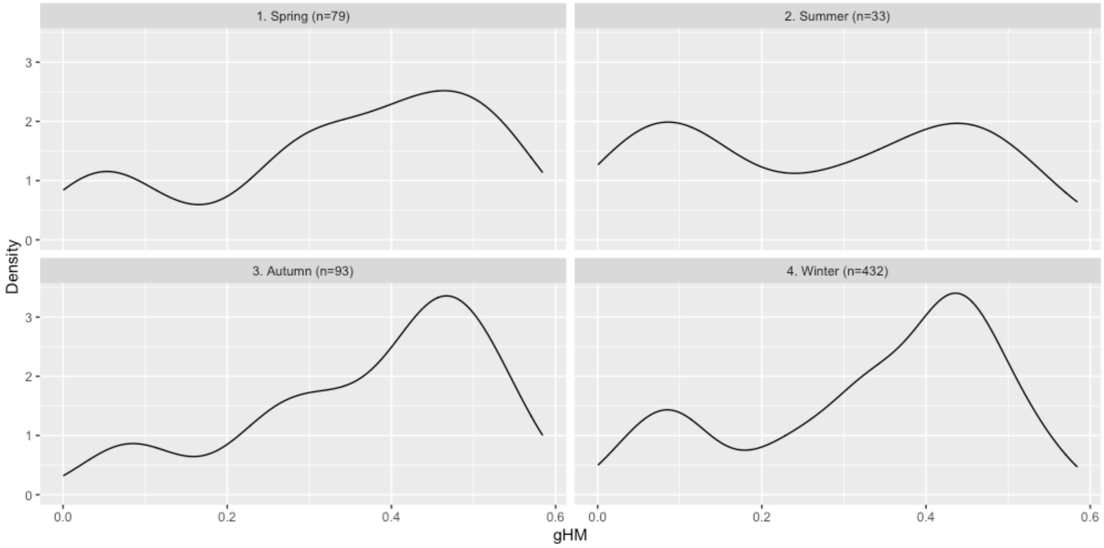

Figure 3-2. Gradient of human modification (gHM) indices at moose (*Alces alces*)-vehicle collision locations in the Matanuska-Susitna Borough, Alaska, USA study area, 2016-2020.

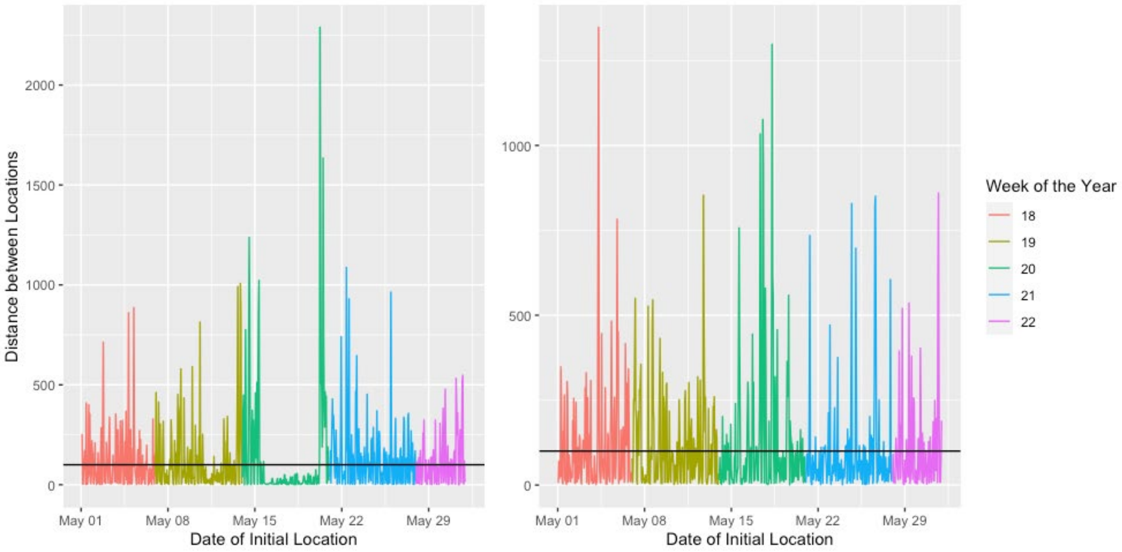

Figure 3-3. Examples of two calving behaviors exhibited by two cow moose (*Alces alces*) in May 2017 in the Matanuska-Susitna Borough, Alaska, USA study area. Calving behavior is typified by a spike during spring followed by a period of sustained movement for 3 or more days and within 100 m, marked in both plots as the horizontal black line. The left plot shows movement typical of a moose that likely calved. The right plot shows movement typical of a moose that likely did not calve.

Table 3-1. Population summary of seasonal cow moose (*Alces alces*) selection coefficient values based on the 80% uncertainty interval (UI) of each variable's posterior estimates, Matanuska-Susitna Borough, Alaska, USA study area, 2017-2020. The % Positive value represents the percentage of samples that were above zero. Covariates include deciduousness (ΔEVI), elevation, and the gradient of human modification index (gHM).

	Summer				Winter			
Coefficient	10% UI	Mean	90% UI	% Positive	10% UI	Mean	90% UI	% Positive
ΔEVI	-0.29	0.16	0.64	0.67	-0.45	0.06	0.59	0.56
elevation	-8.38	0.37	5.54	0.42	-5.19	1.82	9.30	0.55
gHM	-8.31	0.18	15.92	0.56	-7.03	1.71	11.07	0.64
gHM^2	-11.58	-3.69	1.93	0.27	-8.60	-1.96	3.95	0.37

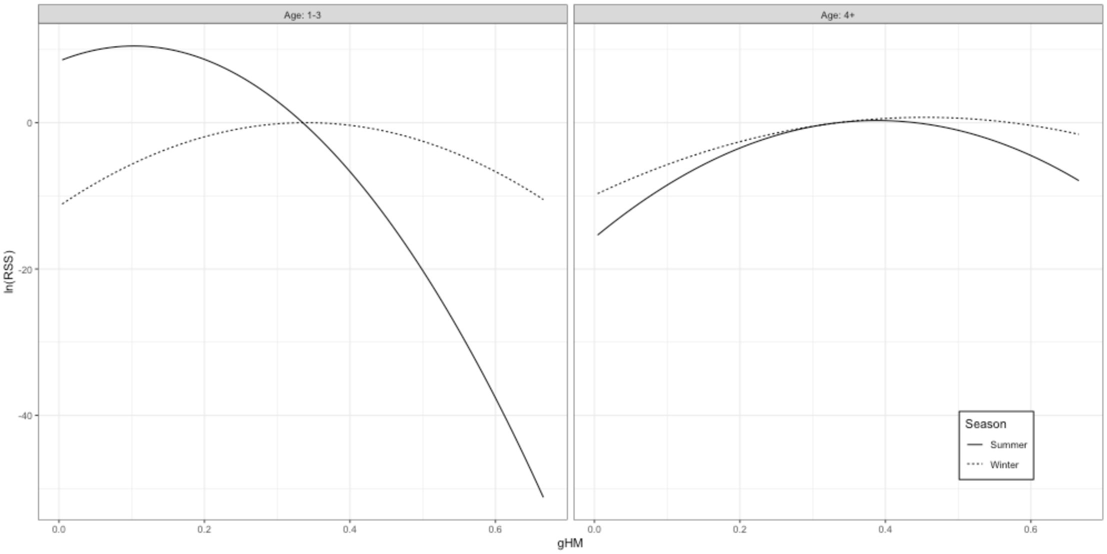

Figure 3-4. Seasonal log-relative selection strength (lnRSS) for selecting a step (x1) with any value of gHM compared to a step (x2) with the average value of gHM for moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA study area, 2017-2020. gHM represents the gradient of human modification index value at x1. lnRSS values were calculated using the average of the coefficients from the urban refugia models' posterior samples. I split the moose-season-year data into two groups based on whether they were aged one to three years old or four plus years old.

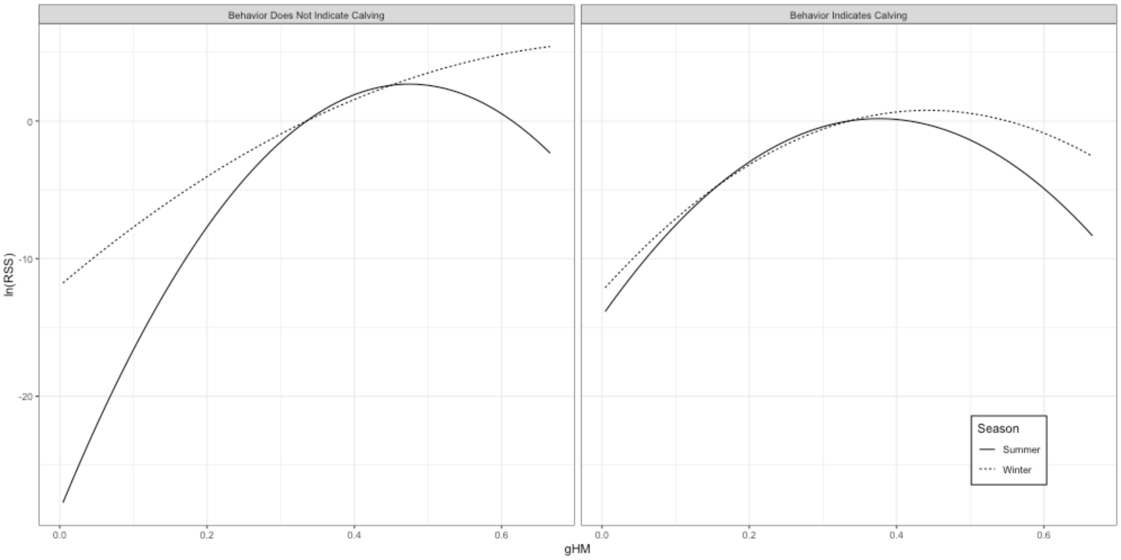

Figure 3-5. Seasonal log-relative selection strength (lnRSS) for selecting a step (x1) with any value of gHM compared to a step (x2) with the average value of gHM for calving and non-calving moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA study area, 2017-2020. gHM represents the gradient of human modification index value at x1. lnRSS values were calculated using the average of the coefficients from the urban refugia models' posterior samples. I split the moose-season-year data of the reproductively aged moose (4+) into two groups based on whether their spring movements exhibited the characteristics of calving.

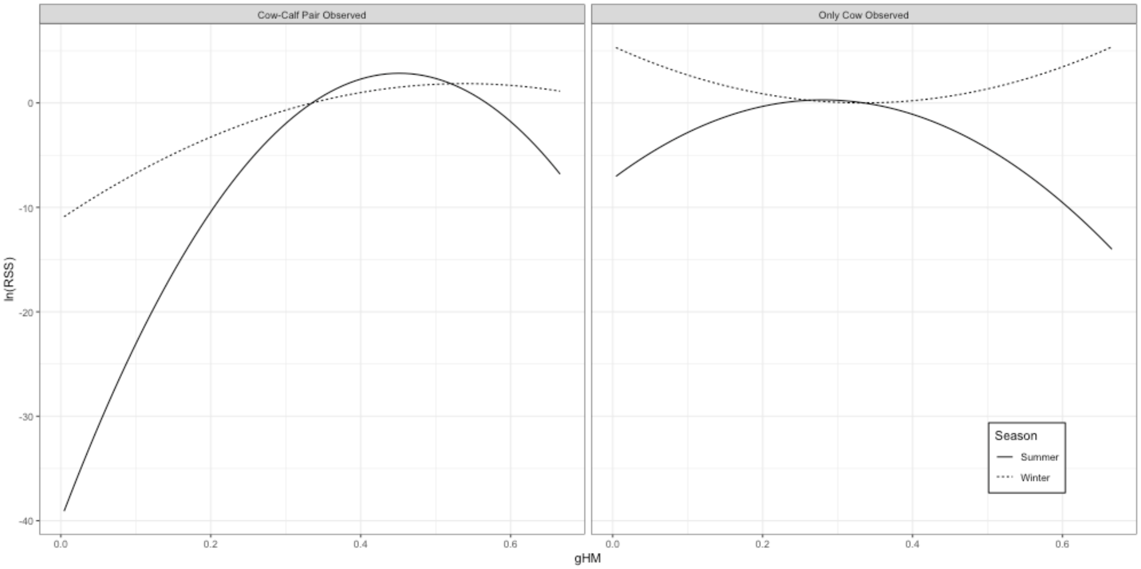

Figure 3-6. Seasonal log-relative selection strength (lnRSS) for selecting a step (x1) with any value of gHM compared to a step (x2) with the average value of gHM for moose (*Alces alces*) observed with and without calves in the Matanuska-Susitna Borough, Alaska, USA study area, 2020. gHM represents the gradient of human modification index value at x1. lnRSS values were calculated using the average of the coefficients from the urban refugia models' posterior samples. I split the moose-season-year data for 16 cows into two groups based on whether they were observed with a calf on December 30, 2020.

APPENDIX A. COEFFICIENT SUMMARIES

Table 1. Age-stratified summary of seasonal cow moose (*Alces alces*) selection coefficient values based on the 80% uncertainty interval (UI) of each variable's posterior estimates, Matanuska-Susitna Borough, Alaska, USA study area, 2017-2020. The % Positive value represents the percentage of samples that were above zero. Covariates include deciduousness (ΔEVI), elevation, and the gradient of human modification index (gHM).

		Summer				Winter			
Age	Coefficient	10% UI	Mean	90%UI	% Positive	10% UI	Mean	90%UI	% Positive
1-3	ΔEVI	-0.27	0.15	0.61	0.67	-0.37	0.13	0.68	0.63
1-3	elevation	-13.07	-2.75	3.11	0.38	-2.13	2.5	9.76	0.63
1-3	gHM	-28.42	-14.95	12.02	0.41	-12.11	0.15	11.29	0.57
1-3	gHM^2	-18.75	-5.33	1.97	0.31	-12.19	-2.7	3.84	0.32
4+	ΔEVI	-0.28	0.15	0.61	0.66	-0.44	0.03	0.5	0.54
4+	elevation	-7.13	1.05	6.22	0.42	-5.91	2.44	10.04	0.52
4+	gHM	-7.42	1.86	15.21	0.56	-5.69	2.03	10.67	0.66
4+	gHM^2	-10.34	-2.91	1.93	0.27	-6.75	-1.41	3.54	0.4

Table 2. Calving behavior-stratified summary of seasonal cow moose (*Alces alces*) selection coefficient values based on the 80% uncertainty interval (UI) of each variable's posterior estimates, Matanuska-Susitna Borough, Alaska, USA study area, 2017-2020. The % Positive value represents the percentage of samples that were above zero. Covariates include deciduousness (ΔEVI), elevation, and the gradient of human modification index (gHM).

		Summer				Winter			
Calving Behavior	Coefficient	10% UI	Mean	90%UI	% Positive	10% UI	Mean	90%UI	% Positive
Yes	ΔEVI	-0.27	0.15	0.59	0.66	-0.31	0.05	0.46	0.55
Yes	elevation	-7.34	1.13	6.27	0.41	-6.43	-3.78	6.74	0.46
Yes	gHM	-7.4	1.38	14.18	0.55	-3.45	2.39	9.63	0.72
Yes	gHM^2	-10.19	-2.77	1.88	0.27	-6.68	-1.84	2.27	0.38
No	ΔEVI	-0.59	0.17	0.78	0.72	-0.52	-0.09	0.27	0.48
No	elevation	-5.58	0.22	6.33	0.5	-3.59	1.38	6.77	0.6
No	gHM	-7.28	6.35	21.57	0.73	-6.08	4.3	14.34	0.8
No	gHM^2	-9.77	-3.76	1.96	0.19	-5.22	-0.8	5.96	0.33

Table 3. Summary of seasonal selection coefficient values for cow moose (*Alces alces*) observed with or without a calf on December 30, 2020. Coefficient estimates are based on the 80% uncertainty interval (UI) of each variable's posterior estimates, Matanuska-Susitna Borough, Alaska, USA study area, 2020. The % Positive value represents the percentage of samples that were above zero. Covariates include deciduousness (ΔEVI), elevation, and the gradient of human modification index (gHM).

		Summer				Winter			
Calf Observed	Coefficient	10% UI	Mean	90%UI	% Positive	10% UI	Mean	90%UI	% Positive
Yes	ΔEVI	-0.35	-0.06	0.32	0.37	-1.08	-0.19	0.5	0.43
Yes	elevation	-12.31	-2.48	3.83	0.33	-11.73	-4.06	7.45	0.53
Yes	gHM	-5.57	8.07	27.64	0.59	-8.33	3	16.94	0.63
Yes	gHM^2	-15.86	-5.74	1.15	0.19	-8	-1.22	3.92	0.43
No	ΔEVI	-0.05	0.17	0.46	0.78	-0.19	0.23	0.77	0.74
No	elevation	-0.84	6.24	28.75	0.69	-14.6	-1.23	7.85	0.37
No	gHM	-10.62	-1.74	12	0.26	-10.47	0.02	9.86	0.62
No	gHM^2	-10.98	-2.63	1.67	0.34	-6.69	1.33	7.66	0.58

CHAPTER IV

IMPLICATIONS OF ROAD AVOIDANCE FOR URBAN MOOSE MANAGEMENT

ABSTRACT

Wildlife develop consistent behaviors to respond to consistent threats, such as predation risk. Road networks are a relatively novel threat to herbivores compared to the native predators with which they have co-evolved, but based on past research, moose (*Alces alces*) and other ungulates typically avoid roads. I hypothesized that the impact of the disturbance on moose behavior would change with traffic and, additionally, would change either temporally or with concealment. If moose perceive roads and their associated traffic as a threat, I predicted that moose would avoid being near or crossing roads as traffic levels increased. If moose use roads for forage or snow-free travel, I predicted that moose would not avoid roads based on traffic level. If moose perceive roads as a predator shield, I predicted that moose would select to be near or cross roads of higher traffic levels. Additionally, if moose perceive roads as a temporally changing threat, I predicted that moose would be more likely to select to be near or cross roads when concealed due to light conditions or nearby vegetation. To test these predictions, I quantified moose selection of road proximity and road crossings for roads of different traffic levels and compared this selection across times of day and in relation to vegetation indices.

Between 2017 and 2020, I studied the winter movements of 86 GPS-collared moose using integrated step selection analysis to quantify avoidance of road proximity and road crossings. Moose in this study rarely crossed roads with high traffic, and on average, this was impacted by time of day, with selection for roads at night and avoidance otherwise. Concealment based on vegetation did not alter moose selection; however, moose did alter their behavior to move more slowly near roads than on average. This study adds to the growing body of research that identifies roads as threats equivalent to predation for ungulates.

KEYWORDS

Alces alces, Alaska, Alaskan moose, human-wildlife conflict, moose-vehicle collisions, risk-disturbance hypothesis, targeted hunting, ungulates

Road networks and their traffic provide spatiotemporally consistent disturbances to wildlife, which will respond to such risk uniquely based on their life histories and individual experiences. Negative impacts, both direct threats such as wildlife-vehicle collisions (WVCs) and increased predator/hunter access, and perceived threats such as traffic-based auditory, visual, and olfactory cues, lead wildlife to avoid road networks and other infrastructure associated with human activity (Forman et al. 2003, Fahrig and Rytwinski 2009). Road networks often negatively influence birds and mammals with large home ranges (Benítez-López et al. 2010, Rytwinski and Fahrig 2012). For example, songbirds avoid 'phantom roads' when traffic noise is transmitted by speakers in otherwise roadless landscapes (Ware et al. 2015). Even when accounting for utilization potential, roads can be barriers to brown bear (*Ursus arctos*) movement (Bischoff et al. 2017). Similarly, elk (*Cervus canadensis*) also avoid roads analogous to their response to predation risk (Prokopenko et al. 2016). Yet, some individuals will inevitably exploit roads, so characterizing how wildlife navigate road networks can guide WVC management by identifying contexts in which roads are crossed.

For ungulate-vehicle collisions (UVCs), managers must consider forage availability, predator/prey densities, and other environmental factors that impact ungulate movement and anti-predator/disturbance behavior to determine where road crossings are most likely to occur. Road edge vegetation management is a commonly provided solution for UVCs because it can be used to reduce forage availability or palatability (Rea 2003, Ng et al. 2008, Meisingset et al. 2014). Ungulates also avoid areas where and when the threat of predation is high (Fryxell and Sinclair 1988, Ouellet et al. 1996, White et al. 2014). This can increase the density of ungulates near roads where human activity acts as a predator shield by reducing predator densities (Berger et al. 2007, Muhly et al. 2011, Shannon et al. 2014). Simultaneously, some predators, such as wolves (*Canis lupus*), may use less trafficked roads for faster travel, increasing the likelihood that prey species will avoid roads (Zimmerman et al. 2014, Dickie et al. 2017). Additionally, anti-predator behavior may include seeking concealment, so lighting conditions and vegetation cover near roads may influence the likelihood that the road will be exploited (Passoni et al. 2021). Hot spots in UVCs may be explained by this differential response to the road system under different contexts.

In the Matanuska-Susitna Borough of Alaska, moose-vehicle collisions (MVCs) are increasing as the human population grows and urban development intensifies. MVCs are clustered in winter, when the distribution of moose shifts to lower elevations, and along the wildland-urban interface, where predation and disturbance risk can be balanced against the availability of forage and the relative lack of snow compared to more mountainous terrain (Ball et al. 2001, McDonald et al. 2019).

To determine how moose respond to roads when navigating urban environments in winter, I quantified selection based on the following hypotheses about the trade-offs moose may experience when traveling near or across roads. The first set of hypotheses is based on the avoidance or exploitation of roads in relation to the risk-disturbance and predator-shield hypotheses (Frid and Dill 2002, Berger 2007). Due to the indirect disturbance and direct threat of traffic, moose may avoid being near and crossing roads as traffic levels increase. Due to the potential for forage along roads and the potential for snow-free travel along roads, moose may select to be closer to roads or to cross them regardless of traffic. Due to the avoidance of roads by predators, traffic may act as a predator shield, encouraging movement near roads of higher traffic.

I developed two additional hypotheses related to time-dependent and context-dependent responses to roads to account for the potential dynamic landscape of fear influenced by traffic disturbance avoidance (Palmer et al. 2022). Due to the temporal variation in traffic disturbances and the potential for concealment without daylight, moose may avoid being near or avoid crossing roads more during the day or twilight periods than during the night. Due to the potential for concealment, moose may select to be near or to cross roads when vegetation cover abuts roads. Additionally, the movement speed of ungulates may change depending upon their behavior near roads (Dickie et al. 2017); for example, a slower pace is typical when foraging. However, if moose are moving much faster near roads than in other contexts, they may be attempting to avoid traffic disturbances. After determining the contexts in which moose select to be near or cross roads, I provide management recommendations for reducing MVCs.

STUDY AREA

I conducted my study within the south-central portion of the Matanuska-Susitna Borough of Alaska between 149.7-151.1°N longitude and 61.2-62.5°W latitude, where most of the borough's human population resides. The area has recently experienced the fastest population growth in Alaska and had a human population of approximately 101,135 in 2017 and 107,360 in 2020 (U.S. Census Bureau 2020). The area's topography ranges between sea level and a peak of 4443 m above sea level.

For the years of the study, 2017–2020, the average annual temperature was 4.1 ℃, with the lowest daily temperature falling to -18.9 ℃ and the highest daily temperature rising to 32.2 ℃. During this time, average rainfall varied between 37.0 and 46.8 cm per year, and average snowfall varied between 147.6 and 237.0 cm annually (Western Regional Climate Center 2020). Forest vegetation typically consists of alders (*Alnus* spp.), cottonwoods (*Populus* spp.), willows (*Salix* spp.), or spruces (*Picea* spp.). The Alaska Department of Fish and Game (ADFG) manages the moose population in this area (Game Management Unit 14A), which had an estimated population of 8756 moose in 2018 (T. C. Peltier, ADFG, personal communication). Approximately 330 MVCs occur annually in the borough. Most roads in the study area are lightly trafficked, but two major highways and one major secondary road dissect the area into four distinct sections (Figure 4-1).

METHODS

Moose captures and monitoring

Beginning in March of 2017, the ADFG deployed 60 necklace-style GPS transmitters (30 Iridium GPS Vertex Plus Collars, 30 Iridium GPS Vertex Lite Collars, VECTRONIC Aerospace GmbH, Berlin, Germany) on moose wintering within the study area using a mixture of ground- and helicopter-based darting methods (IACUC Protocol No. 0032-2018-42). The GPS transmitters provided hourly data on moose movements in the study area, and I downloaded radio-collared moose location data via satellite link (VECTRONIC Aerospace GmbH, Berlin, Germany). As radio-marked moose mortalities were detected, the ADFG redeployed the retrieved GPS transmitters.

Integrated step selection analysis

Integrated step selection analysis simultaneously quantifies resource selection and step selection via conditional logistic regression, wherein the dependent variable represents whether consecutive pairs of GPS locations (steps) were used or available to the animal, and the independent variables represent the resources at either the start or end of the step and the step characteristics (Avgar et al. 2016). Using a series of GPS locations recorded for each animal every 5 hours, I computed the gamma distribution of the step lengths using the distance between consecutive steps and the von Mises distribution of the turn angles using directional persistence between consecutive steps. I used a temporal resolution of 5 hours to get an adequate sampling of each hour of the day while reducing autocorrelation. I computed these movement measurements and their distributions using the *amt* package in R (R Core Team 2022, Signer et al. 2011). Then, I used the resulting distributions to sample 15 available steps the animal could have taken for each location at the start of each step.

I added the covariates deciduousness, slope, distance to road, road crossing, and time of day to each used and available step and paired each series of steps with the same start location to stratify the inputs to the conditional logistic regression model. Deciduousness represented vegetation, slope represented terrain difficulty, distance to road represented road proximity, road crossing represented whether a given step crossed a road, and time of day represented light conditions. Using the *stan_clogit* function from the *rstan* package in R, I computed individual conditional logistic regression models for each moose during each year's winter (December 1 to March 31) life-history period (Ballard and Whitman 1988, Stan Development Team 2022). I sampled using 3 chains, 4000 iterations, and 2000 warmup iterations, resulting in 6000 posterior estimates per moose-season-year combination. The effect sizes of each resource-based covariate are considered movement-independent, while the effect sizes of each movement-based covariate are considered resource-independent (Avgar et al. 2016).

Covariates

Using the *rgee* package implemented in R, I extracted covariates representing deciduousness and slope to each available and used step from Google Earth Engine (Gorelick et al. 2017, Aybar et al. 2020). The deciduousness covariate is represented by the change in phenological measurements across the growing season (Street et al. 2015). To represent phenology, I used Enhanced Vegetation Index (EVI) values from the Terra Moderate Resolution Imaging Spectroradiometer 16-day 250 m vegetation index dataset (MOD13Q1.061) for each year of the study (Land Processes Distributed Active Archive Center 2021). I calculated the change in EVI (ΔEVI) value using the EVI values for July and October for each year to represent summer and fall phenology and extracted the resulting ΔEVI value to each used and available step endpoint. High values of ΔEVI indicate a significant change in productivity across seasons, making ΔEVI a helpful index ranging from no cover (low ΔEVI) to deciduous cover (high ΔEVI). To compute the slope, I used the *Terrain.slope* function in Google Earth Engine on the 3D Elevation Program 10 m Digital Elevation Model and extracted the resulting slope values to each used and available step endpoint (US Geological Survey 2021). Deciduousness and slope covariate values were scaled and centered at zero for analysis.

To define covariates related to road crossing and road distance, I used the Alaska Department of Transportation and Public Facilities Routes shapefile (AK Open Data Geoportal 2016). I clipped the shapefile only to include roads within the Matanuska-Susitna Borough of Alaska and uploaded the resulting shapefile to Google Earth Engine. Using the *distance* function, I calculated raster images representing the distance to the road features contained in the original shapefile using a search radius of 10 km and a resolution of 50 m. I extracted these road distance metrics to each start and end point for each set of used and available steps. I calculated this for each road classification in the dataset representing primary, secondary, tertiary, and all roads. At the 5 hr temporal scale, very few step start or end locations were closer to a highly trafficked primary, secondary, or tertiary road than to other minor roads in the dataset. Due to lack of comparable data between the used and available cases, almost all models based on distance to roads of specific traffic levels would not converge. To identify road crossings, I created individual line objects for each used and available step using the *sf* package in R and used *st_intersect* to identify which steps intersected the road shapefile (Pebesma 2018). I also identified road crossings based on each road classification representing the various traffic levels. As with the road distance metric, very few steps intersected highly trafficked roads, so most models based on road crossings at specific traffic levels would also not converge.

Using the date and time of each used and available step, I labeled each start and end point by time of day using three categorical variables, day, twilight, and night. For each date of observation, I calculated the dawn, sunrise, dusk, and sunset times using the *sunriset* and *crepuscule* functions in the *maptools* R package and labeled each start and end point based on the time the location was recorded (Bivand and Lewin-Koh 2020).

From my iSSA, I included the movement-based covariates log-transformed step length and cosine-transformed turn angle. The effect size of the log-transformed step length represents the difference between the shape of the gamma distribution used to compute the available step lengths and the shape of the gamma distribution used to model the step lengths in the resource-independent movement kernel (Avgar et al. 2016). The effect size of the cosine-transformed turn angle represents the difference between the mean of the von Mises distribution used to compute the available turn angles and the mean of the von Mises distribution used to model the turn angles in the resource-independent movement kernel (Avgar et al. 2016).

Hypothesis testing

Initially, I intended to evaluate my first set of hypotheses by comparing the log-relative selection strength (lnRSS) of road distance and road crossing based on varying levels of traffic. The lnRSS for a given covariate represents the difference in selection between two possible locations, x1 over x2, holding all other covariates equal (Avgar et al. 2017). The first two potential outcomes, traffic as a threat and roads as forage sites, are based on the risk-disturbance hypothesis (Frid and Dill 2002). If traffic is perceived as a threat, moose should avoid being near or crossing roads as traffic levels increase. If traffic is not perceived as a threat, but roads are used as forage sites, moose may be ambivalent to traffic. If traffic is perceived as predator-shield, moose may select to be closer to or cross roads as traffic increases (Berger 2007). However, there were very few road crossings, and moose were not often near highly trafficked roads. Therefore, assessing selection in relation to primary, secondary, and tertiary road classifications was impeded, as most of the models would not converge. Instead, I summarized the distance to each class of road and the frequency that each class of road was crossed for both used and available steps to compare road avoidance across the different road classifications.

To evaluate the second set of hypotheses related to the time-dependent and context-dependent dynamic landscape of fear, I compared the effect size of the distance to all roads and the road crossing covariates at day, night, and twilight and in relation to deciduousness and step length using lnRSS. For each of the 4 models, I used the same core model [deciduousness + slope + log(step length) + cos(turn angle)]. The resource selection-based covariates are represented by deciduousness and slope. The movement-based covariates are represented by log-transformed step length and cosine-transformed turn angle. Model 1 represents the time-dependence of the effect of road distance on selection [core model + log(distance to road) + tod + log(distance to road):tod]. Model 2 represents the time-dependence of road crossings [core model + road-crossed + tod + road-crossed:tod]. Model 3 represents the context-dependence of the effect of road distance on selection [core model + log(distance to road start) + log(distance to road start):deciduousness + log(distance to road start):log(step length)]. Model 4 represents the context-dependence of the effect of road crossing on selection [core model + crossed + road-crossed:deciduousness + road-crossed:log(step length)].

To test the impact of time dependence on selecting steps near roads (Model 1), I added the resource selection-based covariates log-transformed distance between the end of the step and the nearest road, the time of day the step ended, and an interaction term including both covariates to the core model. I compare lnRSS for a given location, x1, starting at 5 m away from a road to a series of locations, x2, increasingly farther from a road during each time of day. If the selection of steps near roads is time-dependent based on traffic, lnRSS should be higher for locations near roads at night when traffic is less common than at twilight and during the day.

I added the resource selection-based covariates road-crossed, represented by true or false, the time of day the step ended, and an interaction between the two covariates to the core model to test the impact of time dependence on selecting to cross a road (Model 2). Then, I compare lnRSS for a given location, x1, that does not cross a road to a location, x2, that does cross a road during each time of day. If the selection of steps that cross roads is time-dependent based on traffic, lnRSS should be higher for steps crossing roads at night than at twilight or during the day.

To test the impact of context dependence on selecting steps near roads (Model 3), I added the log-transformed distance between the start of the step and the nearest road and the interaction between this covariate and deciduousness. Both context dependence models include interactions between the road-based covariate and the log-transformed step length to quantify the change in movement speed as the animal approaches or crosses a road. I compare lnRSS for two given locations, x1, near and far from a road and with mean deciduousness, to a series of locations, x2, near and far from a road but with varying amounts of deciduousness. If the selection of steps near roads is context-dependent based on concealment, lnRSS should be higher at steps near roads when deciduousness values are high. Movement speed should also decrease as road distance decreases if the moose is foraging, whereas movement speed should increase as road distance decreases if the moose is trying to avoid the disturbance of the road.

I added the road-crossed covariate and the interaction between this covariate and deciduousness to test the impact of context dependence on selecting to cross a road (Model 4). I compare lnRSS for a given location, x1, that does not cross a road with mean deciduousness, to a location, x2, that does cross a road but with varying amounts of deciduousness. If the selection of steps that cross roads is context-dependent based on concealment by cover, lnRSS should be higher for steps crossing roads when deciduousness values are high. Movement speed should also decrease as the moose crosses the road if it is foraging, whereas movement speed should increase as the moose crosses the road if it is trying to avoid the disturbance of the road.

Finally, I calculated lnRSS metrics using the linear predictors of each model. I subtracted the linear predictor calculated using the second location (x2) values of each variable from the linear predictor calculated using the first location (x1) values of each variable. The resulting lnRSS value represents how many times more likely the animal is to pick the first location (x1) over the second location (x2; Avgar et al. 2017).

RESULTS

Between 2017 and 2020, I tracked the movements of 101 moose, and 86 of these moose were observed during their winter life history period in at least one year. I had a total of 186 moose-winter datasets after separating observations by year. On average, moose were 0-1947 m from roads at the end of each used step, and available end steps sampled were 0-1995 m from roads. Approximately 1% of used and available steps were farther than 10 km from a road. On average, end points of moose used steps were 2656-6710 m (13.8% > 10 km), 0-4267 m (2.0% > 10 km), 0-3478 m (1.82% > 10 km) from primary, secondary, and tertiary roads, respectively. The distributions of available steps for each road classification were nearly identical to those of used steps. In this collection, moose crossed roads an average of 1.17±0.19 times per week, and 3.49% of used steps crossed roads. Only 6.51% of available steps crossed roads, and available steps crossed roads 2.19±0.67 times per week. To account for differences in the number of used (1) and available steps (15) per stratum, I divided the number of available steps that crossed roads per week by 15. Moose used steps crossed primary, secondary, and tertiary roads 0±0 times per week (0% of used steps), 0.01±0.02 times per week (0.03% of used steps), and 0.3±0.1 times per week (0.08% of used steps) respectively. Available steps crossed primary, secondary, and tertiary roads slightly more (4.98x10^-4, 0.02, and 0.07) times per week than used steps, with 0%, 0.05%, and 0.22% of available steps crossing each road class per week.

Because so few moose used areas near or crossed highly trafficked road classes, I focused on modeling the time-dependent and context-dependent dynamic landscape of fear hypotheses on distances to all roads and all road crossings. When attempting to model based on distances to only primary, secondary, or tertiary roads, most moose-season datasets were rejected due to an inability to converge based on a lack of variation in data for each covariate. The average distance to the nearest road increased as the expected level of traffic on the road increased. The average number of road crossings per week also decreased as the expected traffic on the road increased. When modeling without consideration of road classification, many moose-season datasets were still rejected due to a lack of variation across the categorical responses. For example, if the moose never crossed a road during twilight, that entire moose-season of data could not converge on a posterior estimate without dropping twilight as a variable, making comparison to successfully run models invalid.

I successfully ran 142 time-dependent road avoidance models (Model 1), 37 time-dependent road crossing models (Model 2), 145 context-dependent road avoidance models (Model 3), and 108 time-dependent road crossing models (Model 4). Time-dependent road crossing models were rarely successful because each time of day needed to include at least 2 crossings by available steps in each moose-season to avoid rejection. Among the time-dependent road avoidance models, used end steps were an average of 0-2186 m from the nearest road, and available steps were 0-2233 m from the nearest road. Among the context-dependent road avoidance models, the used and available start steps were 0-2198 m from the nearest road on average. Among the time-dependent road crossing models, used steps crossed roads 2.48±2.01 times per week, and available steps crossed roads 4.58±5.14 times per week. Among the context-dependent road crossing models, used steps crossed roads 0.83±0.27 times per week, and available steps crossed roads 1.52±0.47 times per week.

Among the models summarized below, I found consistent responses to the deciduousness, slope, cosine-transformed turn angle, and time of day variables. The average responses to deciduousness were all positive but near zero. The average responses to increasing slope were all consistently negative except for the time-dependent road crossing model, which was near zero. The average responses to cosine-transformed turn angle were all positive and consistently above zero. For the time-dependent models, the average effects of the night and twilight covariates were consistently near zero. The coefficient means and 80% uncertainty intervals for each covariate above are listed in Tables 1–4 with the remaining covariates.

Time-dependent Road Avoidance

Using the locations of 74 moose tracked during the winters of 2017–2020, I constructed 142 time-dependent road avoidance models (Model 1). The average response to log-transformed road distance was positive ($\beta_{\log(\mathrm{dist})} = 0.27$), and above zero (Table 4-1). The average response to log-transformed road distance decreased at night and twilight, and the effect of the interaction at night ($\beta_{\log(\mathrm{dist}):\mathrm{night}} = -0.33$) was consistently below zero, while the effect of the interaction at twilight was near zero (Table 4-1). The average coefficient for log-transformed step length was negative, but near zero (Table 4-1).

When I computed the lnRSS comparison between a step near a road and a series of steps increasingly far from a road, moose consistently avoided roads during the day, but the avoidance decreased during the twilight period, and on average, moose selected to be closer to roads at night (Figure 4-2). At both night and twilight, uncertainty intervals overlap zero.

Time-dependent Road Crossings

Using the locations of 26 moose tracked during the winters of 2017-2020, I constructed 37 time-dependent road-crossing models (Model 2). The average response to a step that crossed a road was negative (β_{cross} = -0.89) and consistently below zero (Table 4-2). The average responses to steps that crossed a road increased at night and twilight, but the effect of these interactions was also near zero (Table 4-2). The average coefficient for log-transformed step length was positive ($\beta_{log(sl)}$ = 0.04), and slightly above zero (Table 4-2).

When I computed the lnRSS comparison between a step that crossed a road and a step that did not during the three time periods, moose consistently avoided steps that crossed roads during the day, and on average, avoided steps that crossed roads at night and twilight (Figure 4-3). But, at night and twilight, the uncertainty intervals overlapped zero.

Context-dependent Road Avoidance

Using the locations of 76 moose tracked during the winters of 2017-2020, I constructed 145 context-dependent road avoidance models (Model 3). The average response to the start of the step log-transformed road distance and the interaction between this covariate and deciduousness were near zero (Table 4-3). The average coefficient for log-transformed step length was negative, while the interaction between this metric and log-transformed start step road distance was positive, but both coefficients were near zero (Table 4-3).

Comparing a step with average deciduousness to a series of steps with varying deciduousness, higher values of deciduousness were selected for on average, but uncertainty intervals overlapped zero at any distance to a road (Figure 4-4). The selection-free displacement rate for this model was 230.6 m. When I computed the lnRSS comparison between a step of average length (220 m) and a range of step lengths, selection for steps of shorter length increased as the distance to a road decreased (Figure 4-5). Uncertainty intervals also overlapped zero for this interaction, but on average, increasing the distance to a road decreased selection of small steps in favor of average steps.

Context-dependent Road Crossings

Using the locations of 64 moose tracked during the winters of 2017-2020, I constructed 108 context-dependent road avoidance models (Model 4). The average response to steps that crossed roads was negative but near zero (Table 4-4). On average, the effect of the interaction between steps that crossed roads and deciduousness was near zero (Table 4-4). The average coefficient for log-transformed step length was positive, while the effect of the interaction between this metric and steps that crossed road was negative, but both means were near zero (Table 4-4).

When I computed the lnRSS comparison between a step with average deciduousness to a series of steps with varying deciduousness, higher values of deciduousness were selected for on average, and selection for higher values of deciduousness increased when the step crossed a road, but uncertainty intervals overlapped zero regardless of whether a road would be crossed (Figure 4-6). The selection-free displacement rate for this model was 230.6 m. When I computed the lnRSS comparison between a step of average length (220 m) and a range of step lengths, selection for shorter length steps increased when the step crossed a road (Figure 4-7).

Uncertainty intervals also overlapped zero for this interaction, but on average, moose took shorter (slower speed) steps when crossing a road and avoided the same speeds when not crossing a road.

DISCUSSION

I analyzed the winter movements of Mat-Su Valley moose in relation to the road system by quantifying selection of steps based on the distance to the nearest road and whether the step crossed a road. The results support the risk-disturbance hypothesis rather than the predator-shield hypothesis. Moose in my study area rarely crossed roads, which made it difficult to quantify selection for most of the moose I tracked. Still, this inability to model selection based on different levels of traffic provides evidence that moose avoid highly trafficked roads, ultimately responding to them in a similar manner to predation risk at this temporal scale. Almost all the moose in this study were captured near roads and stayed near roads year-round, yet moose rarely crossed primary, secondary, or tertiary roads, which are assumed to have higher levels of traffic. While used and available steps had similar distances to roads of all traffic levels, the average distance to the road did increase with increasing traffic and used steps crossed roads half as many times as available steps. Multiple studies have found similar patterns of road avoidance among ungulates that increases as disturbance intensifies (Leblond et al. 2013, Bartzke et al. 2015, Prokopenko et al. 2017, Wattles et al. 2018).

Ungulates adapt to roads as they would predation risk, avoiding key locations at the riskiest times, and may opt for crossing roadways at night to add concealment or reduce risk. For example, red deer (*Cervus elaphus*) have been found to avoid roads at night when traffic levels are lowest (Meisingset et al. 2013). While time of day did not provoke a significant change to crossing rates or road avoidance in this study, the average response did become positive at night, suggesting in certain circumstances it may be beneficial to move towards roads at night. Including other confounding factors like roadway lighting or a more specific calculation of solar and lunar illumination might help account for concealment as a possible behavioral response when near roads at night. More specific traffic data across space and time would also be beneficial in disentangling rush hour traffic that occurs during daylight from rush hour traffic that occurs at night, as lighting conditions vary more considerably in northern latitudes.

Ungulates also may select to avoid roads when the animal is concealed by vegetation, but response to road distances and road crossings did not change with vegetation cover for this moose population. Multiple studies have found that moose road avoidance changed with forage availability (Dussault et al. 2007, Bartzke et al. 2015, Wattles et al. 2018). Much of the forest cover in the area consists of mixed stands of coniferous and deciduous trees, so the relative effect of deciduousness may not be as influential as road effects and a more specific vegetation metric may be more useful to better reflect selection for available browse. A study that modifies vegetation near roads may provide a better understanding of the interaction between road avoidance and forage conditions (Rea 2003).

Moose in this study did move more slowly near roads than average, suggesting some change in behavior when near roads. This behavior was not expected, as moose and other ungulates typically increase their speed to avoid roads (Dussault et al. 2007, Prokopenko et al. 2017). At the 5-hour temporal scale used in this analysis, this slower movement could be due to moose staying near roads to gain human-shielding or access to forage.

This could also be due to a fear of crossing roads. It would also not be unusual for boreal ungulates to remain still as an antipredator behavior, an *a posteriori* hypothesis to explain this difference in results. Studies to delineate specific behavioral responses should tailor their expectations based on environment, as wildlife respond variably to different conditions. For example, using more specific vegetation and traffic metrics could help movement models better delineate when an animal is moving slowly as they forage as opposed to moving slowly as they wait for traffic to subside.

Generalization to all moose in the study area may be limited to those moose bold enough to cross roads, as I was unable to use datasets without positive cases of road crossings per time of day for the time-dependent road crossing models and without positive cases of road crossings for the context-dependent road crossing models. The inferences about the decision to cross roads may be conservative due to this censorship. If there were a way to include all moose, regardless of whether they crossed roads, the uncertainty intervals of the selection coefficients may better reflect the whole population. Similarly, if the raster dataset of road distance could have been extended to cover all moose locations, I may have been able to better quantify avoidance of roads of all traffic levels, but at the time of analysis, I was unable to calculate distances to roads farther than 10 km using Google Earth Engine.

The temporal resolution of this analysis was 5 hours, but 1 hour relocation data is available. Increasing the resolution to characterize movement at the 1-hr scale may increase identification of crossings that would be missed at the 5-hr scale. Some individuals were also tracked every 5 minutes when near roads, using virtual fencing technology built into the GPS transmitters. Comparing the number of crossings that occur across each time scale should help identify how often crossings may be missing from the higher temporal resolution data. Similarly, the dawn and dusk periods, which are shorter than the nighttime and daytime periods, may also be under observed at the 5-hr scale. Increasing the resolution to 1-hr relocations may be beneficial for understanding the role of traffic, especially during rush hour periods, which will be mostly during dawn, dusk, or nighttime during the winter months in this study area.

This research adds to the growing body of research showing that ungulates respond to human disturbance, and especially roads, as threats, while still selecting to be near them. Like this study, moose captured near roads still avoided crossing them, especially for highways and forest roads (Dussault et al. 2007). Also like this study, moose have been found to avoid areas within 100-250 m of a road (Laurian et al. 2012). As urban sprawl continues to spread road networks farther into previously undeveloped areas and increase intensity of use in currently developed areas, understanding how ungulates and other large mammals respond to these new disturbances will benefit managers trying to conserve or increase the affected populations and reduce human-wildlife conflicts.

By knowing what types of disturbances wildlife will exploit or avoid, wildlife managers will be able to better inform transportation and urban planners how to reduce fragmentation of the landscape and mitigate negative human-wildlife interactions. Analyses of animal behavior like this one can be used to simulate movement across the landscape, providing a rough estimate of where crossings might be most likely to occur. By identifying such chokepoints in the road system where moose, or other ungulates, will cross roads, wildlife managers can better decide where to focus hazing efforts or forage modifications designed to increase road avoidance or crossing structures designed to allow safe passage across the road system. As systems for tracking wildlife and handling such large datasets continue to evolve, managers may be able to use such maps proactively, if the data used to inform the model are useful for predicting resource selection.

MANAGEMENT CONSIDERATIONS

Moose and other ungulates generally avoid road networks, but they are still being impacted by WVCs. There are contexts where road crossings are not as risky, such as at during daylight, which is reflected in reports of WVCs, which are generally higher at night, and in Alaska, are generally higher in winter, when daylight is limited. Removal or hazing of moose near roads may discourage use, but it is unlikely that crossings can be completely eradicated without implementation of crossing structures and fencing, which due to cost will likely be limited to specific road corridors. Educating drivers on the risk of collisions and the contexts in which they occur may also help reduce collisions, but as these events are relatively rare for each individual motorist, this will also not be a complete solution. By identifying where and when road crossings or WVCs occur, a mixture of mitigation methods, including public education, hazing, removal, or infrastructure change, may reduce both road crossings and WVCs. Using analyses to understand movements during time of day and season can allow for a more strategic, pro-active management action.

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REFERENCES

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

Avgar, T., S. R. Lele, J. L. Keim, and M. S. Boyce. 2017. Relative selection strength: quantifying effect size in habitat- and step-selection inference. Ecology and Evolution 7:5322–5330.

Bartzke, G.S., R. May, E. J. Solberg, C. M. Rolandsen, and E. Røskaft. 2015. Differential barrier and corridor effects of power lines, roads and rivers on moose (Alces alces) movements. Ecosphere 6:1–17.

Ballard, W. B., and J. S. Whitman. 1988. Susitna hydroelectric project, final report, big game studies, Vol. II-Moose Upstream. Alaska Department of Fish and Game. https://www.arlis.org/docs/vol1/Susitna/41/APA4128.pdf

Benítez-López, A., R. Alkemade, and P. A. Verweij. 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biological Conservation 143:1307–1316.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.

Bischof, R., S. M. Steyaert, and J. Kindberg. 2017. Caught in the mesh: roads and their network-scale impediment to animal movement. Ecography 40:1369–1380.

Dickie, M., R. Serrouya, R. S. McNay, and S. Boutin. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. Journal of Applied Ecology 54:253–263.

Dussault, C., J. -P. Ouellet, C. Laurian, R. Courtois, M. Poulin, and L. Breton. 2007. Moose movement rates along highways and crossing probability models. The Journal of Wildlife Management 71:2338–2345.

Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society. 14:21.

Forman, R. T. 2003. Road ecology: science and solutions. Island press, Washington, D.C, USA.

Laurian, C., C. Dussault, J. -P. Ouellet, R. Courtois, and M. Poulin. 2012. Interactions between a large herbivore and a road network. Ecoscience 19:69–79.

Leblond, M., C. Dussault, and J.-P. Ouellet. 2013. Avoidance of roads by large herbivores and its relation to disturbance intensity. Journal of Zoology 289:32–40.

McDonald, L. R., T. A. Messmer, and M. R. Guttery. 2019. Temporal variation of moose–vehicle collisions in Alaska. Human–Wildlife Interactions 13:8.

Meisingset, E. L., L. E. Loe, Ø. Brekkum, and A. Mysterud. 2014. Targeting mitigation efforts: the role of speed limit and road edge clearance for deer-vehicle collisions. Journal of Wildlife Management 78:679–688.

Meisingset, E. L., L. E. Loe, Ø. Brekkum, B. V. Moorter, and A. Mysterud. 2013. Red deer habitat selection and movements in relation to roads. Journal of Wildlife Management 77:181–191.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani. 2011. Human activity helps prey win the predator-prey space race. PLoS One 6:e17050.

Ng, J. W., C. Nielsen, and C. C. St. Clair. 2008. Landscape and traffic factors influencing deer-vehicle collisions in an urban environment. Human–Wildlife Conflicts 2:34–47.

Palmer, M. S., K. M. Gaynor, J. A. Becker, J. O. Abraham, M. A. Mumma, and R. M. Pringle. 2022. Dynamic landscapes of fear: understanding spatiotemporal risk. Trends in Ecology and Evolution 37:911–925.

Passoni, G., T. Coulson, N. Ranc, A. Corradini, A. M. Hewison, S. Ciuti, B. Gehr, M. Heurich, F. Brieger, R. Sandfort, et al. 2021. Roads constrain movement across behavioural processes in a partially migratory ungulate. Movement Ecology 9:1–12.

Prokopenko, C. M., M. S. Boyce, and T. Avgar. 2017. Characterizing wildlife behavioural responses to roads using integrated step selection analysis. Journal of Applied Ecology 54:470–479.

Rea, R. V. 2003. Modifying roadside vegetation management practices to reduce vehicular collisions with moose *Alces alces*. Wildlife Biology 9:81–91.

Rytwinski, T., and L. Fahrig. 2012. Do species life history traits explain population responses to roads? A meta-analysis. Biological Conservation 147:87–98.

Shannon, G., L. S. Cordes, A. R. Hardy, L. M. Angeloni, and K. R. Crooks. 2014.

Behavioral responses associated with a human-mediated predator shelter. PLoS One 9:e94630.

Ware, H. E., C. J. W. McClure, J. D. Carlisle, J. R. Barber, and G. C. Daily. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. Proceedings of the National Academy of Sciences of the United States of America 112:12105–12109.

Wattles, D.W., K.A Zeller, and S. DeStefano. 2018. Response of moose to a high-density road network. The Journal of Wildlife Management 82:929–939.

Zimmermann, B., L. Nelson, P. Wabakken, H. Sand, and O. Liberg. 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. Behavioral Ecology 25:1353–1364.

TABLES AND FIGURES

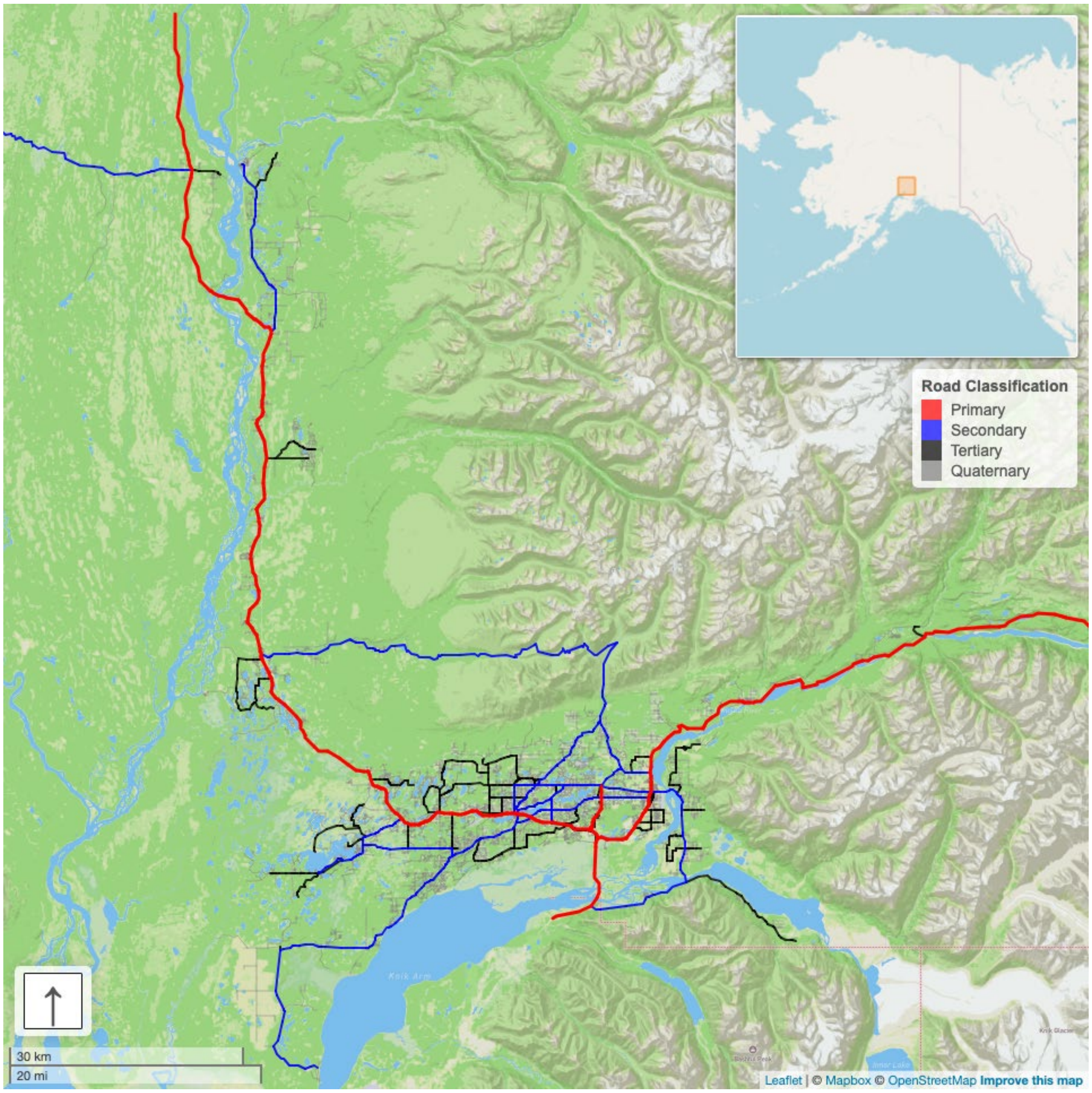

Figure 4-1. Primary, secondary, tertiary, and quaternary roads classified based on traffic level by Alaska Department of Transportation and Public Facilities, in the Matanuska-Susitna Borough, Alaska, USA, 2016.

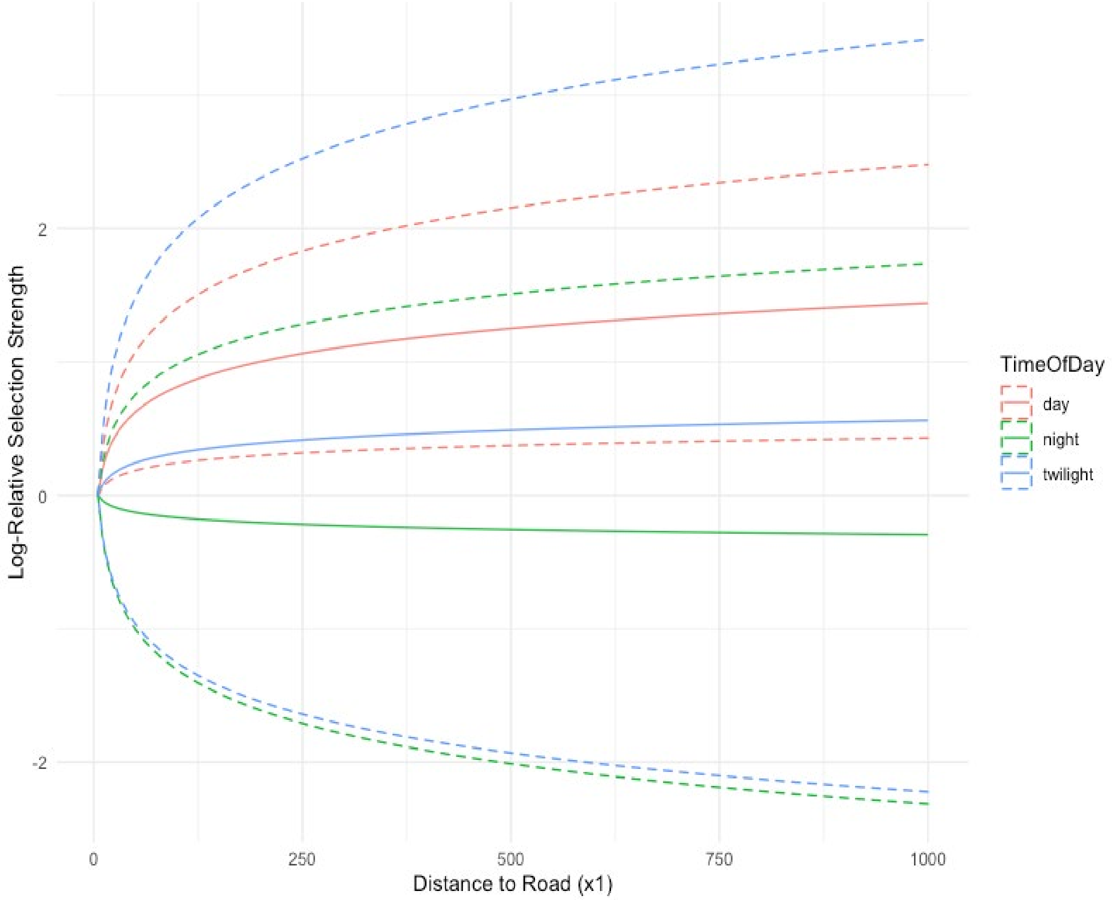

Figure 4-2. Log-Relative Selection Strength of taking a step (x1) that is at various distances to roads at day, night, and twilight compared to taking a step (x2) that is 5 m from a road quantified for moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA, 2017–2020. Solid lines represent the average response at each time of day. Dashed lines represent the 80% uncertainty intervals surrounding the average responses.

Table 4-1. Time-dependent road avoidance (Model 1) results for wintering moose (*Alces alces*), Matanuska-Susitna Borough, Alaska, USA study area, 2017–2020. Coefficient estimates are based on the mean and 80% uncertainty interval (UI) of each variable's posterior estimates. The % Positive values represents the percentage of estimates that were above zero. Covariates include deciduousness (ΔEVI), slope, time of day (Night, Twilight), log-transformed step length (SL), cos-transformed turn angle (TA), the log-transformed distance between roads and the end of the step (D1), and the interaction between time of day and log-transformed distance.

Covariate	Coefficient	10% UI	90% UI	% Positive
ΔEVI	0.06	-0.14	0.26	60.83
Slope	-0.37	-0.55	-0.20	23.82
Night	0.00	-5.39	5.39	49.92
Twilight	-0.01	-9.79	9.76	49.94
log(D1)	0.27	0.08	0.47	77.16
log(D1):Night	-0.33	-0.52	-0.14	9.90
log(D1):Twilight	-0.17	-0.50	0.18	27.58
log(SL)	-0.02	-0.07	0.02	42.72
cos(TA)	0.14	0.05	0.23	87.14

Table 4-2. Time-dependent road crossing (Model 2) results for wintering moose (*Alces alces*), Matanuska-Susitna Borough, Alaska, USA study area, 2017–2020. Coefficient estimates are based on the mean and 80% uncertainty interval (UI) of each variable's posterior estimates. The % Positive values represents the percentage of estimates that were above zero. Covariates include deciduousness (ΔEVI), slope, time of day (Night, Twilight), log-transformed step length (SL), cos-transformed turn angle (TA), whether a road was crossed (Crossed), and the interaction between time of day and road crossing.

Covariate	Coefficient	10% UI	90% UI	% Positive
ΔEVI	0.03	-0.13	0.19	60.28
Slope	-0.07	-0.17	0.02	33.30
Night	-0.04	-5.86	5.78	49.57
Twilight	-0.02	-10.94	10.90	49.81
Crossed	-0.89	-1.36	-0.45	7.56
Crossed:Night	0.17	-0.38	0.73	59.80
Crossed:Twilight	0.11	-0.92	1.09	54.67
log(SL)	0.04	0.00	0.08	61.90
cos(TA)	0.13	0.06	0.21	87.83

Table 4-3. Context-dependent road avoidance (Model 3) results for wintering moose (*Alces alces*), Matanuska-Susitna Borough, Alaska, USA study area, 2017–2020. Coefficient estimates are based on the mean and 80% uncertainty interval (UI) of each variable's posterior estimates. The % Positive values represents the percentage of estimates that were above zero. Covariates include deciduousness (ΔEVI), slope, log-transformed step length (SL), cos-transformed turn angle (TA), the log-transformed distance between roads and the start of the step (D2), and the interactions between deciduousness or log-transformed step length and log-transformed distance.

Covariate	Coefficient	10% UI	90% UI	% Positive
ΔEVI	0.17	-0.80	1.14	48.70
Slope	-0.36	-0.56	-0.17	25.87
log(D2)	0.01	-3.65	3.67	50.12
ΔEVI:log(D2)	-0.02	-0.20	0.17	54.05
log(SL)	-0.09	-0.32	0.15	36.97
log(SL):log(D2)	0.02	-0.03	0.06	61.49
cos(TA)	0.14	0.04	0.24	85.95

Table 4-4. Context-dependent road crossing (Model 4) results for wintering moose (*Alces alces*), Matanuska-Susitna Borough, Alaska, USA study area, 2017–2020. Coefficient estimates are based on the mean and 80% uncertainty interval (UI) of each variable's posterior estimates. The % Positive values represents the percentage of estimates that were above zero. Covariates include deciduousness (ΔEVI), slope, log-transformed step length (SL), cos-transformed turn angle (TA), whether a road was crossed (Crossed), and the interactions between deciduousness or log-transformed step length and road crossing.

Covariate	Coefficient	10% UI	90% UI	% Positive
ΔEVI	0.07	-0.12	0.26	63.08
Slope	-0.14	-0.26	-0.03	29.63
Crossed	-0.22	-3.80	3.26	62.72
ΔEVI:Crossed	0.15	-0.68	1.00	57.80
log(SL)	0.03	-0.02	0.07	54.83
log(SL):Crossed	-0.12	-0.66	0.43	31.02
cos(TA)	0.15	0.07	0.24	88.11

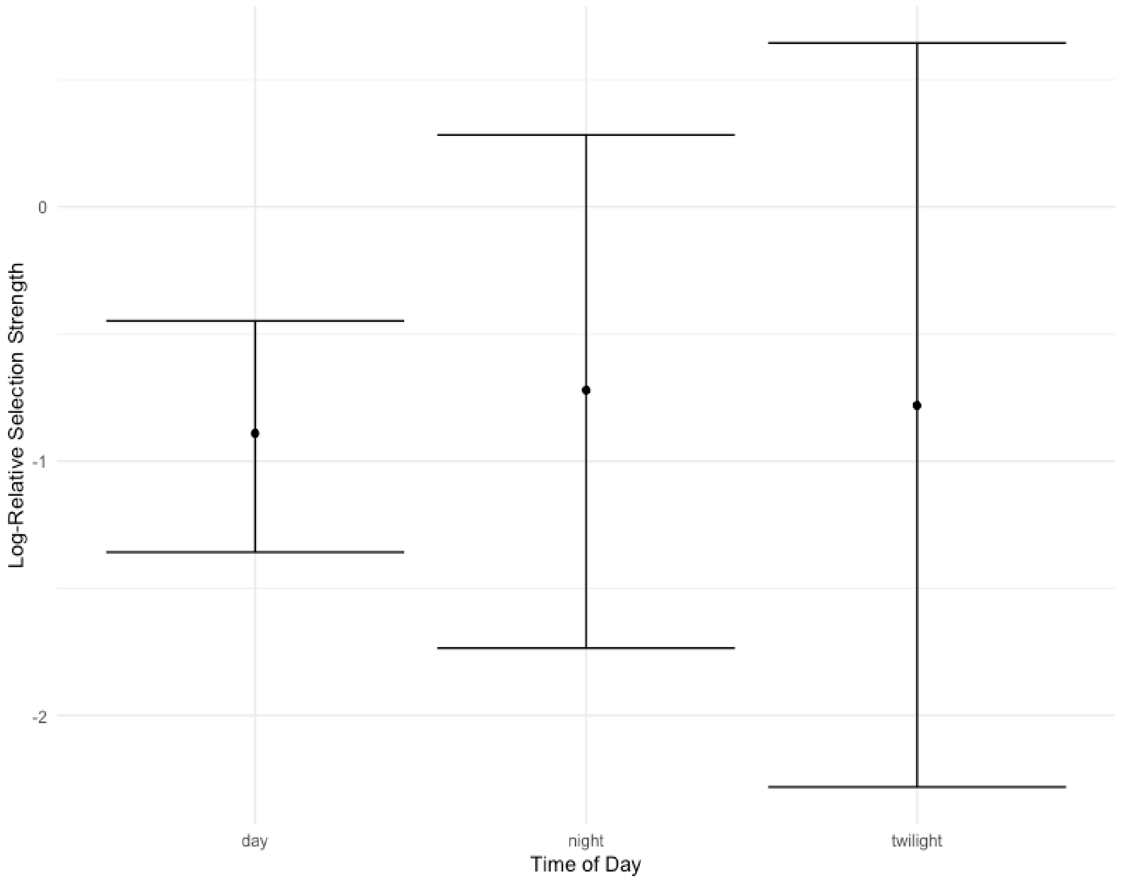

Figure 4-3. Log-Relative Selection Strength of taking a step (x1) that crosses a road at day, night, and twilight compared to taking a step (x2) that does not cross a road quantified for moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA, 2017–2020.

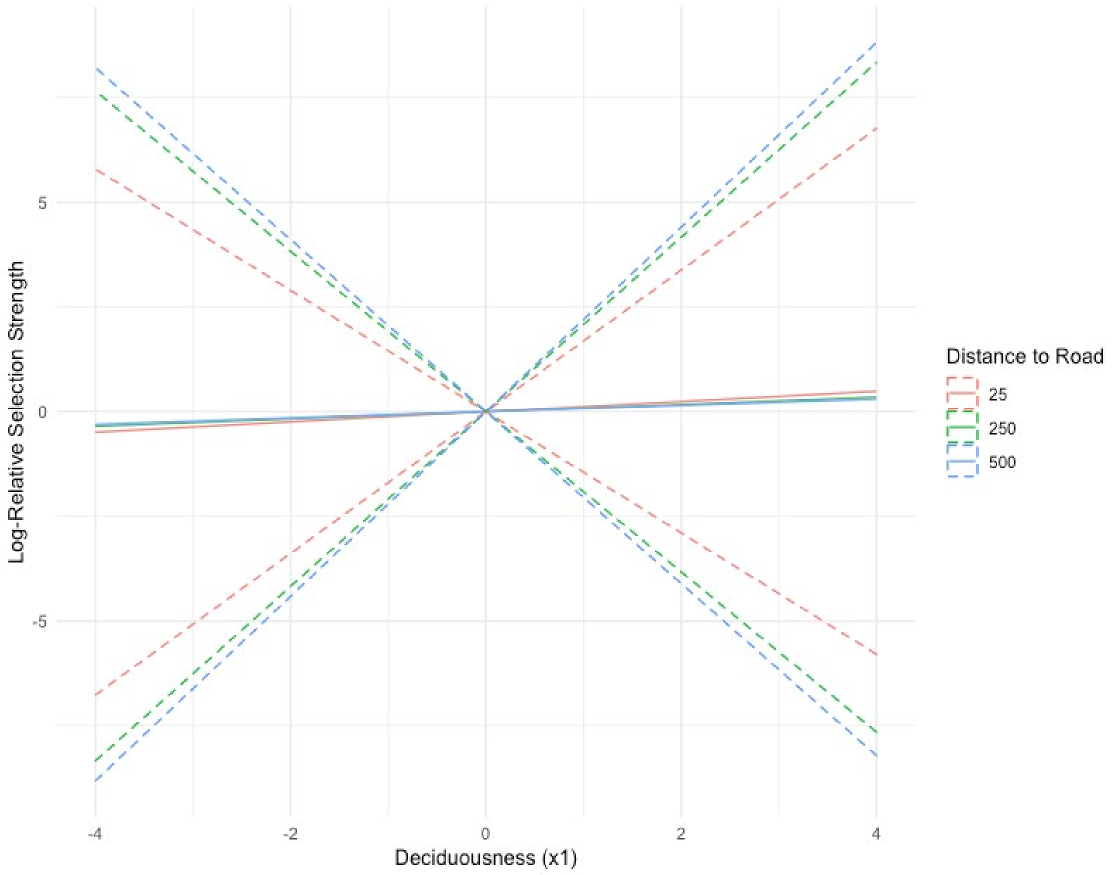

Figure 4-4. Log-Relative Selection Strength of taking a step (x1) of varying deciduousness compared to taking a step (x2) of average deciduousness for steps at varying distances to roads (25, 250, and 500 m) quantified for moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA, 2017–2020. Deciduousness values are highest where deciduous forage is present and lowest where the ground is bare.

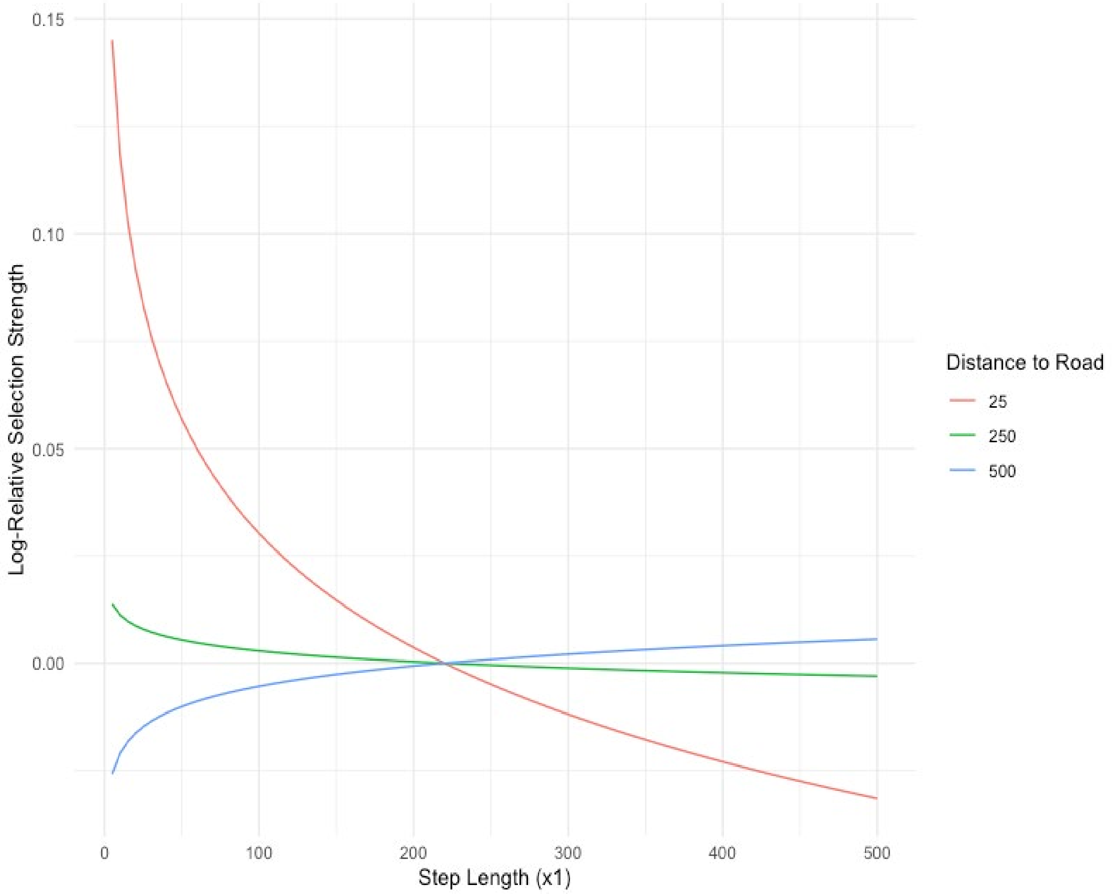

Figure 4-5. Log-Relative Selection Strength of taking a step (x1) of various lengths compared to taking a step (x2) that is the average length (220 m) at various distances to roads (25, 250, and 500 m) quantified for moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA, 2017–2020.

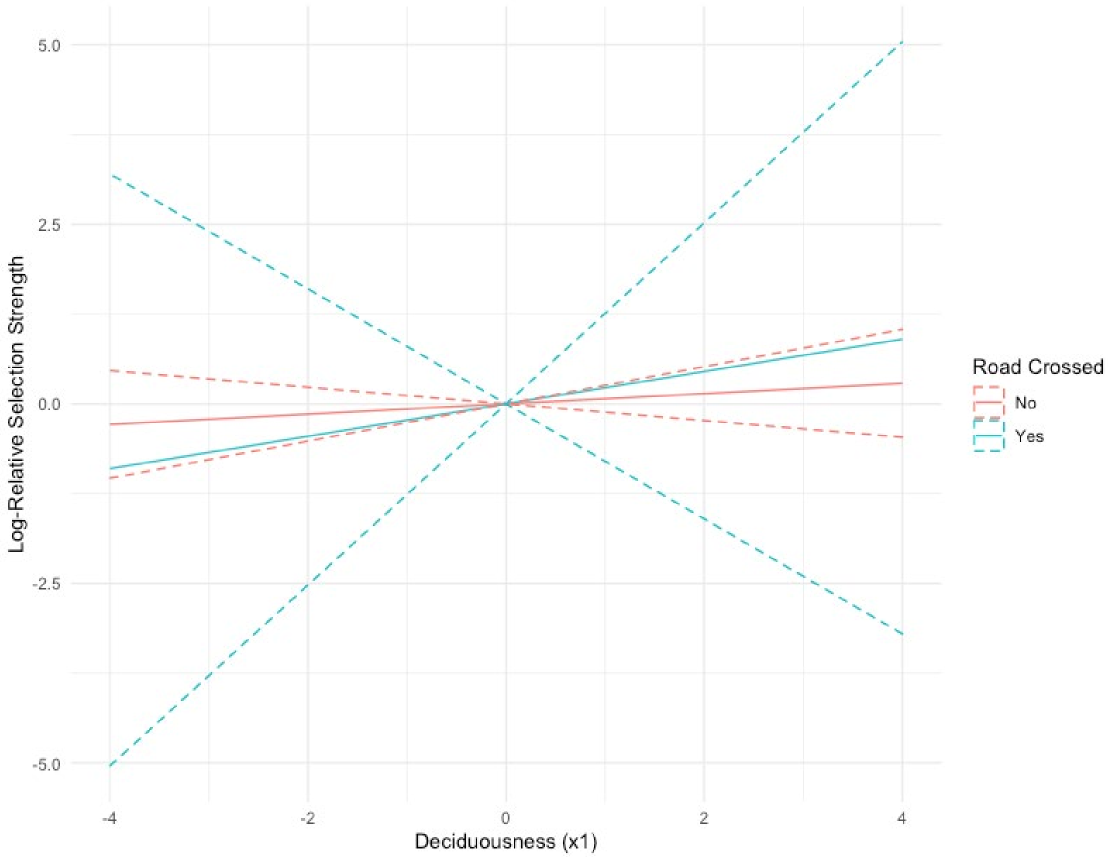

Figure 4-6. Log-Relative Selection Strength of taking a step (x1) of varying deciduousness compared to taking a step (x2) of average deciduousness for steps that either cross or do not cross a road quantified for moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA, 2017–2020. Deciduousness values are highest where deciduous forage is present and lowest where the ground is bare.

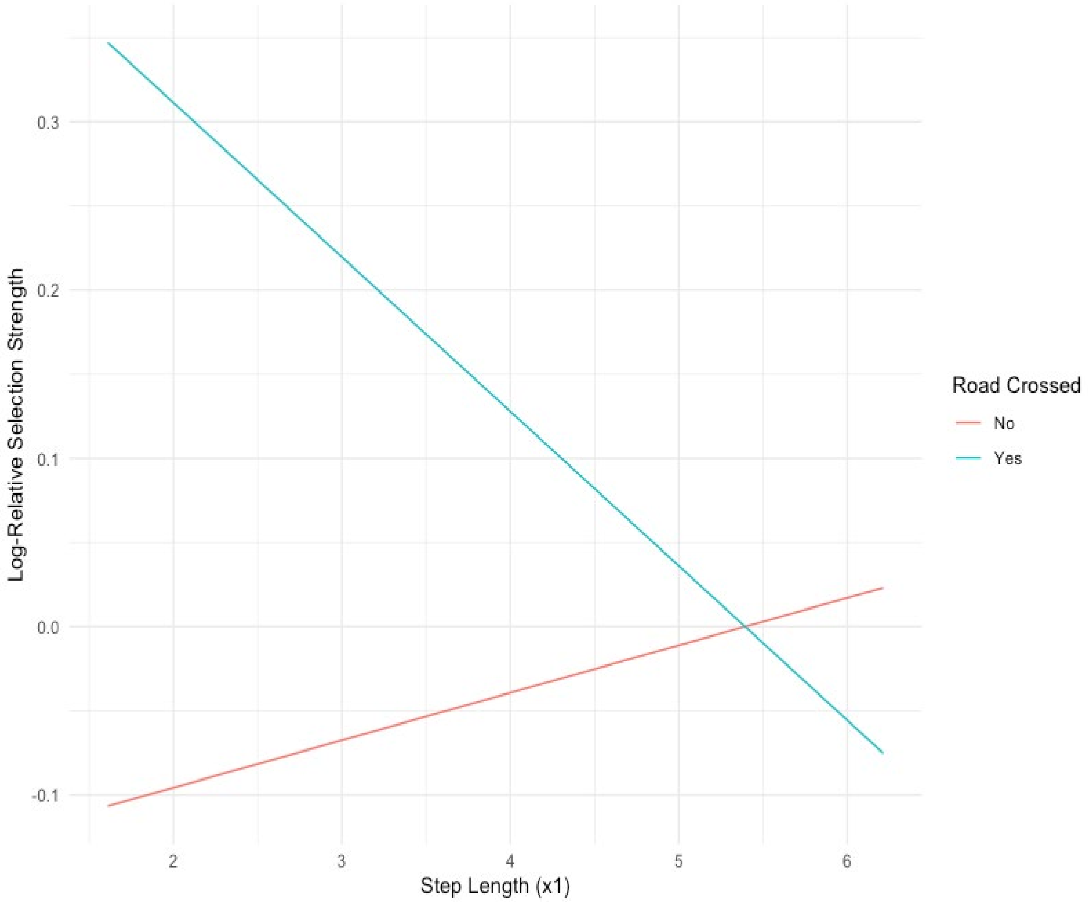

Figure 4-7. Log-Relative Selection Strength of taking a step (x1) of various lengths compared to taking a step (x2) that is the average length (220 m) for steps that either cross or do not cross a road quantified for moose (*Alces alces*) in the Matanuska-Susitna Borough, Alaska, USA, 2017–2020).

CHAPTER V

CONCLUSION

Anthropogenic landscape modification changes the costs and benefits for wildlife seeking to maximize foraging opportunities and minimize mortality risk for themselves and their offspring. As this modification to the environment expands, landscape disturbance, degradation, and fragmentation change the distribution of wildlife populations. This can decouple predator-prey and consumer-producer relationships, reduce the richness and diversity of local species, and alter both wildlife behavior and ecosystem function (McKinney 2002, Foley et al. 2005, Rodewald et al. 2011, Gonzalez et al. 2016).

Moose (*Alces alces*) and other ungulates are regulated top-down by predation and bottom-up by forage (Fryxell and Sinclair 1988). Increasing the amount of vegetation and decreasing predation risk on the landscape can increase populations by reducing calf mortality, increasing overwinter survival, and increasing the density of animals that can survive in an area. Simultaneously, some areas near human settlements with particularly high amounts of disturbance can elicit antipredator behavior in ungulates. This effect may outweigh responses to predation risk, especially for large ungulates who are less vulnerable to predation once they are adults (Theuerkouf and Rouys 2008, Proudman et al. 2020). As ungulates navigate this landscape of fear, the avoidance of both predation and disturbance risk may indirectly lead to selection for intermediately disturbed areas where both risks are minimized (Gaynor et al 2019).

In Chapter II, I refer to this phenomenon as the urban refugia hypothesis. Moose in my study area avoided the most natural and most urban areas, supporting this hypothesis.

This intermediately disturbed area directly overlaps high MVC risk corridors in this study area. This is mirrored in other studies of DVCs, which often find risk is highest in intermediately disturbed areas. Examples include areas where low density roads have high traffic speeds or road densities are average and areas near urban greenspaces or suburban communities (Nielson et al. 2003, Schneiderman 2008, Found and Boyce 2011, Clevenger et al. 2015).

When I compared cow moose selection to cow-calf pair selection in Chapter III, cows that exhibited calving behavior in spring and cows observed with a calf in winter also selected for these intermediately disturbed areas. Ecological traps occur when wildlife selection for areas is maladaptive (Battin 2004). As calves and yearlings are disproportionately impacted by moose-vehicle collisions, this refuge seeking by the cow could be considered an ecological trap for calves in the area. While it is currently unlikely this would push moose to extinction, it may erase any population gains that would be accrued from the lack of neonate predation that is assumed to drive cows with calves to seek such refuge from predators.

When I focused on the impact of roads on winter selection in Chapter IV, moose overwhelmingly avoided road proximity and road crossings, especially on roads with higher average traffic. When not accounting for traffic, moose selected to be closer to roads at night on average, but this effect was minimal. Moose didn’t select to be closer to roads based on vegetation, but they did move more slowly near roads. Slower movement near roads and towards roads with vegetation would have been likely if moose were choosing to forage or conceal themselves near roads (Dickie et al. 2019). Ambivalence towards vegetation near roads may indicate that roads simply impede movement.

Throughout each study, moose behavior changed with increasing urbanization. As moose selected to be farther from natural and urban areas, they likely found themselves in intermediately disturbed areas. Though moose avoided being near roads, MVC rates are still increasing. Gradual urban sprawl may influence this, as current home ranges are encroached by new construction over time, moose already habituated to humans may not respond to the increased risk until a vehicle encounter or other potentially fatal human disturbance. Luckily, moose do respond to these disturbance risks in general, so the population is likely to adjust to humans and will likely be influenced by management techniques designed to reduce the perceived safety of urban refugia. Unfortunately, that does mean that continued urban growth will reduce and fragment the overall land area available to support moose.

IMPLICATIONS FOR MVC MITIGATION

While moose avoid roads and human disturbances, they still inhabit areas near humans and cross roads in some cases, so human-moose conflicts like MVCs are likely to increase as urban sprawl increases the extent of anthropogenically disturbed landscapes and the distance between patches of exploitable forage within these landscapes. By determining when and where these crossings are most likely to occur, managers can better educate the public and mitigate MVCs. Public education has been used to mitigate MVCs in Alaska in the past (Del Frate and Spraker 1991). As a result, motorists in Alaska are typically aware of the risk, but risk to an individual person is rather low (~3 MVCs per 1,000 people per year in my study area). Anecdotally, many Alaskans who have shared their MVC experiences with me throughout this research have been able to identify what to look for when driving and have indicated increased awareness after an encounter, as expected by the risk-perception attitude framework mentioned in Chapter I (Rimal and Real 2003). Any outreach that can similarly influence motorist's ability to identify when and where to be most wary of MVCs when driving will likely be helpful, as roadside moose crossing signage is often mismatched with actual risk and motorists often become habituated to signage over time (Putnam 1997, Sullivan and Messmer 2003, Mastro et al. 2008).

Based on road ecology theory, wildlife-vehicle collisions (WVCs) arise from the interaction between wildlife occurrence, driver behavior, and traffic volumes (Forman et al. 2003). In tandem with public education, agencies attempting to reduce motorist speeds, increase motorist visibility, or reduce traffic levels can also reduce WVCs (Huijser and McGowan 2010). However, wildlife managers can more effectively manage wildlife occurrence than driver behavior or traffic. Using species-specific models to determine how wildlife navigate roads can be an important first step in determining where and when WVCs are likely to occur and how to mitigate them (Gunson et al. 2011, Vistintin et al. 2016). Efficacy of mitigation measures based on such models will depend on the ability of the model to accurately regenerate the behavior of the target species through simulation. For moose in this area, net movement behavior overlaps areas where MVCs are most common, so simulation of movement using models based on human disturbance and road proximity should highlight areas moose are most likely to cross roads.

Mitigation measures designed to limit crossings can be targeted in these locations based on prevalence of MVCs. Population reductions can reduce moose densities near roads, which should reduce crossings, but these measures are short-term due to recolonization by neighboring moose (Huijser and McGowen 2010). Vegetation can also be modified to reduce use of roads by ungulates (Rea 2003), but I found no connection between selection for road proximity and vegetation in this study. Wildlife crossing structures with funnel fencing are the most effective approach, but fencing alone can also reduce crossings (Clevenger and Ford 2010, van der Ree et al. 2015). These structures are often used in major wildlife movement corridors that intersect roads because they are costly to build and maintain.

Hazing, or aversive conditioning, can also condition wildlife to avoid target locations, such as high-risk road corridors. Sensory repellants designed to encourage movement away from roads can reduce MVCs, but these techniques, like whistles, flags, and reflectors, have variable success (Mastro et al. 2008). Hazing could include the use of large guard animals or people on horseback trained to chase ungulates from an area or the use of nonlethal projectiles designed to induce fear in ungulates (Sampson and Van Patter 2020, Jones et al. 2021). Similarly, targeted hunting intended to increase perceived fear in an area could reduce use by ungulates, but moose may not respond to this type of fear-based approach (Cromsigt et al. 2013, Neumann et al. 2009, Neumann and Ericsson 2018). The main downside of hazing is that it is easy for wildlife to become habituated to repellants or hazing techniques if the sensory experience is never reinforced with an immediate, negative consequence (Lajeunesse et al. 2023).

FUTURE RESEARCH DIRECTIONS

Wildlife-vehicle collisions are unlikely to be completely eradicated by mitigation, but by better understanding the species in question, managers can be more confident that the techniques they choose will reduce WVCs. Modeling wildlife movement behavior in relation to more specific metrics could increase their reliability. For example, moose can hear up to a mile away, but cannot see very far. By developing a geospatial map of vegetation based on preference of aromatic compounds, responses to vegetation might be more appropriately scaled and less variable. Continuous vegetation metrics, like the Enhanced Vegetation Index used throughout this study, are coarse in scale and cannot be matched to species or groups of plants, which reduces the ability of researchers to test hypotheses about more specific plant-herbivore relationships. Separation of the sensory experience of plants from the obstacle they impose on movement would also be helpful, so having measures of vegetation density created through LiDAR scans might help differentiate movements that are due to locomotory cost from movements made while foraging. Similarly, disturbance metrics could be dissected into auditory, olfactory, and visual cues, which could be matched to the scale the animal experiences the cue, but information like this is not currently available.

Including the density of predators and conspecifics as predictors could also improve the ability of models to discern the difference between disturbance and predation risk. In this study, predators were assumed to be found in areas where human activity is minimal, but this isn't necessarily accurate and is based on predators' typical responses to human disturbance. A more accurate depiction of the number of encounters that occur between moose, bears (*Ursus spp.*), and wolves (*Canis lupus*) might explain some of the variation found in this study. For example, caribou (*Rangifer tarandus*) quickly move away from an area when predators are within 2.5 km of it (Basille et al. 2015). Moose may respond at a similar scale due to their heightened olfactory senses. Similarly, moose are generally solitary but can become densely populated. Determining how moose define their home range or navigate based on the smells, sounds, or interactions they have with conspecifics may reduce additional variation in responses to vegetation or risks. Models of global wind direction are available, which could help narrow the number of interactions that would need to be accounted for between conspecifics or with their predators. Considering that these types of predictors are not mentioned often in the literature, collecting data on such metrics is likely difficult and expensive, but could provide novel insights into the behavior of moose and other ungulates that sense the world differently than humans.

CONCLUSION

Humans apply dynamic pressures on wildlife populations. Wildlife are increasingly navigating complex mosaics of fragmented forests and urban greenspaces dissected by roads and other linear features of human infrastructure. This dissertation has documented the interplay between predation and disturbance risk that moose must navigate near urban areas.

As urban areas continue to sprawl outwards, anthropogenic disturbances will continue to change large herbivore behavior by changing vegetation and predator distributions. Urban refugia, areas with limited disturbance from humans and predators, are attractive to moose in my study area – but they also overlap areas of high MVC risk. While these areas offer potential safety for cows, their calves may be inadvertently subjected to an ecological trap, as young moose are involved in the majority of MVCs. While adult moose can navigate between these urban refuges and avoid roads, road crossings are inevitable. Identifying differential costs and benefits of this behavior can aid managers in building models and subsequent simulations of where crossings are most likely to occur. This information can then be used to adequately mitigate MVCs.

A multi-faceted approach using public education, hazing, targeted removals, and wildlife crossing structures in key locations may be the best route to long term mitigation. Better models of movement may be needed to adequately capture all the variation exhibited by moose living alongside human settlements, but in my models, the average moose does avoid the most urban areas where highly trafficked roads are located. Simulations based on these results can provide wildlife and transportation network managers valuable information on where moose do choose to cross roads, and should be used to identify where mitigation efforts will be most effective.

REFERENCES

Basille, M., D. Fortin, C. Dussault, G. Bastille-Rousseau, J. P. Ouellet and R. Courtois. 2015. Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. Ecology 96:2622–2631.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482–1491.

Clevenger, A. P., and A. T. Ford. 2010. Wildlife crossing structures, fencing, and other highway design considerations. Pages 17–49 *in* J. P. Beckman, A. P. Clevenger, M. P. Huijser, and J. A. Hilty, eds. Safe Passages–Highways, Wildlife, and Habitat Connectivity. Island Press, Washington, D.C., USA.

Cromsigt, J. P. G. M., D. P. J. Kuijper, M. Adam, R. L. Beschta, M. Churski, A. Eycott, G. I. H. Kerley, A. Mysterud, K. Schmidt, and K. West. 2013. Hunting for fear: innovating management of human–wildlife conflicts. Journal of Applied Ecology

50:544–549.

Del Frate, G. G., and T. H. Spraker. 1991. Moose vehicle interactions and an associated public awareness program on the Kenai Peninsula, Alaska. Alces 27:1–7.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, et al. 2005. Global consequences of land use. Science 309:570-574.

Forman, R. T. 2003. Road ecology: science and solutions. Island press, Washington, D.C., USA.

Found, R., and M. Boyce. 2011. Predicting deer-vehicle collisions in an urban area. Journal of Environmental Management 92:2486–93.

Fryxell, J. M., and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution 3:237–241.

Gonzalez, A., B. J. Cardinale, G. R. Allington, J. Byrnes, K. A. Endsley, D. G. Brown, D. U. Hooper, F. Isbell, M. I. O'Connor, and M. Loreau. 2016. Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. Ecology 97:1949–1960.

Gunson, K. E., G. Mountrakis, and L. J. Quackenbush. 2011. Spatial wildlife-vehicle collision models: a review of current work and its application to transportation mitigation projects. Journal of Environmental Management 92:1074–1082.

Huijser, M. P., and P. T. McGowen. 2010. Reducing wildlife-vehicle collisions. Pages 51–74 *in* J. P. Beckman, A. P. Clevenger, M. P. Huijser, and J. A. Hilty, eds. Safe passages–highways, wildlife, and habitat connectivity. Island Press, Washington, D.C., USA.

Jones, J. D., K. M. Proffitt, J. T. Paterson, E. S. Almberg, J. A. Cunningham, and K. M. Loveless. 2021. Elk responses to management hunting and hazing. The Journal of Wildlife Management 85:1721–1738.

Lajeunesse, G., E. W. Smith, H. W. Harshaw, and C. C. St. Clair. 2023. Proactive use of intensive aversive conditioning increases probability of retreat by coyotes. Ecosphere 14:e4676.

Mastro, L. L., M. R. Conover, and S. N. Frey. 2008. Deer–vehicle collision prevention techniques. Human–Wildlife Conflicts 2:80–92.

McKinney, M. L. 2002. Urbanization, biodiversity, and conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. Bioscience 52:883–890.

Nielsen, C., R. G. Anderson, and M. Grund. 2003. Landscape influences on deer-vehicle accident areas in an urban environment. Journal of Wildlife Management 67:46–51.

Neumann, W., G. Ericsson, and H. Dettki. 2009. The non-impact of hunting on moose *Alces alces* movement, diurnal activity, and activity range. European Journal of Wildlife Research 55:255–265.

Neumann, W., and G. Ericsson. 2018. Influence of hunting on movements of moose near roads: Hunting and rutting effects on moose movement. Journal of Wildlife Management 82:918–928.

Proudman, N. J., M. Churski, J. W. Bubnicki, J. A. Nilsson, and D. P. Kuijper, 2020. Red deer allocate vigilance differently in response to spatio-temporal patterns of risk from human hunters and wolves. Wildlife Research 48:163–174.

Putmam, R.J. 1997. Deer and road traffic accidents: options for management. Journal of Environmental Management 51:43–57.

Rimal, R. N., and K. Real. 2003. Perceived Risk and Efficacy Beliefs as Motivators of Change Use of the Risk Perception Attitude (RPA) Framework to Understand Health Behaviors. Human Communication Research 29:370–399.

Rodewald, A. D., L. J. Kearns, and D. P. Shustack. 2011. Anthropogenic resource subsidies decouple predator–prey relationships. Ecological Applications 21:936–943.

Theuerkauf, J., and S. Rouys. 2008. Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowieża Forest, Poland. Forest Ecology and Management 256:1325–1332.

Sampson, L., and L. Van Patter. 2020. Advancing best practices for aversion conditioning (humane hazing) to mitigate human–coyote conflicts in urban areas. Human–Wildlife Interactions 14:7.

Schneiderman, J. D. 2008. Analysis of landscape characteristics surrounding deer vehicle accidents in St. Louis County, Missouri. Thesis. University of Missouri, Columbia, Missouri, USA.

Sullivan, T. L., and T. A. Messmer. 2003. Perceptions of deer-vehicle collision management by state wildlife agency and department of transportation administrators. Wildlife Society Bulletin 31:163–173.

Visintin, C., R. Van Der Ree, and M. A. McCarthy. 2016. A simple framework for a complex problem? Predicting wildlife–vehicle collisions. Ecology and

Evolution 6:6409–6421.

VITA

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OBJECTIVE:

To leverage research and technology to build a future in which science-backed knowledge is accessible and coherent to the public so that humans can positively interact with the environment and wildlife. Areas of Interest: Human-Wildlife Conflicts & Coexistence, Movement Ecology, Human Dimensions, and Human-Environment Systems.

EDUCATION:

Doctor of Philosophy • *July '19 – Present*

Wildlife Biology, Utah State University, Logan, UT

Master of Science • *Aug '16 – June '19*

Wildlife Biology, Utah State University, Logan, UT

Bachelor of Science • *Aug '12 – May '16*

Wildlife, Fisheries, and Aquaculture, Mississippi State University, Starkville, MS

PUBLICATIONS:

Human–Wildlife Interactions 13(3)

Book Review: *Ecology and Management of Terrestrial Vertebrate Invasive Species in the United States*

Temporal Variation in Moose-Vehicle Collisions in Alaska – Winter 2019

The Alaskan Wildlifer

Mat-Su Moose-Vehicle Collisions – October 2019

Human–Wildlife Interactions 12(3)

Book Review: *Living with Bears Handbook, Expanded 2nd Edition* – Winter 2018

Herpetological Review 47(1): 129

Terrapene carolina carolina (Eastern Box Turtle). High Elevation Record – Spring 2016

PROGRAMMING SKILLSET:

R, Python, Google Earth Engine (Javascript), Git

PROFESSIONAL EXPERIENCE:

Graduate Research Assistant

Utah State University, Logan, UT • Aug 2016 – Present

- Collaborates with stakeholders from the Alaska Department of Fish and Game, the Alaska Department of Transportation and Public Facilities, and the Alaska Department of Public Safety to mitigate moose-vehicle collision risk in the Matanuska-Susitna Borough of Alaska.
- Develops Bayesian modeling techniques for analyzing the spatial and behavioral ecology of moose, the mitigation preferences of the public, and the spatiotemporal risk factors influencing moose-vehicle collision occurrence.

- Manages geospatial datasets, field collected data, and a collection of over 1 million hourly moose relocations retrieved from necklace-style GPS transmitters.
- Conducts focus groups and implements stakeholder attitude surveys using social media marketing techniques.
- Analyzes a variety of data types using local-machine and server-based computing.

Graduate Instructor – Ornithology
Utah State University, Logan, UT • Jan 2024 – Present

- Guided 23 undergraduate students through a survey of the evolution, systematics, physiology, anatomy, ecology, behavior, and identification of birds.
- Designed course material and evaluation methods.

Graduate Instructor – Python Programming for GIS
Utah State University, Logan, UT • Aug 2022 – Present

- Guided 76 natural resource professionals and graduate students as they learned to navigate ArcGIS Pro using arcpy and modules.
- Developed coursework designed to introduce non-programmers to Jupyter notebooks, Python scripting, and geospatial analysis techniques.

Graduate Teaching Assistant – Biology
Utah State University, Logan, UT • Aug 2021 – Dec 2023

- Mentored 140+ introductory biology students studying descriptive and hypothesis-based biology.
- Studied model organisms, such as alfalfa, yeast, seed beetles, and other insects and microorganisms to discuss genetic variation, biodiversity, selection, and evolution in experimental settings.
- Used simple experiments to clarify scientific analysis in R and delineate the scientific writing process from research proposal to manuscript development.

Wildlife Technician
Alaska Department of Fish and Game, Palmer, AK • May – Aug 2016

- Designed a data collection protocol to collect information about moose-vehicle collision sites to identify factors contributing to collision risk.
- Communicated information to the public about local hunting and fishing regulations.

Mississippi State University Extension Service, Starkville, MS • May 2015 – May 2016

- Conducted in-person and telephone surveys pertaining to Mississippi landowners' attitudes regarding feral pigs.

Undergraduate Researcher: High Elevation Ecology
Mississippi State University, Tellico Plains, TN • Aug – Dec 2015

- Surveyed cover boards to quantify high elevation salamander occupancy.
- Banded various bird species using mist nets at migration stop-over sites.
- Discovered a record elevation Eastern Box Turtle at 1,663 meters above sea level.

Undergraduate Researcher: Webster's Salamander Migration
Mississippi State University, Starkville, MS • Jan – May 2015

- Surveyed drift fences to document plethodontid migration habits.

Undergraduate Assistant
Mississippi State University Extension Service, Starkville, MS • Aug 2013 – May 2015

- Organized survey and test data to evaluate student learning outcomes for the Youth Environmental Science Program in the Starkville School District.
- Aided in administrative tasks required to host conferences on human-feral pig conflicts.

Wildlife Telemetry Technician

Mississippi State University, Coldwater Wildlife Refuge, MS • Dec 2014 – Jan 2015

- Captured female Mallards using rocket nets to fit bands and radio-tracking transmitter backpacks for the evaluation of winter habitat use in wildlife management areas.
- Developed telemetry skills using vehicle mounted receivers.

Study Abroad Researcher: Tropical Biology

Mississippi State University, Belize City, Belize • March 2014

- Learned about the local Mayan culture and discussed conservation initiatives to preserve jaguars, prevent poaching of Yellow-headed Parrots, sequester carbon, and sustainably harvest Mahogany woodlands.
- Conducted camera trap surveys for local wildlife, including jaguars, ocelots, tapirs, cassowaries, and jaguarundis.

SCA/Americorps Intern

Iowa Department of Natural Resources, Spirit Lake, IA • May – Aug 2014

- Engaged recreational boaters about invasive species management.
- Surveyed lake fish species using seining and electrofishing.
- Trapped amphibians using wire traps for a wetland education program.
- Developed and implemented environmental education programs for the local community.