UNDERSTANDING INTERNAL STATE TO PREDICT HABITAT SELECTION

by © Levi Newediuk

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ABSTRACT

An important part of managing wildlife populations is predicting how they will distribute after environmental change. Because distributions are driven by selection of habitats, many studies make predictions based on our understanding of how habitat availability and other aspects of the external environment impact habitat selection. However, the external environment is only one driver of habitat selection. Animals are also motivated to move by aspects of their internal state, including energetic state and life-history stage. My thesis focusses on understanding how internal state influences habitat selection decisions by individual animals. I first test whether modelling changes in habitat selection with habitat availability — i.e., the functional response in habitat selection — can improve predictions of habitat selection. I show that only accounting for the functional response does not improve predictions because individuals differ in their responses to changing habitat availability. I next show how internal state might motivate these individual responses to habitat availability, ultimately producing population distributions that depend on the internal states of individual animals in the population. I tested this connection by modelling habitat selection by female elk in response to glucocorticoid hormones, a physiological indicator of their internal state and energetic needs after experiencing stressors. I found that glucocorticoid hormones drive selection for energy-rich forage by female elk. This demonstrates glucocorticoids are a mechanism for habitat selection, and individual differences in its production and physiological effects can shape how individuals respond to stressors.

I next present a novel method for collecting non-invasive samples of glucocorticoids and other physiological biomarkers from wild animals. Finally, I demonstrate glucocorticoids — and thus internal state — reveal how animals manage resource acquisition, competition, and predator avoidance in social contexts. Overall, my thesis provides a framework for integrating internal state with habitat selection. I argue this integration is necessary to make better predictions about wildlife distributions, a critical endeavour as human land use and climate change accelerate environmental change.

GENERAL SUMMARY

Managing wildlife requires an understanding of their responses to human disturbance and climate change. Animals sometimes respond to changes in their environment is by moving to new environments. When we understand which changes cause animals to move, we can predict their responses. However, recent work has shown these responses are difficult to predict because individual animals respond differently to changes in the environment. My thesis focusses on how these unique responses by individual animals relate to underlying physiological differences between them. I show that physiological indicators like hormones, by changing in response to energy needs or fear of predators, are a signal for “internal state”. Internal state differences between individuals coincide with movement differences. I argue that by measuring individual physiology, we can better understand unique individual responses. This understanding will improve our ability to predict animal movement as climate change and human disturbance accelerates.

ACKNOWLEDGMENTS

The data included in this thesis were collected on the original lands of the Anishinaabeg, Cree, Oji-Cree, and Dakota peoples, and homeland of the Métis Nation, in what is now Manitoba. The animals I study are of traditional and contemporary importance to many of these groups today. Memorial University's St. John's campus, where I completed my studies, is located on the ancestral homelands of the Beothuk. The Island of Newfoundland is located on the ancestral homelands of the Mi'kmaq and Beothuk. The Inuit of Nunatsiavut and NunatuKavut and the Innu of Nitassinan and their ancestors, are the original people of Labrador. This thesis is a testament to my privilege as a white settler. I acknowledge that I have not only benefitted from the historic physical and cultural genocide of these groups, but I also continue to benefit from the systemic inequities that keep their descendants from occupying positions like mine. Going forward in my career, I plan to support reconciliation efforts that break down barriers for Indigenous researchers and reluctancy to acknowledge Indigenous ways of knowing in research.

I would like to thank my mentor, Eric Vander Wal, for taking a chance on me four years ago. One of the things I have learned from you is what a substantial time and emotional investment each new student can be. I am grateful that you not only considered that initial investment worthwhile, but also that you gave me the opportunity to learn on my own, make big mistakes, solve them, and start to become the academic I always wanted to be. Your investment in your students is reflected in your own achievements. Thank you for being the best role model I could have asked for.

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I would also like to thank my family. Despite not being academics themselves, my parents never questioned my reluctance to settle down with a conventional career. Thank you for being my biggest fans and always supporting my wild dreams and nomadic lifestyle. I could not have made it this far without your support.

DEDICATION

I dedicate this thesis to my father, Darrell, who taught me to love learning. This thesis is a reminder to me of the many sacrifices you made to get me where I am today.

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CHAPTER 1 INTRODUCTION AND OVERVIEW

1.1 Thesis narrative and chapter outline

I started my PhD with a goal of predicting how human-caused land-use change affects elk populations in Manitoba. Manitoba is an agricultural province. Much of the southern part of the province has been converted to cropland or pastureland, with mainly small and fragmented remnants of natural habitat. I wanted to help guide management of those natural habitats by predicting how their future conversion might affect distribution of the elk populations.

Predicting distributions of animal populations, however, requires an understanding of what drives those distributions. Population distributions take shape when animals use some locations disproportionately relative to their availability. Use depends on characteristics of the environment such as the locations of predators and food resources. Modelling the effect of the environment on current animal distributions, then applying those models to the environment of an extrapolated landscape, is sufficient to make predictions about future animal distributions. Such models do not necessarily require a mechanistic understanding of the processes that drive population distribution. However, both populations and the environmental pressures driving their distributions vary over time and space. Understanding how the importance of these pressures changes, through developing and testing hypotheses, is a necessary precursor of prediction (Mouquet et al. 2015).

My goal is still to make good predictions. However, my thesis mainly focusses on the initial step of generating and testing hypotheses about the drivers that shape population distributions. In the final chapter of my thesis, I discuss how we might — and whether we should — use these insights to predict population distributions. For the rest of this chapter, I provide a background on modelling distributions, introduce some of the environmental pressures behind those distributions, and discuss the historical development of predictive approaches. In Chapter 2, I compare the predictive performance of two modelling approaches that purportedly account for the changing importance of environmental pressures over time and space. What emerges from this comparison is that individual animals respond differently to changing environmental pressures, making population distributions difficult to predict. Accounting for these individual differences is essential to model predictive performance.

Individual differences among animals are partly a product of their internal states. An individual's internal state provides context for how it experiences and responds to the environment. For example, responses to environmental pressures like food limitation are driven by hunger. Hunger and other physiological states are measurable using biomarkers like hormones. In Chapter 3, I discuss how the glucocorticoid hormones drive movement in response to environmental pressures, resulting in population distributions. I demonstrate how to integrate glucocorticoids into movement-based models, making glucocorticoids a potential new tool for improving predictions. Until recently, repeatedly collecting biomarkers like glucocorticoids from wild animals has been challenging, limiting the ability to consider internal state in population distribution models. In Chapter 4, I introduce a new method for noninvasively collecting these physiological samples, making it possible to build models that make predictions based on internal state.

Understanding the relationship between internal state and environmental pressures also helps explain when animals do not distribute as predicted. Animals are expected to distribute to maximize their access to resources (Charnov 1976). In Chapter 5, I show that counter to this expectation as predicted by the ideal free distribution (Fretwell & Lucas 1969), elk must also distribute in a way that minimizes exposure to competition. I find individuals can lower their predation risk by sharing space with others. However, direct associations between individuals that share space, while making it possible to exchange information about resources, likely trigger competition. Since the extent to which animals require safety and energy modifies their responses to predation and competition, knowledge of their internal state is important context for understanding their distributions in response to these environmental pressures. This understanding is a step towards better predictions.

1.2 Why we need to predict the distributions of animal species

1.2.1 Impact of climate and humans on animal distributions

As of its latest report, the IUCN Red List reports 28 percent of its assessed species are threatened with extinction (IUCN 2020). Much of the current extinction crisis is driven by a cascade of ecological effects underpinned by climate change; global temperatures have increased by 1 degree since pre-industrial levels (IPBES 2019). Temperature-caused changes in the distribution and phenology of plants, for example, correspond to rapid spatial shifts in resources for herbivores. Consequently, herbivores must follow temperature-based cues like spring snowmelt (Laforge et al. 2020) and vegetation green-up (Merkle et al. 2016) to track them. The fitness consequences of closely tracking resources places pressure on those herbivores to change their own distributions in landscapes affected by climate change (Middleton et al. 2018).

Coinciding with climate change, human-caused land use change currently affects an estimated 30% of terrestrial environments (IPBES 2019). New habitats — i.e., points in the environment characterized by unique combinations of resources, conditions, and risks (Northrup et al. 2021) — are shaped by the joint impacts of climate and land use changes. Agriculture leads land use changes, with a threefold increase in production value of the industry since 1970 (IPBES 2019). Ecological impacts of the oil and gas industry are also of concern to conservationists, particularly surrounding their impacts on behavioural interactions among large mammals (e.g., caribou *Rangifer tarundus*; Hebblewhite 2017). For example, seismic lines, pipelines, and roads associated with oil and gas make it easier for wolves to target caribou prey in landscapes normally difficult for wolves to access (Dickie et al. 2017). But even species with unrestricted access to food under rates of current land use change may be at risk from other stressors as land use change intensifies in the future. For example, as wildlife aggregate in agricultural areas to take advantage of productive food sources, they risk increasing rates of pathogen transmission from higher contact rates (Becker et al. 2015).

Most animals must move to track resources as habitats shift in response to changing climates and land use or face potential maladaptation and extinction (Abrahms et al. 2018; Merkle et al. 2022). Because mismatches between appropriate habitat and species distributions are so consequential for fitness, predicting movements of species across changing landscapes is essential to stave off further extinctions. Species distribution modelling is a suite of techniques aimed at predicting these movements and the resulting geographic distributions of species after the environment has changed. Incorporating information about the external environment is purported to improve their predictions (Matthiopoulos et al. 2011; Jachowski and Singh 2015), allowing us to target environmental interventions to support species persistence.

For the remainder of this chapter, I show how so-called “internal states” (*sensu* Nathan et al. 2008) of individuals interact with external environments to shape movement behaviour and animal distributions. In the following section, I show how the class of species distribution model I primarily focus on in my thesis — habitat selection functions (HSFs) — are fit to predict species distributions. I begin by reviewing the development of habitat selection analysis (HSA) and its use as a predictive approach. I then discuss how HSF predictions are improved when they incorporate information from the external environment and internal state.

1.3 Predicting distributions by quantifying habitat selection

1.3.1 Predicting space use from a geographic and environmental perspective

Animals that move to new geographic locations, or remain in the same locations over time, find themselves in changing environments with habitats characterized by new sets of resources, risks, and conditions. To predict their distributions requires an understanding of the relationship between movement, space use, and the environment. Characteristics of the environment, along with a mobile animal's ability to assess those characteristics, drive its movement behaviour (Nathan et al. 2008). Movements in response to the environment lead to habitat selection, whereby some habitats are used disproportionately more than their availability (Manly et al. 2002). The simplest expression that measures this proportion — the selection ratio — compares used to available but unused habitat within a spatially- and temporally-bound geographic area (Boyce and Mcdonald 1999). The selection ratio, for example, might constitute a comparison between the home range area selected by an animal and the entire geographic area used by the population to which it belongs. When applied to a new geographic space or the same space following environmental change, the animal's selection ratio both serves as a prediction for its expected space use pattern and sheds light on the behavioural response to the environment that produces it.

The selection ratio is the conceptual basis for HSA. HSFs estimate the relative probability of selection for aspects of the environment that characterize used locations in geographic space (Manly et al. 2002; Northrup et al. 2021). Use of geographic locations is often recorded using geographic positioning system points collected by biotelemetry devices affixed to an animal.

However, because biotelemetry devices only record animal locations at regular intervals (e.g., every two hours), unused but available habitat, to which the environmental characteristics of used locations are compared in the selection ratio, is usually unquantifiable. Instead, available locations are often a random sample of those locations accessible to the animal (Lele and Keim 2006). The combination of environmental characteristics, X, at used locations are compared to characteristics at available locations to estimate their relative probability of selection, β, using logistic regression: $\exp(\beta_0 + \beta_1 X + \cdots + \beta_n X)$. Because they are estimates of selection in environmental space, the coefficients, β, from these "use-availability" HSFs can be applied like selection ratios to predict the distributions of animals in new geographic spaces (Boyce and Mcdonald 1999).

1.3.2 The problem of prediction: inconsistency in space and time

Despite their popular use for prediction and improvements over the selection ratio, the current process for fitting HSFs makes them surprisingly unreliable for predicting the actual distributions of animals through time and after environmental change (Gerber and Northrup 2020). This paradox can be explained in part by the tension between model complexity and generality. Models that are especially biologically informative for one population or species may lack *transferability*, or the ability to make predictions outside of the systems in which they were created (Wenger and Olden 2012). The earliest applications of HSF to the problem of prediction relied on this tenuous assumption of model transferability; an animal's distribution in a new location or at a later time period was simply assumed to be the product of relative selection for each habitat and its new availability (Boyce and Mcdonald 1999).

But habitat selection often changes over space and time. For example, as populations grow toward equilibrium, territorial individuals exclude others from preferred habitats (O'Neil et al. 2019). Habitats that are hyper-available in new locations may no longer be selected for because the resources they provide are no longer limiting (Wilber et al. 2020). Such variability limits transferability, but the severity of its effect is impossible to quantify when estimates of selection are only available from a single point in time or space. Transferability of HSFs when the environment changes, therefore, means understanding the dynamic relationship between habitat selection and availability (Matthiopoulos et al. 2020).

HSF models generally assume the relationship between habitat selection and availability is linear; that is, a unit increase in habitat availability results in a unit increase in its selection according to the habitat-specific coefficient. However, this is often not the case. Resource requirements have thresholds, meaning the habitat use-availability relationship often plateaus at higher resource levels (Arthur et al. 1996; Mysterud and Ims 1998). For example, a prey species may require forest habitat as a resource for hiding from predators, and selection for it may be strong when only 10 ha of forest are available. But the difference between 10 and 1,000 ha of forest may not yield a similar increase in selection — the species does not need more forest to hide from predators just because it is available. Instead, use of forest may remain the same as its availability increases, or even decline if a different required habitat becomes less available, resulting in a negative selection-availability relationship. Accounting for the relationship between availability and habitat selection improves transferability because it generalizes the biological processes by which animals seek resources (Matthiopoulos et al. 2011).

Understanding how groups of animals seek resources also improves transferability of HSF models because population density affects resource competition. As more individuals compete for resources in preferred habitats, they reduce resources to the point where previously less-preferred habitats offer more resources to new animals entering the population (Fretwell and

Lucas 1969). At each population size, therefore, the equalization of resources amongst individuals results in a density-dependent pattern of habitat selection (Morris 2003). But habitat selection-density relationships are not exclusively negative. Density itself acts as a resource when individuals dilute predation risk for others (Lehtonen and Jaatinen 2016). Individuals also learn information about potential predators and locations of resource via social information from others (Gil et al. 2018). Whether social information increases access to resources or competition reduces it, population density is essential context for transferability of HSF model predictions (Avgar et al. 2020).

To some extent, step-selection analysis (SSA) solves the issues of interdependency between geography, habitat availability, and selection. Whereas traditional HSFs assume all locations within a defined geographic and temporal area are simultaneously available (Aarts et al. 2012), step-selection functions (SSFs) constrain the availability sample to “steps” accessible from each successive location (Fortin et al. 2005). Because availability of successive steps is conditional on the previous step, changing selection can be estimated along with changing availability over time. Constraining availability also means SSFs can estimate the effects of transient variables like predation (Basille et al. 2015) and competition for resources (Merrill et al. 2020) on selection. However, the qualities of SSFs that help solve the issue of availability — i.e., constraining availability by step — also complicates their use for predicting animal distributions. Predictions made by traditional HSFs typically differ from those of SSFs in which the long-term relative probability of selection, and therefore the expected distribution, depends on how observed locations are sampled (Michelot et al. 2017).

1.4 Learning about individuals to understand species distributions

Two distinct factors influence habitat selection behaviour and the predictions we can make using HSFs. The first, discussed in the previous section 1.3, comprises differences in the external environments to which individuals are exposed (e.g., local habitat availability, predation risk, and conspecifics). Variation in selection, however, does not only arise from differences in the external environment. Even when two individuals share an environment, intrinsic differences between them can result in different space-use behaviour. In their seminal movement ecology framework, Nathan et al. (2008) described these intrinsic differences among individuals as internal sate. In this section, I describe how internal state factors — specifically, individual differences in physiology or habitat selection behaviour — influence movement, habitat selection, and ultimately species distributions. I provide additional information on incorporating these data into HSA (Box 2.1) and SSA (Box 3.1) in subsequent chapters.

1.4.1 Individual differences influence movement and habitat selection

Some internal factors remain static over the lifetime of the individual, producing consistent individual differences in habitat selection behaviour. For example, personality-based differences in resource exploitation efficiency and risk perception may lead to spatial separation of individuals among habitats to which they are best suited (Spiegel et al. 2018). As another illustration, more explorative and bold brown bears (*Ursus arctos*) were more likely to use a high-risk, high-reward habitat (Hertel et al. 2019).

Differences may also be state-based or variable over time within individuals. Hungrier individuals, for example, may select riskier habitats (Blecha et al. 2018). However, the same individuals, when well-fed, might make different habitat selection decisions. The degree to which selection decisions vary between states might depend on individual variation in capacity for behavioural adjustment across contexts. Behavioural plasticity, a measure of this variation, is a component of personality that differs among individuals (Dingemanse et al. 2010). For example, periwinkles (*Littoraria irrorata*) with shyer personalities were more plastic in their responses to environmental change than were bold individuals whose responses were unchanging over the same environmental gradient (Cornwell et al. 2019). Consistent individual differences in personality and behavioural plasticity also have important implications for animal distributions in response to environmental change at large spatial scales. For example, partially migratory species with more plasticity in their timing and propensity to migrate may be better adapted to respond to environmental change (Xu et al. 2021).

Personality-based habitat selection implies that individuals respond differently when the external environment changes. For example, provided with two foraging habitats from which an animal can expect to gain the same amount of energy, the optimal habitat selection decision would be to forage in the less risky habitat (Brown 1988). However, predation risk and food availability also take different priority for different individuals. Priorities might mean degree of plasticity interacts with internal state to shape habitat selection For example, individuals with dependent offspring, or older individuals with fewer future reproductive opportunities, generally respond less to risk because they place greater value on current reproduction (Heidinger et al. 2006). Behaviourally, these individuals might forage more in a risky habitat than would other individuals. Individual differences in risk taking can also arise from personality traits. For example, jumping spiders (*Marpissa muscosa*) with more active and bold personalities took more chances when risky foraging habitat was available (Steinhoff et al. 2020).

Knowledge of individual state or personality itself is often not necessary to detect individual differences if there are repeated observations of behaviour by the same individuals in different contexts (Dingemanse et al. 2010). For example, several years of brown bear (*Ursus arctos*) relocation data showed bears had little plasticity in selection for bog and forest cut-block habitat, demonstrating consistent individual differences in their habitat preferences (Leclerc et al. 2016). That the internal factors driving bear preferences were unknown was inconsequential to their detection. However, not having information about internal state with which to parameterize HSF models limits transferability of their predictions to new contexts. For example, a population may inhabit a relatively risky area, such as a cut-block, when we observe them. The same overall preference for risky habitats might be expected after the environment changes. But when the environment becomes less risky, individuals may respond differently depending on their consistent or state-based differences. Unless accounted for, these individual differences will increase residual variance in the environment-habitat selection relationship.

In the following section, I argue that physiology is a mechanistic link with which we can both make better predictions and better understand how internal factors influence individual habitat selection. Physiological biomarkers like hormones underpin both transient internal states like hunger (Saper et al. 2002) and persistent personality differences (Niemelä and Dingemanse 2018). With movement-based habitat selection models like integrated step selection analysis (iSSA), we can directly model the effect of these biomarkers on movement, habitat selection, and population distribution. Importantly, building mechanistic models of animal distribution also precludes the need for repeated measures of individuals, reducing the need for large and expensive datasets.

1.4.2 Taking an "internal state" approach to species distribution modelling

Physiological data — in particular, energy-regulating hormones like glucocorticoids and thyroid hormones —might help us model habitat selection and predict distributions when the environment changes. Glucocorticoids and thyroid hormones like triiodothyronine fluctuate in response to changes in energetic state and feeding (Eales 1988). Glucocorticoid production is also tied to habitat differences. For example, California ground squirrels (*Ostospermophilus beecheyi*) in human-disturbed habitats had higher fecal glucocorticoid metabolites (Hammond et al. 2019). Suppressing glucocorticoid production is posited as an adaptive response to the environment, developed by animals to cope with sensitive life history stages like reproduction (Wingfield and Sapolsky 2003). Because physiological biomarkers are tied to energy, feeding, space use, and reproduction, measuring them reveals behavioural motivations of individuals and may help us anticipate habitat selection decisions in reaction to environmental change.

Internal state has occupied relatively little research space in predictive models compared to the research space afforded to the external environment (Holyoak et al. 2008; Jachowski and Singh 2015). A large contributor to this lack of attention is methodological. In addition to increasing access to physiological data from wild animals, HSF methods like iSSA capable of incorporating these data are only recently available. Another reason for the lack of attention is the scale at which we manage animals. Historic conservation focus has been on populations and landscapes, and shifting to focus on individuals has been slow (Merrick and Koprowski 2017). However, I argue that a sizable part of this barrier is conceptual. Until we test approaches for studying individual differences in habitat selection behaviour (Chapter 2), recognize internal state as an important driver of those behaviours (Chapter 3), and use it to interpret unexpected responses to the environment (Chapter 5), internal state will remain a peripheral concern in predicting species distributions.

1.5 Study species and study areas

1.5.1 Elk as a behavioural model for responses to environmental change

There is a long history of behavioural and ecological research on the North American elk (hereafter elk, *Cervus canadensis*). In the past decade, attention has been given to personality-based differences in habitat selection behaviour that affect their exposure to environmental pressures from humans. For example, bolder elk moved more in open habitat, making them more likely targets for hunters (Ciuti et al. 2012). Human-caused environmental change also affects their habitat selection, attracting elk when it increases resource availability (Barker et al. 2019) and stimulating avoidance behaviour when it increases perceived risk (Prokopenko et al. 2017). Finally, there is a demonstrated connection between the environment and elk glucocorticoid levels (Creel et al. 2009), providing a physiological basis for habitat selection in response to environmental change. This rich background literature makes elk an ideal model for testing hypotheses and making predictions about the relationships among internal state, habitat selection, and human-caused environmental pressures.

1.5.2 Natural history of elk of the Canadian prairies

The present-day distribution of Canadian prairie elk was shaped by direct and indirect effects of land use change over the past century. Historical and genetic evidence suggests elk were once a continuous species ranging from Manitoba to Alberta, composed of the common ancestors of what are today considered Manitoban elk (*Cervus canadensis manitobensis*) and Rocky Mountain elk (*C. canadensis nelsoni*; Polziehn et al. 2000). Habitat loss at lower elevations around the Rocky Mountain foothills in Alberta to Manitoba as early as the 1700s restricted populations to higher elevations and protected areas (Speller et al. 2014). Hunting pressure intensified at lower elevations during the same period, when populations of prairie Manitoban elk may have suffered a genetic bottleneck while the Rocky Mountain subspecies was spared from hunting and maintained genetic diversity (Speller et al. 2014). In Alberta, Manitoban elk populations are still genetically and geographically connected to Rocky Mountain elk along the mountain-prairie interface (Polziehn et al. 2000). However, most of the Manitoban elk further east became restricted to relict populations near the Canada-US border (Soper 1946). By the 1940s the once widespread elk populations in southern Manitoba were largely restricted to a stronghold in the newly designated Riding Mountain National Park where their numbers fluctuated but generally remained large (Banfield 1949).

1.5.3 Riding Mountain elk population

Riding Mountain National Park (RMNP) in Manitoba is a vestige of the former shores of glacial Lake Agassiz, rising approximately 1,000 m above the surrounding lower-elevation parkland it borders. In contrast to the more open parkland and agriculture surrounding it, only small pockets of wetland and native fescue prairie interrupt a largely forested RMNP. Concerns over maintaining the forest as a fuel source amidst white settler encroachment prompted its establishment as a timber reserve in 1895 and later as a national park in 1929 (Dupuis 2005). Though the interior of the park was once also used for grazing, land outside its boundaries continued to transition to a largely agricultural landscape through the 20th century (Walker 2002). The stark separation between agriculture and parkland today mirrors historical changes in the distribution of the RMNP elk.

The distribution of the RMNP elk population was likely shaped by colonial influence in addition to land use changes over the past century. The land designated as RMNP in the mid-20th century, including the elk and other animals within it, are part of Treaty 2 territory and culturally significant to First Nations bands in the area. Historically, elk were thought to have migrated between the higher elevations of Riding Mountain and the surrounding prairie where they were seasonally abundant and hunted by the bands (Green 1933). However, unregulated hunting by settlers in the early 20th century generated concerns over the instability of the population (Brook 2009). Between 1914 and the late 1940s, elk reportedly all but disappeared outside the park while those within its borders fluctuated between several thousand and as few as 500 (Green 1933; Banfield 1949). In response to these and other declines, reserve lands within park were forcibly expropriated from the Keeseekoowenin band in 1935 (Dupuis 2005). Despite restrictions, the band made ventures into the park through the 20th century to hunt and fish, risking arrest by park wardens (Peckett 1998). No attempts to rectify restrictions were made until 1994 (Peckett 1998), and the original reserve lands were only returned to the Keeseekoowenin First Nation in 2004 (Dupuis 2005). Today, the Coalition of First Nations, including the Keeseekoowenin First Nation, partners with Parks Canada in management planning within the park. However, historic hunting restrictions within the park, combined with land use change and hunting pressure outside, meant only a subset of elk use farmland outside the park boundary today (Brook 2010).

One important implication of farmland use by elk are concerns surrounding their transmission of bovine tuberculosis (TB) to livestock. These concerns have guided management and research on the RMNP elk since the early 2000s. The first RMNP elk tested positive for TB in 1992, with infection rates increasing to approximately three percent by 2002 (Lees et al. 2003). In that year, farmers were highly concerned about widespread TB infection and crop damage, and many advocated either for eradication of the population or measures to keep elk within the park boundaries (Brook and McLachlan 2006). RMNP elk were regularly killed in defense of crops and livestock for the better part of the 20th century, but a TB management group was officially established in 2001 (Brook 2009). Subsequent culling measures to control infected individuals reduced the population from an estimated 5,500 in the late 1990s to 1,200 in the late 2010s (Parks Canada 2018).

Despite the intentional population decline, the culling program yielded several years of global positioning system data from collared elk and a rich collection of research on their social and habitat selection behaviour. For example, RMNP elk select mostly deciduous and mixed forest because the trees and shrubs are suitable for browsing while also providing protection cover from their main predators in the park, wolves (Carbyn 1983). Use of forest is especially important seasonally as parturient females require cover habitat to protect their vulnerable calves. A substantial number, however also use agricultural land along the park boundary, even around parturition (Brook 2010). Use of agricultural land increases, and mixed forest decreases, in years of greater elk density as competition for forage intensifies (van Beest et al. 2016). Despite apparent forage competition, female elk groups in particular grow larger and more aggregated with density to mitigate predation risk (Vander Wal et al. 2013).

1.5.4 Vita-Caribou elk population

Less is known about the distribution, behaviour, or origin of the Vita-Caribou elk population than many of the other Manitoban populations. The Vita-Caribou elk occupy an agricultural area bordering Minnesota in southeastern Manitoba. Since many of the smaller herds in southern Manitoba disappeared through the late 19th and early 20th centuries (Soper 1946), the population could be composed of surviving individuals from remnant herds, reintroduced individuals from other populations, or both. I was told by a local Vita, Manitoba resident that he recalled a horse trailer releasing elk along Provincial Trunk Highway 59 in the early 1970s (Farmer, personal communication). These animals might come from as near as Riding Mountain, but many populations in Manitoba were also restocked with relocated animals from Elk Island National Park, Alberta in the mid-20th century (Speller et al. 2014). Despite historic restocking and continued reintroductions, the Vita-Caribou population remains much smaller than the RMNP population at approximately 150 animals (Franke 2019).

The Vita-Caribou elk population straddles the Canada-US border, with geographic proximity to a cluster of smaller elk populations in northern Minnesota. Some of the Vita elk may have originated in these Minnesota populations, which have their own origin and reintroduction stories. Throughout the 20th century after the Minnesota populations suffered declines similar to those of the Manitoban populations, the local government supported efforts to relocate animals throughout the state to bolster smaller herds. Later relocations aimed to reduce crop predation as elk populations began to grow (Minnesota Department of Natural Resources 2017). These redistributions continued until recently. An individual in the Lancaster, Minnesota area, for example, told me about an elk farmer who intentionally released animals in the area in the 1990s (Farmer, personal communication).

Like the RMNP population, the distribution of the Vita elk is largely shaped by hunting restrictions and local land use. Elk in the population rely on agricultural land as a source of forage and hiding cover, spending most of their time within approximately 1 km of crops like corn, soybeans, and alfalfa (Hinton et al. 2020). Crop use positions them close to humans for most of the year, resulting in some human-wildlife conflict on both sides of the border. Conflict is mitigated in Minnesota through regulated hunting seasons to help limit elk population growth (Minnesota Department of Natural Resources 2017). However, other than occasional rights-based harvest by mostly Métis hunters, no licensed hunting is permitted for animals in Manitoba.

Differences in hunting risk in Minnesota and Manitoba may be responsible for some of the seasonal movements of elk across the border in late fall (personal observation).

1.6 COVID-19 impact statement

Though in some respects the COVID-19 pandemic positively changed the direction of my thesis, its effects on my field work were nonetheless significant. The field time I lost impacted the data I was able to collect and the chapters I was able to complete, ultimately changing the narrative direction of my thesis from the one I originally proposed.

I originally proposed a thesis with four data chapters, all of which focused on how we could use existing relationships between human-caused land use change and habitat selection to predict the distribution and health of Manitoba elk herds. Data collection began in early 2019 when we captured and fit 18 female elk from the Vita-Caribou population with global positioning system collars. We programmed the collars with a three-year battery life (i.e., 2019–2021), with the expectation that I would be in the field from May–August of each year using the collars to collect health-related data. My first data chapter changed the least from its proposal stage. I hypothesized the availability of habitats altered by land use change would affect habitat selection by elk, and consequently our ability to predict their future distribution. I test this hypothesis in Chapter 2 of my thesis using existing data from the RMNP population (see the following section 1.7 for details on the dataset). In my second data chapter, I proposed to test the effect of habitat selection by the Vita-Caribou elk on levels of hormones — glucocorticoids and triiodothyronine — often used as a proxy for wildlife health. Since then, I identified a more compelling gap in our understanding of how hormones influence habitat selection, which now forms the conceptual basis of Chapter 3 and accompanying proof-of-concept. My final two data chapters centred around testing the effect of habitat selection on elk reproductive success. In a preceding chapter I would use movement patterns of the Vita-Caribou elk to develop a modelling method for detecting birth and potential death events of their calves. The proposed method involved locating newborn calves in the field and fitting them with radio collars capable of tracking mortality signals. Given our sample of 18 female elk over three calving seasons, I expected to track at least 30 calves. After using the model to predict births and deaths of the remaining calves, I would then test relationships among habitat selection, hormone levels, and reproductive success in my final data chapter.

The delayed 2020 field season resulted in major changes to what is now Chapter 3 and the complete pivot of my final two proposed data chapters. My 2019 field season, the pilot season for my PhD, was a big success. From May through August, myself and several volunteers and field staff located and collared 10 elk calves. Though we confirmed the death of only one calf within the first two months of monitoring, we located the birth sites of 12. These births helped me predict the parturition dates for the remaining elk, information I used in Chapter 3 of my thesis. We also collected nearly 200 elk hair and fecal samples from which we extracted the hormone and genetic data used in Chapters 3–5. Despite our initial success, however, the 2020 and 2021 field seasons were also critical because I needed to observe more calf deaths to build my model. Unfortunately, Memorial University’s travel and field work restrictions in 2020 kept me from travelling to Manitoba until I received an exemption in June, resulting in almost two months of lost field work. A skeleton crew of Manitoba government staff took over locating and collaring calves on my behalf in 2020. However, with a combination of their inexperience, limited staff, and their own field restrictions, we only collared four calves that year. Like the 2019 cohort, calf survival was notably high in 2020 and no calves died during the monitoring period. Continued waves of restrictions prevented any 2021 fieldwork, and collars deployed in

2019 finally failed and were removed throughout that year. Having observed only one calf mortality, I could not build a model to predict reproductive success, preventing me from completing my final two data chapters as proposed.

I completed three new thesis chapters between 2020 and 2022. One of these, now Chapter 4, was in progress as of fall 2019 as I needed to identify the fecal and hair samples collected the previous summer. This chapter became especially critical in 2020 after I collected fewer than 100 hair and fecal samples over my shortened field season. My larger sample size after predicting the identity of unidentified samples ensured sufficient hormone observations for the proof-of-concept analysis in Chapter 3. Chapter 4 also complements some of my recommendations in Chapter 3 where I advocate a need for more repeated hormone observations from individuals. Chapter 5 was a late 2021 addition. I conceived of this idea with the goal of using some pre-existing data to better understand additional factors responsible for animal distributions.

1.7 Co-authorship statement and data sources

The data for my thesis came out of two separate long-term studies on the RMNP and Vita-Caribou elk populations. From 2003–2016, Parks Canada collared elk in Riding Mountain National Park to monitor the local TB outbreak. Three PhD students at the time — Eric Vander Wal, Ryan Brook, and Christina Prokopenko — in part collected and managed the biotelemetry data from the over 70 adult elk collared throughout the decade. I use these data in Chapter 2. Though Manitoba Agriculture and Resource Development (ARD) surveyed the Vita elk over approximately the same period, no GPS collars were deployed in the population until 2016. Manitoba ARD deployed the initial set of collars on 14 female elk with the support of the Vita Elk Partnership, having representatives from Memorial University of Newfoundland, Nature

Conservancy of Canada, Manitoba Hydro, and the Rural Municipality of Stuartburn. The partnership approved deployment of a second set of collars on 18 elk in 2019 after I proposed my PhD project. I use these 2019–2020 data in Chapters 3–5. While data were collected in 2019 and 2020, I also led the capture and collaring of Vita-Caribou elk calves used to infer calving dates in Chapter 3 and personally collected the fecal samples I used for genetic and glucocorticoid analyses in Chapters 3–5.

Though I am lead author on all thesis chapters, my data chapters were all collaborative efforts with multiple coauthors. My mentor, Eric Vander Wal, contributed both intellectually and in a supportive role on Chapters 2–5. Christina Prokopenko is an intellectual contributor and co-author on Chapter 2. Gabriela Mastromonaco both extracted and analyzed glucocorticoid hormones from the fecal samples and contributed intellectually on Chapter 4. Alec Robitaille is a coauthor and assisted with the analysis on Chapter 5. Additional acknowledgments accompany my published thesis chapters.

Chapter 2. Newediuk L, Prokopenko CM, Vander Wal E. 2022. Individual differences in habitat selection mediate landscape level predictions of a functional response. *Oecologia* 198: 99-110 doi: 10.1007/s00442-021-05098-0.

Chapter 3. Newediuk L, Mastromonaco GF, Vander Wal E. Unifying adaptive stress and adaptive habitat selection hypotheses through movement ecology will be submitted to *Proceedings of the Royal Society B*.

Chapter 4. Newediuk L, Vander Wal E. 2021. Predicting the individual identity of non-invasive faecal and hair samples using biotelemetry clusters. *Mammalian Biology* doi: 10.1007/s42991-021-00173-8.

Chapter 5. Newediuk L, Robitaille AL, Vander Wal E. Separating shared space from shared social information reveals the antipredator benefit of home range overlap will be submitted to *Behavioral Ecology*.

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CHAPTER 2 INDIVIDUAL DIFFERENCES IN HABITAT SELECTION MEDIATE LANDSCAPE LEVEL PREDICTIONS OF A FUNCTIONAL RESPONSE

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2.1 Abstract

Predicting future space use by animals requires models that consider both habitat availability and individual differences in habitat selection. The functional response in habitat selection posits animals adjust their habitat selection to availability, but population-level responses to availability may differ from individual responses. Generalized functional response (GFR) models account for functional responses by including fixed effect interactions between habitat availability and selection. Population-level resource selection functions instead account for individual selection responses to availability with random effects. We compared predictive performance of both approaches using a functional response in elk (*Cervus canadensis*) selection for mixed forest in response to road proximity, and avoidance of roads in response to mixed forest availability. We also investigated how performance changed when individuals responded differently to availability from the rest of the population. Individual variation in road avoidance decreased performance of both models (random effects: ß = 0.69, 95% CI = 0.47, 0.91; GFR: ß = 0.38, 95% CI = 0.05, 0.71). Changes in individual road and forest availability affected performance of neither model, suggesting individual responses to availability different from the functional response mediated performance. We also found that overall, both models performed similarly for predicting mixed forest selection ($F_{1,58} = 0.14$, $p = 0.71$) and road avoidance ($F_{1,58} = 0.28$, $p = 0.60$). GFR estimates were slightly better, but its larger number of covariates produced greater variance than the random effects model. Given this bias-variance trade-off, we conclude that neither model performs better for future space use predictions.

Keywords: Species distribution models, behavioural reaction norms, *Cervus canadensis*, resource selection, space use, habitat availability

2.2 Introduction

We conserve and manage landscapes for wildlife populations in ways we assume make them most profitable for their use (Gaillard et al. 2010). The profitability of landscapes depend on which habitats individuals within those populations are best adapted to use (Merrick and Koprowski 2017). Individuals select habitats to which they are adapted, and when changing environments produce gradients of habitat availability, their selection changes (Mysterud and Ims 1998). This idea — known as the functional response in habitat selection (Mysterud and Ims 1998) — is becoming central to forecasting the distributions of populations in new environments (Clark et al. 2019; Muhly et al. 2019; Wilber et al. 2020). Thus, our approaches to forecasting population distributions must be robust to the influences of both individual variation and habitat availability on space use. However, habitat selection models that account for availability typically disregard individual differences in habitat selection, even while a number of recent studies have explicitly highlighted their importance (e.g., Lesmerises and St-Laurent 2017; Montgomery et al. 2018; Schirmer et al. 2019; Perrig et al. 2020; McCabe et al. 2021). Indeed, variation in space use among individuals provides behavioural redundancy that can maintain population-level fitness, i.e., population growth, when environmental change imposes selection pressure (Edelaar and Bolnick 2019). Given our understanding of functional responses to habitat selection and the adaptive importance of individual differences in habitat selection, we suggest there is a need to ascertain whether models based on the functional response should indeed improve our ability to forecast the distributions of individual animals when they are faced with environmental change.

Habitat selection is an individual's behavioral response to the environment that nests within the functional response framework. Resource selection functions (RSFs) model selection as the relative probability that an animal will select a location based on the availability of habitat at that location (Matthiopoulos et al. 2020). Methods like the RSF-based generalized functional response (GFR) further incorporate the functional response by allowing habitat selection coefficients to vary with local habitat availability (Matthiopoulos et al. 2011). Thus, based on the environment alone, a GFR model should be better able to forecast distributions outside of the context in which it is developed. As a result, the GFR approach has garnered use in models aimed at understanding how to best manage habitat to preserve its use by animal populations facing large scale disturbances (Morato et al. 2018; Mumma et al. 2019).

However, the compositions of populations change over time and space, and these changes may have implications for habitat selection independent of the environment. For example, female black bears (*Ursus americanus*) avoid males in spring to protect their cubs, resulting in different habitat selection between the sexes (Lesmerises and St-Laurent 2017). At a larger scale, conspecific density in elk (*Cervus canadensis*) motivates some individuals to migrate while others remain resident (Eggeman et al. 2016). The ratio of resident to migratory individuals and demographic characteristics should affect how larger populations select habitat in response to changing availability. Thus, even if models account for habitat availability, not accounting for individual variation in habitat selection may lead to model error and misleading forecasts of distribution.

Individuals within populations also exhibit consistent differences in habitat selection even when faced with the same changes in the environment. These differences in habitat selection are often not correlated with sex or population density, but instead depend on personality traits that are more difficult to measure in wildlife populations. For example, more active and exploratory southern red-backed voles (*Myodes gapperi*) and deer mice (*Peromyscus maniculatus*) selected forests with higher ground cover and light levels than their less active conspecifics (Brehm and Mortelliti 2021). However, all individuals need not follow the same patterns of habitat use when the environment changes. Instead, different personalities may respond with different plasticity to changes in habitat availability. In the previous example, active and exploratory voles and mice converged on the same habitat selection strategies as their less active conspecifics after silvicultural changes to the forest structure (Brehm and Mortelliti 2021), indicating they responded more strongly to the change in habitat availability. These variable responses to availability by individuals are analogous to behavioural reaction norms (BRNs; Dingemanse et al. 2010). BRNs may be correlated with the functional response in habitat selection. However, if the slope of an individual's BRN differs from that of the functional response, then its future habitat selection will not agree with the population-level model used to predict it (Box 2.1).

One approach to deal with individual differences is to challenge the assumption that all individuals sharing a common environment will also make similar habitat selection decisions (Carlson et al. 2021). An alternative model construction approach is to include random coefficients for selection of habitat by individuals. This allows habitat selection models to accommodate both individual differences and the functional response (Muff et al. 2020). Like the slope of a BRN, random slopes account for plasticity, or the magnitude of the change in habitat selection across contexts (Gillies et al. 2006). They can be regressed against mean availability to estimate the functional response, similar to fitting a separate logistic regression model for each individual (Holbrook et al. 2017) without having to explicitly account for availability as in the GFR. Random slopes can also be incorporated into a GFR framework to account for the effects of individual differences on populan-level estimates (Muhly et al. 2019). However, models with only random effects instead make a single estimate of habitat selection for the population, potentially reducing the variance between individual-level and population-level models when variation among individuals is high. Ultimately, the ability of a habitat selection model to forecast animal distributions when the environment changes depends on its ability to reconcile individual differences with population-level patterns.

Here, we tested whether the GFR model or the random effects model better predicts habitat selection by individual elk (*Cervus canadensis*), an animal with demonstrated individual differences in habitat selection (Eggeman et al. 2016, Prokopenko et al. 2017, Montgomery et al. 2018). We first measured the relative strength of selection for two habitat covariates by individuals during two consecutive time periods. We then compared the ability of the population-level GFR and random effects models, fit with data from the earlier period, to predict selection strength by individuals in the later period. The GFR model makes predictions based on the context of current habitat availability, and thus we expected its predictions to agree with future habitat selection effect sizes if individual selection follows the same functional response in both periods (Box 2.1: Fig. IA). Since the random effects model fits a single selection coefficient for the population and thus does not assume individuals also follow a functional response, we expected it to perform best if the functional response changes between periods (Box 2.1: Fig. IB). To investigate how agreement with the functional response affects performance, we compared the extent to which the performance of each population-level model depended on how much availability and individual selection strength for covariates differed from the population-level response. Because its predictions are based on population-level responses, we expected the GFR model to perform worse for individuals whose response to changing availability between the two periods differed most from the population response, while this would not affect performance of the random effects model.

2.3 Methods

2.3.1 Study Area

Our study area is in Riding Mountain National Park (50.83º N, 100.20º W), a protected area at the interface of the Boreal Plains and Prairie ecozones in Manitoba, Canada. The region is characterized by long, cold winters, and precipitation falls primarily as snow between November and April. The park is within Treaty 2 Territory, the original lands of the Anishinaabeg people and the homeland of the Métis Nation. The underlying Manitoba Escarpment consists of rugged terrain, natural habitats, and elevations from 333 to 757 m. The largely agricultural land surrounding the park imposes a distinct boundary: deciduous (43%), coniferous (4%), mixed coniferous-deciduous forests (32%), wetlands (13%), and fescue grassland (1%) within the park give way to open farmland and communities outside the park connected by a dense road network. We recognize the continued relationships between the people of the Tootinaowaziibeeng, Ebb and Flow, Sandy Bay, Rolling River, Keeseekoowenin, Waywayseecappo, and Gambler First Nations from Treaties 1, 2, and 4, and the land and wildlife within and surrounding the park, including the elk population in this study.

2.3.2 Elk Data

Global Positioning System (GPS) collars were deployed on elk in northwest Riding Mountain National Park from 2003 to 2016. Elk were captured between late January and early February during three periods in 2003–2005, 2011–2012, and 2015–2016 using a net gun fired from a helicopter. To prevent sex-related and seasonal differences in habitat selection behaviour from influencing our models, we included only data from female elk during 8 weeks in the winter season from December 1 to January 29. All collars collected relocations at either 1– or 2–hour frequencies.

We divided the 8–week study period into four 2–week blocks to test the performance of the GFR and random effects models for predicting selection by individuals. Individual collars collected data either during the first two blocks (blocks 1 and 2) from December 1–15 and December 16–30, or during the second two blocks (blocks 3 and 4) from December 31–January 14 and January 15–January 29. Thus, data were available for all individuals only during two consecutive blocks. In all cases, we used models fit using data from the earlier period to predict selection by individuals during the later period (i.e., block 1 used to predict block 2, block 3 used to predict block 4). To facilitate model convergence, we excluded any individual with fewer than 60% of the minimum expected location points in either of its 2–week blocks (the equivalent of 100 relocations for collars with 2–hour relocation frequencies). We also screened the data for two-dimensional fixes, step lengths longer than could be travelled by the animal within a time step, and spikes in movement between duplicate points (Bjørneraas et al. 2010). After cleaning, our data included 35 individuals with between 109 and 343 GPS points per 2–week block.

2.3.3 Fitting Resource Selection Functions with Functional Responses

RSFs are a suite of widely used methods to quantify habitat selection, or the relative probability of habitat use by an individual or population compared to that available (Matthiopoulos et al. 2020). We estimated habitat selection ($w(x)$) by elk using exponential form logistic regression RSFs (Manly et al. 2002):

$$w(x_i) = \exp\left[\beta_1 h_1(x_i) + \beta_2 h_2(x_i) + \cdots \beta_n h_n(x_i)\right] \qquad \text{eqn 1}$$

Which describes the selection of a location x_i in habitats h_1 to h_n, where β denotes selection coefficients for habitats. Many use-availability resource selection functions model selection at the third order (Johnson 1980), drawing a sample of availability from within the home range of an individual to compare to observations of use. We drew a separate sample of available points from a 100% minimum convex polygon (MCP) surrounding the used points in each individual 2–week block home range. We confirmed the entire home range was available by comparing the mean home range diameter (3.1 km, 95% CI 0.9, 7.9) with the largest distance travelled by elk from our population within 1 hr (3.9 km). We then generated 10 available points per used point as a compromise between minimizing time required for model convergence and limiting the bias that can be introduced in RSFs when the landscape is not represented by a large availability sample (Northrup et al. 2013).

To test the performance of the GFR and random effects models, we conducted a preliminary analysis to identify where a functional response was likely to occur. We targeted our efforts based on inferences from previous work on elk space use. The Riding Mountain elk population frequently uses mixed forest because it provides both forage and cover from predators (van Beest et al. 2016). Other populations of elk are known to avoid roads because they are associated with risk from humans (Prokopenko et al. 2017). Particularly in areas of higher human use where roads are difficult to avoid entirely, elk also cope by using denser vegetation cover (Dugal et al. 2013). Thus, in addition to individual selection for mixed forest as a function of mixed forest availability, we were interested in selection for mixed forest as a function of their average distance to road. We expected the strongest response from Riding Mountain elk during our study period because it coincides with rifle season — approximately December 1st to January 31st. Based on our preliminary analysis, we detected a weak functional response trade-off in which individuals that were closer to roads on average selected mixed forest more strongly. The relationship between distance to road and selection for mixed forest was similar between blocks

1 and 2 and blocks 3 and 4 (Fig. 2.1b), suggesting individual BRNs followed the same functional response. We also expected elk with more available mixed forest — those within the park that do not use human-modified habitat (Brook 2010) — to avoid roads more strongly. Thus, in addition to a functional response for road avoidance as a function of average distance to roads, we also modelled a functional response for road avoidance as a function of mixed forest availability. However, unlike selection for mixed forest, road avoidance by some individuals differed between their blocks. Individuals with more mixed forest in their home ranges did avoid roads more strongly, but only in the fourth block. The same individuals did not change their response to roads in the previous third block, suggesting their BRNs did not follow the same functional response as individuals with data in blocks 1 and 2 (Fig. 2.1a).

We tested whether modelling the functional response improved predictions of individual selection for mixed forest and distance to road by comparing predictions made by the GFR and random effects models. We fit two individual-level RSF models per individual using data from its earlier and later blocks, and a single population-level GFR and random effects model per individual using data from the remaining individuals collected during its earlier block. We fit the GFR and random effects models 200 times per individual to obtain a bootstrapped set of models with confidence intervals around coefficients, each time sampling the remaining individuals with replacement. All models included the same fixed effect covariates: distance to road as a continuous variable and presence in mixed forest habitat as a categorical variable. We centred and scaled both covariates to facilitate convergence. We obtained roads data from Manitoba Conservation (1994, 2006) and land cover data from Agriculture and Agri-Food Canada Annual Crop Inventory (2019), both at 30 m resolutions.

Random coefficients are used to incorporate individual differences in habitat selection resulting from differences in availability (Muff et al. 2020), including in GFR models (Muhly et al. 2019). We included random coefficients for both covariates in the random effects model, allowing the model to accommodate individual differences in selection without modelling the functional response as a fixed effect:

$$w(x_{ik}) = \exp\left[(\beta_0 + \gamma_{0k}) + \beta_1 h_1(x_{ik}) + \gamma_{1k} h_1(x_{ik}) + \beta_2 h_2(x_{ik}) + \gamma_{2k} h_2(x_{ik})\right] \quad \text{eqn 2}$$

Where γ_0 is the individual intercept, β_n is the coefficient for habitat h_n, γ_{nk} is the random coefficient for habitat h_n for individual k, and x_{ik} is the ith location for individual k. We included random intercepts to control for uneven sample sizes among individuals, which were uncorrelated with random coefficients (Gillies et al. 2006).

We modelled the functional response by including four pair-wise fixed effect interactions between selection for habitat covariates and the mean availability of each covariate for individuals in the GFR model (Matthiopoulos et al. 2011):

$$\begin{aligned} w(x_{ik}) = \exp\big[&(\beta_0 + \gamma_{0k}) + (\beta_1 + \gamma_{1k}) h_1(x_{ik}) + (\beta_2 + \gamma_{2k}) h_2(x_{ik}) + \beta_{11k} h_{11k}(x_{ik}) + \\ &\beta_{12k} h_{12k}(x_{ik}) + \beta_{22k} h_{22k}(x_{ik}) + \beta_{21k} h_{21k}(x_{ik})\big] \end{aligned} \quad \text{eqn 3}$$

Where β_{n1k} is the coefficient for habitat h_n given the mean proportion of habitat h_1 in the home range of individual k, β_{n2k} is the coefficient for habitat h_n given the mean proportion of habitat h_2 in the home range of individual k. Finally, we assigned weights of 1,000 to the set of available points in equations 2 and 3 to ensure our logistic regression models approximated an inhomogenous Poisson point process model (Fithian and Hastie 2013).

2.3.4 Evaluating Performance of Resource Selection Functions

We used relative selection strength (RSS) to evaluate individual differences in selection for mixed forest and distance to road from population-level responses. RSS is the ratio of selection estimates between two locations, x_i and x_j, i.e., $RSS(x_i, x_j) = w(x_i)/w(x_j)$ (Avgar et al. 2017). If values of habitat covariates differ between the two locations, RSS can be used to understand how habitat characteristics influence selection. RSS can also be used to compare how the relative direction and magnitude of selection for a habitat changes across a gradient of availability when the model includes interactions between covariates (Box 1; Prokopenko et al. 2017). This provides a means to assess how closely individual selection coefficients follow the functional response, or in our example how selection of mixed forest is influenced by average distance to road, or vice-versa, in the GFR model.

We first calculated log-RSS by each individual in the latter of their two blocks. We then calculated the log-RSS from each bootstrapped random effects, GFR, and individual model from the individual's earlier block. We made comparisons between the earlier and later blocks by setting the values of distance to road and mixed forest at locations x_i and x_j to different values that compared selection for forest and distance from roads. We calculated log-RSS for distance to road by setting distance to road at location x_i to the 0.05 quantile of the population, distance to road at location x_j to the 0.95 quantile of the population, and mixed forest at both locations x_i and x_j to zero (i.e., outside of forest). These quantiles allowed us to compare changes in habitat selection across most of the range of habitat availability experienced by the population. We calculated log-RSS for mixed forest by setting distance to road at both locations x_i and x_j to the 0.95 quantile of the population, and mixed forest at locations x_i and x_j to zero and 1 (i.e., in versus outside of forest). We set the values of h_{2nk} and h_{1nk} in the GFR model — which includes fixed effect interactions between selection and availability — to the mean distance to road or mean mixed forest availability from the individual's later block.

We considered models from the earlier block to be better predictors when their log-RSS was closer to that of individual log-RSS from the second block. To compare individual with random effects and GFR log-RSS between blocks, we calculated the Z-score of the individual log-RSS on the bootstrapped distribution of the population-level model log-RSS. We considered individuals with a lower absolute value of their Z-score to be better predicted by their population-level model. We also compared individual selection between their earlier and later blocks by calculating the difference in log-RSS between the two periods. We used these comparisons to test the prediction that the performance of the GFR model depends on either within-individual variation in habitat selection or availability. Specifically, we fit a linear regression with Z-score as the response variable and the difference in availability and individual selection between blocks as predictor variables, weighted by the inverse of the variance of the bootstrapped distributions of the GFR and random effects models.

2.4 Results

2.4.1 Variation in Selection and Availability

Individuals varied more in availability of mixed forest than distance to road. Between blocks, individual home ranges differed in availability of mixed forest by a median of 4.82% cover (95% CI = 0.28, 22.17). Individual distances to roads varied between blocks by a median of 0.41 $m \cdot km^{-1}$ (95% CI = 0.04, 1.64). Individuals varied in their responses to mixed forest and distance to road, with some selecting and others avoiding (Supplementary Fig. S.2-1).

2.4.2 Model Performance

Though the population-level models predicted future selection for distance to road (Fig. 2.2) and mixed forest (Fig. 2.3) for some individuals better than others, we detected no overall difference in predictive performance between the random effects and GFR models. The GFR model performed slightly better than the random effects model; Z-scores comparing individual log-RSS for mixed forest in the later block with population-level mixed forest log-RSS distributions were closer to zero in the case of the GFR model than the random effects model (Fig. 2.4). However, when we weighted the Z-score comparisons between models by the inverse of the variance of the log-RSS distributions, there was no difference in their abilities to predict selection for either distance to road ($F_{1, 58} = 0.28$, $p = 0.60$) or mixed forest ($F_{1, 58} = 0.14$, $p = 0.71$). The variance of the GFR model log-RSS distributions was generally higher than the random effects distributions (Figs. 2.3 and 2.4). The variance of the individual slopes from the GFR model (Supplementary Fig. S.2-2) was higher than that of the individual slopes from the random effects model (Supplementary Fig. S.2-3). Fixed effect coefficients and variance of random effects from all bootstrapped models are summarized in Supplementary Figs. S.2-2 and S.2-3.

2.4.3 Effects of Variation in Availability and Selection on Model Performance

Changes in habitat selection by individuals affected the performance of both the GFR and random effects models. Z-scores comparing individual log-RSS for distance to road in the later block with distance to road log-RSS distributions increased with individual differences in selection for distance to road between the earlier and later blocks (random effects: ß = 0.69, 95% CI = 0.47, 0.91; GFR: ß = 0.38, 95% CI = 0.05, 0.71; Fig. 2.5a). In contrast, individual differences in selection for mixed forest between blocks did not affect Z-scores (random effects: ß = 0.61, 95% CI = -0.37, 1.59; GFR: ß = 0.08, 95% CI = -0.25, 0.41; Fig. 2.5b). Similarly, changes in habitat availability between the earlier and later blocks did not affect Z-scores comparing either individual log-RSS with log-RSS for mixed forest (random effects ß = -0.44, 95% CI = -2.78, 1.90; GFR ß = 0.17, 95% CI = -1.52, 1.86; Fig. 2.6b) or distance to road (random effects ß = 0.69, 95% CI = -1.92, 3.30; GFR ß = 0.69, 95% CI = -1.59, 0.41; Fig. 2.6a).

2.5 Discussion

Forecasting future distributions of animals requires modelling approaches that capture habitat selection in light of near-and long-term environmental changes. We compared the ability of two widely used modelling approaches to predict habitat selection by elk when habitat availability varied in the near term. Random effects models account for individual differences in habitat selection by including random intercepts and random coefficients for each habitat. In addition to random effects, the generalized functional response (GFR) model includes fixed effect interactions between habitat selection and availability, allowing coefficient estimates to account for the effect of availability. We found that the random effects and GFR models both performed similarly for predicting near-term selection (Fig. 2.4); without interactions between selection and availability, random effects in the random effects model accounted for more of the variance in selection (Supplementary Fig. S.2-2). Performance of neither model declined when availability changed (Fig. 2.6), but predictions worsened for both models when individual selection changed across time (Fig. 2.5), suggesting differences from the population response affected performance of both models. Overall, our results suggest the random effects model can perform as well as the GFR model for capturing responses to changing availability, but individual variation in response to availability affects the performance of both models. Though this result poses a difficult problem for prediction, it also frames a fruitful discussion about the most appropriate approach to forecast near- and long-term animal distributions. We submit that the GFR makes use of functional response patterns that may be useful for forecasting future distributions, but consideration should be given to whether or not individuals respond similarly to changes in habitat availability.

Models should be evaluated on whether they represent the individual mechanisms that produce population-level patterns (Johnston et al. 2019). When all individuals follow the population-level pattern, the functional response performs well for predicting individual habitat selection (Box 2.1: Fig. IA). However, when habitat selection by some individuals deviates from the population-level pattern, the functional response is a less reliable predictor for those individuals (Box 2.1: Fig. IB). We found the GFR performed well for predicting the functional response for mixed forest as average distance from roads increased, which was largely consistent between blocks (Fig. 2.1). However, the performance of both models depended on individual differences in the way in which mixed forest availability affected their road avoidance (Fig. 2.5), and ultimately the GFR model did not outperform the random effects model. Similarly, Gillies et al. (2006) found no functional response in grizzly bear (*Ursus arctos horribilis*) selection for elevation due to a large amount of individual variation. Like grizzly bears, elk are also known to exhibit variation in habitat selection both within populations (Montgomery et al. 2018) and across time (Eggeman et al. 2016). Given the effect of this variation on model performance, our results suggest the random effects model might be just as appropriate as the GFR model for predicting the distributions of animals that characteristically exhibit large amounts of individual variation. Future studies should assess individual variation by quantifying changes in selection between periods of time (e.g., Fig. 2.1). Individual variation in the functional response could also be captured within the GFR model itself by including random slopes for the functional response terms. Application of this approach in other systems may improve the predictive performance of the GFR model over the random effects model.

Our results also demonstrate that we can reveal individual differences by leveraging the comparative performances of different model evaluation methods. RSS allowed us to estimate selection for each habitat individually while holding availability of the other constant. Including an interaction between selection for each habitat and the availability of each habitat within home ranges allowed us to determine how the GFR model effect sizes compared to effect sizes from individual models with different habitat availability. For many individuals that did not follow the functional response, the GFR and random effects models predicted selection for one of the habitats better than the other (e.g., both models accurately predicted road avoidance but not selection for mixed forest by individual 40 in Figs. 2.2 and 2.3), decreasing the overall performance of the population-level models. Bootstrapping the models also revealed that for many individuals, the variance in RSS for mixed forest based on GFR model coefficients was larger than the variance in RSS based on random effects coefficients (Fig. 2.3). The larger variance of the GFR RSS distributions may be the result of it greater number of covariates, which increased the accuracy of its estimates at the expense of greater variance. This bias-variance trade-off ultimately led us to conclude no difference in predictive performance between models. Whether such variance result from meaningful variation in response to availability by the sample of individuals used to fit the models, or uncertainty in GFR coefficient estimates, is likely to impact the predictive performance of the GFR model in any study system.

Because individual differences underlie population-level patterns, it is important to consider both the functional response (Wittemyer et al. 2019) and individual differences (Merrick and Koprowski 2017) in applied management. GFR model applications attest to its effectiveness for managing wildlife habitat, predicting wolf (*Canis lupus*) distribution in response to anthropogenic disturbance (Muhly et al. 2019) and guiding habitat conservation for lynx (*Lynx canadensis* – Holbrook et al. 2017). However, it is also critical to evaluate its performance for populations with varying degrees of individual variation in habitat selection in response to availability. Individual differences in behaviour mediate factors like mortality risk that ultimately determine reproductive success and population-level performance (Ofstad et al. 2020). Moreover, even when they comprise the minority of behaviours, individual differences in habitat selection can influence effective management and conservation recommendations. For example, by detecting individual differences in Andean condor (*Vultur gryphus*) habitat selection independent of environmental context, Perrig et al. (2020) identified new areas of the species range in need of protection. Their study demonstrates that effective conservation requires both an individual and population perspective. The dual focus on individuals and populations also aligns with our finding that we need more than just patterned responses to availability to comprehensively predict habitat selection. As we found, both the GFR and random effects models reveal habitat selection patterns, but added terms may improve their ability to account for individual variation. If we are to make management recommendations to preserve individual variation in habitat selection, we need to expand our criteria for measuring habitat selection model performance.

As a complementary approach to understanding the effects of individual variation on model performance, future efforts should test how habitat diversity and heterogeneity affect model performance. Many habitat selection models make the reasonable assumption that the most important habitats are where individuals are currently best adapted (Hebblewhite and Merrill 2009; Dupke et al. 2017; Palmer et al. 2017). But population-level habitat selection is adaptive either when different individuals select the habitats to which they are adapted, or the environment changes to suit their adaptations (Edelaar and Bolnick 2019). Past environmental pressure causes some, but not necessarily all, individuals to adjust how they select habitat (Box 2.1: Fig. 2.IB), potentially over evolutionary time (Trevail et al. 2021). We found that both population-level models performed worse for individuals whose response to road distance changed most between blocks, but performance did not depend on changes in availability. Depending on the existing capacity of individuals to respond to availability, greater magnitudes of environmental change could induce more or less agreement between individual BRNs and the functional response. We focussed on how small, near-term changes in the environment and individual variation affect the performance of habitat selection models. Future studies could compare model performance between populations having different historic and current exposure to environmental variation. If past exposure to variable environments primes individual capacities to respond in the future, models that account for individual variation may be a particularly important in diverse and heterogeneous environments.

Forecasts of animal distributions both in human-modified landscapes (Stjernman et al. 2019) and in the face of climate change (Hein et al. 2013) benefit from the expectation that populations change their habitat selection across contexts. However, while population-level changes in selection might be captured by the functional response, we demonstrated that simpler random effects models perform just as well when individual habitat selection deviates from the functional response. Individuals are the units underlying context-dependent habitat selection patterns (Merrick and Koprowski 2017). Recognizing their importance can help prioritize habitat conservation (Perrig et al. 2020) and promote behavioural diversity (Ofstad et al. 2020). Ultimately, we need to consider both habitat availability and individual differences to understand which drives animal distribution patterns and best inform landscape management decisions.

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Box 2.1 The link between individual differences and the functional response

The functional response in habitat selection posits that animals adjust their habitat selection as availability changes (Mysterud and Ims 1998). However, agreement between the population-level functional response and individual habitat selection depends on how much individual variation affects the ability of the functional response to predict the selection of individuals when availability changes.

In Fig. I, each coloured line represents a single individual. Individuals exhibit a behavioural reaction norm for a habitat, the direction and magnitude of which varies along an environmental gradient as an individual's home range changes between two time periods. The functional response for the habitat is positive, i.e., the slope of the increase in selection for the habitat increases along the environmental gradient. Such a response could occur if the environmental gradient measures risk of predation, and the habitat provides cover from that risk. When all individuals respond similarly to the environmental gradient as their positions vary along the environmental gradient, their individual behavioural reaction norms (BRNs) are correlated with the functional response pattern (panel a). In such cases, the functional response is a good predictor of individual selection.

However, if some individuals exhibit a response to the environmental gradient that differs from the majority of the population, the functional response is less reliable for predicting individual selection (panel b). Deviation from the functional response could occur if individuals exhibit consistent differences in their habitat selection regardless of the environmental gradient. In such cases, the mean selection by all individuals in the population (dashed line) is likely to be a better predictor than the functional response because it minimizes the variation between all individuals and their predicted selection.

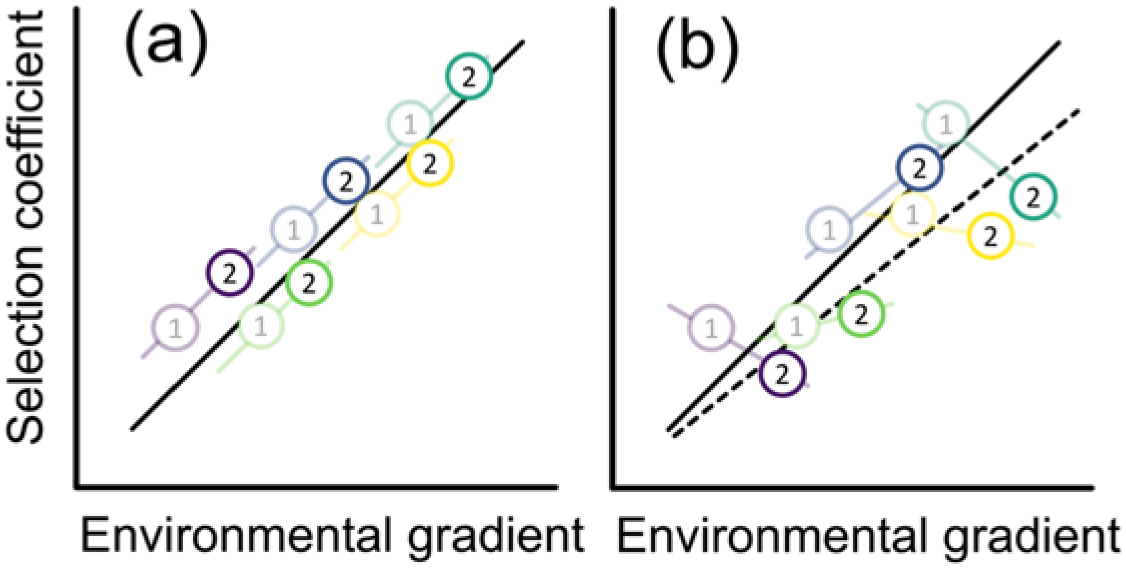

Fig. I The effect of individual variation on the ability of the functional response to predict individual habitat selection. Coloured circles show selection for the habitat by individuals measured during an earlier period (1) and later period (2), resulting in behavioural reaction norms (coloured lines) along the environmental gradient to which individuals are exposed. The solid black line shows the population-level functional response for the habitat along the environmental gradient during the earlier period. The dashed black line shows the resulting change in functional response in the second period when individual responses to the environmental gradient vary.

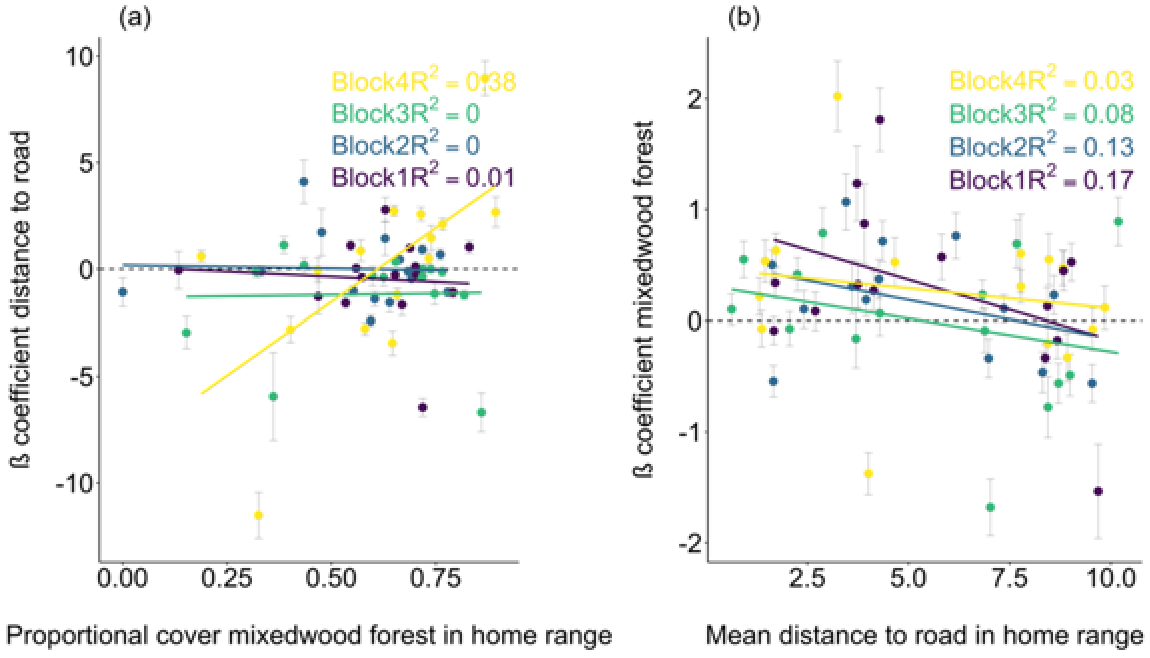

Figure 2.1: Change in selection for distance to road (a) or mixed forest (b) as the availability of the other covariate changes in individual home ranges. Points represent selection coefficients ± SE from individual resource selection functions, and solid lines represent the population-level functional response in each of four blocks: (1) December 1–15, (2) December 16–30, (3) December 31–January 14, and (4) January 15–January 29. Functional responses are based on preliminary analysis to target models for comparing the generalized functional response and random effects models.

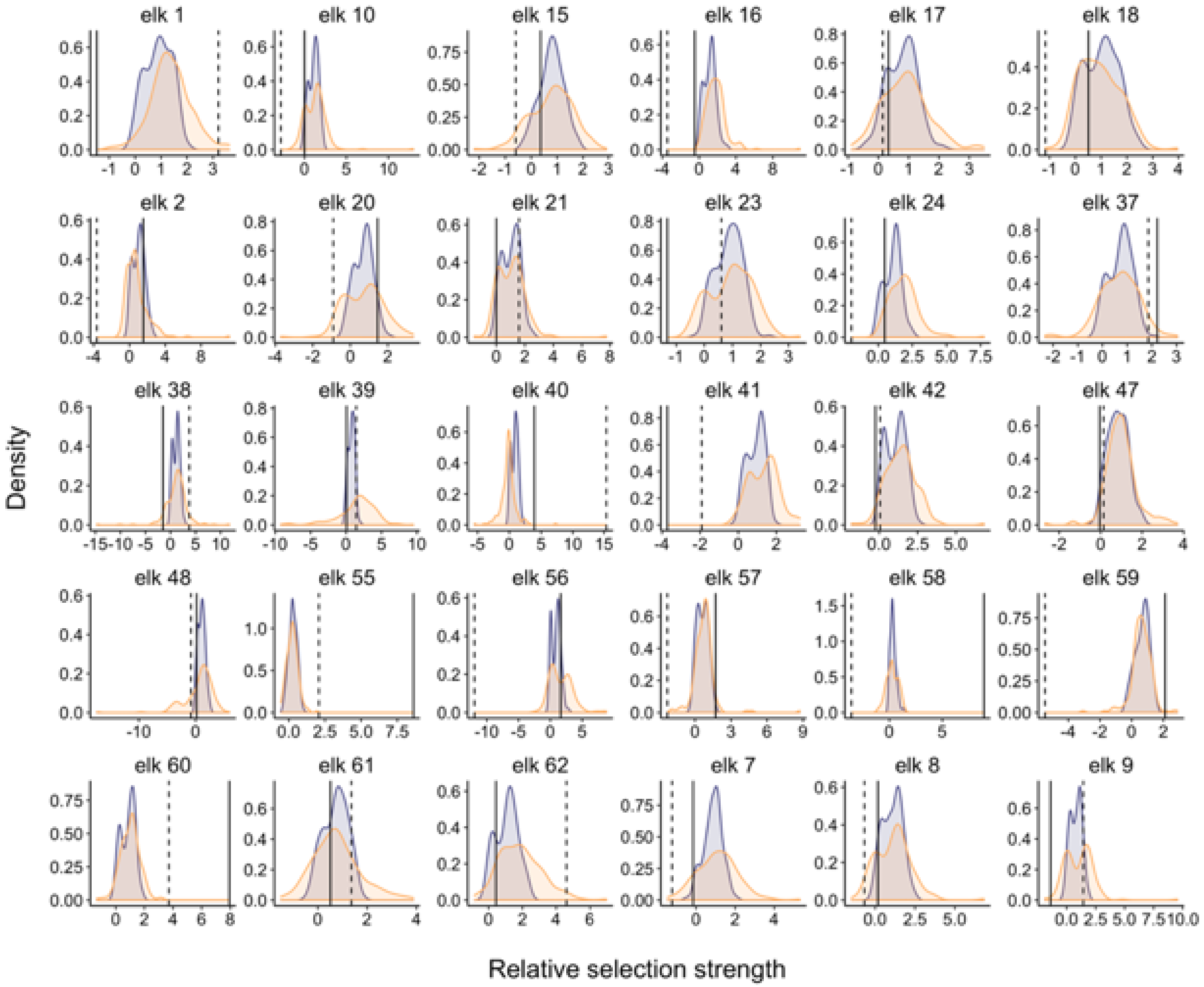

Figure 2.2: Relative selection strength (RSS) for a location in mixed forest 300 m from the nearest road versus a location in mixed forest 5 km from the nearest road, compared among the generalized functional response model (orange distributions), random effects model (purple distributions), and individual models from an earlier period (dashed vertical lines). True RSS from later-period individual models (solid vertical lines) are shown to contextualize predictive model performance. Population-level models are considered better predictors when their distributions overlap the individual model lines. Arabic numerals above plots represent individual identifications. Distributions are comprised of RSS calculated from 200 bootstrapped models per individual, using data collected from the remaining individuals in the earlier period.

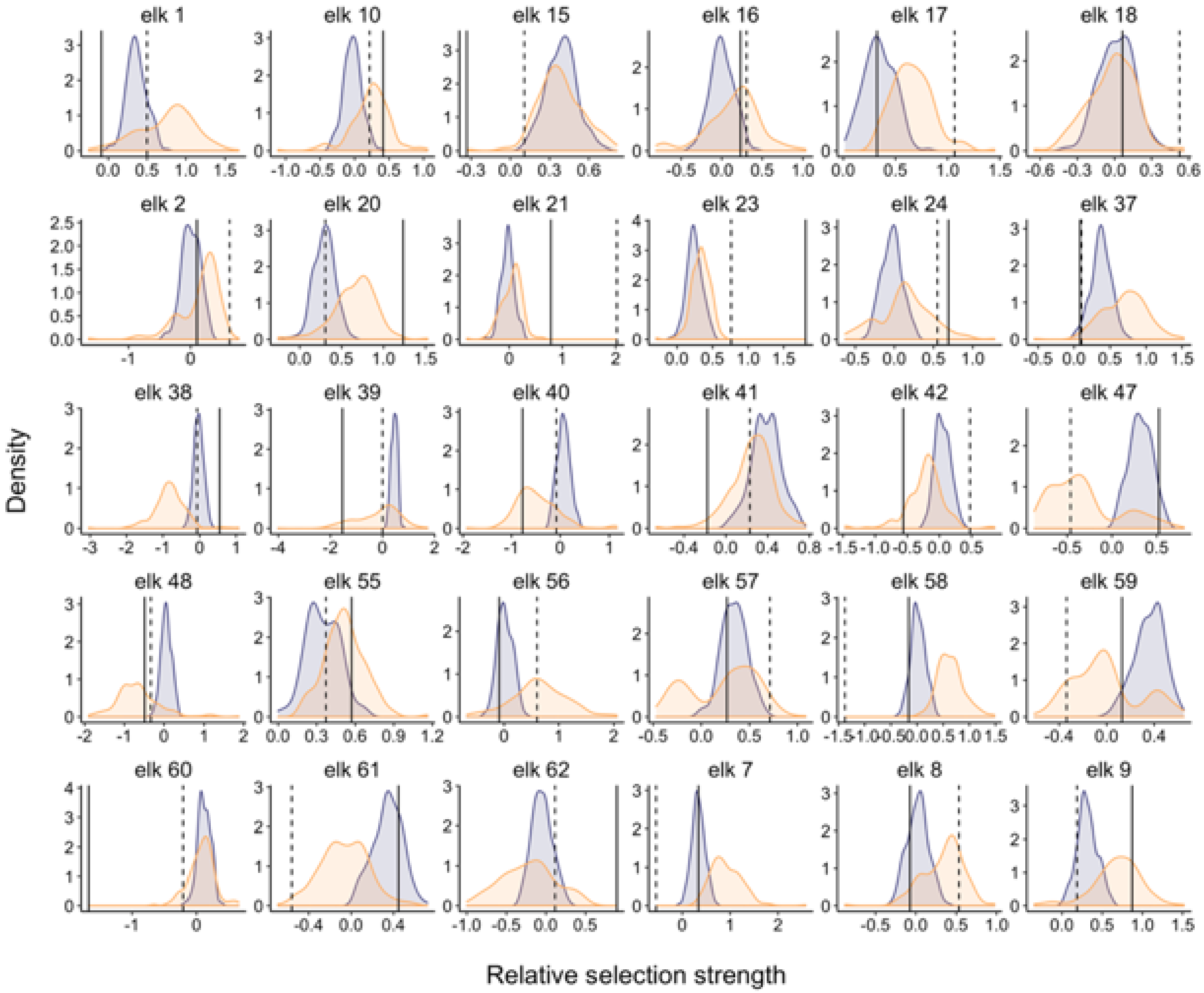

Figure 2.3: Relative selection strength (RSS) for a location in mixed forest versus outside mixed forest and located 5 km from the nearest road, compared among the generalized functional response model (orange distributions), random effects model (purple distributions), and individual models from an earlier period (dashed vertical lines). True RSS from later-period individual models (solid vertical lines) are shown to contextualize predictive model performance. Population-level models are considered better predictors when their distributions overlap the individual model lines. Arabic numerals above plots represent individual identifications. Distributions are comprised of RSS calculated from 200 bootstrapped models, using data collected from the remaining individuals in the earlier period.

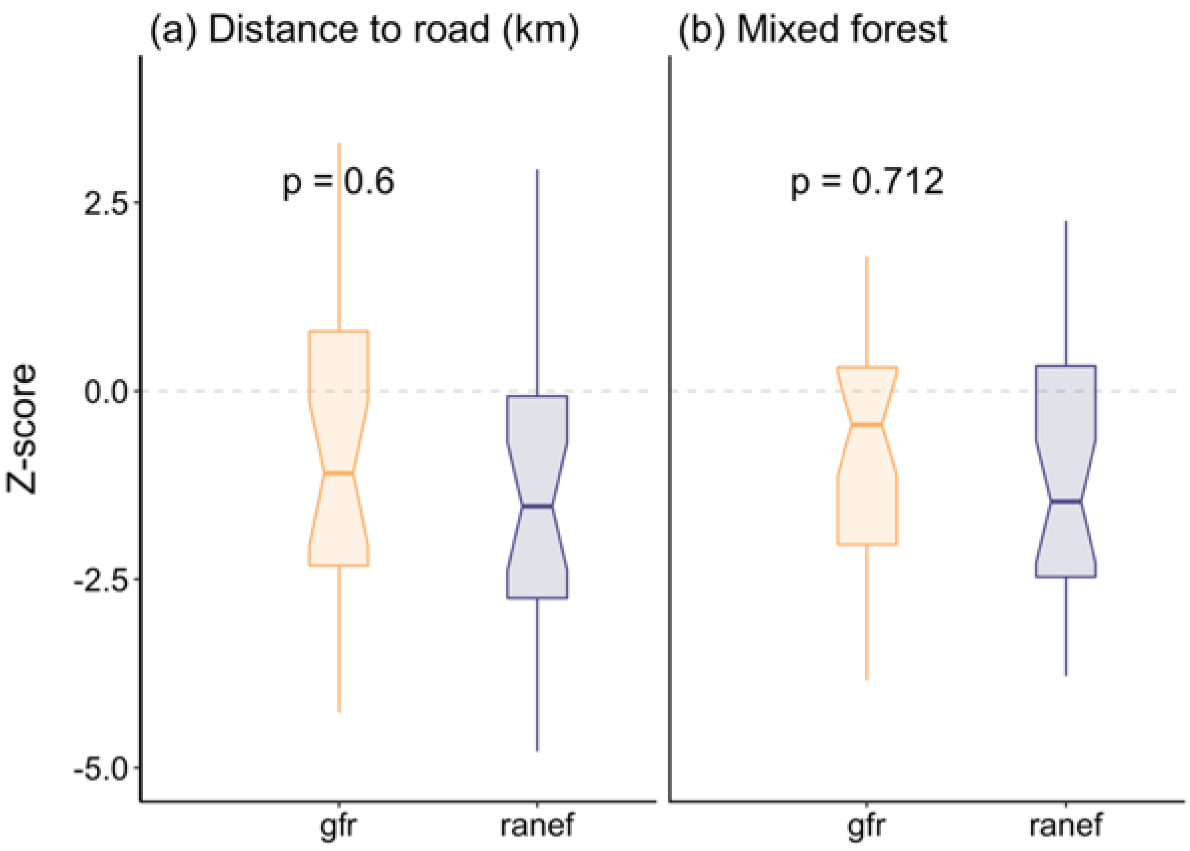

Figure 2.4: Comparison of the ability of random effects (ranef) and generalized functional response (gfr) models using data from an earlier time block to predict selection for distance to road (a) and mixed forest (b) in the next time block. Boxplots measure Z-scores of individual log-RSS on a bootstrapped distribution of log-RSS from each population-level model. P-values are from linear models comparing Z-scores between the gfr and ranef, weighted by the variance of the bootstrapped distribution.

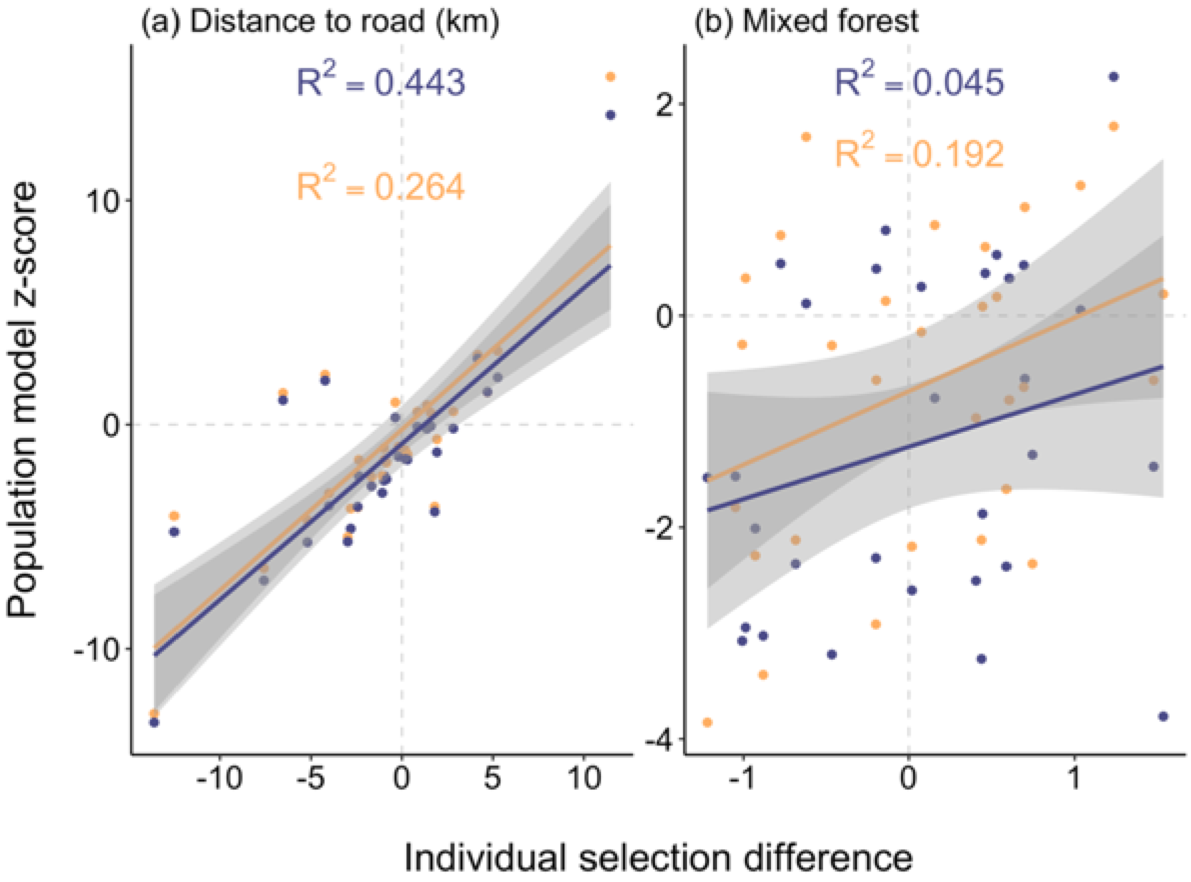

Figure 2.5: Variation in Z-scores of individual log-RSS on bootstrapped distributions of population model log-RSS as individual selection for distance to road (a) and mixed forest (b) changes between an earlier and later time block. Blue points represent individual log-RSS measured along the bootstrapped distribution of the random effects model, and gold points represent individual log-RSS measured along the distribution of the generalized functional response model.

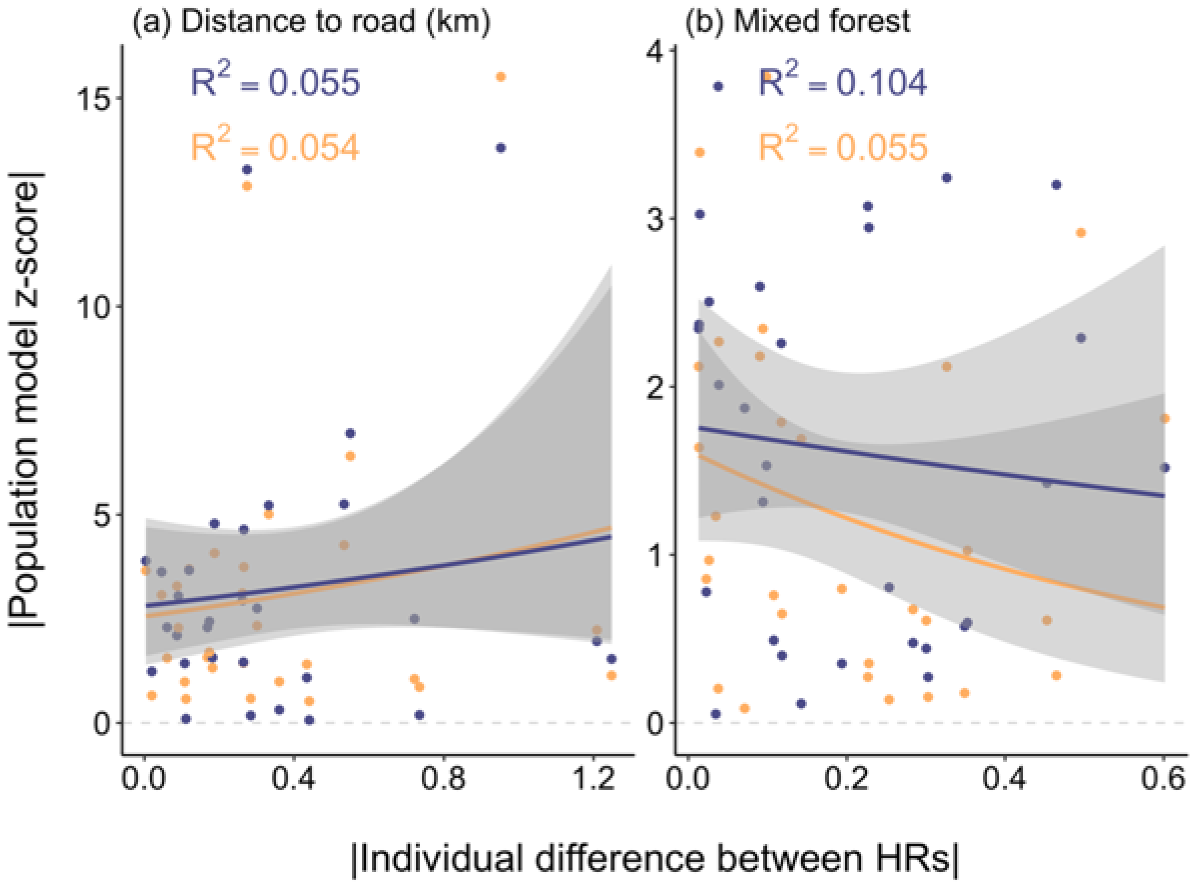

Figure 2.6: Variation in Z-scores of individual log-RSS on bootstrapped distributions of population model log-RSS as availability of distance to road (a) and mixed forest (b) changes between home ranges (HRs) at an earlier and later time block. Blue points represent individual log-RSS measured along the bootstrapped distribution of the random effects model, and gold points represent individual log-RSS measured along the distribution of the generalized functional response model.

CHAPTER 3 UNIFYING ADAPTIVE STRESS AND ADAPTIVE HABITAT SELECTION HYPOTHESES THROUGH MOVEMENT ECOLOGY

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3.1 Abstract

Habitat selection is adaptive, but habitats where animals exhibit elevated glucocorticoid production are often associated with lower fitness. The perception of fitness costs persists in part because glucocorticoid samples rarely represent the internal state of individuals at the time of sampling, making it difficult to demonstrate a causal link between glucocorticoid production and habitat selection. We show how to test this causal link by integrating movement ecology with stress physiology. We first synthesize physiological evidence for the effect of glucocorticoid production on movement with habitat selection theory. We then distinguish when habitat selection exposes individuals to stressors that elevate their glucocorticoid levels, or when elevated glucocorticoids stimulate selection for better habitat. We test the directionality of the two pathways using movement-based habitat selection analysis, capitalizing on a combination of movement data and the predictable time required for glucocorticoids to peak in samples like hair, feathers, and feces. Our proof-of-concept shows how to distinguish when glucocorticoids stimulate adaptive habitat selection. Finally, we suggest a potential evolutionary role for glucocorticoids in habitat specialization, offering a mechanism by which populations might adapt to their environments over generations.

3.2 Introduction

Animals are adapted to their environments, physiologically through glucocorticoid production and behaviourally through habitat selection. Habitat selection is the process by which animals use some habitats disproportionately to their availability. For example, animals might relocate to sparser foraging patches that maximize energetic intake (Charnov 1976) while mitigating the stress of competition for forage (Fretwell and Lucas 1969). Movement between foraging patches is driven in part by glucocorticoid hormone production. Glucocorticoids stimulate appetite when energy reserves are low (Pecoraro et al. 2004) and make energy available for movement to find foraging resources (Dallman et al. 1993). Their role in energy regulation makes glucocorticoids a key indicator for internal state, which is integral to movement and habitat selection (Nathan et al. 2008). But glucocorticoid production is also associated with exposure to stressors that can compromise fitness (Bonier et al. 2009). Glucocorticoids have pleiotropic effects under stress, reducing body mass when they stimulate catabolism of energy reserves (Landys et al. 2004), and lowering reproductive success when they stimulate behaviours that interfere with reproduction (Vitousek et al. 2014). While these costs usually only arise when animals face chronic and inescapable stressors (Boonstra et al. 1998), studies considering possible adaptive benefits of glucocorticoids are the minority. The benefits of glucocorticoid production are least considered when their production coincides with selection of stressful habitats.

Glucocorticoids decrease fitness directly when their long-term production becomes physiologically harmful or otherwise compromises reproduction or survival. Reproductive output, for example, declines after long-term experimental exposure to stressors (Vitousek et al. 2018). Oxidative stress can accumulate even after short-term glucocorticoid exposure (Majer et al. 2019). Though the physiological and behavioural consequences of glucocorticoid production can compromise fitness, glucocorticoid production is not inherently pathological. In fact, its production is often an adaptive response to stressors faced in the wild (Boonstra 2013). For example, depletion of body reserves is associated with elevated glucocorticoids (Jeanniard du Dot et al. 2009; Krause et al. 2017), but breakdown of protein and lipid reserves are is not always harmful over longer time scales. For example, when food availability is low or energetic demand is high, mobilizing lipid and protein reserves prevent starvations (Landys et al. 2004). Sacrificing body condition might eventually compromise survival, but lifetime reproductive success may also be higher for animals that select habitat favouring their own survival when conditions are not favourable for offspring survival (Jaatinen et al. 2014). Quantifying survival and reproductive success associated with glucocorticoid production can help distinguish when glucocorticoid-driven habitat selection is adaptive, but this requires knowing whether glucocorticoids caused habitat selection, or habitat selection caused glucocorticoid production.

One way to establish causation between glucocorticoids and habitat selection is to identify the timing of habitat selection relative to associated glucocorticoid production. When glucocorticoids are already elevated before selecting a particular habitat, stressors in the selected habitat could not have caused their production. Instead, glucocorticoid production might have driven selection of the habitat, motivated by stressors experienced elsewhere. For example, migratory animals elevate glucocorticoids in spring as stressors intensify on winter ranges (Anderwald et al. 2021), energetically preparing them for migration to summer ranges (Landys-Ciannelli et al. 2002). Thus, during migration the glucocorticoids causing habitat selection are adaptive. In contrast, when glucocorticoids become elevated after selecting habitat, their production might represent reactions to stressors. For example, sandgrouse (*Pterocles alchata*) inhabiting a recreational area had elevated glucocorticoids only after weekends with high tourist traffic, suggesting human disturbance triggered their stress responses (Casas et al. 2016).

The sequence from glucocorticoid production to habitat selection is clearer when glucocorticoids are elevated in response to measurable stressors like human disturbance, but many natural stressors facing wild animals are not readily observable. For example, when a wild animal selects a risky habitat where it briefly encounters a predator, the hypothalamic-pituitary-adrenal axis might stimulate an acute stress response. Eventually, glucocorticoids produced during the stress response can be measured in non-invasive samples like hair and feces. However, non-invasive samples are difficult to age and could represent stressors that occurred hours, days, or even weeks in the past (Gormally and Romero 2020). The disconnect between stressor and sample makes the exact timing of the predator encounter, and therefore the relative order of habitat selection and glucocorticoid production, ambiguous.

Responses to short-term stressors are also difficult to manipulate and measure where multiple stressors co-occur (Gaynor et al. 2019). For example, predator abundance can be compared between habitats, but assumed stress responses to predation risk may instead be caused by other associated stressors like food shortages or conspecific density (Petrullo et al. 2022). The consequence is that only correlations can normally be made between habitats, glucocorticoid production, and fitness under natural conditions. The most common interpretation of these correlations is that selection of stressful habitat caused harmful glucocorticoid production that reduced fitness, even without causal evidence (Table 3.1).

We show how the movement ecology lens (*sensu* Nathan et al. 2008) can help distinguish adaptive production of glucocorticoids from their purported harmful effects. To demonstrate, we first synthesize evidence that glucocorticoids are mechanistically responsible for adaptive habitat selection behaviour. Our examples show how habitat selection changes when animals in different life-history stages manipulate glucocorticoid levels to support either reproduction or survival. Next, we discuss the time lag between stressor and peak glucocorticoid concentrations in tissues like blood, feces, and hair. Normally considered a challenge for researchers aiming to connect glucocorticoids with movement and habitat selection, we demonstrate how the consistency of this time lag presents an opportunity to pinpoint the stressor responsible for habitat selection. Once the timing of the stressor is known, movement-based analyses can test causal links between glucocorticoids and adaptive habitat selection responses to the stressor. We demonstrate this analysis with a proof-of-concept. Our proof-of-concept acts as a template for promising research questions to which the same approach could be applied in the future.

3.3 Physiology of glucocorticoids as a mechanism and motivation for movement

Patterns of glucocorticoid production correlate with movement activity over daily and seasonal time periods. Baseline glucocorticoid levels, regulated by the autonomic nervous system (Herman et al. 2003), coincide with energy needs for locomotion at predictable times. For example, circadian activity patterns in mice coincide with the rise and fall of circulating glucocorticoids (Malisch et al. 2008), and in turn, glucocorticoid rhythms adapt to regular feeding periods when energy is available for movement (Rovirosa et al. 2005). The interplay among energy availability, movement, and these baseline glucocorticoid levels is a mechanistic explanation for diel habitat selection patterns that help prey species access forage while avoiding their predators (Smith et al. 2019). Seasonal activity patterns like migration track longer-term baseline glucocorticoid rhythms (Landys et al. 2006). Because baseline glucocorticoid levels are seasonally elevated during migration (Landys-Ciannelli et al. 2002), birds are primed to adjust movement quickly in response to cues like wind assistance (Eikenaar et al. 2017) and stressors upon arrival at migration stopover sites (Falsone et al. 2009). Non-migratory birds also elevate baseline glucocorticoids during reproduction when offspring require the most active provisioning (Bonier et al. 2009). Thus, via extension of their effects on activity and locomotion, glucocorticoids form the physiological connection between environmental pressures and adaptive patterns of behaviour to overcome them.

Environmental pressures, like predation risk, induce stress responses that make prey species avoid risky foraging habitat. Predator cues stimulate a cascade of hormone release via the hypothalamic-pituitary-adrenal (HPA) axis, the main products of which include glucocorticoids and other faster-acting hormones such as catecholamines. While catecholamines are mainly involved in increasing blood pressure, heart rate, and driving other more immediate responses to stress (Sapolsky et al. 2000), glucocorticoids have a primary role in helping to regulate blood glucose levels. Glucose is mobilized when glucocorticoids prevent its uptake by adipose and muscle tissue (Carroll et al. 2018) and stimulate gluconeogenesis (Dallman et al. 1993), thereby providing needed energy to forgo foraging while escaping predators. Continued effects of elevated predation risk on glucocorticoid production can have long-term effects on habitat selection patterns. For example, decadal shifts in predation pressure by grey seals in Atlantic Canada caused Atlantic cod (*Gadus morhua*) and white hake (*Urophycis tenuis*) to redistribute to safer areas with less food (Swain et al. 2015). In such cases, the potential cost of predation outweighs the value of energy gain.

The continued need to replenish calories under long-term predation risk, however, can also encourage selection for risky habitats that offer more productive foraging. As risk attenuates after a stress response, glucocorticoid levels return to baseline levels through a combination of negative feedback on the HPA axis and reduced glucocorticoid production. When reduction in

HPA axis activity follows a stress response, still-elevated baseline levels stimulate feeding behaviour (Dallman et al. 1993) and a preference for high-calorie foods (Pecoraro et al. 2004). If lower feeding rates during the stress response eventually compromise energy storage, peripheral satiety signals also decline and animals seek to replace energy stores (Dallman et al. 1993). For wildlife, replacing energy stores means movement to foraging habitats. Consequent hunger encourages animals exposed to chronic risk to spend even more time foraging (McNamara and Houston 1990). Preferences for richer foods are reinforced over time because their consumption gradually blunts mounting of stress responses (Foster et al. 2009), keeping baseline glucocorticoid levels in a slightly elevated state. Similarly, predation risk elevates respiration rate, changing C:N ratios of animal tissue and stimulating selection of forage with greater carbon content (Hawlena and Schmitz 2010). Over time, habitat selection patterns emerge that prioritize energy gain over avoidance of predation risk. For example, rather than moving to unproductive areas with less poaching, elephant groups in Kenya responded to intense ivory poaching by moving to ranges with higher primary productivity (Goldenberg et al. 2018). Thus, glucocorticoid-stimulated movement mediates trade-offs between energy-motivated and risk-avoidant habitat selection, which is ultimately adaptive.

3.4 Integrating glucocorticoids into individual habitat selection

Testing when glucocorticoids stimulate adaptive habitat selection is difficult in the wild because glucocorticoid samples are imprecise measures of stressors faced by individuals. Precision comes from placing movement appropriately along the timeline from glucocorticoid production to sample collection. Glucocorticoids are incorporated into growing hair cells from the plasma, and depending on the rate of hair growth, represent circulating levels over periods from weeks to months (Burnard et al. 2017). Feathers also require weeks or months to incorporate glucocorticoids, and only do so during growth periods prior to moult (Gormally and Romero 2020). Fecal samples represent circulating glucocorticoids processed by the liver and deposited as metabolites within several hours to days depending on species-specific gut transport times (reviewed in Palme 2019). In contrast, the temporal resolution of biotelemetry data is often hourly or finer, making glucocorticoid samples a relatively coarse representation of stressors faced during habitat selection. The mismatch between habitat selection and glucocorticoid production makes it necessary to pool movement data over weeks, months, or even years. The more data are pooled, however, the more challenging it becomes to assess whether glucocorticoid production is a cause or consequence of habitat selection behaviour. Addressing the problem of causation requires validating the time required for glucocorticoids to peak in samples after stressors, then determining whether the behaviour occurred before or after the hormone peak.

Determining whether behaviours caused or were caused by elevated glucocorticoid levels is especially important in the wild where stress responses are often inferred instead of observed. The general expectation is that perceived stressor severity determines the quantity of glucocorticoids produced in response (Luttbeg and Grindstaff 2022). However, the bioactive component of glucocorticoids, and not the overall amount produced in response to stressors, triggers behavioural responses. Habitat selection behaviours driven by baseline glucocorticoid levels, like foraging and migration, arise when glucocorticoids bind to low-affinity mineralocorticoid (MR) receptors (Landys et al. 2006). For immediate behavioural effects during a stress response, glucocorticoids bind high-affinity glucocorticoid (GR) receptors (Dallman 2005). Receptor binding is controlled in part by corticosterone binding globulins (CBGs) which bind glucocorticoids in the plasma and prevent them binding receptors (Breuner et al. 2020). As a result, the effects of glucocorticoids on behaviour saturate when either high CBG concentrations, downregulated receptor transcription (Lattin and Romero 2013), or negative feedback on the stress response slow receptor binding rates downstream (Lattin et al. 2016). Estimating the amount of circulating glucocorticoids available to bind to receptors, however, requires either blood samples (e.g., Breuner et al. 2020) or experimental hormone challenges (e.g., Mastromonaco et al. 2014). The controlled conditions required for these protocols make it difficult to link CBGs, receptors, and negative feedback to habitat selection under natural conditions. Alternatively, modelling glucocorticoid-habitat selection relationships could reveal when these downstream mediators adjust how the hormones affect behaviour. This is because when downstream mediators interact with glucocorticoids at high concentrations, their relationship with behaviour becomes nonlinear. For example, Adélie penguin (*Pygoscelis adeliae*) locomotory behaviour had a U-shaped relationship with glucocorticoid supplementation, where glucocorticoid effects on behaviour at high circulating concentrations were buffered by high CBG concentrations (Spée et al. 2011).

Adjusting behavioural responses to glucocorticoids downstream is beneficial for some individuals and during some seasons. For example, as day lengths shorten in winter, the effect of cortisol supplementation on white-crowned sparrow (*Zonotrichia leucophrys gambelii*) activity saturates (Breuner and Wingfield 2000). Saturating effects of endogenous glucocorticoids on behaviour are also common during reproduction (Lattin and Romero 2013), when habitat selection must adjust to meet the needs of breeding individuals and those provisioning offspring (Amor et al. 2019). Individuals having more experience with a stressor sometimes develop stronger negative feedback to prevent pathology from chronic stress (Cyr and Romero 2009). The result is that the same stressor might produce different peak glucocorticoid levels in two individuals or differences in how glucocorticoid effects are mediated downstream (Baldan et al. 2021). These differences might manifest in different adaptive habitat selection patterns by individual or by season in response to the environment.

Differences in how individuals respond to the environment pose a problem for disentangling cause and effect because they introduce variation into the glucocorticoid-habitat selection relationship. To control for this variation, individual movement must be linked to glucocorticoid samples collected from individual animals at known times. While repeated sampling of individual animals is often infeasible in the wild, biotelemetry data can help link individuals with opportunistically collected field samples. Feathers, hair, and feces contain genetic material in addition to glucocorticoids, allowing anonymous samples from populations to be matched to individuals with genetic data using genetic capture-mark-recapture techniques (Palme 2019). Conspicuous species like ungulates can be observed defecating or shedding hair (Dulude-de Broin et al. 2020). When individuals also carry biotelemetry tags, areas like trails and locations of kill or rest sites can be targeted for sampling specific individuals (e.g., Giroux et al. 2012), especially when fine-scale timestamped location data link individual movements to their circulating glucocorticoids during the same period (Newediuk and Vander Wal 2021).

When the timing of sample collection, estimated age of the sample, and the time required for glucocorticoids to peak in hair, feces, or feathers are known, the approximate timing of stressors can also be pinpointed. Movement-based models can then be used to interpret whether the stressor caused or was a product of habitat selection. One possible interpretation of elevated glucocorticoids is that the habitat selected by an animal exposed it to a stressor that affected its circulating glucocorticoid levels. This interpretation might be tested with double hierarchical models that include a coefficient for movement characteristics describing behaviours related to foraging (e.g., tortuous movements) over the “steps” preceding the glucocorticoid peak (outlined in (Hertel et al. 2020)). Another interpretation is that glucocorticoid levels became elevated by the stressor, which then stimulated habitat selection. Habitat selection analysis might be used to test this interpretation. Integrated step selection analysis (Avgar et al. 2016), a specialized class of habitat selection analysis, can be used to test whether glucocorticoids produced before the beginning of a step affect the relative probability of habitat selection at its end (Box 3.1). In the following section, we provide a proof-of-concept demonstrating this approach.

3.5 Proof-of-concept: Glucocorticoid-mediated fine-scale habitat selection by elk

For species that provide parental care, the fitness consequences of habitat selection manifest around parturition as an energetically demanding life stage. Female ungulates must both maintain sufficient body condition prior to calving and compensate for the demanding energetic costs of spring lactation via summer nutrition (Cook et al. 2013). In part, these nutritional needs are met by shifting habitat use toward better forage. Increased used of forage rich habitat also coincides with elevated baseline glucocorticoid levels typical of ungulate calving periods (Lehman et al. 2019). However, calves are vulnerable to predation and in some species of ungulate are typically hidden for a few weeks following birth. To ensure reproductive success, mothers must compromise some of their nutritional needs for safety needs of the calf (Duchamp et al. 2019). Safety typically requires use of cover habitat like forests and shrubland despite better foraging opportunities elsewhere (Alves et al. 2013).

We used integrated step selection analysis (Box 3.1; Avgar et al. 2016) to test whether selection for cover habitat by 13 female elk (*Cervus canadensis*) shifted in response to fecal glucocorticoid metabolite levels, and whether the response changed during the approximate 16-d window when their calves are most vulnerable (see Supplementary 1 for detailed methods). We collected fecal glucocorticoid samples, which for elk correspond to circulating levels approximately 20 hours prior to defecation (Huber et al. 2003; Ashley et al. 2011). Our global positioning system-collared study population in southeastern Manitoba, Canada (49.134, -96.557) uses forest as cover habitat (Hinton et al. 2020) to safely avoid humans in the largely agricultural landscape that acts as a source of calving season forage (Amor et al. 2019). Because animals forage to recover from stressors (Dallman et al. 1993), we predicted that prior to calving and during the approximately 20 hours following glucocorticoid peaks, elk would select locations farther from cover. Foraging to recover energy after stress responses risks calf safety by exposing them to potential encounters with predators. However, lactating elk also require more energy. Thus, during the 16-d window of calf vulnerability we expected elk to use locations either farther from or closer to cover habitat depending on their priority for energy versus safety. If elk prioritized safety, those with young calves should remain closer to cover habitat even after glucocorticoid production increased. Alternatively, if they prioritized energy, they might have an even stronger preference for areas further from cover when glucocorticoid production increased. Importantly, a change in behaviour after calving might indicate either CBG concentration, receptor number, negative feedback, or all three are adjusted downstream to support calf survival.

Elk habitat selection differed with glucocorticoid levels and presence of young calves. Before calving and when calves were able to escape predators, their mothers were 50% more likely to select locations farther from cover habitat for each unit increase in glucocorticoids (Fig. 3.1, “pre” period). Elevated glucocorticoids increased the likelihood that elk selected locations further from cover even more strongly within the 16-d window when calves were most vulnerable (Fig. 3.1, "post" period). These results suggest the non-linear effects of glucocorticoids on habitat selection may be mediated post-partum either by CBG concentration, receptor availability, or negative feedback on glucocorticoid production. Glucocorticoid-mediated habitat selection characterizes a transition in life-history for the elk, making it an adaptive strategy that supports lifetime reproductive success. See Supplementary 2 for comprehensive results.

3.6 Conclusions and future directions

One of the most pervasive ideas about glucocorticoid overproduction is that it is an indicator of exposure to stressors that decrease fitness (Bonier et al. 2009). We interpreted the fitness implications of glucocorticoid production through its relationship to adaptive behaviours like habitat selection. In our proof-of-concept, elk with elevated glucocorticoid levels selected locations further from cover habitat, suggesting a preference for forage-rich agriculture. Selection for forage aligns with physiological evidence that glucocorticoids help animals recover energetically after a stress response (Dallman et al. 1993). When they had young calves, elk with elevated glucocorticoids exhibited even stronger selection for locations further from cover, suggesting they prioritized energy over remaining close to cover habitat for their calves (Fig. 3.1). We suggest the change in behaviour associated with young calves might have been brought about by a change in CBG concentration (Lattin and Romero 2013) or other downstream effects. We demonstrated that glucocorticoid production and downstream mediation are adaptive with a modelling approach that could demonstrate a causal relationship between glucocorticoid production and habitat selection. Key to our inference was knowing the time required for glucocorticoids to peak in fecal pellet samples and which samples belonged to which individuals. These two pieces of information, already available or collected in many studies, hold promise for testing existing hypotheses in habitat selection and stress physiology and for exploring new links between individuals and their environments (Box 3.2).

One promising extension of our approach is to test whether adjusting habitat selection through glucocorticoid production helps individuals and populations respond to stressors over multiple generations. Individuals respond to stressors by adjusting glucocorticoid production over their lifetimes to support either survival or reproduction. For example, as they age and fewer reproductive opportunities remain, individual terns (*Sterna hirundo*) produce fewer glucocorticoids to support reproductive behaviours (Heidinger et al. 2006). These age-dependent changes in reproduction are adaptive at the population level because they align with age-dependent reproductive investment as predicted by life-history theory. Stress-coping mechanisms are also transmissible to offspring (Jenkins et al. 2014), meaning selection might act on habitat-specific glucocorticoid production as individuals are exposed to different stressors in the habitats they occupy (Patterson et al. 2014). Disruptive selection on both habitat selection and glucocorticoid profiles could reinforce differences among individuals, resulting in both the physiological and spatial separation of populations over time (Lema 2020). For example, frogs adapted to habitats with long-term exposure to anthropogenic noise both produced fewer glucocorticoids in response to noise and had developed physiological coping mechanisms to equalize fitness with their noise-free habitat counterparts (Tennessen et al. 2018). The evolutionary effects of glucocorticoid-habitat selection feedback might be preceded by habitat specialization at smaller scales, likely testable using our movement-based approach (Box 3.2).

Our synthesis highlighted a limitation in the way we currently interpret associations between habitat selection and glucocorticoids: namely that we rarely consider glucocorticoids an agent of adaptive habitat selection. The association between poor habitat selection and glucocorticoid production persists because it is more challenging to test whether different levels of glucocorticoids drive adaptive habitat selection. We showed the tools to test for these adaptive relationships readily available where ecologists collect biotelemetry data, non-invasive glucocorticoid samples, and are willing to integrate new modelling approaches. The challenge going forward will be to remain receptive to alternative interpretations about glucocorticoid production in the context of habitat selection.

3.7 References

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Box 3.1: Primer on habitat selection analysis and glucocorticoids

Habitat selection analysis (HSA) quantifies how stressors influence which habitats — or points in space characterized by a unique set of resources, risks and conditions (Northrup et al. 2022) — are used preferentially or avoided by animals:

$$w_i = {}^{u_i}/_{a_i}$$

Where w_i is the "selection ratio" for habitat i, u_i is the proportion of habitat i used by the animal, and a_i is the proportional representation of habitat i within a landscape (Boyce and Mcdonald 1999). Note that use is often quantified using locations from biotelemetry devices. Unused locations are generally unknown, rendering proportion of use indeterminable. In these cases, selection for habitats can be estimated using logistic regression:

$$w_x = exp(\beta_0 + \beta_1 k_i + \cdots + \beta_n k_j)$$

Where the used locations are compared to a larger sample of "available" locations. Instead of probability of selection as in the selection ratio, coefficients β_1 to β_n represent selection for habitats variables, k, *relative* to j others in the model (Fieberg et al. 2021).

Later adjustments to the HSF model stemmed from technological advances in biotelemetry data collection. Modern biotelemetry devices collect used location data at regular time intervals. Intervals are often frequent enough that not all available locations are necessarily accessible, making biological constraints on movement a likely constraint on habitat availability. For example, locations visited within a day may not be accessible between hourly locations because the distance an animal can travel within an hour is limited. Step selection functions (SSF) address this constraint by drawing available locations from a set of trajectories to which the animal could move from each location point (Fig. I; Fortin, Morales, & Boyce, 2005). Turn angle and step length between location points become additional variables in the model, drawn from empirical distributions of the animal's movements. Movement, however, is also influenced by stressors habitat-specific stressors encountered along a movement path. Integrated step selection functions (iSSF) extend the SSF approach by incorporating this interdependency between movement and habitat selection within the modelling process (Avgar et al. 2016).

Aside from its statistical justification, constraining availability and integrating movement into the habitat selection process makes iSSF models convenient for testing hypotheses about glucocorticoids and movement. Just as movement depends on habitats encountered along a movement path, it also depends on the animal's glucocorticoid production. Glucocorticoid samples from known time points along the movement path can be integrated into the iSSF model as interactions between habitat and movement covariates (Fig. I). Interaction coefficients test hypotheses about the effects of glucocorticoids on both capacity and motivation for movement. For example:

Step length and turn angle interaction with glucocorticoids at the start of a step: When animals produce more glucocorticoids, are their movements faster and more directed (Fig. I a)?

Interaction between glucocorticoids at the start of a step and habitat at the end of the step: Do animals that produce more glucocorticoids select safer habitat or habitats with resources to replenish energy reserves (Fig. I b)?

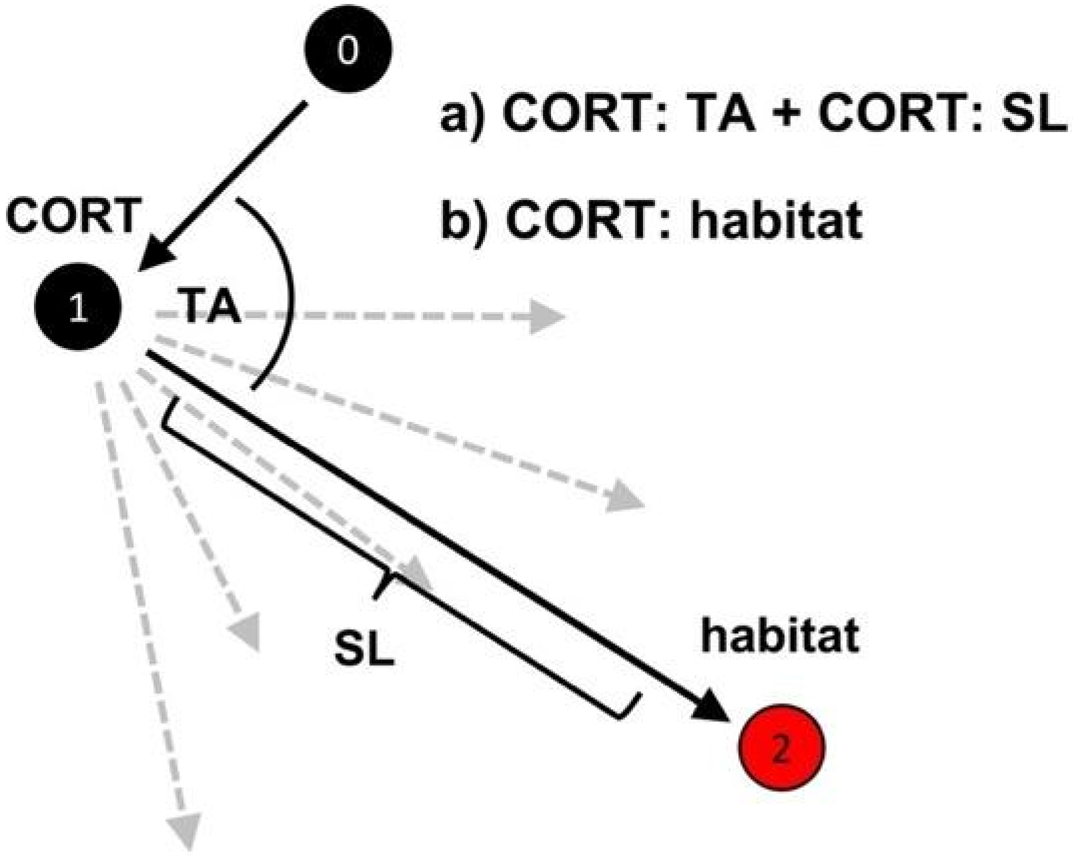

Figure I. Schematic representation of used locations (circles) along a movement path from $t = 0$ through $t = 2$. Solid arrows represent the movement path between location points, and dashed arrows represent five available trajectories an animal could have taken at $t = 1$, drawn from assumed distributions of the animal's step lengths (SL) and turn angles (TA) between movement paths with parameters based on its movement characteristics. Effects of glucocorticoids (CORT) at $t = 1$ on movement between $t = 1$ and $t = 2$ can be tested using its interaction with TA (between $t = 0$ and $t = 1$) and SL (between $t = 1$ and $t = 2$) as variables in an iSSF model (a). Its interaction with habitat at $t = 2$ tests how glucocorticoids at $t = 1$ affect habitat selection.

Box 3.2 Future directions

Integrating glucocorticoid hormones and habitat selection can both test the assumptions of some foundational hypotheses in stress physiology and space use ecology and generate new testable hypotheses that integrate both.

Glucocorticoid production can cause oxidative stress and reduce reproductive success (MacLeod et al. 2018), but elevated baseline levels often increase lifetime reproductive success if they facilitate immediate investment in current offspring (*cort-adaptation hypothesis*; Bonier, Martin, et al., 2009). Some investment behaviours, such as foraging trips by nesting birds, are based in habitat selection. By integrating glucocorticoids and habitat selection with iSSF models, we can detect proximate effects of glucocorticoids on investment behaviours. Are these investment behaviours repeatable within individuals? If so, how much does investment strategy contribute to individual differences in lifetime reproductive success?

The *landscape of fear* is a popular space use ecology concept linking habitat selection to predation risk: animals facing predation are expected to avoid unsafe habitats or use antipredator strategies like vigilance or safety in numbers to mitigate risk (Laundré et al. 2001). However, predator cues rather than presence are often used in practice as a proxy for risk, making fear itself difficult to quantify (Peers et al. 2018). Can we use glucocorticoids to quantify the landscape of fear, and iSSF models to measure its responsibility for antipredator habitat selection strategies?

Just as glucocorticoids drive adaptive habitat selection behaviour, the habitats individual animals select should also affect future changes in their hormone levels. This two-way relationship between habitat and hormones may drive a positive feedback loop that reinforces habitat selection behaviour. Evidence is emerging that habitat selection behaviour is indeed repeatable (Stuber et al. 2022), and that adults continuously exposed to stressors can epigenetically alter offspring hormonal responses to the same stressors (Brass et al. 2020), do intergenerational glucocorticoid-habitat selection feedback loops underlie specialization of populations on habitats?

Looking beyond populations, an integrated approach to studying glucocorticoids and habitat selection may also provide insights into ecosystem functioning and the ability of species to respond to environmental change.

The *carbon stress hypothesis* (Hawlena and Schmitz 2010) purports animals facing predation stress have higher cellular respiration rates, making them carbon limited. To maintain C:N ratios, stressed animals should seek forage with more of digestible carbon. Animals also select foraging habitat when they produce more glucocorticoids under stress physiology theory (Boudreau et al. 2019). Can we use iSSF and spatial data of elemental landscape composition (Leroux et al. 2017) to reconcile expectations of stress physiology with the carbon-stress hypothesis? Preferences for carbon-rich forage and resulting spatial variation in carbon-rich additions to detrital pools could fundamentally alter ecosystem structure (Hawlena and Schmitz 2010).

Even if glucocorticoids drive adaptive habitat selection, animals unable to access habitats that counteract stressors may instead behave in a manner that compromises fitness. Fitness costs may be particularly high in human-modified landscapes. For example, anthropogenic structures present physical barriers to movement and limit assessment of habitat selection costs (i.e., ecological traps; Lamb, Mowat, McLellan, Nielsen, & Boutin, 2017). Can we use the null expectation that both habitat selection and glucocorticoid production are adaptive to identify cases where animals are not free to move? Glucocorticoids in these cases may measure need for management intervention.

Table 3.1. Examples of recent field studies reporting negative relationships among habitat-associated stressors, glucocorticoid production, and fitness, without testing for causal relationships among the three. We searched for articles on Web of Science in June 2021 using the search query habitat AND glucocorticoid* OR corticosterone OR cortisol AND fitness AND chronic stress.

Topic	Findings	Interpretation	Citation
Effect of human footprint on feather glucocorticoids and survival rate of Eurasian griffon vultures (*Gyps fulvus*)	Glucocorticoids elevated among birds living in areas with higher human footprint. Previous studies found lower survival rates in areas with greater footprint.	Chronic stress is associated with living in areas with higher human footprint	(Gangoso et al. 2021)
Effect of habitat quality on fecal glucocorticoids and population growth rate in Cape mountain zebra (*Equus zebra zebra*)	Glucocorticoids elevated in lower-quality habitat. Glucocorticoids also highest among populations with lower female fecundity and growth rates.	Populations in lower-quality habitat suffering from chronic stress due to poorer nutrition	(Lea et al. 2018)
Effect of invasive species on urinary glucocorticoids on reproduction and survival in Fijian ground frog (*Platymantis vitiana*)	Glucocorticoids elevated in enclosures with invader. Body condition and reproduction, but not survival, also lower with invader.	Competition with invader causes chronic stress that suppresses reproduction.	(Narayan et al. 2015)

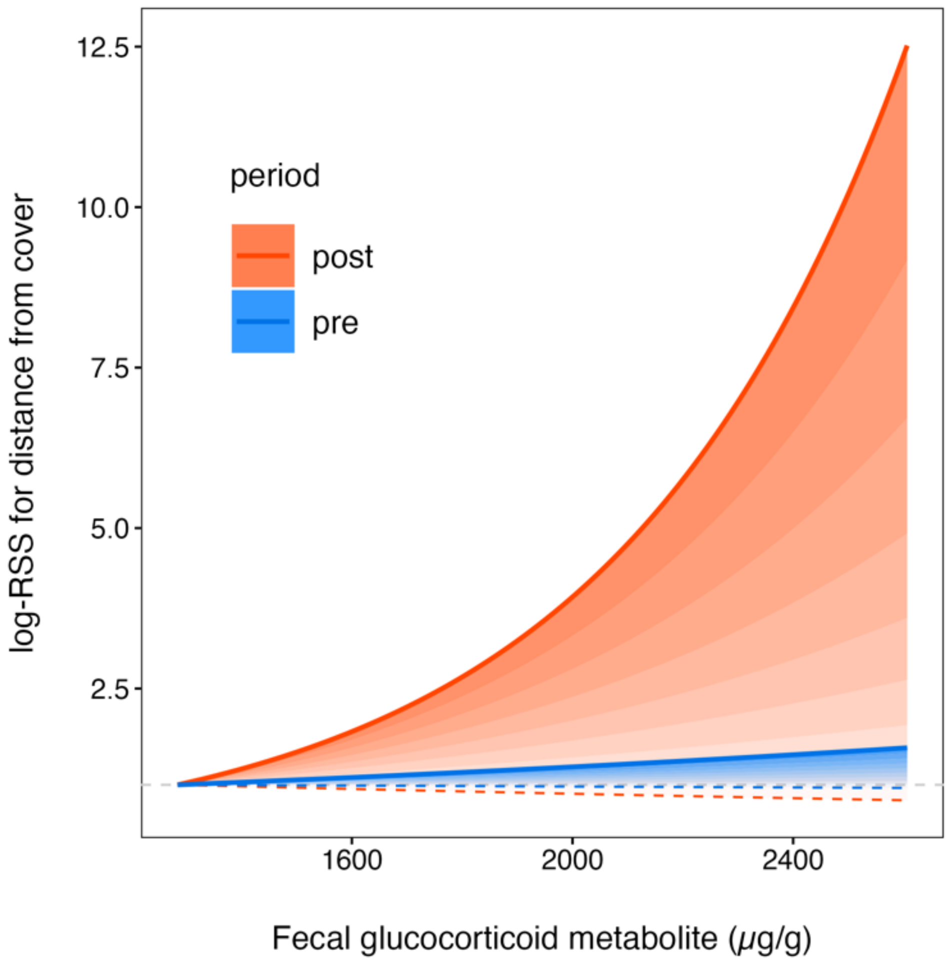

Figure 3.1: Log relative selection strength (RSS) for a location within cover (dashed lines) versus 450 m from cover (solid lines) with increasing fecal glucocorticoid metabolite (FGM) levels. Blue ribbons show the change in RSS between these locations in the 16-d window ("pre" period) when young calves are most vulnerable, and orange ribbons outside of this period ("post" period). Distance between the solid and dashed lines indicate relative selection strength is stronger for locations closer to cover as FGM levels increase. Higher elevation of the orange ribbon indicates a stronger effect during the 16-d window of calf vulnerability, suggesting lower corticosterone binding globulin concentration, fewer receptors, or reduced negative feedback may be driving selection for foraging habitat when energy needs are greatest.

CHAPTER 4 PREDICTING THE INDIVIDUAL IDENTITY OF NON-INVASIVE FECAL AND HAIR SAMPLES USING BIOTELEMETRY CLUSTERS

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4.1 Abstract

Animal diet and health influence fitness, making individual variation in these markers essential for understanding how individuals and populations respond to their environments. Fecal and hair samples provide a record of this information and can be non-invasively collected from animals in the field. However, physiology, diet, and susceptibility to parasitic infections vary within individuals, requiring repeated samples from individuals. We developed a technique using biotelemetry data for individual identification of non-invasive fecal material and hair sampled from female elk (*Cervus canadensis*). We non-invasively collected individually genotyped fecal and hair samples from resting sites, then compared the accuracy of supervised machine learning models to predict the individual identities of the samples. We found both the tightness of Global Positioning System point clusters and activity level surrounding the sample allowed us to positively identify samples belonging to specific individuals with 77% accuracy. Our approach can be applied to other populations for which biotelemetry data are available and is potentially adaptable for other species. Furthermore, application of our approach will reduce the need for individual identification of non-invasive samples using genetic analysis, which is costly and prone to low recovery success. Increased access to physiological, dietary, and health information obtainable from individual non-invasive samples will strengthen our understanding of animal responses to their environments.

Keywords: Biotelemetry, fecal DNA, non-invasive sampling, cluster analysis, ungulates, individual differences

4.2 Introduction

Diet and health are essential components of fitness that vary among individual animals. Thus, quantifying individual variation in diet and physiological markers is an important part of understanding how individuals and populations interact with and respond to their environments. Animal hair and fecal material contain a record of such information from a point in space and time, allowing them to be linked to the environment experienced by an individual. For example, microhistological analysis of fecal material (Hoy et al. 2019) and stable isotopes of carbon and nitrogen obtained from individual hair samples (Bryan et al. 2013) reveal how changes in environmental conditions affect differences in diet composition between populations. Using parasites shed in fecal material, the prevalence of infections in social species can also be linked to factors such as density and group size (Snaith et al. 2008). Glucocorticoid hormones help to restore homeostasis following acute exposure to stressors like predator encounters (Romero 2004), and thus fecal material with relatively high glucocorticoid concentrations is indicative of populations facing elevated predation risk (Hammerschlag et al. 2017). Because it is not always possible to examine stomach contents or blood, non-invasive sampling of hair and fecal material has become a common approach for obtaining diet (Leighton et al. 2020), parasite load (Snaith et al. 2008), and stress information from wild mammals (Sheriff et al. 2011). However, physiology, diet, and susceptibility to parasitic infections varies within populations, a complication that can be resolved by collecting repeated non-invasive samples from individuals.

Individual variation is prevalent in animals (Dingemanse et al. 2010; Guindre-Parker 2020), and at the population level it can reduce the precision of information obtained from non-invasive samples. For example, the existence of dietary specialists within a population of mostly generalists can decouple measurements of stable isotopes from measurements of local food availability (Ramos et al. 2020). Similarly, if a population exhibits a glucocorticoid response to a stressor but variation in stress responses is high, individual responses might not reflect the level of stressor to which the population is exposed (Guindre-Parker et al. 2019). In some cases, high individual variation in glucocorticoid responses can even mask detection of population level responses to the environment (Coppes et al. 2018). Individuals also differ in their susceptibility to parasitic infections depending on age and life history stage, meaning the demographic structure of populations can skew fecal pellet parasite counts (Seeber et al. 2020). Thus, while untargeted collection of non-invasive samples provides a general overview of responses to the environment, repeated samples from individual animals adds context to help interpret how the environment impacts populations.

In addition to distinguishing individual variation from population level patterns, sampling individual animals strengthens the inferences that can be drawn from non-invasive sampling. For example, pairing individual diet samples with changes in body mass over time makes it possible to track the interacting effects of the environment and individual foraging behaviour on fitness (Giroux et al. 2016). Repeated glucocorticoid samples from individuals can reveal endocrine plasticity, which may be important for individuals to ensure reproductive success in fluctuating environments (Guindre-Parker et al. 2019). While samples from individuals provide more information than non-invasive samples collected at random from the population, planning their collection, and their subsequent assignment to individual animals, is not straightforward.

The individual identities of non-invasively collected samples can be confirmed by comparing individual genotypes of microsatellite loci recovered from hair and fecal material (Bryan et al. 2013; Jesmer et al. 2020). While some collection methods identify individuals relatively successfully (Bach et al. 2022), genetic information recovered from fecal material can be degraded by high temperatures and precipitation, often resulting in low recovery success or restricting sample collection to winter and temperate climates (Rea et al. 2016). Physiological measurements can also be attributed to known individuals by collecting fecal material after observing the individual defecate (Fattorini et al. 2018; Dulude-de Broin et al. 2019; Hunninck et al. 2020). While this individual observation technique mitigates the issue of sample degradation in genetic analysis because exposure to the elements is reduced, the substantial time investment required to observe defecation limits sample size. In comparison to fecal samples the genetic material contained in hair is stable over longer periods of time, but this stability also makes it difficult to determine when the sample was left by the individual (Lukacs and Burnham 2005). Uncertainty in the age of the sample could prevent the physiological information therein from being linked to short-term and transient environmental factors. Thus, an efficient and reliable technique for locating a large number of individually identifiable samples could disentangle the effects of individual differences from the environment.

A potential solution for linking individuals to non-invasively collected hair and fecal samples capitalizes on remote sensing of animal space use. Inference of location and movement characteristics from remotely sensed Global Positioning System (GPS) data has made it possible to identify areas used by individual mammals for parturition (Bonar et al. 2018) and foraging (McNeill et al. 2020). Tracking individual animals to these areas of high use reduces time spent in the field because areas can be prioritized for collection of samples that are more likely to belong to specific individuals. For example, Giroux et al. (2012) linked fecal material to individual GPS-collared white-tailed deer (*Odocoileus virginianus*) by following their foraging tracks. Though genetic analysis or individual observation are the only methods that can conclusively confirm the identities of individual samples (Coppes et al. 2018), the high resolution at which GPS data are now available facilitates the collection of a large number of samples that do not rely on successful extraction of genetic material. However, the performance of these techniques for targeting known individuals must be evaluated on a species-by-species basis.

Here, we developed and truthed a technique for individual identification of non-invasively sampled fecal material and hair from female elk (*Cervus canadensis*) using GPS data, motivated by a need to disentangle individual differences in physiology, diet, and parasite load from environmental effects. Elk are well suited for individual collection of non-invasive samples because they must stop moving while ruminating or bedding (Cook 2002), producing discrete GPS location clusters. Particularly during spring and autumn shedding (O'Gara 2002), it is common to find hair at their bedding locations. Furthermore, elk defecate at an average frequency of once every two hours (Neff et al. 1965), meaning an individual is also likely to leave a fecal sample at location clusters where it has spent at least two hours. This increases the probability of collecting a sample from a known individual. In spring and summer, we collected fresh fecal material and hair samples from location clusters indicative of bedding sites suspected to belong to known genetic individuals from the population. After confirming the identity of the individual at each bedding site by genetic analysis of the samples, we compared the predictive performances of supervised machine learning models to distinguish positively and negatively identified samples based on characteristics of the target individual's GPS location clusters.

4.3 Methods

4.3.1 Study system

We conducted all field work using the elk population in Vita, Manitoba within the traditional lands of the Anishinaabe peoples (49.134, -96.557). The study area is characterized by hot summers, with approximately 300 mm of rain and temperatures regularly in excess of 30°C from May to August. The approximately 150 adult elk in our study population (Manitoba Agriculture and Resource Development, unpublished data) inhabit an area that comprises privately owned agricultural land and public land dominated by marshes, wet hardwood forests, and shrubland. In February 2019, 18 individual females were captured using a net gun fired from a helicopter and each was fit with an Iridium satellite Global Positioning System collar (Vertex Plus 830 g, VECTRONIC Aerospace GmbH, Berlin, Germany). The collars were programmed to collect locations every 30 minutes from May to August 2019 and we calculated a mean fix success rate of 89.4% (i.e., the proportion of locations successfully transmitted, an average of 3,948 locations per individual). All capture procedures were in accordance with approved animal care protocols (Memorial University of Newfoundland animal use protocol #19-01-EV).

4.3.2 Sample collection and preprocessing

We collected elk fecal pellet and hair samples from May to August 2019. To increase the number or samples collected per individual, we targeted 11 of the 18 collared individuals (hereafter "target individuals"). Collars recorded locations of the elk every 30 minutes during the period of collection, subjectively allowing us to identify potential bed-sites by looking for areas with a relatively large number of location points close to one another (hereafter "cluster"). After identifying clusters we searched for recently shed hair and fresh fecal pellets with the appearance of a fresh mucous layer (Le Saout et al. 2016). We collected fecal samples in a sealable plastic bag and stored them in a -18°C freezer as quickly as possible following collection, since exposure to warm temperatures, typical of our study area during the sampling period, degrades the genetic material in fecal samples (Rea et al. 2016). All samples were stored in the freezer between 29– and 410–minutes following collection and remained frozen until DNA extraction.

We attempted to increase the odds of sampling a target individual by preferentially collecting samples on or within 5 m of its suspected bed, identifiable as an area of depressed vegetation within the cluster. In many ungulates, a single bedding bout typically only lasts between one and a few hours (Cederlund 1989; Kuzyk and Hudson 2007). However, inactive bedding periods are interspersed with alternating periods of feeding in the same vicinity (Green and Bear 1990; Naylor et al. 2009), and in our study the long periods of time target individuals spent in the vicinity of their samples introduced some uncertainty about which cluster of points was recorded at the time the sample was deposited. To ensure our models were robust to this uncertainty, we specified three location points belonging to the target individual that were closest to each sample as "cluster centres" for use in our machine learning models. Finally, we counted the number of other bed sites within 20 m of the sample as a measure of the number of other elk in the same area (hereafter "activity level"; Fig. 4.1). We chose search radius of 20 m as a compromise between selecting a search area larger than the accuracy of the GPS collars (8-15 m; VECTRONIC Aerospace GmbH, Berlin, Germany) and maintaining a small enough area to visually keep track of which beds we had already counted.

During elk captures, whole blood samples were taken from each collared individual to serve as a genetic benchmark. We determined whether non-invasive samples belonged to target individuals by comparing DNA extracted from them to the genetic benchmarks. We sent all fecal pellets, hair samples, and blood samples collected during capture to the Natural Resources DNA Profiling & Forensics Centre in Peterborough, Ontario for extraction and processing of genetic material. Extractions were performed on 10–15 hairs with roots or 1–2 fecal pellets subsampled from each of the original samples using the DNeasy 96 Blood and extraction protocol (Qiagen, Germany). Individuals were then identified by amplifying and sizing between 8 and 9 microsatellite loci (BM4513, BM1009, IGF, AF102257, BM4107, BM1225, BM848, BM5004, BL42) using GeneMarker software (SoftGenetics, USA). We assigned each fecal pellet and hair sample a classification of either “positive” or “negative” based on whether its genetic material matched the target individual at the cluster.

4.3.3 Supervised machine learning

We used supervised machine learning to build a model that could distinguish which samples belonged to the target individual, i.e., were positively identified. Machine learning is a suite of algorithm-based techniques aimed at making predictions about “testing” data based on observed patterns in “training” data used to build the model. When supervised, the patterns in both training and testing data are known, and the machine learning algorithm seeks to maximize the predictive performance of the model. In classification applications, machine learning classifiers predict whether observations fall into one of two or more classes, such as positive and negative identifications.

To prioritize locations for sampling, we wanted to build the best model for classifying positively and negatively identified samples using only predictor variables that could be collected remotely. Based on the duration of bedding bouts in other ungulate species (Cederlund 1989), we anticipated the use of bedding sites associated with samples would not exceed four consecutive hours. Thus, we used nine 30-min location points centred at each of the potential cluster centres, i.e., four location points before and after each cluster centre, to measure characteristics of the target individual’s movement track capable of distinguishing bedding behaviour. First, we measured cluster tightness by determining how many of the eight surrounding location points fell within a 32 m buffer of the cluster centre, including the cluster centre (Fig. 4.1 B; also see Supplementary S.4 for details about how we determined the buffer radius). We also calculated the average nearest-neighbour distance among each of the nine location points, including the cluster centre (Fig. 4.1 C). In addition to movement characteristics, we used the activity level in the area of the cluster (i.e., the number of bed sites within 20 m of the sample) and proximity of the sample to each cluster centre (i.e., the nearest point to the sample from each cluster) as predictor variables. While both the activity level and proximity to cluster centre predictors must be collected in the field, they could improve predictive performance of the model.

We applied five different classifiers to the training model to determine which best predicted the two classes of samples in our testing data: linear discriminant analysis (LDA), naïve Bayes (NB), K nearest neighbour (KNN), classification and regression trees (CART), and support vector machines (SVM). We also explored the random forest (RF) classifier as an alternative regression tree method, owing to its popularity and demonstrated performance for classification (Bahn and McGill 2013). However, performance of the random forest classifier was negligibly different from CART (data not shown), so we considered only CART and not RF in our final analysis. Classifiers can be categorized based on the process by which they assign observations to classes. For example, LDA and NB compute decision boundaries between the classes based on the Bayesian probability that each observation belongs to either class (Casella et al. 2013; Genoud et al. 2020). KNN makes classifications based on the majority class of the K observations closest to a given observation, and CART iteratively builds decision trees based on the attributes of all observations, then assigns observations to classes according to the class to which the majority of observations belong on that branch of the tree (Casella et al. 2013). SVM separates classes by hyperplanes that maximize the distance between classes, with its position dependent on observations termed “support vectors” that occur along the margin of the hyperplane (Casella et al. 2013).

The performance of a machine learning classifier is based on it being able to provide a flexible fit to patterns in the training data without overfitting. Overfitting is a consequence of too much flexibility: the model fits to noise in the training data, ultimately reducing its accuracy when applied to testing data. The machine learning classifiers we used all vary in their levels of flexibility, with nonlinear methods like radial SVM some of the more flexible, and LDA and linear SVM some of the least flexible. In addition to selection of the classifier itself, changing the values of constants within the equation used to calculate the probability of an observation belonging to either class, provides further control over the degree of flexibility. For each classifier we tested a range of these constants, termed “tuning parameters”, which adjusted the algorithms across a range of flexibility. We selected the optimal tuning parameter values to maximize the classification accuracy of each classifier. We also selected among three types of SVM models at this stage: linear, polynomial, and radial SVM range from least to most flexible based on the shape of the hyperplane that separates classes. Details about the tuning parameters tested in each classifier are provided in the section Supplementary S.4. After selecting the tuning parameters, we assessed the performance of all combinations of the five classifiers and four predictor variables based on the mean percent accuracy of their classification of the testing data.

We also compared model performance using receiver operating characteristics (ROC). ROC curves convey predictive accuracy by plotting the rate of true positive identifications against false positive identifications predicted by a model. The area under the curve (AUC) quantifies this comparison, with AUC values closer to 1 indicating higher model performance (Fawcett 2006).

4.3.4 Model validation

We used 10-fold cross validation with five repeats to first select the optimal tuning parameters for each algorithm, and then again to select the combination of algorithm and predictor variables that maximized model accuracy. Cross validation is a resampling method that evaluates the predictive ability of a model by repeatedly testing it on new sets of training and testing data split from the initial data set. In 10-fold cross validation, the data are randomly partitioned into 10 "folds", one of which is used for testing and the remaining nine for training. After all 10 folds are used successively for both training and testing, 10 new folds are partitioned, and the process is repeated. Imbalance between observations in the testing and training set – such as in our study, where positively identified samples outnumbered negatively identified samples 3:1 – can result in misclassification of the minority class (Liu et al. 2011). Thus, we also under-sampled the majority class in each cross-validation fold, matching it to the number of samples in the minority class. We compared performance across the five models according to their mean accuracy from all cross-validation iterations. To ensure neither sample type nor collar relocation frequency influenced model accuracy, we also ran the models again with hair and fecal pellet data separated, and after having rarefied the GPS data to 1–hr relocations by removing every second location in the cluster.

10-fold cross validation is used for supervised machine learning applications when an independent testing set is not available to test the predictive capabilities of a model (Kindschuh et al. 2016; Sánchez-González et al. 2018). However, when training and testing data are not independent, dependence structures – where nearby observations are more correlated than distant ones – can lead to overly optimistic conclusions about model performance that do not necessarily hold when the model is applied to a novel data set (Roberts et al. 2017; Gregr et al. 2018). As a solution, blocked cross validation has been shown to produce more realistic assessments of model performance (Roberts et al. 2017). In blocked cross validation, the data are partitioned by dependence structures rather than randomly into folds. We suspected that the predictor variable data belonging to a single elk may be correlated, and that this dependence structure may bias model performance estimates. Thus, we also performed a separate blocked cross validation to confirm whether the accuracy of the top model agreed with 10-fold cross validation. We partitioned the 11 elk into folds and used the data from 10 elk as training data to predict the positively identified samples of the remaining elk.

4.4 Results

We collected 114 hair and fecal pellet samples between May and August 2019. Of those, 43 yielded recoverable genetic material that we could compare to known individuals in the population. While we recorded three cluster centres for 42 of 43 samples, for one of the samples it was only possible to identify a single cluster, leaving us with a total of 126 clusters in the dataset. After calculating cluster tightness and the nearest neighbour distance between cluster points, we then compared the performance of these two predictors, activity level (i.e., number of bed sites within 20 m of the sample), and distance between the cluster centre and sample for predicting whether samples were positive or negatively identified as belonging to a target individual. In total, we tested 75 different combinations of predictor variables and machine learning classifiers.

Positively and negatively identified samples differed across two of the predictor variables. There was less activity, i.e. there were fewer bed sites within 20 m of the sample, for positively identified versus negatively identified samples ($F_{1,124}$ = 13.91, p = 0.0003; Fig. 4.2 A). The clusters surrounding positively identified samples were also tighter than those surrounding negatively identified samples, i.e., there were more location points within 32 m of a positively identified cluster centre than those negatively identified ($F_{1,124}$ = 13.69, p = 0.0003; Fig. 4.2 B). However, neither the average nearest neighbour distance between cluster points ($F_{1,124}$ = 2.354, p = 0.13; Fig. 4.2 C) nor the proximity of the sample to the cluster centre ($F_{1,124}$ = 0.389, p = 0.53; Fig. 4.2 D) differed between positively and negatively identified samples.

Overall, cluster tightness and activity level were the best predictor variables for positively identified samples (Table 4.1). The NB classifier performed best according to 10-fold cross validation, with its predictive accuracy averaging 77% when both cluster tightness and activity level were included as predictor variables in the same model. However, the accuracy of the best model that included only remotely sensed data, i.e. cluster tightness, was less accurate at 71% (Table 4.1). This was largely due to a decrease in sensitivity of the model, which refers to its ability to correctly classify positive identifications, i.e. its ability to avoid false negatives. When activity level was removed, sensitivity dropped from 64% to 37%. However, specificity – which refers to the ability of the model to correctly classify negative identifications, i.e. its ability to avoid false positives, was still high at 85% even without the activity level predictor (Table 4.1). ROC curves corroborated that the combination of cluster tightness and activity level better balanced specificity and sensitivity (AUC = 0.73 versus AUC = 0.55 for cluster tightness only; Table 4.1, Fig. 4.3). For the remaining combinations of predictor variables and classifiers, neither the addition of nearest neighbour distance between cluster points nor the proximity of the sample to the cluster centre improved predictive accuracy (Table 4.1). Models were slightly more accurate (0.7-1%) when we modelled the hair and fecal pellet data separately (Supplementary Table S.4-1), and model accuracy declined by only 1% when we rarefied the

GPS data to 1–hr relocations (Supplementary Table S.4-2). However, accuracy of the cluster tightness only model declined by > 10% when we rarefied the data to 1–hr relocations.

Results from the blocked cross validation largely agreed with 10-fold cross validation, with cluster tightness and activity level as the best predictor variables. However, the model lost accuracy and specificity in comparison to 10-fold cross validation, dropping from mean 77% accuracy to 71% accuracy, and mean 83% specificity to 74% specificity when blocked cross validation was used (Supplementary Table S.4-3). In contrast, the sensitivity of the blocked cross validation model increased in comparison to 10-fold cross validation from 64% to 71%. The model with only cluster tightness followed a similar pattern, decreasing from 71% accuracy to 63% accuracy, and 85% specificity to 65% specificity, while sensitivity increased from 36% to 53%. A full list of model predictor variables, classifiers, and their performance metrics are provided in section Supplementary section S.4.

4.5 Discussion

We assigned non-invasively collected hair and fecal pellets to individual elk by capitalizing on the characteristics of bed sites identified by their GPS point clusters. This approach can improve how we interpret information from non-invasive samples because stronger inferences can be gained by accounting for variation among individual animals. Indeed, opportunistically collecting multiple samples from the same individuals in the wild is challenging (but see Giroux et al., 2016; Fattorini et al., 2018; Dulude-de Broin et al., 2019; Hunninck et al., 2020). Furthermore, labour-intensive fieldwork and financial costs associated with non-invasive sample collection from individuals can be prohibitive (Taberlet et al. 1999). In our study, supervised machine learning models including both the tightness of GPS point clusters and activity level, i.e., the number of bed sites within 20 m, at the bed sites allowed us to confirm that samples belonged to a specific individual. We also found that naïve Bayes and linear discriminant analysis outperformed more flexible classifiers like support vector machines and decision trees that are often reported to be highly accurate (Elith et al. 2008; Genoud et al. 2020), which may be the result of the more flexible classifiers overfitting the patterns in our small dataset (Raudys and Jain 1991). While other machine learning approaches have used GPS point clusters to remotely interpret elk behaviour (Van Moorter et al. 2010), ours links individuals to fecal or hair samples from which diet, physiology, and parasite load information might be obtained. We submit our approach is also general enough to adapt for other species with similar GPS point clusters, making it a promising way forward for investigating responses of individuals within animal populations to their environment.

We found that cluster tightness, measured as the number of points occurring within a 32 m buffer of the cluster centre, allowed us to distinguish positively and negatively identified samples with high accuracy. We also expected the nearest-neighbour distance between cluster points to provide another indication of the individual spending time in the vicinity of the sample. However, it did not improve the predictive performance of the model. Others have found distance measures useful for predicting carcass visitation by carnivores that exhibit different movements from bedding ungulates. For example, the maximum distance of nearby non-cluster points to the cluster was predictive of carcass type scavenged by brown bears (*Ursus arctos*; Ebinger et al., 2016). Carcass visitation by carnivores is characterized by multiple and lengthy visits to the same location, interrupted by periods of rest or other unrelated activity (Zimmerman et al. 2007; Ebinger et al. 2016). In contrast, elk and other herbivores forage at multiple locations interspersed with movements between patches and long latency to return to the same patch (Seidel and Boyce 2015). Thus, while nearest neighbour distance within a cluster may indicate a return to the carcass in carnivores, in herbivores like elk it may instead measure directed movements between different foraging patches and resting sites. These differences in their movement behaviour from carnivores would make the number of points within a 32 m buffer of the target point a more consistent predictor of herbivore location clusters than nearest-neighbour distance, and therefore a better predictor of correctly identified samples.

We also expected the distance between the nearest cluster centre and the sample to distinguish positively and negatively identified samples. While this variable did not appear in the most accurate model, we suspect it was excluded because of collar location accuracy rather than elk behaviour. While our mean collar location accuracy according to the manufacturer specifications is 8-15 m (VECTRONIC Aerospace GmbH, Berlin, Germany), the majority of distances between the cluster centre and sample in our study were well under 20 m for both positively and negatively identified samples. However, GPS collar locations are only accurate if the distance between subsequent locations is large and exceeds measurement error of the device (Jerde and Visscher 2005). This suggests that any differences in distance between positively and negatively identified samples and cluster centres might have been masked by measurement error. Indeed, Frair et al. (2005) were unable to parse movement behaviour of elk at spatial scales finer than the measurement accuracy of their GPS collars. Interestingly, this measurement error can produce the appearance of spurious 180° angles between subsequent location points even when the collar is stationary (Hurford 2009; Bjørneraas et al. 2010). Future applications of this approach may be able to use the presence of these 180° turn angles to more precisely pinpoint the location of the target individual relative to the sample.

Our goal was to develop a model that could distinguish correctly from incorrectly identified samples without site-level characteristics to prioritize sampling locations. However, we found that activity level substantially improved model accuracy when paired with cluster tightness (Fig. 4.3). Similarly, cluster models for identification of foraging in GPS-collared animals are also often improved by site-level information such as vegetation productivity (Seidel and Boyce 2015), habitat characteristics (Knopff et al. 2009), and the availability of alternate food sources (Ebinger et al. 2016). However, for those applications models without site-level characteristics are often more important because the objective is to remotely identify foraging behaviour without ground truthing. In contrast, our framework is better suited to the collection of site-level characteristics because each cluster must be visited to obtain a fecal or hair sample. Thus, as a compromise between purely remotely sensed data for prioritization of sampling locations and the need for site-level information to confirm sample identification, we suggest a two-step approach. Areas for sampling can first be targeted using the less accurate model that includes only cluster tightness as a predictor, then the positive identification of those samples confirmed by the addition of activity level to the model. However, we caution that the accuracy of models using only remotely sensed data should be assessed for relocation frequencies less frequent than 30 mins, as our remotely sensed only models were substantially less accurate when we rarefied the data to 1–hr relocation frequencies.

While the cluster tightness and activity level model accurately predicted positively identified samples using 10-fold cross validation, accuracy declined when we cross-validated the model blocked by individuals. One explanation for this loss in accuracy is related to data. Unlike 10-fold cross validation where we balanced classes by under-sampling, we were unable to do so for individually blocked cross-validation because six of the 11 individuals had either all positively or all negatively identified samples. Thus, the class imbalance in blocked cross-validation may have led to a greater number of misclassifications (Liu et al. 2011). Alternatively, the reduction in model accuracy with blocked cross validation may be explained by the presence of additional individuals at some bed sites that was not captured by our bed site activity measure. In elk, home range size fluctuates with local competition for forage (Barker et al. 2019). However, because of selective encounters among familiar individuals, fine-scale social interactions saturate even as home range overlap continues to increase (Vander Wal et al. 2014). Thus, we may have underestimated the presence of individuals that shared space but did not bed with our target individuals, particularly if some of the individuals occupied home ranges with higher resource availability and thus a greater density of individuals. Future versions of this analysis could test whether a variable to account for productivity at the sample location, such as habitat type or normalized difference vegetation index, improves classification accuracy.

Though our approach is appropriate for any species with periodic bedding behaviour, we only tested its performance on female elk during the calving season, raising several important considerations for its application to other systems. While female elk only isolate themselves for several days before and after parturition (Altmann 1952), they typically spend weeks following birth of their calves in smaller nursery herds with other female elk (Geist 2002), many of which were also collared in our study. Thus, the probability of our sampling a specific individual was likely different than it would have been during other seasonal periods like winter that are characterized by larger, mixed sex groups. Furthermore, male and female elk differ in both their minimum group size and group dispersion, which depend on increasing population size for female elk (Vander Wal et al. 2013). Thus, the accuracy of the models we tested may differ for male elk. The importance of predictors like activity level may also differ for less gregarious ungulate species like moose, where, for example, adult bed sites are found less frequently in close proximity (McCann et al. 2016). The duration of bedding bouts also varies seasonally and across species (Cederlund 1989; Kuzyk and Hudson 2007), and thus adjusting the temporal period represented by clusters may affect model performance.

We demonstrated that characteristics of GPS point clusters can be used to target individual female elk for collection of hair and fecal samples, providing information about physiology, diet, and parasite load. Accounting for individual differences in physiological markers like hormone levels is essential for correct interpretation of population level responses to stressors (Bonnot et al. 2018). Similarly, tracking individual differences in diet can reveal how populations of herbivores balance competition for food and cope with plant chemical defenses (Jesmer et al. 2020). Linking parasite load to age and sex of individuals can disentangle the influence of life history stage and environmental conditions on their susceptibility (Seeber et al. 2020). Our approach offers an efficient, cost-effective solution for sampling individual elk, and possibly other species fit with biotelemetry collars. For example, our approach is also applicable for other species like moose (McCann et al. 2016) and large carnivores (Knopff et al. 2009; Ebinger et al. 2016) that produce clusters of GPS locations at bedding and feeding sites. This increased access to physiological, dietary, and health information from individuals will strengthen our understanding of animal responses to their environments.

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Table 4.1: Performance comparison of all combinations of predictor variables for distinguishing positively from negatively identified samples according to 10-fold cross validation, divided into models including both remotely sensed and site-level data versus remotely sensed data only, and ranked in order of mean percent accuracy. The bolded predictor variable combinations correspond to the most accurate model with both remotely sensed and site-level data (*buffer* + *bed*), and the most accurate model using only remotely sensed data (*buffer*).

		Performance metric (95% CI)			
Predictor variables[1]	Classifier[2]	Percent accuracy	Percent sensitivity	Percent specificity	AUC
Remotely sensed and site-level					
buffer* + *bed	**NB**	**76.6 (72.8, 80.3)**	**64.3 (56.3, 72.2)**	**82.6 (78.3, 86.8)**	**0.73**
bed	LDA	74.7 (71.5, 77.8)	47.0 (39.4, 54.5)	86.4 (83.2, 89.6)	0.65
buffer + *nn_dist* + *bed*	NB	74.6 (71.1, 78.0)	55.4 (47.1, 63.6)	82.0 (78.3, 85.7)	0.69
buffer + *bed* +*nearest*	NB	74.3 (71.7, 76.9)	60.9 (54.4, 67.4)	80.5 (77.4, 83.5)	0.69
bed + *nearest*	LDA	73.8 (70.8, 76.8)	52.3 (45.0, 59.5)	81.5 (77.3, 85.7)	0.65
nn_dist + *bed*	LDA	73.2 (69.6, 76.8)	59.8 (50.9, 68.7)	79.2 (75.6, 82.9)	0.66
buffer + *nn_dist* + *bed* + *nearest*	LDA	71.5 (68.7, 74.3)	63.1 (54.3, 71.8)	74.2 (70.3, 78.0)	0.71
nn_dist + *bed* + *nearest*	SVM	67.7 (64.0, 71.3)	61.1 (52.4, 69.8)	70.7 (65.4, 76.0)	0.69
Remotely sensed only					

buffer	**NB**	**70.5 (66.7, 74.3)**	**35.7 (28.9, 42.5)**	**84.7 (80.3, 89.1)**	**0.55**
buffer + *nearest*	NB	68.3 (65.3, 71.3)	39.5 (32.3, 46.6)	81.2 (77.7, 84.8)	0.60
buffer + *nn_dist*	NB	67.5 (63.7, 71.2)	35.5 (28.2, 42.7)	81.3 (76.7, 85.9)	0.58
buffer + *nn_dist* + *nearest*	NB	65.8 (62.0, 69.7)	37.9 (29.2, 46.5)	79.0 (74.3, 83.6)	0.59
nearest	NB	60.9 (57.0, 64.8)	28.3 (19.7, 36.8)	74.4 (68.1, 80.7)	0.46
nn_dist	NB	60.3 (55.8, 64.8)	27.0 (19.5, 34.4)	76.2 (69.6, 82.8)	0.47
nn_dist + *nearest*	NB	59.7 (56.7, 62.6)	33.4 (26.5, 40.2)	76.6 (72.8, 80.5)	0.47

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[1] Predictor variables include *buffer* = cluster tightness (number of points within 32 m buffer of cluster centre); *nearest* = distance from sample to nearest cluster centre; *nn_dist* = average nearest neighbour distance among points in cluster; *bed* = number of beds within 20 m of sample

[2] Classifiers include naïve Bayes (NB), linear discriminant analysis (LDA), and radial support vector machines (SVM)

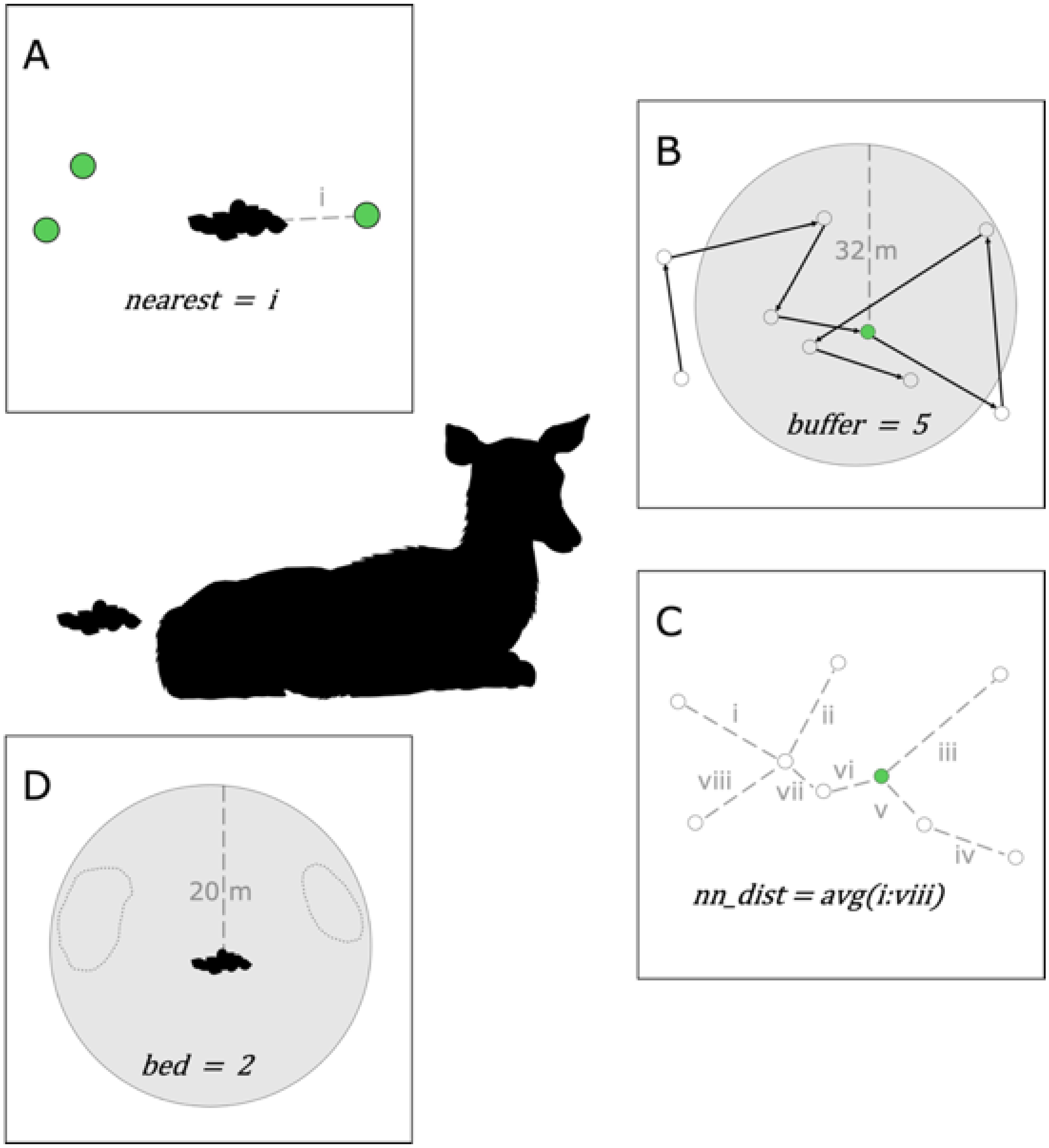

Figure 4.1: Predictor variable data collected at sample locations. A) The three nearest GPS location points to the sample are cluster centres (green circles), and *i* is the distance to the nearest point. B) Cluster tightness is the number of points in the cluster (white circles) falling within 32 m of each cluster centre. C) Average nearest-neighbour distance between all points in the cluster. D) Number of beds within 20 m of the sample.

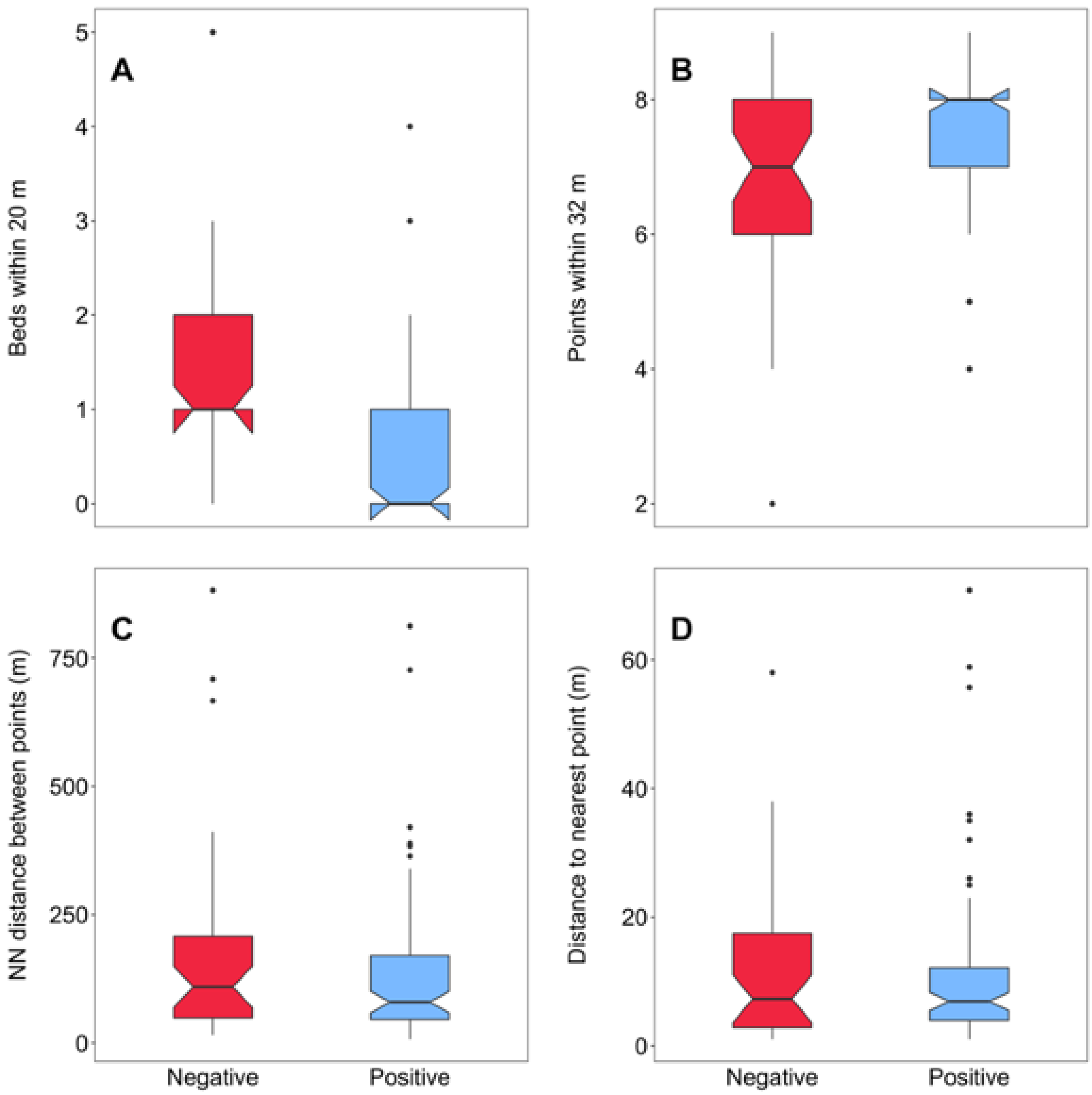

Figure 4.2: Box plots showing the median (horizontal black line), quartiles (box ends and vertical lines), and outliers (points) of each predictor variable, separated by positive and negative identification of samples. A) displays compares activity level (the number of other bed sites within 20 m of the sample location), B) compares cluster tightness (the number of points within a 32 m buffer of the sample location), C) compares the average nearest neighbour distance among all points in a cluster, and D) compares the distance between the sample and cluster centre.

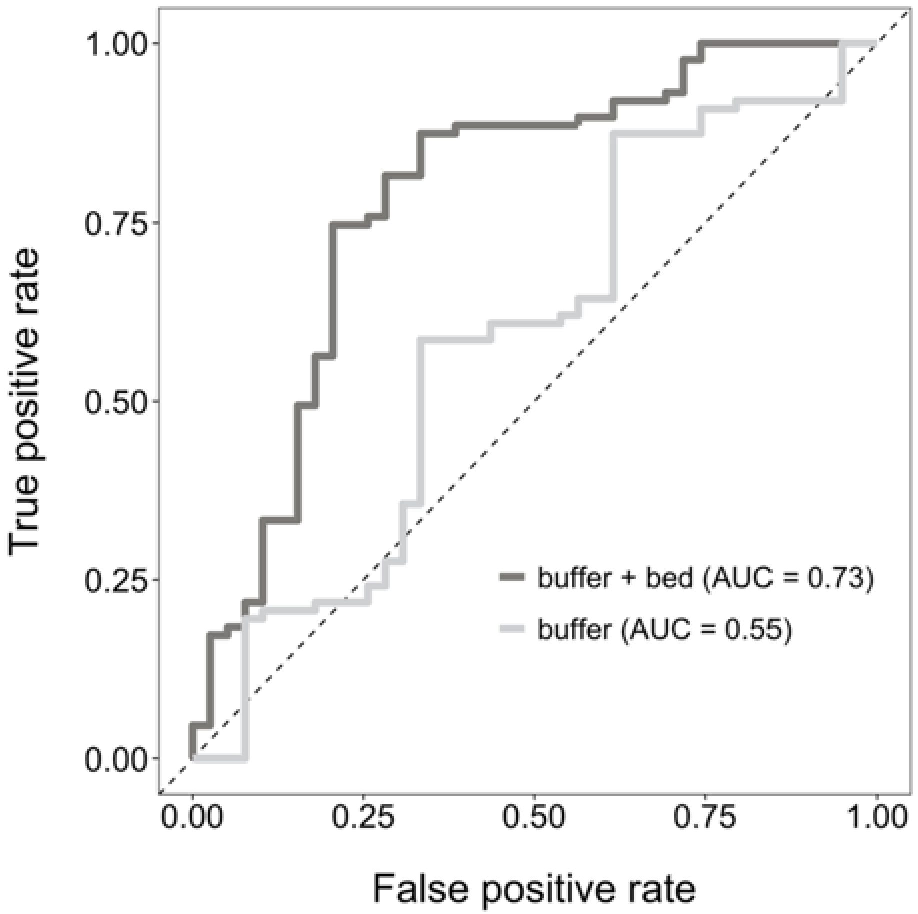

Figure 4.3: Receiver operating characteristic (ROC) curves for the most accurate model (buffer + bed), and the most accurate model including only remotely sensed predictor variables (buffer). ROC curves were drawn based on the model's iterative classification of samples as positively and negatively identified. The dashed diagonal line represents a model with a random success rate of classifying positively and negatively identified samples, and curves in the upper left portion of the graph represent models with classification performance better than random (*buffer* = cluster tightness, number of points within 32 m buffer of cluster centre; *bed* = activity level, number of bed sites within 20 m of sample). Area under the curve (AUC) provides a numerical measure of model performance, where AUC = 1 indicates a model with perfect prediction capability.

CHAPTER 5 SEPARATING SHARED SPACE FROM SHARED SOCIAL INFORMATION REVEALS THE ANTIPREDATOR BENEFIT OF HOME RANGE OVERLAP

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5.1 Abstract

Home range overlap is often used to distinguish whether animals use social information to track resources. Its distinction from personal information use is important in variable environments where both information sources become less reliable with change. However, home ranges also overlap spatially when animals independently track the same resources, making it difficult to isolate the contribution of social information to resource-tracking. We distinguished social from personal information use by testing the ability of elk (*Cervus canadensis*) to track resources when they shared spatial overlap but did not associate closely enough to share social information. Elk that consistently overlapped with the same individuals across years tracked resources most effectively, but since shared spatial overlap did not coincide with more social associations, those elk did not have an opportunity to exchange social information. In support of this interpretation, neither social associations nor shared spatial overlap improved resource-tracking. However, individuals with more spatial overlap had lower glucocorticoid levels, while those with more social associations did not, suggesting sharing space diluted predation risk but may have increased resource competition when elk shared space at the same time. Our results indicate when animals like elk track resources in variable environments, personal information contributes more to space use decisions than direct social information. However, spatial overlap remains an important antipredator strategy, particularly when temporally coarse enough to avoid interference competition. More broadly, as environmental change accelerates, we demonstrate the importance of distinguishing shared spatial overlap from social associations to understand the importance of social information exchange for resource-tracking.

5.2 Introduction

Animals face changing environments. When those changes are predictable between periods, animals can use personal information — i.e., memory of past resources or experience acquired while exploiting resources (Kendal et al. 2005) — to make space use decisions that maximize access to resources that change across space and time (i.e., resource tracking *sensu* Abrahms et al. 2021). A key aspect of of resource tracking is home range placement. Frequently, animals remain in their home ranges when resources are available and move after unfavourable periods (Morrison et al. 2021). Much of this decision hinges on having sufficient information to anticipate where resources will be. However, when locations of resources vary over time, personal information may be insufficient to predict future resource changes. Animals can access novel resources by moving their home ranges, but face inconsistent access to resources if the environment changes (Patrick and Weimerskirch 2017). To increase the precision and reduce the variability with which they track resources, animals can glean social information from behaviours of others (Stamps 1988). Reliability of social information for tracking resources, however, also decreases with environmental variability if rates of information exchange do not keep pace with shifting resources (Kendal et al. 2005). Given the diminishing returns of both personal and social information in variable environments, it is unclear how animals facing the accelerating pace of environmental change should filter information to optimize resource-tracking.

Social information is most valuable for resource-tracking when individuals lack enough personal information about resources to make good space use decisions (Boyd and Richerson 1988). For example, the more outdated their own personal information, the more sticklebacks (*Pungitius pungitius*) relied on social information to find foraging locations (van Bergen et al.

2004). Individuals foraging in new environments and lacking any personal information often use the locations of conspecifics as indicators of resource availability (i.e., conspecific attraction; (Stamps 1988). Translocated ibex (*Capra ibex*), for example, found high-quality resources by cueing in on where resident ibex placed their home ranges in their novel landscapes (Scillitani et al. 2013). Individuals face a similar situation in highly variable environments where they cannot anticipate the locations of resources. In such cases, individuals that capitalize on social information also tend to track resources more effectively (Carroll et al. 2018). The corollary is that when resources are variable, individuals relying only on personal information might fail to exploit social information about novel resources. Thus, socially connected individuals may track resources more effectively when they supplement their personal information in variable environments.

Supplementing with social information is also adaptive in variably risky environments where potential fitness costs of acquiring personal information are high (Laland 2004). Familiarity with the environment allows individuals to find refuge from predators, thereby avoiding injury or mortality while seeking resources (Gehr et al. 2020). In contrast, acquiring personal information in unfamiliar environments through trial-and-error can increase exposure to predators, making it a potentially costly behaviour (Kendal et al. 2005). To avoid costly outcomes associated with acquiring personal information, individuals facing predation risk sometimes tolerate competition to live in groups where they have access to social information about both resources and predators (Shrader et al. 2007). Even individuals that do not associate directly can capitalize on social information available from observing other individuals feed (i.e., local enhancement). For example, minnows (*Phoxinus phoxinus*) exposed to higher risk used social cues about foraging from demonstrators with knowledge of the environment (Webster and

Laland 2008). Information need not even be exchanged for social associations to mitigate risk; prey animals at higher densities also benefit from the dilution effect, or the phenomenon where predation risk to individual group members declines as group size increases (Lehtonen and Jaatinen 2016).

Though individuals can still benefit from associating with others with whom they do not interact directly, resource-tracking may be optimized when individuals rely selectively on social information from familiar conspecifics. Familiarity is especially important in environments that are both variable and risky. For example, familiar pairs of guppies (*Poecilia reticulata*) were more likely to exchange social cues and associate with one another in a novel, risky situation (Granroth-Wilding and Magurran 2013). Learning may also be more fruitful when individuals copy behaviours of more experienced individuals with whom they are more familiar (Granroth-Wilding and Magurran 2013). In kin-based social groups, the most familiar individuals may also be relatives. Indeed, kin selection makes social information from closer relatives both more transmissible (Schwab et al. 2008) and more beneficial for finding high-quality resources (Lynch et al. 2020).

Despite advantages of social information use in risky and variable environments, its use also entails some costs that can instead render personal information more reliable. Social information may be unreliable in extremely variable environments where conditions change before the information can be exchanged (Stodola and Ward 2017; Morinay et al. 2018). Individuals that use outdated social information risk making maladaptive behavioural decisions (Giraldeau et al. 2002; Aoki and Feldman 2014). For example, bison (*Bison bison bison*) followed social cues about resources to a new agricultural area but failed to cue in on higher hunting pressure that increased mortality and caused the population to decline (Sigaud et al.

2017). Given the negative fitness repercussions of social information, many populations in highly variable environments instead use personal information when making foraging decisions. For example, chickadees (*Poecile gambeli*) sought more personal information about food resources at higher elevations where the environment was more variable, and the risk of starvation increased costs of using potentially unreliable social information (Heinen et al. 2021). Responding to unreliable social information about predators also represents a cost if time spent foraging is also lost (McLachlan et al. 2019). However, animals in variable environments face a dilemma: because the environmental variability that makes social information less reliable often coincides with predation risk that makes personal information acquisition costly, animals placing their home ranges in variable environments must ultimately weigh two imperfect sources of information.

Quantifying this trade-off using only information about space use is challenging; although home range overlap between individuals provides opportunity for social information exchange (e.g., Hansen et al. 2022), individuals with overlapping home ranges may not interact closely enough. The distinction is especially pertinent in variable environments. For example, individuals can track shifting resource patches by moving and acquiring new personal information. However, if their between-year movements result in home range overlap with others, they may appear to be using social information to track resources (Stamps 1988) even if they arrive at the same patches independently of others (Fig. 1 a). A key distinction between social and personal information use in this context is whether spatial overlap also coincides with finer scale interactions between individuals. For example, overlapping home ranges of two individuals whose paths never cross suggests they use only personal information to arrive independently at the same resource patches (Fig. 1 b). Conversely, individuals that consistently share spatial overlap with the same individuals across years suggests some degree of familiarity among them, and the likely exchange of social information to track changing resources (Francesiaz et al. 2017; Fig. 1 c). Ultimately, distinguishing use of personal versus social information when animals share space is necessary to understand the significance of animal aggregations in variable environments.

We tested the degree to which home range overlap between individuals is underpinned by use of personal information or the opportunity for social information exchange. We compared whether only overlap between home ranges, or home range overlap combined with familiarity or social associations indicative of social information exchange, improved the ability of group-living elk (*Cervus canadensis*) to track resource changes in an agricultural landscape. Annual land cover change is a feature of agricultural landscapes that makes them variable. Individuals in variable environments may either use social information to locate resources or arrive independently at the same resource patches, in either case resulting in shared space at locations of better resources. Thus, we predicted elk with higher shared spatial overlap would better track resources between years (Prediction 1). If social information exchange but not personal information was responsible for better resource-tracking, we predicted that individuals sharing more space would also have more social associations (P2), and that individuals with more social associations (P3) and mutual familiarity (P4), would track resources most effectively. Finally, in addition to being variable in terms of resource availability, agricultural landscapes are risky; human disturbance increases access to prey by predators and hunting and trapping increases wildlife mortality (Robertson et al. 2013). We hypothesized that having to cope with mortality risk would make it beneficial for individuals to dilute risk by sharing space, whether they used social or personal information to find resources. We predicted elk that both shared more space (P5) and had more social associations (P6) would perceive lower predation risk.

5.3 Methods

5.3.1 Study system

Our study area in southeast Manitoba, Canada (49.134, -96.557) has a temperate climate with cold winters and brief, hot summers. The short growing season supports productive agricultural land use, including production of both crops and livestock, interspersed with wetlands, shrubland, and natural aspen forests. A combination of steady aspen encroachment into open grassland and forage fields and frequent crop rotations create a rapidly changing landscape with large inter-annual changes in land cover.

Eight adult female elk from the study area's approximate 150-animal Vita population were captured with a net gun fired from a helicopter and fit with GlobalStar satellite Global Positioning System (GPS) collars (LifeCycle Pro 500 g, Lotek, Newmarket, Ontario, Canada) in January 2016. An additional six animals were collared the following year in 2017. In February 2019, 18 more female elk were captured and fit with Iridium satellite GPS collars (Vertex Plus 830 g, VECTRONIC Aerospace GmbH, Berlin, Germany). All capture procedures were in accordance with approved animal care protocols (Memorial University of Newfoundland animal use protocol #19-01-EV).

We resampled collar locations to a common rate to prevent differences in the frequency of locations from biasing our home range estimates. The GlobalStar collars collected location data at 12-hr intervals throughout the year, while the Iridium collars collected locations at 30-min intervals from May 1 to July 31, and otherwise at 4-hr intervals. To ensure a consistent frequency, we resampled all collar locations by removing all locations closer than 12 hr to the next relocation, beginning at a randomly selected initial row for each animal. Finally, we cleaned the location data by removing any 2D locations, locations within 24 hr of deployment or collar retrieval, any inter-location intervals suggesting a biologically impossible movement rate, and individuals with fewer than two consecutive years of data. Our final data set included 22 individuals, each with exactly two years of data.

5.3.2 Home range estimates, fidelity, and social connections

We estimated home ranges using autocorrelated-Kernel density estimation (AKDE). AKDE corrects for bias due to small samples and autocorrelation in location data in addition to estimating confidence intervals around home ranges (Winner et al. 2018). As a result, confidence intervals can also be generated around estimates of home range overlap. Our three-month home ranges included locations beginning at the approximate final calving date for the population (August 2) and ended in late fall (November 1). This period overlaps with agricultural growing and harvest seasons in our study system and represents a relatively risky time of year when we expected all elk calves to be born and most vulnerable to predation.

We used overlap of AKDE home ranges as a measure of shared spatial overlap. We calculated the 95% confidence intervals of dyadic Bhattacharyya coefficient values between individuals, in the second year of the two years over which each individual was tracked, using the *ctmm* package (Calabrese et al. 2016) in R version 4.0.3 (R Core Team 2020). Higher Bhattacharyya coefficient values indicate greater overlap between two home ranges (Winner et al. 2018). We weighted social network edges with the dyadic Bhattacharyya coefficient values, then summed the edge weights by individual as a measure of its graph strength, calculated using the *igraph* package (Csardi and Nepusz 2006). Higher graph strength indicates overall greater overlap with other individuals within the network, i.e., higher shared spatial overlap. We weighted graph strength by the current number of individuals collared because a different number of individuals were collared in the three periods 2016–2017, 2017–2018, and 2019–2020.

We also quantified association rates using finer-scale relocation data to confirm whether shared spatial overlap represented social information sharing among individuals. We limited this sub-analysis to the 18 individuals collared during the 2019–2020 comparison. Iridium collars used on this group provide finer scale (i.e., 30-min versus 12-hr) location data required for distinguishing direct social associations. We weighted social network edges with the simple ratio index (SRI), calculated as the number of timepoints overlapping by 5 mins when members of a dyad were within 50 m of one another, divided by the total number of timepoints in the dataset when the locations of each dyad member overlapped by 5 mins (Lesmerises et al. 2018). We then calculated the sum of the edge weights as above, without weighting graph strength by collared individuals since the same number were collared in both 2019 and 2020. We performed all association rate analyses using the *spatsoc* package in R (Robitaille et al. 2019).

We developed a metric for familiarity among individuals that compared the identities of their network edges between years. We assumed that the smaller the total between-year difference in an individual's edge weights, the more familiar that individual was with the others with which it shared space. We summed the absolute differences in edge weights between years for individuals:

$$F_j = \sum |o_{ji2} - o_{ji1}|$$

Where F_j is familiarity for individual j, o_{ji1} is the shared spatial overlap of individual j with individual i in year 1, and o_{ji2} is the shared spatial overlap of individual j with individual i in year 2. Smaller F_j indicate greater familiarity.

5.3.3 Landscape metrics and resource-tracking

We quantified resources using both land cover metrics and vegetation quality. Normalized Vegetation Difference Index (NDVI) is a remotely sensed measure of vegetation greenness, often serving as a proxy for vegetation quality for browsing herbivores like elk (e.g., Barker et al. 2019). Vegetation quality increases as NDVI takes higher values. We calculated NDVI as the difference in reflection between red and near infrared bands in U.S. Geological Survey Landsat 8 images.

We also quantified habitat structure using contrast-weighted edge density (CWED). CWED measures the density of edges between adjoining patch types, weighted by the contrast between classes to which the patches belong (McGarigal and Marks 1995). Since natural habitat in our study system is dominated by forest, shrubland, and wetlands with tall emergent species like *Typha* spp., edges between natural habitat and cropland represent abrupt structural changes. This structure provides cover for species like elk to hide from predators and humans while foraging in cropland (DeVore et al. 2016). We considered the contrast between crops and natural habitat to be higher than the contrast between any two different crop classes. However, elk also use crop classes differently based on their relative height and growing stage. Elk mostly use crops like soybeans and alfalfa for foraging, while taller cereal crops like wheat are mainly used for hiding cover (Hinton et al. 2020). Corn is a multi-use habitat type; it provides hiding cover late in the growing season, but in its mature stage, like it was in the earlier half of our study period, it is also used for foraging (DeVore et al. 2016). We assigned each habitat class a value between zero and one, making larger CWED values — i.e., more patch edges connecting natural habitat with cropland or connecting two crop classes having different value in terms of forage and hiding cover — a measure of habitat structure. See Supplementary Table S.5-1 for all contrast weights. We obtained land cover data from the USDA National Agricultural Statistics Service Cropland Data Layer (2016–2020) and Agriculture and Agri-Food Canada Annual Crop Inventory (2016-2020), reclassifying each land cover dataset to common classifications (Supplementary Table S.5-1). We calculated CWED using the *landscapemetrics* package (Hesselbarth et al. 2019) in R. Resolution of all spatial datasets was 30-m.

We measured the ability of elk to track resources by comparing the between-year change in habitat structure and vegetation quality within home ranges, relative to the larger landscape. We assumed that elk better tracked habitat structure when CWED within their home ranges changed less between years relative to the larger landscape. We quantified this relative change between years as the absolute difference in the between-year change in CWED at the landscape and home range scales. In contrast, we assumed elk better tracked foraging resources when they had access to greater NDVI. We measured NDVI tracking by the mean NDVI across their home ranges in the second year of their between-year comparison.

5.3.4 Measuring perceived predation risk

We used the average level of fecal glucocorticoids as a proxy for the degree of predation risk individuals experienced. When animals encounter acute stressors such as predators, the HPA axis initiates release of a suite of chemical signals into the blood that includes the glucocorticoid hormones. A fraction of these glucocorticoids is metabolized and eliminated in feces where it provides an integrated average of glucocorticoid release — and stressors faced — over a period of several hours (Gormally and Romero 2020). From May—August in 2019 and 2020 we non-invasively collected fecal pellet samples from 11 of the 18 elk collared in 2019. We assigned the samples to individual elk using either pair-wise genetic relatedness with blood samples collected at the time of capture or a machine learning approach that matched samples to individuals based on movement characteristics (Newediuk and Vander Wal 2021; also see Chapter 4 and Newediuk et al. 2022). We assumed individuals with higher average glucocorticoid levels perceived higher predation risk on average. To confirm within-individual variation in predator exposures did not obscure among-individual differences in glucocorticoid production, we calculated glucocorticoid repeatability. We fit generalized linear models with the *rptR* package (Stoffel et al. 2017) in R, including individual as a random effect. We used 1,000 bootstraps to account for uncertainty in the repeatability estimate.

5.3.5 Analysis

When social network analysis tests the effect of social structure on a response variable, such as the effect of shared spatial overlap and association rates on resource tracking in our analysis, observed associations among individuals may be the result of either social connection or spatial aggregations of resources that attract individuals to the same locations. Uncertainty about the causes of spatial aggregations can bias social network measures (Spiegel et al. 2016). We controlled for potential biases in our social network measures within the models themselves (Franks et al. 2021). More specifically, we visualized the causal structure of our system using directed acyclic graphs (DAGs; Supplementary Fig. S5-1), then carefully selected covariates to control for non-causal effects (Arif and MacNeil 2022), e.g., by including shared spatial overlap as a covariate to test the effect of SRI on resource-tracking.

Network randomization is an alternative and more widespread approach to control for biases in social network measures (Spiegel et al. 2016). Briefly, the order of GPS track sections belonging to individuals in the network are repeatedly randomized, and a null model is fit to test the relationship between the new random network and the response variable (Farine and Whitehead 2015). This approach, known as *data stream permutation*, purportedly breaks the covariance between social associations and the response variable. However, data stream permutations face criticism for reducing variance in the null model response variable, which can make it appear as if the relationship between social associations and the response variable is stronger in the observed than null model, i.e., a type II error (Weiss et al. 2021). To avoid such spurious results, and since our analyses were already designed to test the distinction between aggregation due to social connection versus attraction to resources, we opted against performing network randomizations in our study.

We fit an initial set of Markov Chain Monte Carlo (MCMC) generalized linear models to test our initial prediction that shared spatial overlap improves resource-tracking (Prediction 1). We separately tested the effects shared spatial overlap on resource-tracking in terms of habitat structure and vegetation quality (i.e., CWED and NDVI). Based on the causal structure of our system, we suspected the relationship between shared spatial overlap and resource-tracking to be conditional on an indirect effect of the overall amount of change in the environment between years (Supplementary Fig. S.5-1). To avoid biasing our inferences, we included the overall amount of change in either CWED or NDVI in the same model with a covariate for shared spatial overlap.

Our second set of models tested whether social information exchange was responsible for better resource-tracking. To test whether individual that shared space had more social associations (P2), we modelled the effect of shared spatial overlap on SRI. We also tested whether social information exchange facilitated by these social associations improved resource-tracking by modelling the effects of SRI (P3) and familiarity (P4) on resource-tracking. Again, we tested resource-tracking in terms of CWED and NDVI separately. We included only the 2019–2020 subset of data in models testing Predictions 2 and 3 because we only calculated SRI for elk with fine-scale data. We suspected the causal relationship in both models was influenced by an indirect effect of shared spatial overlap on the predictor variable (Supplementary Figure S.5-1). To control for potential bias, we included a covariate for shared spatial overlap in all models.

Our final set of models tested the effects of shared spatial overlap and social associations on risk perception. The first model tested whether elk with more shared spatial overlap had lower glucocorticoid levels on average, suggesting they perceived less risk (P5). The second model tested whether social associations lowered risk perception by modelling the effect of SRI on glucocorticoid levels (P6). Here, we suspected an indirect effect of shared spatial overlap on SRI (Supplementary Figure S.5-1), so also included it as a covariate in the model.

We fit all MCMC models with multinomial distribution and Gaussian link function using the *brms* package (Bürkner 2017). We scaled and centred all variables prior to modelling. We used weakly informative priors with a normal distribution, 4 chains, and the default 2,000 iterations with a warmup of 1,000 iterations. We visually assessed trace plots to ensure adequate warmup and iterations and to assess model convergence.

5.4 Results

We quantified shared spatial overlap in the second of two years for 7 elk collared from 2016–2018 and 15 from 2019–2020. For the 2019–2020 group, we also quantified mean fecal glucocorticoid metabolite levels (µg/g) and associations rates using the simple ratio index (SRI). Unscaled SRI values ranged from 0.03–1.11 (n = 15), while average proportion of shared spatial overlap among individual home ranges ranged from 0.11—0.5 (n = 22). Mean fecal glucocorticoids ranged from 1,734–3,714 µg/g (n = 11), but the repeatability estimate was low at 0.16 ± 0.11 SE, suggesting high within-individual variation in glucocorticoid levels relative to variation among individuals. Trace plots for MCMC models indicated convergence and adequate sampling of posterior distributions given our warmup and number of iterations. All trace plots and posterior distributions are provided in Supplementary Figures S.5-2–S.5-8.

Shared spatial overlap did not affect the ability of elk to track vegetation quality (P1; 89% credible interval -0.40, 0.40) nor habitat structure (89% CI -0.19, 0.69). Similarly, elk did not track NDVI more effectively when they had higher SRI values, i.e., when they associated more with other individuals (P3; 89% CI -0.52, 0.76 Fig. 5.2 a). However, elk that overlapped more with the same individuals between years — i.e., those that were more familiar — were better at tracking NDVI (P4; 89% CI -0.96, -0.29 Fig. 5.2 b). Neither association rates (89% CI -0.12, 0.93) nor familiarity (89% CI -0.20, 0.57) were associated with tracking CWED.

Perceived risk depended on whether individuals shared only space, or space in addition to social associations. Elk had association rates decreased with shared spatial overlap (P2; 89% CI -0.96, -0.05 Fig. 5.3). Those with greater shared spatial overlap perceived less risk, i.e., had lower fecal glucocorticoid metabolite levels (P5; 89% CI -1.11, -0.03 Fig. 5.4 a). In contrast, association rates had no effect on fecal glucocorticoids (P6; 89% CI -67, 0.65 Fig. 5.4 b).

5.5 Discussion

Shared spatial overlap can arise either when individuals exchange social information about resources or when multiple individuals use their own personal information to arrive at the same resource patches. We distinguished shared space from shared social information by testing whether social associations, familiarity, or shared spatial overlap among individual elk improved their ability to track resources in a variable agricultural landscape. Individuals whose home ranges overlapped with one another consistently across years, i.e., those we assumed were more familiar, tracked resources more effectively (support for P4). However, resource-tracking improved with neither the amount of spatial overlap shared among individuals (no support for P1) nor with their finer scale association rates (no support P3). Furthermore, social associations did not increase with spatial overlap (no support for P2), suggesting individuals that overlapped consistently exploited the same profitable resource patches at different times. This behaviour produced a pattern of shared spatial overlap among individuals independent of social information exchange. However, shared spatial overlap had other benefits. Social association rates did not coincide with fewer glucocorticoids (no support for P6), but individuals with more shared spatial overlap had lower glucocorticoid levels regardless of the individuals with which they shared space (support for P5). Thus, even without exchange of social information, individuals in densely used areas may perceive less predation risk. Together, our results suggest that while shared spatial overlap may not necessarily be driven by social information exchange, it still provides benefits for animals living in variable environments.

Shared spatial overlap among individuals involves exchange of social information about resources (Hansen et al. 2022). In variable environments, however, social information quickly becomes outdated and is devalued (Heinen and Stephens 2016). We suggest elk in our study devalued social information since shared spatial overlap did not coincide with more social associations (Fig. 5.3), nor did it affect the ability of elk to track either habitat structure or vegetation quality. Instead, elk likely relied on personal information to track resources. Site fidelity, a strategy based on personal information, is often effective in variable environments because individuals reduce long-term costs from having inconsistent access to resources in spaces with which they are familiar (Traisnel and Pichegru 2019; Gerber et al. 2019). Familiar places hold most value for individuals that are consistently site-faithful, especially if they begin to accumulate personal information early in life (Piper 2011). Older site-faithful elk in our study may have benefited from this long-term personal information, especially about features like crop rotations or localized hunting pressure that are consistent over long but not necessarily shorter periods. In contrast, higher shared spatial overlap may have been characteristic of individuals with lower site fidelity that moved frequently between periods. While our comparison period was limited to two years, comparing the efficacy of personal and social information use for resource tracking likely requires longer study periods, especially in variable environments.

Our brief study period likely also complicated our assessment of familiarity with other individuals. Though individuals we assessed as being more familiar overlapped spatially for two years, we also found individuals that shared more space did not share more social information. By extension, those individuals that shared spatial overlap across years may not have been familiar with one another. Over short periods, as in our study, individuals that track the same resources independently may share spatial overlap by chance. Consistent shared spatial overlap in other studies, in contrast, is often a proxy for familiarity among individuals followed for several years from juvenile to adulthood (Robinson et al. 2015; Hansen et al. 2022). Had we followed individuals over multiple years, we might have also been able to distinguish familiar individuals from those that shared spatial overlap by chance alone. Despite this limitation in our study, decomposing shared spatial overlap into finer-scale association rates helped us understand its connection to social information exchange.

That individuals shared spatial overlap, but not closer associations, is consistent with the hypothesized costs of social information in variable environments (Kendal et al. 2005).

However, while these costs purportedly stem from unreliable information, our results suggest closer associations also pose a cost in terms of interference competition. This additional cost is evident in the patterns of glucocorticoid production we found. While we expected glucocorticoid levels to decrease with association rates that lowered perceptions of predation risk, there was no relationship (Fig. 5.4 b). In addition to predation risk, however, elevated glucocorticoid levels are also an indicator for low energy reserves (Jesmer et al. 2017). We suggest elk having to compete directly for the best foraging sites may have foraged less efficiently. This competitive effect was likely exacerbated by the costs of lactation by reproductive females in our study system; for ungulates like elk, lactation represents a substantial physiological cost requiring high energy intake and thus high-quality foraging resources (Lehman et al. 2019). Not being able to meet these foraging demands may have also increased the frequency of aggressive interactions among individuals (Weckerly 1999). Together, aggressive interactions and forage competition could have both elevated glucocorticoid levels and offset any antipredator benefit of associating closely with others.

Elk appeared to overcome competitive costs by exploiting the same resources at different times. Prey species use a similar temporally conservative strategy to lower predation risk, restricting foraging in productive areas to times when predators are inactive or easier to avoid (Smith et al. 2019). In our study, individuals might avoid interference competition and aggressive interactions by trading off between foraging sites. This behaviour could have additional foraging benefits for lactating elk. Intermittent use of foraging sites, or foraging at lower intensities, keeps some plant species at an immature and more nutritious stage by promoting compensatory growth (Van Der Graaf et al. 2005). Thus, elk could have improved forage nutrition for all individuals by foraging in the same places at different times. This hypothesis is consistent with seasonal behaviour of female elk; during the calving season, female elk often form small nursery groups in contrast to the large, multi-sex groups typical of other seasons (Paquet and Brook 2006). While smaller groups are primarily considered a predator avoidance strategy (Hebblewhite and Pletscher 2002), they may also be adaptive for lactating elk that benefit both from less competition and more nutritious forage.

Individual differences in coping with forage limitation versus predation risk might provide another explanation for the patterns of shared spatial overlap and resource-tracking we found. While higher association rates did not coincide with lower glucocorticoid levels, suggesting closely associating individuals did not dilute their predation risk, we found glucocorticoid levels were lowest among individuals with the highest spatial overlap (Fig. 5.4 a). This result suggests spatial proximity to others might still dilute predation risk. Importantly, since shared spatial overlap did not also improve resource-tracking, this antipredator benefit likely persists even in areas with relatively fewer resources and without exchange of social information about resources. The benefits of social information exchange diminish with increasing group size (Gil et al. 2017), but because predators are limited by the number of prey they can kill at one time, the level of risk experienced by individuals continues to decrease as prey density increases (i.e., functional response *sensu* Holling 1959). Furthermore, attack rates are higher when individuals group together (Hebblewhite and Pletscher 2002), which may have incentivized individuals in our study to avoid closer associations while still remaining in high-density areas. While elk with higher spatial overlap and lower association rates avoided predation risk, those at lower densities — possibly those with consistent shared spatial overlap between years — instead tracked the best resources. Since the best resources in agricultural environments are often on cropland where risk is also high, these individuals probably tolerated elevated risk. Uncovering the causes of variation in tolerance of predation risk versus forage limitation is an avenue for future research.

Overall, we suggest shared space by individuals in this system is not driven by exchange of social information. We suggest the preference for personal over social information use stems from a need to balance risk and resource, rather than from low reliability of information in variable environments. On one hand, individuals with limited knowledge about predation might be drawn to dilute their risk by overlapping spatially with others. Individuals that share space, however, also compete for resources, incentivizing site fidelity or use of lower-density areas with higher predation risk. In either case, a combination of personal motivation and personal information likely drives space use decisions. Ultimately, understanding the motivations behind shared spatial overlap in variable environments requires distinguishing it from social information exchange.

5.6 References

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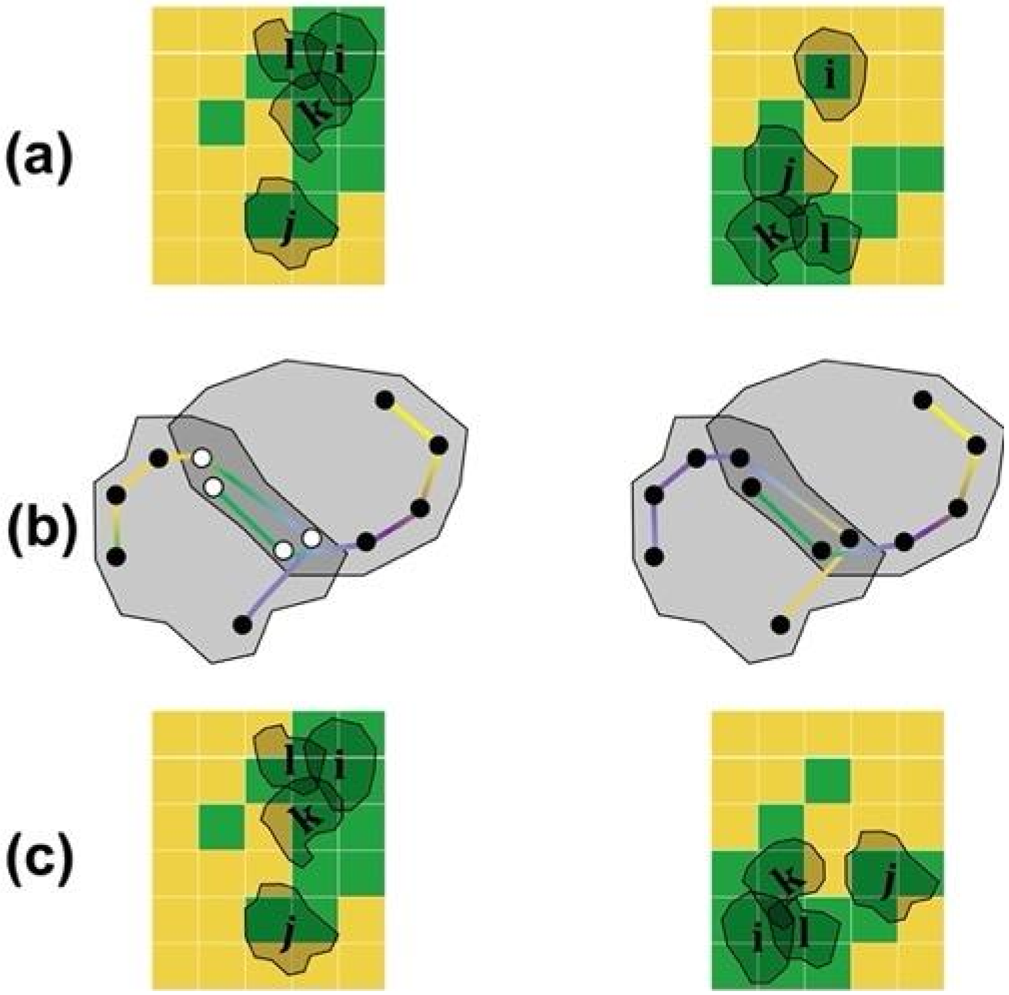

Figure 5.1: Scenarios in which individuals with overlapping home ranges (grey polygons) do not necessarily exchange social information when resource patches (green tiles) change between years (left to right). In (a), individuals *k* and *l* maintain the same home range overlap in both years but arrive at the resource patch independently of *i* and *j*, suggesting no social information exchange with *i* and *j*. In (b), two home ranges overlap, but individuals only interact closely enough to exchange social information in the first year, indicated by the same track colour and white locations. Finally, in (c) individuals *i*, *k*, and *l* are familiar, i.e., their home range overlap is coordinated across years, providing an opportunity for social information exchange.

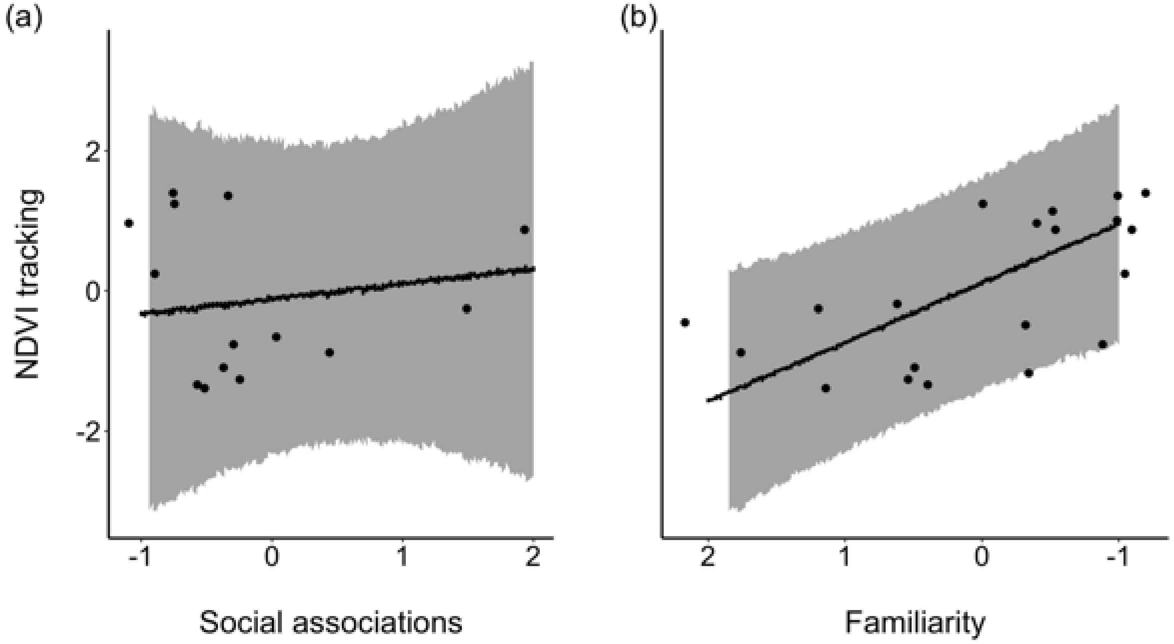

Figure 5.2: Conditional effects of social associations (a) and familiarity of individuals with others with which they share social connections (b) on resource-tracking in terms of normalized difference vegetation index (NDVI). Black lines and ribbons are mean predictions and 89% percentile intervals of samples from the posterior distribution. Black points are scaled raw data points. In (b), more negative values along the x-axis indicate greater familiarity among individuals.

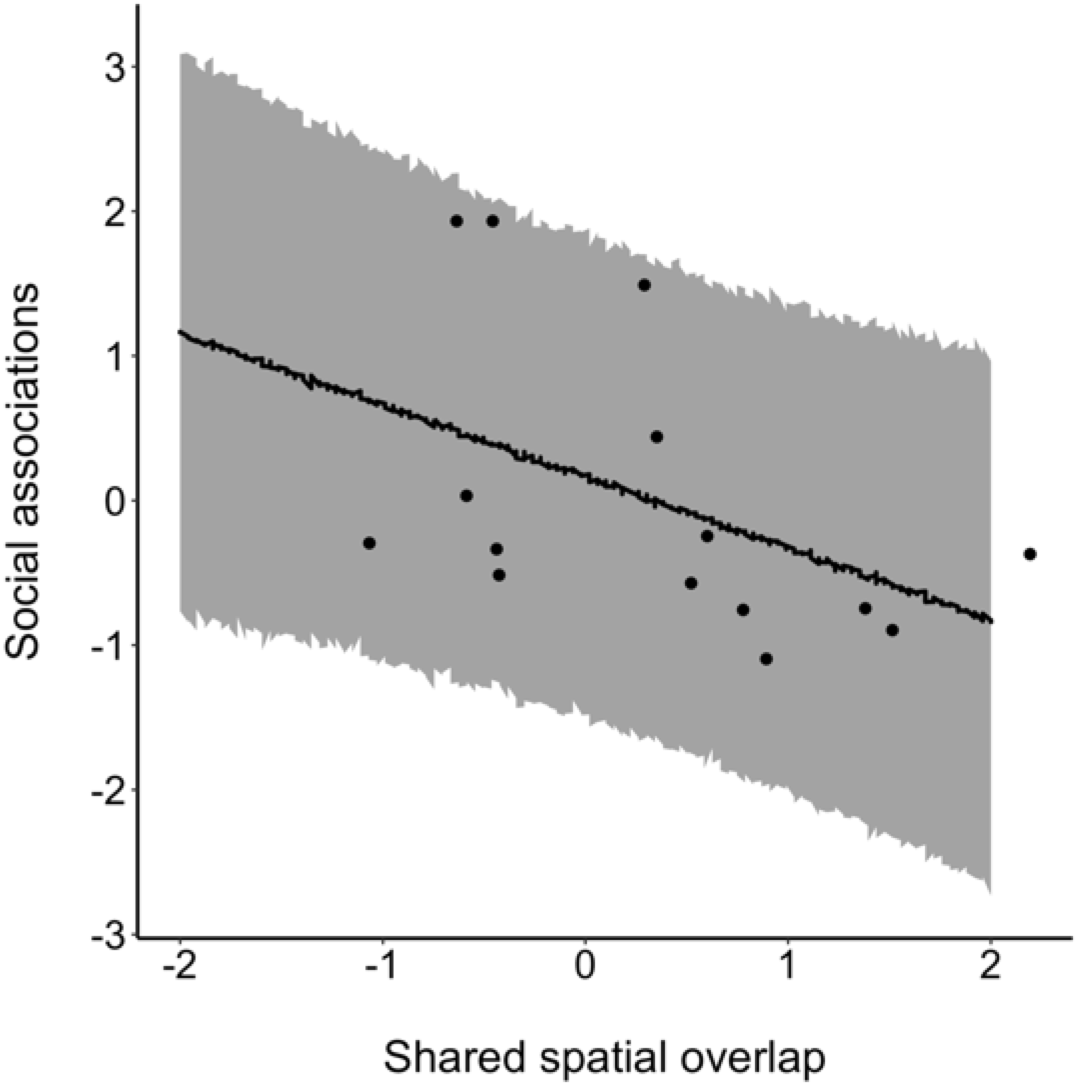

Figure 5.3: Conditional effects of shared spatial overlap on social association rates. Black lines and ribbons are mean predictions and 89% percentile intervals of samples from the posterior distribution. Black points are scaled raw data points.

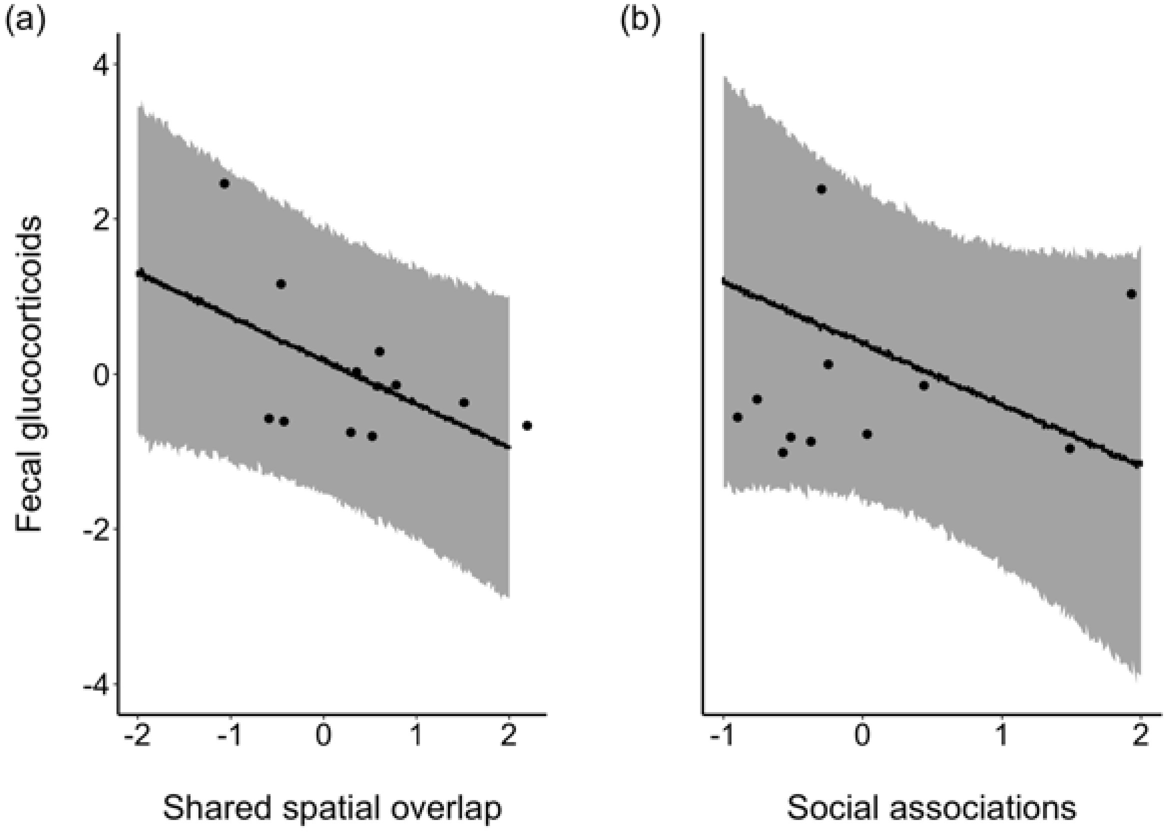

Figure 5.4: Conditional effects of shared spatial overlap (a) and association rates (b) on fecal glucocorticoids levels. Black lines and ribbons are mean predictions and 89% percentile intervals of samples from the posterior distribution. Black points are scaled raw data points.

CHAPTER 6 CONCLUSIONS

6.1 Summary

Climate change models (Thomas et al. 2010) and estimates of future land use change (Regos et al. 2018) are used in conjunction with predictions of species distributions to identify species facing extinction from habitat loss. Models that predict species distributions accurately after habitat change — i.e., those that are transferable — are essential for this task. Even very recently, methodological focus has been limited to how model transferability is impacted by changes in the external environment (e.g., Rousseau and Betts 2022). But this focus on the external environment may not be enough.

In the latter half of my thesis, I showed that characteristics of individual animals' internal environments — i.e., their internal state (Nathan et al. 2008) — interact with the external environment to shape their distributions. The influence of internal state highlights its equally important role in predictive modelling, despite its slow uptake by movement ecologists over the past decade (Holyoak et al. 2008; Jachowski and Singh 2015). Fortunately, the importance of recognizing internal state while working towards species recovery is a premise already espoused by conservation biologists (Madliger et al. 2016; Merrick and Koprowski 2017), and movement ecologists can take their lead to integrate them into predictive habitat selection analysis (HSA).

My thesis makes several important contributions to species distribution modelling using HSA. First, I probe the assumption that HSA model transferability requires explicitly accounting for the functional response in habitat selection, i.e., the relationship between habitat selection and availability (Mysterud and Ims 1998). In Chapter 2, I showed that accounting for this relationship did not improve model transferability in comparison to simpler HSA models. Simpler models sometimes perform better because internal state differences among individuals influence whether they follow the expectations of the functional response, and thus expected distributions after the environment changes.

While I focus on understanding how internal state drives habitat selection rather than predicting habitat selection in Chapters 3 and 4, findings from these two chapters nonetheless have value for improving HSA predictions. In Chapter 3, I showed that glucocorticoids help produce the movements and habitat selection patterns estimated by HSA. HSA provides a mechanistic link between the external environment, internal state, and animal distributions on the landscape when models are parameterized with physiological data like glucocorticoids measured from hair and feces. In Chapter 4, I showed how we can use biotelemetry data to link hair and fecal samples to individual animals as a measure of their physiological state. Repeatedly sampling internal state as individuals move is essential for their integration into movement-based integrated step-selection analysis.

Finally, in Chapter 5, I showed how internal state might help us understand how animals balance their needs to avoid risk and acquire resources in social contexts. Even if they do not associate closely enough to share information about resources, individuals facing predation may share space with others to reduce their risk. Risk perception, therefore, is the internal state that mediates how individuals respond to changes in resources like forage availability. Predicting animal distributions requires not only that we anticipate where resources will be when the environment changes, but that we understand how internal state influences how important those resources are relative to other environmental pressures.

Integrating the fields of physiology and habitat selection will be an important milestone toward mainstreaming the use of internal state in movement ecology (Jachowski and Singh 2015). My thesis demonstrates the theoretical connection between movement ecology and physiology. To conclude my thesis I discuss, in a more applied sense, how we can invoke physiology to uncover the physiological mechanisms for habitat selection and use them to parameterize HSFs. Finally, I discuss some technical challenges to putting these physiology-based HSFs into practice for predicting animal distributions.

6.2 How data might be integrated into habitat selection functions

6.2.1 Finding the physiological mechanism for movement and habitat selection

For physiology to be useful for predicting species distributions, clear mechanistic links must be made and tested between the environment, physiology, and habitat selection behaviour. My third and fifth chapters show how glucocorticoids might act as a mechanism for making behavioural trade-offs as animals seek resources and avoid predation risk. There are also excellent examples of such links from previously hypothesized relationships in the literature. In some partially anadromous salmonids, for example, residency versus migration is thought to be under control of environmental factors like temperature, food supply, and competition that together influence growth rate and whether the fish will be reproductively successful in its rearing environment (Kendall et al. 2015). Here, an individual's habitat selection in response to the environment depends in its physiology. Similarly, the carbon-stress hypothesis proposes a physiological mechanism for habitat selection by individuals under predation risk. Stress responses stimulated by predation risk increase metabolic demand, causing individuals to meet their greater metabolic requirements by selecting habitat with more energy available in the form of carbon (Hawlena and Schmitz 2010). Importantly, both the carbon-stress hypothesis and partial migration in salmon suggest pathways by which physiological reactions to stress and slower growth rates — factors normally associated with lower fitness — can improve fitness when accompanied by the appropriate habitat selection response.

We can also use existing theory about physiological mechanisms to hypothesize new relationships between habitat selection and untested physiological biomarkers. Androgen hormones, for example, correlate with reproductive and aggressive behaviour (Fattorini et al. 2018). Outcomes of aggressive competition for limited resources around breeding time, fueled by rising androgens, could be responsible for determining whether birds move to breeding grounds in partially migratory populations (Watts et al. 2018). Other biomarkers are also promising candidates for modelling relationships between energetic requirements and habitat selection. Reproductive female mammals produce the biomolecule C-peptide as a by-product of insulin production. C-peptide levels track the transition from higher to lower levels of required carbohydrates through the course of lactation (Ellison and Valeggia 2003), suggesting a possible physiological mechanism for preference of forage-rich habitats after parturition (Panzacchi et al. 2010; Heffelfinger et al. 2020).

Just as physiology influences habitat selection behaviour, habitat selection also influences physiology. At larger scales, these relationships may reveal how animal distributions shift within the lifetimes of individuals and over ecological time. For example, stable diet preferences of red knots (*Calidris canutus islandica*) contributed to lower gizzard mass even though gizzard mass did not affect diet preference (Oudman et al. 2016), suggesting behavioural effects on physiology. In some cases, behavioural or physiological traits are stable. However, in cases where both habitat selection and physiological traits like gizzard size are plastic, continuous feedback between them could represent a pathway by which individuals might adapt to their environments over their lifetimes. In Chapter 5, elk with lower glucocorticoid levels — and possibly facing higher predation risk — also shared more space with others. However, they did not do so in locations with the most foraging resources, which may have also been most risky.

Elk opting for risk dilution via spatial overlap with others might limit their need to seek the highest-quality resources, while those facing greater risk would require more energy from higher-quality resources. Both behavioural types could be bound to specialize on either lower-resource habitat with low risk, or higher-resource habitat with greater risk, with glucocorticoid production as the mediator between them.

Even if an individual does not experience an environment itself, habitat specialization might arise through epigenetic or cultural transmission of habitat preferences. Many parents select the natal habitat for their offspring, which can have profound developmental effects through the lifetime of the individual (Stamps et al. 2009). When natal habitat preferences confer a fitness advantage, cultural transmission of distributions might become stabilized in populations. For example, consistent differences in bottlenose dolphin (*Tursiops aduncus*) habitat use was inherited through maternal transmission of behaviour (Strickland et al. 2021). In some cases, such transmission may have an underlying epigenetic component. In a different bottlenose dolphin population, ecotypes adjusted to coastal and offshore habitats also exhibited unique DNA methylation patterns, suggesting epigenetic differences with behaviour (Tatsch et al. 2021). Thus, as the environment changes over time and causes cultural and epigenetic shifts in habitat selection behaviour, species distributions will likely also continue to change.

6.3 Challenges with incorporating physiology into predictive habitat selection models

Three important considerations still require work before use of physiology-based HSFs to predict future distributions is widespread. First, predicting the effects of physiology on future distributions requires both integrating the physiological data into movement-based iSSFs and estimating the predicted utilization distribution in the new landscape. For traditional HSFs, the utilization distribution can be estimated simply by multiplying the selection coefficients by habitat availability in the new landscape if availability is adequately sampled (Boyce 2006). Availability in the case of iSSF, however, changes with each step. Thus, the utilization distribution predicted by the iSSF is sensitive to time and location; it is only at its “steady state” when the temporal and spatial extent of availability at each step approaches that of a traditional HSF, i.e., assuming all points are simultaneously available (Signer et al. 2017). This definition of availability, of course, is inconsistent with iSSA. Instead, the steady state distribution of the iSSF has been sought by using individual-based simulations of short-term distributions (Signer et al. 2017) or by sampling repeatedly from the posterior of the utilization distribution using methods like Markov Chain Monte Carlo (Michelot et al. 2019). It is unclear how the added complexity of physiological markers — which vary both among individuals and within individuals across time — will affect estimation of the utilization distribution.

A second caveat related to the variability of physiological markers concerns balancing model complexity and generality. Behavioural responses to physiological markers might vary across contexts. For example, in Chapter 3 I showed that habitat selection in response to acute stress responses depending on reproductive status. Because the relationship between stress response and habitat selection is not general, including glucocorticoid markers as interactions in iSSF models may not improve transferability. After all, I showed in Chapter 2 that modelling the added complexity of the functional response did not improve transferability because individual responses to changing habitat availability varied. Thus, it is unclear how modelling selection based on variable physiological states will perform in predictive applications. Performance may be particularly unpredictable for situations in which the environment feeds back on physiology and further impacts selection. Combining physiology-based HSFs with new HSFs designed to test habitat selection based on energetic needs (Klappstein et al. 2022) may be useful for uncovering these feedbacks.

Finally, translating model predictions into management actions will require moving physiology-based HSFs from theory to the practice. Making physiology-based HSA practical will require more demonstrations of how hormones and other physiological markers influence habitat selection. A first step might be to foster cross-disciplinary work between physiologists and movement and habitat selection ecologists. The field of conservation physiology is a model of this cross-disciplinary approach, where experts in disease ecology, fisheries, restoration, and other disciplines already work with stress physiologists (Madliger et al. 2016). Many physiological markers obtained from animals while tagging or trapping can also be collected noninvasively from the environment using movement data (Giroux et al. 2012). Working with field ecologists can normalize collection of "panels" of non-invasive physiological data (Madliger et al. 2016). For wildlife managers, physiology-based HSFs could be used to produce a range of possible future distributions that reflect anticipated habitat responses to landscape change given known physiological markers. Managers would need only match the land use scenario with the best outcome for future distributions. Importantly, it will be necessary to theorize and test for clear mechanisms connecting physiological markers with habitat selection. This will require a culture shift from a literature dominated by the notion that glucocorticoids are synonymous with stress.

6.4 Concluding remarks

In my thesis, I proposed we incorporate internal state into HSFs to better predict species distributions after environmental change. I began by highlighting how internal state is an often neglected but important gap in species distribution modelling (Chapter 2), showing how we might collect the appropriate data to measure internal state and incorporate it into movement-based HSFs (Chapters 3 & 4), and finally provided examples of how incorporating physiology-based HSA can enrich our ecological understanding of species distributions (Chapters 3 & 5). In my concluding chapter, I looked forward to opportunities for improvement and prospective challenges for future research. Most notable of these challenges is the problem of whether we can generalize the relationships between internal state and movement across individuals, populations, and species. Testing transferability of physiology-based HSF predictions is an important area of future research. However, transferability of these HSF models will only be testable when we collect the physiological data needed to measure internal state and the perspective that physiological responses to the environment drive adaptive distributions in response to environmental change.

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SUPPLEMENTARY MATERIALS

The following contains a glossary of terms (section S.1) and supplementary materials for Chapters 2–5 (sections S.2–S.5). Chapters 1 and 6 have no associated supplementary material.

S.1 Glossary of terms

Table S.1-1: Glossary of terms.

Autocorrelated kernel density estimation	A method of home range estimation that both corrects for small sample sizes and the autocorrelation inherent in animal movement data and estimates confidence intervals around the home range area.	(Winner et al. 2018)
Baseline glucocorticoid level	Predictable daily and seasonal levels of circulating glucocorticoids that fluctuate in response to predictable stressors that change over time (e.g., seasonal food limitation.	(Landys et al. 2006)
Behavioural plasticity	The capacity of an animal to adjust its behaviour over a range of environmental conditions.	(Dingemanse et al. 2010)
Chronic stress	Overstimulation of emergency responses to chronic stressors (e.g., persistent food limitation) associated with higher risk of stress-related pathology.	(Romero et al. 2009)
Cort-fitness hypothesis	The notion that baseline glucocorticoid levels have a negative relationship with fitness because glucocorticoids are produced in response to environmental challenges, and those environmental challenges compromise fitness.	(Bonier et al. 2009)
Functional response in habitat selection	The change in relative use of a habitat with its changing availability or the changing availability of a different habitat type.	(Mysterud and Ims 1998)
Habitat	A point in environmental space (as opposed to geographic space) characterized by a unique combination of resources, risks, and conditions.	(Northrup et al. 2021)

Habitat selection	Proportional of a habitat in comparison to available or unused units of the habitat.	(Manly et al. 2002)
Habitat selection function	A function describing the relative probability that a habitat is selected depending on its characteristic resources, risks, and conditions.	(Boyce and Mcdonald 1999; Matthiopoulos et al. 2020)
Human-induced rapid environmental change	Changes to the environment including habitat loss and fragmentation, invasive species, harvest, pollutants, and climate change that typically occur more rapidly than natural changes, and often too quickly for evolutionary responses.	(Sih et al. 2011)
Integrated step-selection function	A class of habitat selection function that separates the process of movement from the process of habitat selection, allowing the interdependency between movement and habitat selection to be incorporated in the model.	(Avgar et al. 2016)
Internal state	Physiological state of an individual (e.g., hunger, fear) that influences its motivation to move to a new habitat.	(Nathan et al. 2008)
Model transferability	A measure of the degree to which a model can be applied to make predictions on data outside of the datasets from which they were developed.	(Wenger and Olden 2012)
Personal information	Individually held information acquired either from memory or in real time.	(Kendal et al. 2005)
Relative selection strength	In the context of habitat selection functions, the relative selection for two locations in space according to their characteristic resources, risks, and conditions, and assuming both locations are equally available.	(Avgar et al. 2017; Fieberg et al. 2021)
Resource	An aspect of the external environment (e.g., food source, affiliative interaction) having both a positive effect on either survival or reproduction.	(Matthiopoulos et al. 2020)

Resource-tracking	Change in position of an organism over space and time to exploit spatiotemporal fluctuations of resources.	(Abrahms et al. 2021)
Risk	An aspect of the external environment (e.g., predator encounter, antagonistic interaction) having a negative effect on individual fitness either by reducing either survival or reproduction directly or reducing access to resources that support either survival or reproduction.	(Matthiopoulos et al. 2020)
Social information	Information produced either actively (e.g., communication about resources) or as passive cues (e.g., observations of resource exploitation) that is relevant to reproduction or survival of other individuals	(Gil et al. 2018)
Species distribution model	A modelling approach, including habitat selection analysis, that describes associations between the position of an organism in space and time and characteristics of the environment including resources, risks, and conditions.	(Morris et al. 2016)
Stress response	Elevation of circulating glucocorticoids above seasonal or daily baseline levels that activate alternative coping strategies to deal with life-threatening and unpredictable stressor.	(Landys et al. 2006)

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S.2 Supplementary materials for Chapter 2

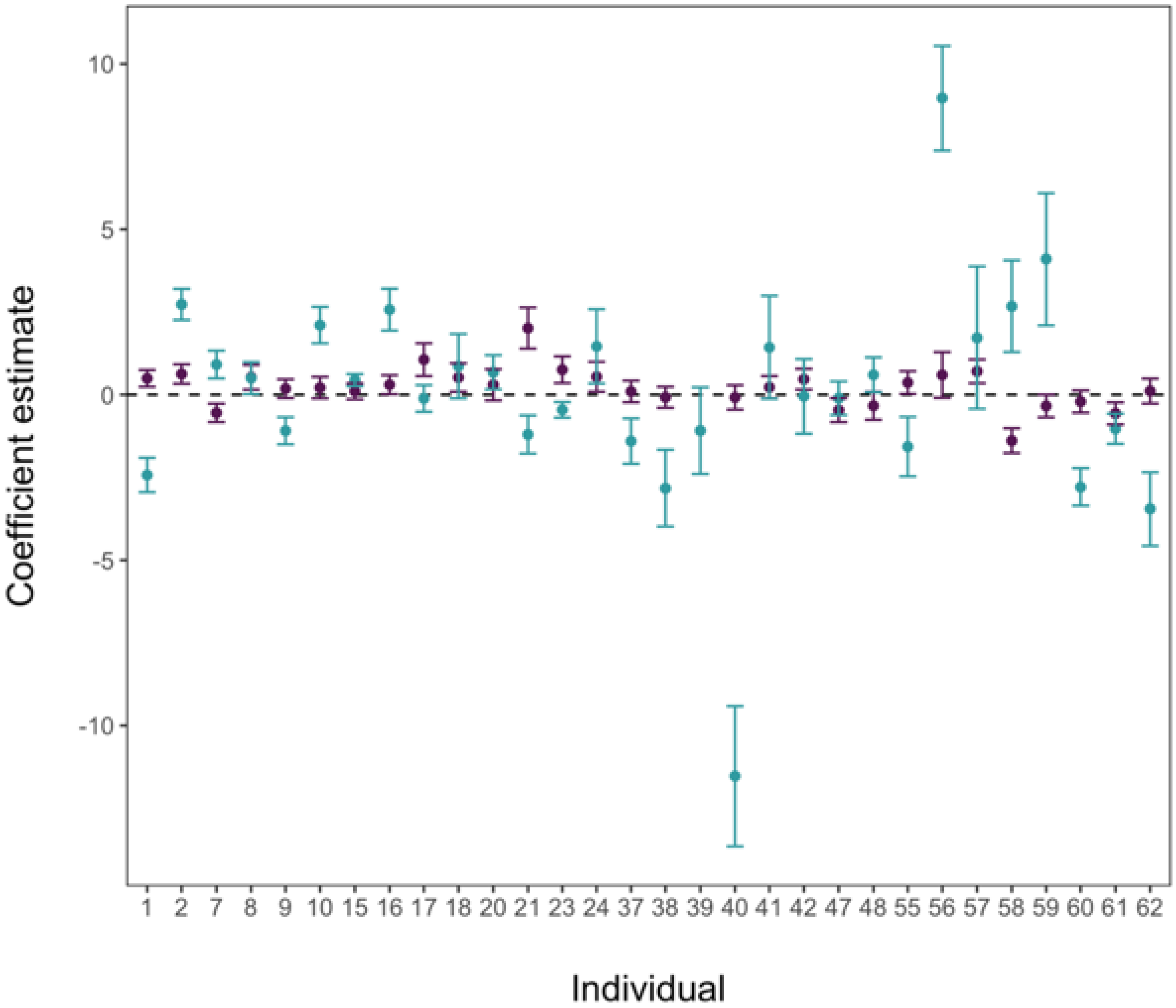

Figure S.2-1 Summary of model coefficients from individual models from the second block. Points represent the coefficient estimates (purple = mixed forest, seafoam = distance to road) and error bars represent the 95% confidence interval of the estimate. Error bars that do not cross the dashed line at zero are significant at $p < 0.05$.

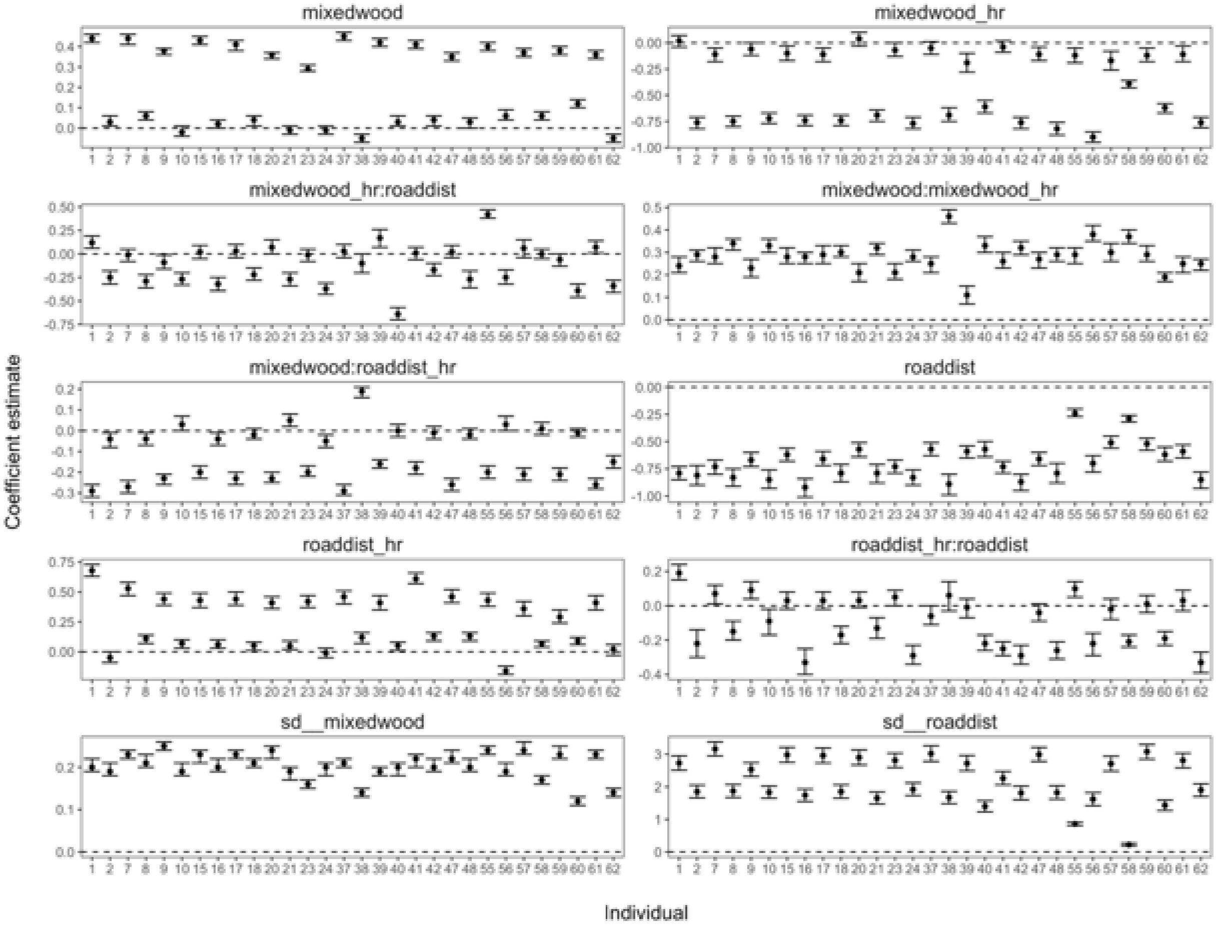

Figure S.2-2 Summary of individual mean fixed effect coefficients and variance of random effects from bootstrapped GFR models (hr = proportion of covariate within the home range of the individual). Points represent the coefficient estimates and error bars represent the 95% confidence interval of the estimate. Error bars that do not cross the dashed line at zero are significant at $p < 0.05$.

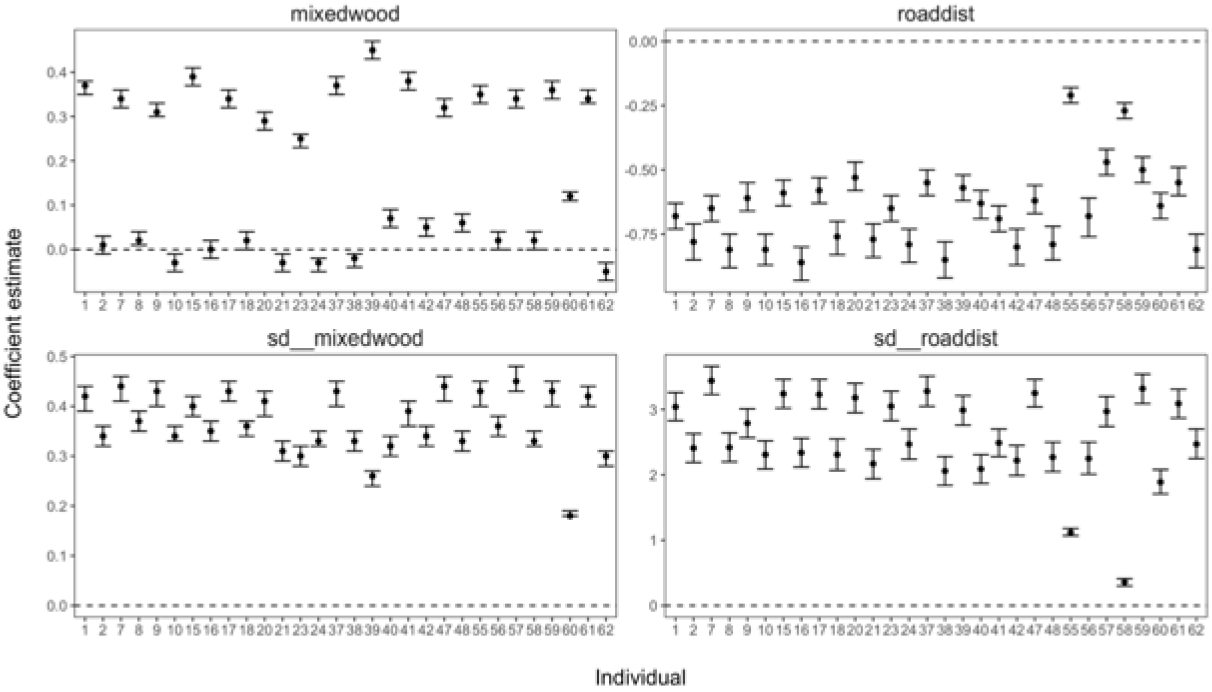

Figure S.2-3 Summary of individual mean fixed effect coefficients and variance of random effects from bootstrapped random effects models. Points represent the coefficient estimates and error bars represent the 95% confidence interval of the estimate. Error bars that do not cross the dashed line at zero are significant at $p < 0.05$.

S.3 Supplementary materials for Chapter 3

Proof-of-concept methods

Estimating parturition dates

We used global positioning system (GPS) locations of adult female elk to both characterize habitat selection and identify calving dates. In February 2019, 18 adult female elk were captured in southeast Manitoba, Canada (49.134, -96.557) from a population of approximately 150 individuals. Individuals were fit with GPS collars (Vertex Plus 830 g, VECTRONIC Aerospace GmbH, Berlin, Germany) that collected locations every 30 minutes during the calving season (May through July). We identified potential 2019 and 2020 calving sites by monitoring the mothers' movement patterns. After locating calves, we fit each with a very high frequency (VHF) radio collar (V6C 83 g, Lotek, Newmarket, Ontario, Canada) for monitoring calf survival. Both adult female and calf capture procedures were in accordance with approved animal care protocols (Memorial University of Newfoundland animal use protocol #19-01-EV).

We used location data from the adult female GPS collars to estimate unobserved calving events. Elk calves hide for 4-5 days following parturition and require approximately 16 days until they are mobile enough to escape predators (Geist 2002). This limited mobility causes elk mothers to reduce their own movement rates to remain close to the calf (Brook 2010). We used the frequency of return visits to the potential calf to estimate parturition date using a machine learning approach (Marchand et al. 2021). We used the *recurse* package (Bracis et al. 2018) to calculate the number of return visits by each elk to within a buffer of each of its location points between May 15 and July 20 in both 2019 and 2020. Unlike some other ungulate species, elk calves select new hiding spots away from the calving site shortly after parturition (Johnson et al. 2006), meaning mothers might make return visits to different locations. To account for distance in return location compared to the birth site, we used a 300 m radius buffer (Wallace and Krausman 1992) to calculate recursive movements to the calf rather than the 100 m radius buffer suggested by (Marchand et al. 2021).

We used elk movements surrounding 16 confirmed parturition events as training data to predict the remaining 11 unconfirmed events. We defined parturition as the period between the confirmed parturition date up to 5 d following parturition to account for the hiding phase. After down sampling the training data to balance the number of points within and outside the parturition period, we used a random forest classifier to predict the probability of each training data point belonging to the parturition period. We averaged the probability of parturition for each point falling within the known parturition period and used this as a threshold for detecting parturition periods in the testing data. Specifically, we located where average probabilities exceeded the known calving threshold within a 5-d rolling window in the testing data. After repeating this process 100 times, we selected the 5-d window of points with the highest probability of belonging to the parturition period. We set the estimated the parturition date as the first date within that period.

Hormone sampling

We were able to collect 181 fecal pellet samples to monitor glucocorticoid levels of 13 of 18 collared elk from May–August 2019 and 2020. We identified clusters of location data indicative of bedding, and after confirming bedding by visiting the locations within 24 h of the individual being present in the area, we collected any visible fecal material. Because fecal glucocorticoid metabolites (FGM) are the product of circulating glucocorticoids metabolized over a period of hours to days (Gormally and Romero 2020), elevated levels can indicate one or more responses to exogenous (e.g., predator encounters) or endogenous (e.g., calving) stressors during that time.

For many ungulate species (e.g., reindeer, *Rangifer tarandus* (Ashley et al. 2011); roe deer, *Capreoulus capreoulus* — Escribano-Avila et al. 2013) FGM levels remain elevated for approximately 20 h following stress responses. The validated metabolization period for the Roosevelt elk (*Cervus canadensis roosevelti*) is 22 h (Ashley et al. 2011), and 18 h in red deer (*Cervus elaphus*), a close relative of the North American elk (Huber et al. 2003). This makes FGM an integrated proxy for both baseline and stress-induced circulating glucocorticoids during the 18-22 h preceding defecation.

FGM recovery from samples is affected by moisture in the field and failure to promptly store samples after collection (Romero and Wingfield 2016). Thus, we avoided sampling after rain, collected samples within 24 hours of suspected defecation, and froze samples as soon as possible (< 8 hours) after collection (Sheriff et al. 2011).

We identified individuals by comparing DNA extracted from fecal samples to that from whole blood samples taken from individuals at the time of capture. However, like FGM concentration fecal DNA is susceptible to degradation from inclement weather and storage conditions, and only approximately 20% of extractions were successful. For those samples we could not identify using DNA (117 of 181 samples), we used supervised machine learning to assign suspected individuals to samples based on movement patterns and level of elk activity in the vicinity of the sample. The training model identified whether samples belonged to the suspected individual with 77% accuracy (Newediuk and Vander Wal 2021); see also for further details on DNA extraction and machine learning models). We used this accuracy as a threshold for correct identification, predicting the accurate identification of testing samples over 500 iterations. We assumed samples belonged to the suspected individual when the mean predicted accuracy of testing samples exceeded the threshold accuracy. When mean predicted accuracy was less than the threshold, we tested whether samples could have belonged to a different collared individual in the same area around the time of defecation. We identified candidate individuals as those with any location points within 20 m of the sample up to 2 d prior to the time of sample collection. We repeated the same machine learning procedure for these new individuals, replacing the original individual that did not meet the threshold for correct identification with the new suspected individual. As above, we assumed samples belonged to the new individual if the predicted accuracy across 500 iterations exceeded the threshold accuracy.

Habitat selection analysis

To test whether elk habitat selection responses to glucocorticoid levels depended on calving period, we used integrated step selection analysis (iSSA). Habitat selection analyses quantify the relative probability of selection for habitat characteristics within a logistic regression framework by comparing the distribution of habitat values at used locations to another sample of habitat values at available locations (see Box 3.1). Step selection analyses draw available locations from empirical distributions of observed step length and turn angle movement parameters, thereby constraining available locations to the step level. However, habitat selection is linked to the movement process; if movement is unaccounted for in available step samples model coefficients may be biased. To avoid this bias, iSSA steps are sampled from pre-specified distributions of turn angles and step lengths parameterized on observed steps (Avgar et al. 2016b). Constraining available steps in this way simultaneously estimates movement and habitat selection coefficients (Fieberg et al. 2021), making it possible to test the effect of temporally dynamic variables — such as changes in glucocorticoid levels — on habitat selection.

We fit population-level iSSA models to test the effect of glucocorticoid levels on selection of safer cover habitat (Agriculture and Agri-Food Canada Annual Crop Inventory

2019-2020) depending on calf vulnerability. To limit our selection inferences to movement bouts associated with known FGM levels, we subsampled GPS data to the 20–h preceding each sample (i.e., within the metabolization period). We sampled available steps from gamma distributions (turn angles) and von Mises distributions (step lengths) parameterized with movement characteristics of used steps (Avgar et al. 2016a). We determined how many available steps were required to estimate selection coefficients by repeatedly fitting the model using ratios of between 1 and 1,000 available: used steps. We included three fixed effect predictors of selection: distance to cover habitat (i.e., safer habitat) at the end of each step, an interaction between distance to cover and FGM at the start of the movement bout, and a three-way interaction between the distance to cover-FGM interaction and a binary variable describing whether the movement bout occurred within the 16-d window of lower calf mobility (post-calving) or outside of that window (pre-calving). We included movement bouts up to 3 d before the calving date to account for uncertainty in its estimate. We also included in the model the natural log of the step length to account for the movement process. Finally, to account for correlation between samples from individuals (Hebblewhite and Merrill 2007), differences in sample size among individuals, and individual differences in habitat selection (Gillies et al. 2006), we included random intercepts and slopes for both distance to cover and the interaction between distance to cover and FGM. However, random effects models are challenging to fit within the conditional logistic regression framework typically used in step selection analysis because of the large number of step-specific strata. To deal with this challenge, we reformulated the conditional logistic model as a Poisson model with large, stratum-specific fixed intercepts (Muff et al. 2020).

We used relative selection strength (RSS) a measure of habitat selection effect size. We calculated RSS across the 0.2–0.8 quantile range of population-level FGM levels (approximately

1,200–2,600 μg•g^{-1}). RSS quantifies the ratio of the relative strength of selection for one location compared to selection at another location. When a single habitat characteristic varies between locations, RSS quantifies the change in selection for that characteristic (Avgar et al. 2017). In our case, we quantified the RSS for distance to cover habitat at the 0.2 quantile FGM versus a range of FGM values over the 0.2–0.8 quantile range. The difference in selection strength across this range predicts the change in effect size for selecting distances further from cover habitat as FGM increases. We compared the difference between these effect sizes by calving period.

We validated our models with used-habitat calibration (UHC) plots (Fieberg et al. 2018). UHC plots measure model calibration, or the agreement between distributions of habitat values at observed locations and distributions of habitat values at locations predicted as used by the model. UHC plots also compare used distributions to the distributions of habitat values at available locations to determine whether model covariates are important for predicting selection. Unlike other methods, UHC is appropriate for validating stratified habitat selection analyses like iSSA (Fieberg et al. 2018).

Proof-of-concept results

We used 68 fecal glucocorticoid metabolite samples from between May 14 and August 16 in 2019 and 2020, representative of 13 sampled individuals. Individuals each had between one and 16 fecal samples (median = 4) and between 14 and 554 location points (median = 153) across the pre- and post-parturition periods (Fig. S.3-1). We used a ratio of 40 available: used points for all models as our sub-analysis suggested model coefficient estimates and standard errors remained relatively consistent from 30 to 1,000 available: used points (Fig. S.3-2). Though individual sample sizes and location points per individual were few, small samples are still sufficient for RSF inference when selection strength is strong and landscape heterogeneity is low (Street et al. 2021).

Selection for distance from cover habitat depended on glucocorticoid levels and changed over the calving season. Elk exhibited a slight avoidance of locations further from cover habitat ($e^{ß} = 0.93$, 95% CI 0.85, 1.00). They were also 50% more likely to select locations further from cover for each unit increase in glucocorticoid levels ($e^{ß} = 1.49$ 95% CI 1.12, 1.98). Outside of the 16-d parturition window when calves were most vulnerable but nutrition requirements were high, the effect of glucocorticoids on selection of locations further from cover was even stronger ($e^{ß} = 0.72$, 95% CI 0.54, 0.97). Our model validation supported these inferences as model coefficients discriminated used from available locations. The model was relatively well calibrated, with observed habitat use close to that predicted by models, and differences in distribution of used and available habitat values (Fig. S.3-3).

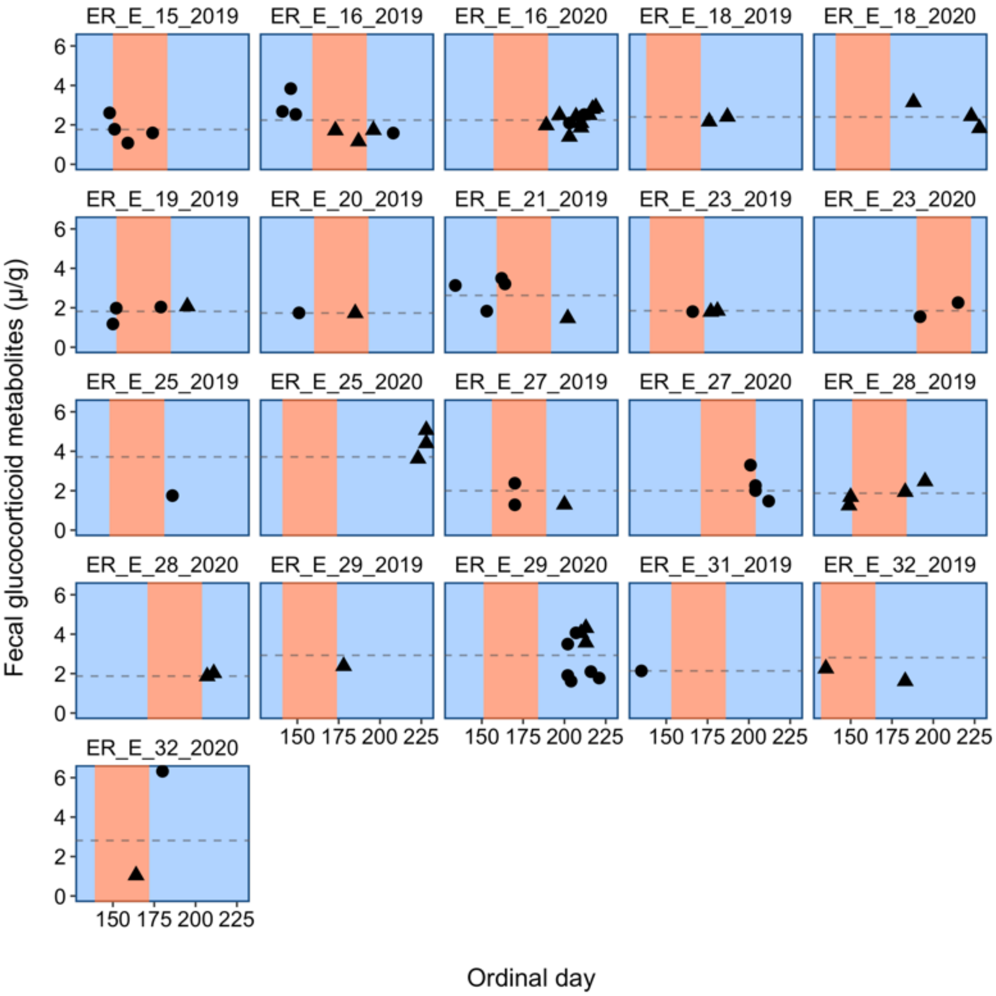

Figure S.3-1: Collection dates and glucocorticoid metabolite levels from 68 fecal samples from 13 individual elk over two years. Each panel represents a single elk, with blue indicating the individual's pre-parturition period, and red indicating the post-parturition period (i.e., within 30 d of calving). Circles denote samples identified as belonging to individuals by matching DNA, and triangles denote samples identified as belonging to individuals based on machine learning. Horizontal dashed lines show the median fecal glucocorticoid metabolite level for individuals collected across both calving seasons in 2019 and 2020.

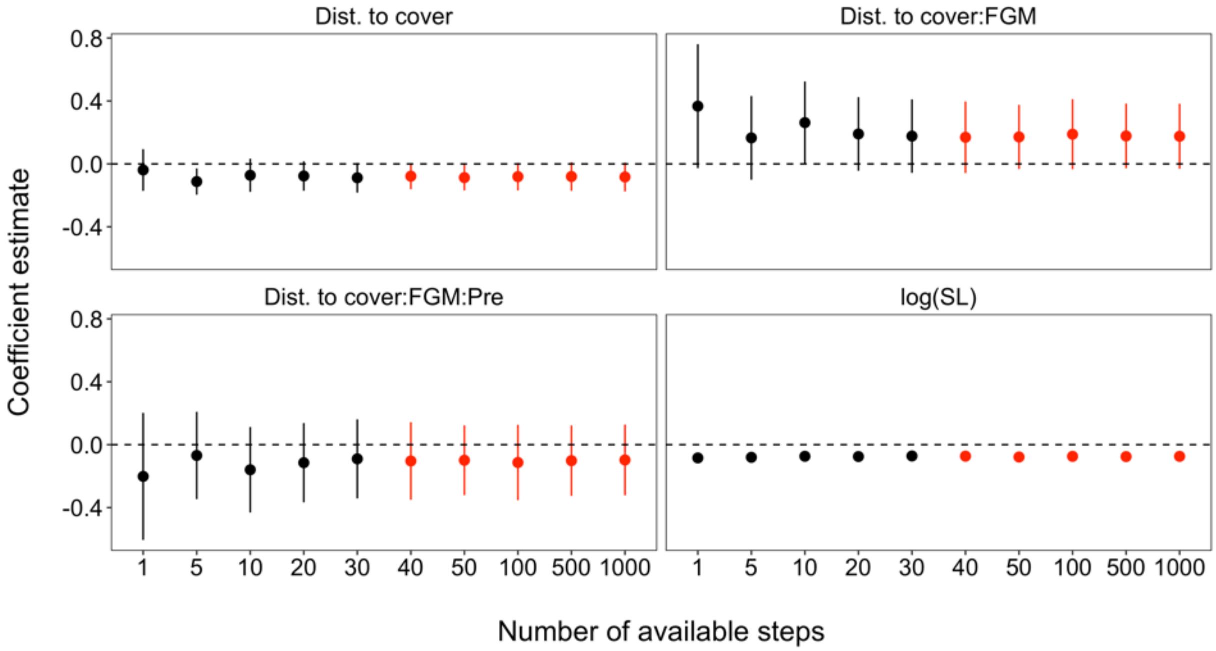

Figure S.3-2: Model coefficient estimates (points) and standard errors (vertical lines) from sub-analysis of model across increasing ratios of available: used points. Black points and lines indicate available: used ratios below 40, and red points and indicate ratios above. Coefficients and standard errors remain relatively consistent at available: used ratio equal to 30. SL = step length, pre = pre-parturition period (reference category relative to post-parturition period), and FGM = fecal glucocorticoid metabolite levels.

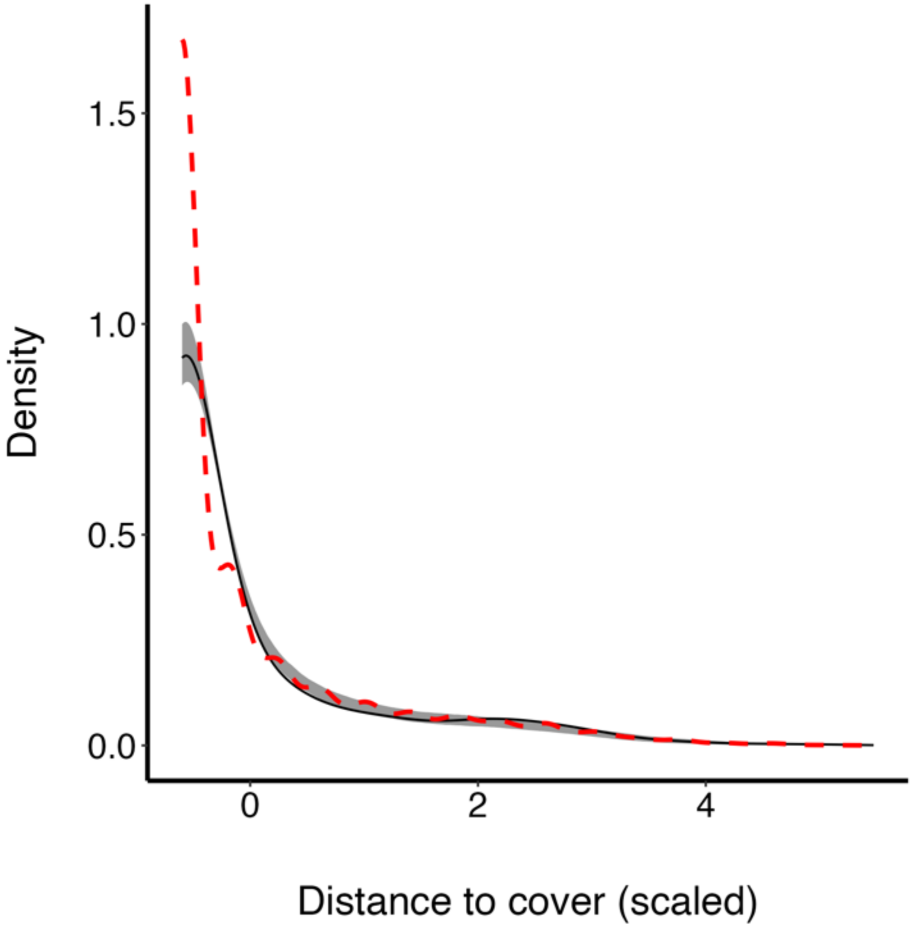

Figure S.3-4: Used-habitat calibration plot comparing distributions of habitat values at used locations (black solid line) to habitat values at available locations (red dashed line) and 95% confidence intervals of used locations predicted by the cropland model (grey ribbon). Predicted values agree with observed values — i.e., the model is well-calibrated — when grey ribbons overlap with black lines. Differences between black-solid and red-dashed lines indicate elk are likely to be found at locations with dissimilar characteristics to those available.

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S.4 Supplementary materials for Chapter 4

Methods for deciding on the buffer radius of the cluster tightness variable

We wanted to determine which movement track characteristics were most important for distinguishing positively and negatively identified samples. In a similar cluster-based method, Knopff et al. (2009) identified kill sites using the number of cougar (*Puma concolor*) location points within a buffer of the geometric centre of a cluster. Similarly, we used the number of location points within a buffer of some radius from the cluster centre (hereafter “cluster tightness”) as a predictor in our models. However, we also wanted to determine the buffer radius that maximized the difference in number of location points between positively and negatively identified samples. Thus, we created a series of buffers with radii ranging from 1 to 100 m by increments of 1 m. We first determined the average number of location points within each buffer that were associated with either positively or negatively identified samples (Figure S.4-1 A). We then selected the buffer radius for the cluster tightness predictor that maximized the difference in number of location points between the positively identified samples. We determined this optimum radius to be 32 m (Figure S.4-1 B).

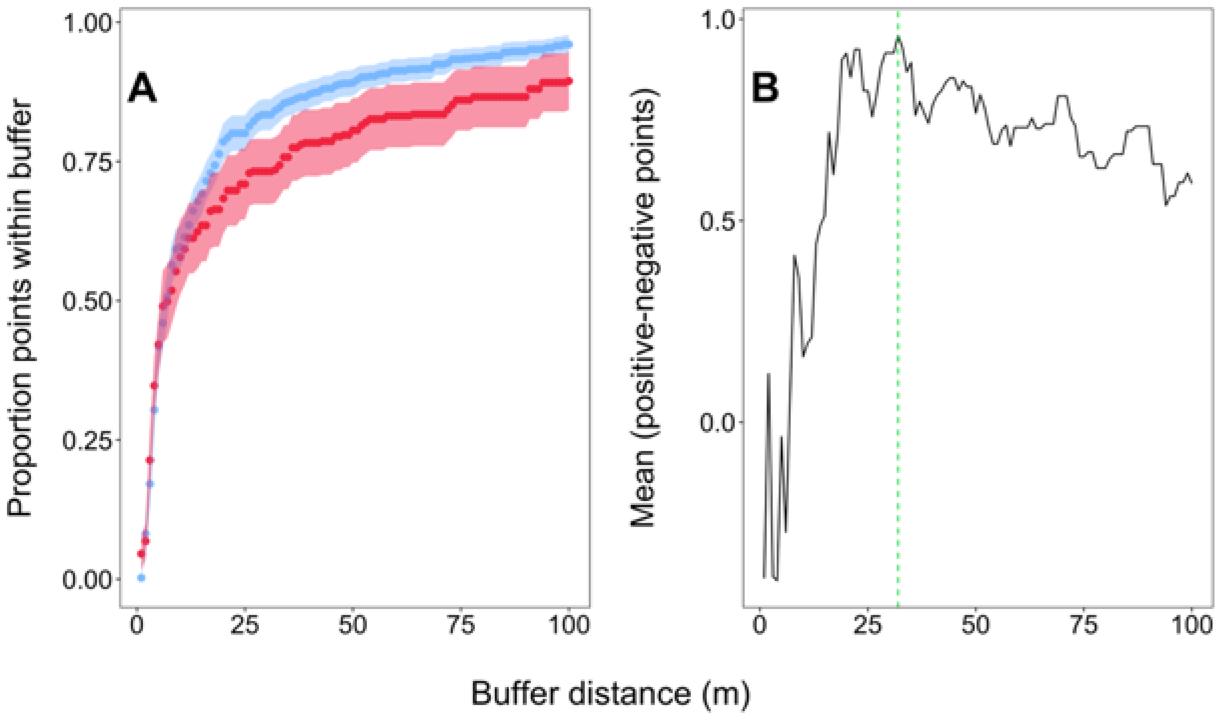

Figure S.4-1: Comparison of cluster tightness between positively and negatively identified samples, where tighter clusters have more points falling within a smaller-radius buffer surrounding the cluster centre. In A, the proportion of points falling within a buffer of each radius from 1 to 100 m is shown for positively identified (blue) and negatively identified (red) samples. In B, the mean difference in the number of points within the buffer is shown between positively and negatively identified samples. The green dashed line indicates the largest mean difference at buffer radius of 32 m.

R code for specifying tuning parameters in machine learning models

```
# K nearest neighbour: K (number of nearest neighbours upon which
# classification is based) varies from 1 to the number of negative
# samples in the training set minus 2
knn_tp <- data.frame(.k = seq(1,nrow(dsample_data[correct==0])-2,1))

# Naive Bayes: Model fit with and without kernel estimator
nb_tp <- data.frame(.usekernel = c(TRUE, FALSE), .fL=0, .adjust=1)

# Linear SVM: C (number of observations allowed to be in violation
# of the hyperplane margin) varies gradually from 0.1 up to 2, then
# 10, and all points in training data
svmLinear_tp <- data.frame(.C = c(seq(0.1,2,0.1), 10, nrow(dsample_data)))

# Polynomial SVM: Polynomial degree varies up to 3; C (number of
# observations allowed to be in violation of the hyperplane margin)
# varies gradually from 0.1 up to 2, then 10, and all points in training
# data; scale fixed at 0.1
svmPoly_tp <- data.frame(.degree = c(1,2,3), .C = c(seq(0.1,2,0.1),
nrow(dsample_data)), .scale=0.1)

# Radial SVM: C (number of observations allowed to be in violation
# of the hyperplane margin) varies gradually from 0.1 up to 2, then
# 10, and all points in training data; sigma fixed at 1.438348
svmRadial_tp <- data.frame(.sigma = 1.438348, .C = c(seq(0.1,2,0.1),
nrow(dsample_data)))

# Classification and regression trees: CP (tree complexity parameter
# varies from 0 up to 0.3
rpart_tp <- data.frame(.cp=seq(0,0.3,0.01))
```

Comparison of performance metrics from models performed on subsets of data

Table S.4-1: Accuracy comparison of hair and fecal pellet models to full dataset model for distinguishing positively from negatively identified samples. Models include all combinations of predictor variables for distinguishing positively from negatively identified samples according to 10-fold cross validation. The most accurate combination of predictor variables using remotely sensed and site-level predictors, and remotely sensed predictors only, are bolded. Predictor variables include *buffer* = cluster tightness; *nearest*= distance from sample to nearest cluster centre; *nn_dist* = average nearest neighbour distance among points in cluster; *bed* = number of beds within 20 m of sample. Classifiers include naïve Bayes (NB), linear discriminant analysis (LDA), and radial support vector machines (SVM).

	Full dataset		Fecal Pellets		Hair	
Predictor variables	Classifier	Percent accuracy (95% CI)	Classifier	Percent accuracy (95% CI)	Classifier	Percent accuracy (95% CI)
Remotely sensed and site-level						
buffer + bed	**NB**	**76.6 (72.8, 80.3)**	**NB**	**77.6 (74.2, 81.0)**	**NB**	**77.3 (74.3, 80.4)**
bed	LDA	74.7 (71.5, 77.8)	LDA	74.6 (71.8, 77.3)	NB	75.2 (71.2, 78.4)
buffer + nn_dist + bed	NB	74.6 (71.1, 78.0)	SVM	74.6 (71.7, 77.5)	NB	73.9 (70.6, 77.3)
buffer + bed +nearest	NB	74.3 (71.7, 76.9)	NB	73.0 (70.0, 76.2)	NB	74.2 (70.6, 77.7)
bed + nearest	LDA	73.8 (70.8, 76.8)	NB	72.4 (69.1, 75.6)	LDA	71.3 (57.4, 75.2)
nn_dist + bed	LDA	73.2 (69.6, 76.8)	NB	75.1 (71.8, 78.3)	SVM	76.5 (72.7, 80.3)
buffer + nn_dist + bed + nearest	LDA	71.5 (68.7, 74.3)	NB	73.0 (69.9, 76.2)	NB	71.0 (67.4, 74.6)

nn_dist + bed + nearest	SVM	67.7 (64.0, 71.3)	LDA	69.9 (66.3, 73.6)	LDA	72.8 (69.2, 76.5)
Remotely sensed only						
buffer	**NB**	**70.5 (66.7, 74.3)**	**NB**	**69.4 (66.1, 72.8)**	**NB**	**71.5 (68.3, 74.7)**
buffer + nearest	NB	68.3 (65.3, 71.3)	NB	67.6 (63.9, 71.2)	NB	67.2 (63.8, 70.5)
buffer + nn_dist	NB	67.5 (63.7, 71.2)	NB	66.9 (63.1, 70.8)	LDA	66.2 (62.2, 70.2)
buffer + nn_dist + nearest	NB	65.8 (62.0, 69.7)	NB	66.3 (62.4, 70.2)	NB	64.0 (60.2, 67.9)
nearest	NB	60.9 (57.0, 64.8)	NB	59.7 (55.7, 63.7)	NB	57.2 (52.6, 61.8)
nn_dist	NB	60.3 (55.8, 64.8)	NB	61.7 (57.4, 66.0)	NB	64.1 (60.4, 67.7)
nn_dist + nearest	NB	59.7 (56.7, 62.6)	NB	58.1 (53.6, 62.7)	LDA	57.3 (53.5, 61.1)

Table S.4-2: Accuracy comparison between 1–hr relocation frequency data and 30–min relocation frequency data for distinguishing positively from negatively identified samples. Models include all combinations of predictor variables for distinguishing positively from negatively identified samples according to 10-fold cross validation. The most accurate combination of predictor variables using remotely sensed and site-level predictors, and remotely sensed predictors only, are bolded. Predictor variables include *buffer* = cluster tightness; *nearest*= distance from sample to nearest cluster centre; *nn_dist* = average nearest neighbour distance among points in cluster; *bed* = number of beds within 20 m of sample. Classifiers include naïve Bayes (NB), linear discriminant analysis (LDA), and radial support vector machines (SVM).

	30–min relocations		1–hr relocations	
Predictor variables	Classifier	Percent accuracy (95% CI)	Classifier	Percent accuracy (95% CI)
Remotely sensed and site-level				
buffer + bed	**NB**	**76.6 (72.8, 80.3)**	NB	75.6 (72.5, 78.8)
bed	LDA	74.7 (71.5, 77.8)	NB	74.2 (70.9, 77.5)
buffer + nn_dist + bed	NB	74.6 (71.1, 78.0)	NB	72.3 (68.8, 75.8)
buffer + bed +nearest	NB	74.3 (71.7, 76.9)	NB	72.1 (68.2, 76.0)
bed + nearest	LDA	73.8 (70.8, 76.8)	NB	73.3 (70.2, 76.4)
nn_dist + bed	LDA	73.2 (69.6, 76.8)	**SVM**	**(76.9 (73.8, 80.0)**
buffer + nn_dist + bed + nearest	LDA	71.5 (68.7, 74.3)	NB	69.1 (65.4, 72.8)

nn_dist + bed + nearest	SVM	67.7 (64.0, 71.3)	NB	71.7 (68.1, 75.3)
Remotely sensed only				
buffer	**NB**	**70.5 (66.7, 74.3)**	NB	60.1 (56.2, 63.8)
buffer + nearest	NB	68.3 (65.3, 71.3)	NB	56.1 (52.5, 59.8)
buffer + nn_dist	NB	67.5 (63.7, 71.2)	NB	59.9 (56.0, 63.8)
buffer + nn_dist + nearest	NB	65.8 (62.0, 69.7)	NB	57.2 (53.0, 61.3)
nearest	NB	60.9 (57.0, 64.8)	NB	59.6 (55.5, 63.7)
nn_dist	NB	60.3 (55.8, 64.8)	**NB**	**61.5 (57.1, 65.8)**
nn_dist + nearest	NB	59.7 (56.7, 62.6)	NB	57.3 (52.6, 62.0)

Performance metrics of all models using both 10-fold and blocked cross validation

Table S.4-3: Model accuracy output from 10-fold cross validation of models for distinguishing positively from negatively identified samples. Predictor variables include *n_within_dist* = cluster tightness; *nearest_pt*= distance from sample to nearest cluster centre; *nn_avg* = average nearest neighbour distance among points in cluster; *beds_in_20_m* = number of beds within 20 m of sample. Classifiers include naïve Bayes (nb), linear discriminant analysis (lda), radial support vector machines (svmRadial), K-nearest neighbour (knn), and classification and regression trees (rpart).

Classifier	Model predictor variable set	Accuracy	Lower 95% CI	Upper 95% CI
nb	n_within_dist.beds_in_20_m	0.76589744	0.72842932	0.80336556
lda	beds_in_20_m	0.74666667	0.71495023	0.7783831
nb	n_within_dist.beds_in_20_m.nn_avg	0.74602564	0.71196298	0.7800883
svmRadial	n_within_dist.beds_in_20_m	0.745	0.71154542	0.77845458
nb	n_within_dist.beds_in_20_m.dist_nearest_pt	0.74294872	0.71669385	0.76920359
svmRadial	beds_in_20_m.nn_avg	0.74192308	0.70326067	0.78058548
nb	beds_in_20_m	0.73935897	0.70462255	0.7740954
lda	beds_in_20_m.dist_nearest_pt	0.73794872	0.70758696	0.76831048
lda	beds_in_20_m.nn_avg	0.73217949	0.69605252	0.76830645
svmRadial	n_within_dist.beds_in_20_m.nn_avg	0.73128205	0.69430623	0.76825787
svmRadial	beds_in_20_m	0.72820513	0.69468184	0.76172841
lda	beds_in_20_m.dist_nearest_pt.nn_avg	0.72564103	0.6974644	0.75381765
knn	beds_in_20_m	0.725	0.69082525	0.75917475
knn	n_within_dist.beds_in_20_m	0.72166667	0.68599052	0.75734281
lda	n_within_dist.beds_in_20_m	0.72153846	0.6865147	0.75656222

nb	beds_in_20_m.nn_avg	0.71653846	0.67871938	0.75435755
nb	beds_in_20_m.dist_nearest_pt	0.71538462	0.68851664	0.74225259
lda	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.71474359	0.68695784	0.74252934
lda	n_within_dist.beds_in_20_m.dist_nearest_pt	0.71320513	0.68563924	0.74077102
nb	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.71294872	0.67879841	0.74709903
nb	beds_in_20_m.dist_nearest_pt.nn_avg	0.71076923	0.68127945	0.74025901
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt	0.70961538	0.67952303	0.73970774
nb	n_within_dist	0.70512821	0.66708708	0.74316933
lda	n_within_dist.beds_in_20_m.nn_avg	0.7024359	0.6681147	0.73675709
rpart	beds_in_20_m	0.69461538	0.65929559	0.72993518
rpart	n_within_dist.beds_in_20_m	0.68512821	0.65471556	0.71554086
nb	n_within_dist.dist_nearest_pt	0.68294872	0.65286288	0.71303456
rpart	beds_in_20_m.dist_nearest_pt	0.67692308	0.63718703	0.71665912
svmRadial	beds_in_20_m.dist_nearest_pt.nn_avg	0.67666667	0.64018321	0.71315012
nb	n_within_dist.nn_avg	0.67474359	0.63736229	0.71212489
rpart	n_within_dist.beds_in_20_m.nn_avg	0.67307692	0.63511889	0.71103496
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt	0.67166667	0.64162566	0.70170767
rpart	n_within_dist	0.67089744	0.63211722	0.70967765
svmRadial	beds_in_20_m.dist_nearest_pt	0.66871795	0.63325492	0.70418098
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.66705128	0.63399364	0.70010892
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.66076923	0.62266069	0.69887777
nb	n_within_dist.dist_nearest_pt.nn_avg	0.65833333	0.61972857	0.6969381
rpart	beds_in_20_m.nn_avg	0.65384615	0.61912942	0.68856289
lda	n_within_dist.dist_nearest_pt.nn_avg	0.65371795	0.62001163	0.68742426
lda	n_within_dist.nn_avg	0.65307692	0.61383421	0.69231963
rpart	beds_in_20_m.dist_nearest_pt.nn_avg	0.64615385	0.6024267	0.68988099
lda	n_within_dist.dist_nearest_pt	0.63807692	0.59885463	0.67729922
knn	n_within_dist	0.63192308	0.58885499	0.67499116

rpart	n_within_dist.dist_nearest_pt.nn_avg	0.62641026	0.58943931	0.6633812
rpart	n_within_dist.nn_avg	0.62320513	0.57955867	0.66685158
knn	n_within_dist.beds_in_20_m.dist_nearest_pt	0.62153846	0.57986656	0.66321036
lda	n_within_dist	0.61435897	0.57261385	0.6561041
svmRadial	n_within_dist	0.61410256	0.57253433	0.6556708
nb	dist_nearest_pt	0.60910256	0.5699538	0.64825133
nb	nn_avg	0.60346154	0.55852229	0.64840078
knn	beds_in_20_m.dist_nearest_pt	0.60064103	0.5696791	0.63160295
nb	dist_nearest_pt.nn_avg	0.59653846	0.56706229	0.62601463
lda	nn_avg	0.59615385	0.55179037	0.64051733
svmRadial	n_within_dist.dist_nearest_pt	0.58782051	0.55090501	0.62473601
knn	n_within_dist.dist_nearest_pt	0.58474359	0.54356579	0.62592139
svmRadial	n_within_dist.nn_avg	0.58435897	0.54184307	0.62687488
lda	dist_nearest_pt.nn_avg	0.58153846	0.55026844	0.61280849
rpart	n_within_dist.dist_nearest_pt	0.58012821	0.54433817	0.61591824
svmRadial	n_within_dist.dist_nearest_pt.nn_avg	0.575	0.53432288	0.61567712
svmRadial	dist_nearest_pt	0.56512821	0.52922474	0.60103167
svmRadial	dist_nearest_pt.nn_avg	0.56115385	0.52148887	0.60081882
lda	dist_nearest_pt	0.55474359	0.51242995	0.59705723
rpart	dist_nearest_pt	0.54435897	0.51021706	0.57850089
knn	dist_nearest_pt	0.52551282	0.48956966	0.56145598
knn	beds_in_20_m.dist_nearest_pt.nn_avg	0.51153846	0.48013692	0.54294
knn	n_within_dist.nn_avg	0.50820513	0.47234893	0.54406133
knn	dist_nearest_pt.nn_avg	0.50615385	0.47013106	0.54217663
knn	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.50512821	0.46910356	0.54115285
knn	n_within_dist.dist_nearest_pt.nn_avg	0.50153846	0.46629208	0.53678484
rpart	dist_nearest_pt.nn_avg	0.49897436	0.46113301	0.53681571
svmRadial	nn_avg	0.49820513	0.45205767	0.54435259

knn	beds_in_20_m.nn_avg	0.49307692	0.45040147	0.53575238
knn	nn_avg	0.4824359	0.43711859	0.52775321
rpart	nn_avg	0.48064103	0.43614487	0.52513718
knn	n_within_dist.beds_in_20_m.nn_avg	0.47807692	0.44402902	0.51212482

Table S.4-4: Model sensitivity output from 10-fold cross validation of models for distinguishing positively from negatively identified samples. Predictor variables include *n_within_dist* = cluster tightness; *nearest_pt*= distance from sample to nearest cluster centre; *nn_avg* = average nearest neighbour distance among points in cluster; *beds_in_20_m* = number of beds within 20 m of sample. Classifiers include naïve Bayes (nb), linear discriminant analysis (lda), and radial support vector machines (svmRadial), K-nearest neighbour (knn), and classification and regression trees (rpart).

Classifier	Model predictor variable set	Sensitivity	Lower 95% CI	Upper 95% CI
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt	0.71333819	0.65440474	0.77227164
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.70166667	0.63144717	0.77188616
svmRadial	n_within_dist.beds_in_20_m	0.66525753	0.59430758	0.73620748
svmRadial	n_within_dist.dist_nearest_pt.nn_avg	0.66015873	0.57402835	0.74628911
knn	n_within_dist.beds_in_20_m.dist_nearest_pt	0.65381438	0.58567795	0.72195081
svmRadial	n_within_dist.dist_nearest_pt	0.64938095	0.57723027	0.72153164
knn	beds_in_20_m.dist_nearest_pt	0.64460641	0.57463004	0.71458279
knn	n_within_dist.beds_in_20_m	0.64280855	0.56382801	0.7217891
nb	n_within_dist.beds_in_20_m	0.64280855	0.56330058	0.72231652
lda	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.63065079	0.54330159	0.718
lda	n_within_dist.beds_in_20_m	0.62696793	0.55422686	0.699709
svmRadial	beds_in_20_m.dist_nearest_pt.nn_avg	0.61119048	0.52453435	0.6978466
svmRadial	n_within_dist.beds_in_20_m.nn_avg	0.61038095	0.52439328	0.69636863
nb	n_within_dist.beds_in_20_m.dist_nearest_pt	0.60940233	0.54438754	0.67441712
lda	n_within_dist.dist_nearest_pt.nn_avg	0.60555556	0.52220831	0.6889028
lda	n_within_dist.beds_in_20_m.nn_avg	0.60347619	0.52137542	0.68557696
rpart	n_within_dist.dist_nearest_pt	0.60128571	0.51599393	0.6865775
lda	beds_in_20_m.dist_nearest_pt.nn_avg	0.59838095	0.52337062	0.67339129

lda	beds_in_20_m.nn_avg	0.59792857	0.50915533	0.68670181
svmRadial	beds_in_20_m.nn_avg	0.5972619	0.51363909	0.68088472
rpart	n_within_dist.beds_in_20_m	0.59504373	0.51130569	0.67878178
lda	n_within_dist.beds_in_20_m.dist_nearest_pt	0.59492225	0.53052279	0.65932172
svmRadial	beds_in_20_m.dist_nearest_pt	0.58372206	0.50307382	0.6643703
nb	beds_in_20_m.nn_avg	0.58209524	0.49284291	0.67134756
rpart	beds_in_20_m.dist_nearest_pt.nn_avg	0.57304762	0.48383811	0.66225713
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt	0.57184159	0.49036728	0.65331591
lda	n_within_dist	0.56972789	0.48520925	0.65424654
rpart	beds_in_20_m.dist_nearest_pt	0.56841594	0.49812568	0.6387062
knn	n_within_dist.dist_nearest_pt	0.55866667	0.47627597	0.64105736
lda	n_within_dist.nn_avg	0.55694849	0.4734856	0.64041139
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.55465079	0.46168316	0.64761843
nb	n_within_dist.beds_in_20_m.nn_avg	0.55385714	0.47122189	0.63649239
nb	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.5535873	0.47372915	0.63344545
rpart	dist_nearest_pt.nn_avg	0.54966667	0.46569365	0.63363968
rpart	dist_nearest_pt	0.5462619	0.45747682	0.63504699
rpart	beds_in_20_m.nn_avg	0.53559524	0.45159121	0.61959927
rpart	n_within_dist.dist_nearest_pt.nn_avg	0.53131746	0.43601218	0.62662274
lda	n_within_dist.dist_nearest_pt	0.52852381	0.45193864	0.60510898
lda	beds_in_20_m.dist_nearest_pt	0.52283771	0.45047228	0.59520314
rpart	n_within_dist.beds_in_20_m.nn_avg	0.52085714	0.44229432	0.59941996
rpart	nn_avg	0.52028571	0.43175698	0.60881445
svmRadial	n_within_dist.nn_avg	0.5196793	0.43705999	0.60229861
knn	beds_in_20_m	0.51257143	0.4333372	0.59180566
rpart	beds_in_20_m	0.50809524	0.43058762	0.58560286
nb	beds_in_20_m.dist_nearest_pt	0.49868805	0.42712365	0.57025244
svmRadial	beds_in_20_m	0.49809524	0.42183067	0.57435981

nb	beds_in_20_m.dist_nearest_pt.nn_avg	0.49328571	0.41174536	0.57482607
svmRadial	n_within_dist	0.49314869	0.40725131	0.57904606
svmRadial	dist_nearest_pt.nn_avg	0.48790476	0.41559938	0.56021014
rpart	n_within_dist.nn_avg	0.48566569	0.39473517	0.57659622
nb	beds_in_20_m	0.47957143	0.40370042	0.55544244
knn	n_within_dist	0.46987366	0.39444904	0.54529829
lda	beds_in_20_m	0.46957143	0.39396363	0.54517922
knn	dist_nearest_pt	0.46302381	0.39675532	0.5292923
knn	nn_avg	0.44338095	0.36284902	0.52391288
knn	beds_in_20_m.dist_nearest_pt.nn_avg	0.44104762	0.3550703	0.52702493
knn	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.40147619	0.31874472	0.48420766
rpart	n_within_dist	0.39961127	0.31808102	0.48114153
knn	n_within_dist.nn_avg	0.39888241	0.32372033	0.47404449
nb	n_within_dist.dist_nearest_pt	0.39461905	0.32349639	0.4657417
lda	dist_nearest_pt	0.39328571	0.31337369	0.47319774
knn	dist_nearest_pt.nn_avg	0.38885714	0.31270251	0.46501177
knn	n_within_dist.dist_nearest_pt.nn_avg	0.38489683	0.30013711	0.46965654
knn	beds_in_20_m.nn_avg	0.37888095	0.30031727	0.45744464
nb	n_within_dist.dist_nearest_pt.nn_avg	0.37860317	0.29211537	0.46509098
knn	n_within_dist.beds_in_20_m.nn_avg	0.3677619	0.284214	0.45130981
nb	n_within_dist	0.35726433	0.2893809	0.42514777
nb	n_within_dist.nn_avg	0.35466472	0.28228211	0.42704734
lda	dist_nearest_pt.nn_avg	0.33366667	0.26484729	0.40248605
lda	nn_avg	0.32585714	0.24748436	0.40422993
svmRadial	nn_avg	0.31271429	0.23617461	0.38925396
svmRadial	dist_nearest_pt	0.29554762	0.22256772	0.36852752
nb	dist_nearest_pt	0.28288095	0.19735729	0.36840462
nb	nn_avg	0.26971429	0.19539043	0.34403815

nb	dist_nearest_pt.nn_avg	0.19642857	0.14044981	0.25240734

Table S.4-5: Model specificity output from 10-fold cross validation of models for distinguishing positively from negatively identified samples. Predictor variables include *n_within_dist* = cluster tightness; *nearest_pt*= distance from sample to nearest cluster centre; *nn_avg* = average nearest neighbour distance among points in cluster; *beds_in_20_m* = number of beds within 20 m of sample. Classifiers include naïve Bayes (nb), linear discriminant analysis (lda), radial support vector machines (svmRadial), K-nearest neighbour (knn), and classification and regression trees (rpart).

Classifier	Model predictor variable set	Specificity	Lower 95% CI	Upper 95% CI
lda	beds_in_20_m	0.86391991	0.83221024	0.89562959
nb	beds_in_20_m	0.84810101	0.79931236	0.89688966
nb	n_within_dist	0.84719625	0.80328733	0.89110517
nb	n_within_dist.beds_in_20_m	0.82573238	0.78332259	0.86814217
svmRadial	beds_in_20_m	0.82206926	0.76970114	0.87443739
nb	n_within_dist.beds_in_20_m.nn_avg	0.8201176	0.78338809	0.85684712
svmRadial	beds_in_20_m.nn_avg	0.81780087	0.77571937	0.85988237
knn	beds_in_20_m	0.81521212	0.76468996	0.86573428
lda	beds_in_20_m.dist_nearest_pt	0.81513276	0.77281439	0.85745113
nb	n_within_dist.nn_avg	0.8129697	0.76650451	0.85943488
nb	n_within_dist.dist_nearest_pt	0.81248846	0.77658865	0.84838826
nb	n_within_dist.beds_in_20_m.dist_nearest_pt	0.80451804	0.77413043	0.83490564
nb	beds_in_20_m.dist_nearest_pt.nn_avg	0.79991919	0.76626222	0.83357617
nb	beds_in_20_m.dist_nearest_pt	0.79697475	0.75759479	0.83635471
lda	beds_in_20_m.nn_avg	0.79212771	0.75552706	0.82872835
svmRadial	n_within_dist.beds_in_20_m	0.78983145	0.74628032	0.83338258
nb	n_within_dist.dist_nearest_pt.nn_avg	0.78971934	0.74332462	0.83611406
nb	beds_in_20_m.nn_avg	0.78499206	0.74000108	0.82998305

nb	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.7834899	0.7446026	0.8223772
lda	beds_in_20_m.dist_nearest_pt.nn_avg	0.78302237	0.7479812	0.81806353
rpart	n_within_dist	0.77698846	0.72579208	0.82818483
rpart	beds_in_20_m	0.77193939	0.72039145	0.82348734
nb	dist_nearest_pt.nn_avg	0.76635209	0.72762237	0.80508182
lda	n_within_dist.beds_in_20_m	0.7661771	0.72060275	0.81175145
nb	nn_avg	0.76191703	0.69589208	0.82794198
svmRadial	n_within_dist.beds_in_20_m.nn_avg	0.76070491	0.71665586	0.80475395
lda	n_within_dist.beds_in_20_m.dist_nearest_pt	0.75816667	0.72279223	0.79354111
knn	n_within_dist.beds_in_20_m	0.75727955	0.70784509	0.80671402
nb	dist_nearest_pt	0.74392136	0.68096028	0.80688243
lda	n_within_dist.beds_in_20_m.nn_avg	0.74218759	0.70127631	0.78309887
lda	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.74178499	0.70341897	0.78015101
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt	0.72738672	0.68489872	0.76987472
rpart	beds_in_20_m.dist_nearest_pt	0.72552237	0.66422168	0.78682306
rpart	n_within_dist.beds_in_20_m.nn_avg	0.72114863	0.66876445	0.77353281
rpart	beds_in_20_m.nn_avg	0.71735426	0.66797308	0.76673543
rpart	n_within_dist.beds_in_20_m	0.71441447	0.66653327	0.76229568
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.71255267	0.66224911	0.76285623
lda	nn_avg	0.70897691	0.66412611	0.75382772
svmRadial	beds_in_20_m.dist_nearest_pt.nn_avg	0.70702814	0.65377099	0.76028529
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt	0.70225108	0.65992356	0.74457861
knn	n_within_dist	0.69477778	0.64099801	0.74855754
lda	n_within_dist.nn_avg	0.69326679	0.64435185	0.74218172
svmRadial	beds_in_20_m.dist_nearest_pt	0.6874899	0.62821047	0.74676932
lda	n_within_dist.dist_nearest_pt	0.68733405	0.63480289	0.73986522
svmRadial	dist_nearest_pt	0.68541414	0.62816925	0.74265903
lda	dist_nearest_pt.nn_avg	0.68294733	0.64152903	0.72436563

rpart	n_within_dist.nn_avg	0.67808403	0.60289678	0.75327128
lda	n_within_dist.dist_nearest_pt.nn_avg	0.67720491	0.62916483	0.72524498
rpart	beds_in_20_m.dist_nearest_pt.nn_avg	0.67271645	0.60975899	0.73567391
svmRadial	n_within_dist	0.65669841	0.60460763	0.70878919
rpart	n_within_dist.dist_nearest_pt.nn_avg	0.65145094	0.58739539	0.71550649
lda	n_within_dist	0.62094228	0.56979917	0.67208539
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.62032035	0.56749219	0.6731485
svmRadial	n_within_dist.nn_avg	0.6189854	0.56943644	0.66853437
lda	dist_nearest_pt	0.61455123	0.54656214	0.68254032
knn	n_within_dist.beds_in_20_m.dist_nearest_pt	0.60893362	0.56022823	0.65763901
knn	n_within_dist.dist_nearest_pt	0.59050072	0.53653041	0.64447103
svmRadial	dist_nearest_pt.nn_avg	0.5899531	0.53424963	0.64565657
rpart	n_within_dist.dist_nearest_pt	0.57347619	0.51161265	0.63533973
knn	beds_in_20_m.dist_nearest_pt	0.56541919	0.51889133	0.61194705
svmRadial	nn_avg	0.55965945	0.48931245	0.63000645
svmRadial	n_within_dist.dist_nearest_pt	0.55917605	0.50393623	0.61441586
knn	n_within_dist.nn_avg	0.55706482	0.51147425	0.60265539
knn	beds_in_20_m.dist_nearest_pt.nn_avg	0.55384343	0.50440715	0.60327972
knn	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.55177994	0.49818773	0.60537216
knn	beds_in_20_m.nn_avg	0.54818326	0.4886556	0.60771093
knn	n_within_dist.dist_nearest_pt.nn_avg	0.54591126	0.4955404	0.59628211
knn	dist_nearest_pt.nn_avg	0.54585714	0.49858456	0.59312973
knn	dist_nearest_pt	0.54510173	0.4943985	0.59580497
rpart	dist_nearest_pt	0.52765224	0.46965642	0.58564805
svmRadial	n_within_dist.dist_nearest_pt.nn_avg	0.52432179	0.47309327	0.57555031
knn	n_within_dist.beds_in_20_m.nn_avg	0.5018254	0.4528147	0.55083609
knn	nn_avg	0.50156349	0.4405589	0.56256808
rpart	nn_avg	0.47795238	0.40699202	0.54891274

rpart	dist_nearest_pt.nn_avg	0.47371284	0.4179429	0.52948279

Table S.4-6: Model accuracy output from blocked cross validation of models for distinguishing positively from negatively identified samples. Predictor variables include *n_within_dist* = cluster tightness; *nearest_pt*= distance from sample to nearest cluster centre; *nn_avg* = average nearest neighbour distance among points in cluster; *beds_in_20_m* = number of beds within 20 m of sample. Classifiers include naïve Bayes (nb), linear discriminant analysis (lda), radial support vector machines (svmRadial), K-nearest neighbour (knn), and classification and regression trees (rpart).

Classifier	Model predictor variable set	Accuracy	Lower 95% CI	Upper 95% CI
knn	n_within_dist.beds_in_20_m	0.72423833	0.53321135	0.91526532
lda	beds_in_20_m	0.72187462	0.51552861	0.92822062
lda	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.72019793	0.56863856	0.8717573
svmRadial	n_within_dist.beds_in_20_m	0.71837811	0.52402389	0.91273233
lda	n_within_dist.beds_in_20_m	0.71670143	0.56899725	0.86440561
lda	beds_in_20_m.nn_avg	0.71581401	0.52316632	0.9084617
nb	beds_in_20_m.dist_nearest_pt	0.7082771	0.51633383	0.90022038
nb	n_within_dist.beds_in_20_m	0.69856459	0.50912141	0.88800777
nb	beds_in_20_m	0.69157159	0.49249652	0.89064665
svmRadial	n_within_dist.beds_in_20_m.nn_avg	0.68512248	0.49878402	0.87146094
rpart	n_within_dist.beds_in_20_m	0.68422279	0.49352107	0.87492452
lda	beds_in_20_m.dist_nearest_pt.nn_avg	0.68200221	0.48191026	0.88209416
lda	beds_in_20_m.dist_nearest_pt	0.68108208	0.44932916	0.912835
rpart	beds_in_20_m	0.67921727	0.47010741	0.88832714
knn	beds_in_20_m	0.66709606	0.47324372	0.8609484
svmRadial	beds_in_20_m	0.66709606	0.47324372	0.8609484
lda	n_within_dist.beds_in_20_m.nn_avg	0.65959187	0.53537938	0.78380436
nb	n_within_dist.dist_nearest_pt	0.65737128	0.52903982	0.78570275

nb	n_within_dist.beds_in_20_m.nn_avg	0.64805954	0.45907428	0.83704481
svmRadial	beds_in_20_m.nn_avg	0.64249785	0.45846558	0.82653013
lda	n_within_dist.beds_in_20_m.dist_nearest_pt	0.63938985	0.50944074	0.76933896
lda	n_within_dist.nn_avg	0.63199607	0.50437114	0.75962101
nb	beds_in_20_m.nn_avg	0.62925612	0.4534683	0.80504395
nb	n_within_dist	0.62699055	0.47977704	0.77420407
nb	n_within_dist.beds_in_20_m.dist_nearest_pt	0.62490492	0.43496389	0.81484595
knn	n_within_dist.beds_in_20_m.dist_nearest_pt	0.62456958	0.47769173	0.77144743
svmRadial	n_within_dist.dist_nearest_pt	0.62263935	0.48700318	0.75827552
rpart	beds_in_20_m.nn_avg	0.62190733	0.42552493	0.81828973
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.61859894	0.4578427	0.77935519
lda	n_within_dist	0.61455854	0.46942037	0.75969671
rpart	n_within_dist.dist_nearest_pt.nn_avg	0.61082894	0.4638725	0.75778537
svmRadial	n_within_dist.nn_avg	0.60607696	0.49858552	0.71356841
lda	n_within_dist.dist_nearest_pt.nn_avg	0.59948473	0.45435011	0.74461934
nb	n_within_dist.nn_avg	0.59341185	0.44864347	0.73818024
nb	beds_in_20_m.dist_nearest_pt.nn_avg	0.58924058	0.39995901	0.77852216
nb	dist_nearest_pt.nn_avg	0.58088169	0.40491463	0.75684875
rpart	n_within_dist	0.5785057	0.46012757	0.69688384
knn	n_within_dist	0.57336523	0.46621196	0.68051851
svmRadial	n_within_dist	0.57336523	0.45919875	0.68753172
lda	n_within_dist.dist_nearest_pt	0.57232241	0.44021678	0.70442805
nb	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.57217928	0.39831301	0.74604555
svmRadial	beds_in_20_m.dist_nearest_pt.nn_avg	0.56549708	0.39357913	0.73741502
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.56534168	0.39230473	0.73837862
svmRadial	beds_in_20_m.dist_nearest_pt	0.55298736	0.3392975	0.76667723
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt	0.55174416	0.36387014	0.73961818
rpart	n_within_dist.beds_in_20_m.nn_avg	0.54754836	0.37734541	0.71775131

nb	n_within_dist.dist_nearest_pt.nn_avg	0.54618247	0.34683127	0.74553368
knn	nn_avg	0.52896577	0.38644025	0.67149129
lda	dist_nearest_pt	0.52765714	0.36199678	0.69331749
nb	nn_avg	0.52458185	0.34403066	0.70513305
svmRadial	nn_avg	0.51626794	0.3562359	0.67629999
knn	n_within_dist.beds_in_20_m.nn_avg	0.51001922	0.41912424	0.60091421
rpart	dist_nearest_pt.nn_avg	0.50689895	0.36856523	0.64523266
knn	n_within_dist.dist_nearest_pt	0.49897354	0.35329227	0.64465481
lda	dist_nearest_pt.nn_avg	0.49804114	0.33792938	0.6581529
svmRadial	n_within_dist.dist_nearest_pt.nn_avg	0.49493314	0.37702992	0.61283636
knn	beds_in_20_m.dist_nearest_pt	0.49053695	0.33853676	0.64253714
rpart	n_within_dist.dist_nearest_pt	0.48211262	0.32625545	0.6379698
lda	nn_avg	0.48195722	0.30226549	0.66164896
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt	0.47668589	0.28548902	0.66788275
rpart	nn_avg	0.47195436	0.37041967	0.57348906
knn	dist_nearest_pt.nn_avg	0.46636405	0.32373286	0.60899523
svmRadial	dist_nearest_pt	0.45803787	0.25787838	0.65819736
svmRadial	dist_nearest_pt.nn_avg	0.45788247	0.26881144	0.6469535
rpart	beds_in_20_m.dist_nearest_pt	0.45715045	0.24433651	0.6699644
knn	dist_nearest_pt	0.44495972	0.26914359	0.62077584
knn	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.44037541	0.34479974	0.53595108
rpart	beds_in_20_m.dist_nearest_pt.nn_avg	0.43856786	0.22686205	0.65027368
knn	n_within_dist.nn_avg	0.43841246	0.35106767	0.52575726
nb	dist_nearest_pt	0.43177524	0.24125958	0.62229091
rpart	n_within_dist.nn_avg	0.42355948	0.24662564	0.60049332
knn	beds_in_20_m.dist_nearest_pt.nn_avg	0.40020447	0.27715642	0.52325253
rpart	dist_nearest_pt	0.39982824	0.21442588	0.5852306
knn	beds_in_20_m.nn_avg	0.37193391	0.24098702	0.5028808

knn	n_within_dist.dist_nearest_pt.nn_avg	0.32065186	0.186524	0.45477973

Table S.4-7: Model sensitivity output from blocked cross validation of models for distinguishing positively from negatively identified samples. Predictor variables include *n_within_dist* = cluster tightness; *nearest_pt*= distance from sample to nearest cluster centre; *nn_avg* = average nearest neighbour distance among points in cluster; *beds_in_20_m* = number of beds within 20 m of sample. Classifiers include naïve Bayes (nb), linear discriminant analysis (lda), radial support vector machines (svmRadial), K-nearest neighbour (knn), and classification and regression trees (rpart).

Classifier	Model predictor variable set	Sensitivity	Lower 95% CI	Upper 95% CI
rpart	n_within_dist.beds_in_20_m	0.74404762	0.51007879	0.97801645
lda	beds_in_20_m.nn_avg	0.72619048	0.47686006	0.97552089
svmRadial	n_within_dist.beds_in_20_m.nn_avg	0.72321429	0.48396356	0.96246501
knn	n_within_dist.beds_in_20_m	0.70758929	0.47419961	0.94097896
rpart	beds_in_20_m	0.70535714	0.45164829	0.959066
lda	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.7046131	0.47156829	0.9376579
nb	n_within_dist.beds_in_20_m	0.70238095	0.47637478	0.92838712
svmRadial	n_within_dist.beds_in_20_m	0.70238095	0.47637478	0.92838712
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.69717262	0.47067083	0.92367441
lda	n_within_dist.beds_in_20_m	0.69494048	0.45397624	0.93590471
lda	beds_in_20_m.dist_nearest_pt.nn_avg	0.6875	0.41680225	0.95819775
svmRadial	beds_in_20_m.nn_avg	0.66369048	0.38792066	0.93946029
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.66071429	0.37912787	0.9423007
nb	n_within_dist.beds_in_20_m.nn_avg	0.63988095	0.4227544	0.8570075
svmRadial	n_within_dist.dist_nearest_pt	0.63988095	0.44999396	0.82976795
svmRadial	n_within_dist.dist_nearest_pt.nn_avg	0.63095238	0.45747924	0.80442552
lda	beds_in_20_m.dist_nearest_pt	0.62723214	0.34130413	0.91316016
nb	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.62425595	0.39097234	0.85753956

lda	n_within_dist.beds_in_20_m.nn_avg	0.62127976	0.41397434	0.82858518
nb	beds_in_20_m.dist_nearest_pt	0.61681548	0.35299012	0.88064083
lda	beds_in_20_m	0.61160714	0.32992187	0.89329241
knn	n_within_dist.beds_in_20_m.dist_nearest_pt	0.60565476	0.42245061	0.78885892
nb	n_within_dist.beds_in_20_m.dist_nearest_pt	0.60342262	0.38752122	0.81932402
rpart	beds_in_20_m.nn_avg	0.60119048	0.32101376	0.88136719
knn	beds_in_20_m	0.58035714	0.2999597	0.86075459
svmRadial	beds_in_20_m	0.58035714	0.2999597	0.86075459
rpart	n_within_dist.beds_in_20_m.nn_avg	0.57738095	0.30147656	0.85328534
knn	n_within_dist.beds_in_20_m.nn_avg	0.56919643	0.41858897	0.71980389
lda	n_within_dist.beds_in_20_m.dist_nearest_pt	0.56473214	0.33692301	0.79254128
nb	n_within_dist.dist_nearest_pt	0.55654762	0.37905527	0.73403997
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt	0.55654762	0.32486406	0.78823118
nb	beds_in_20_m	0.54910714	0.28286861	0.81534567
lda	n_within_dist.nn_avg	0.54017857	0.39141557	0.68894157
lda	n_within_dist.dist_nearest_pt.nn_avg	0.53497024	0.39373281	0.67620767
svmRadial	beds_in_20_m.dist_nearest_pt	0.53348214	0.23722471	0.82973957
lda	n_within_dist	0.52827381	0.39606979	0.66047783
nb	beds_in_20_m.nn_avg	0.52306548	0.23833003	0.80780092
lda	n_within_dist.dist_nearest_pt	0.50892857	0.33368127	0.68417587
rpart	n_within_dist.dist_nearest_pt.nn_avg	0.50744048	0.28153014	0.73335081
rpart	dist_nearest_pt.nn_avg	0.4985119	0.27691503	0.72010878
svmRadial	n_within_dist.nn_avg	0.48809524	0.31691986	0.65927062
knn	beds_in_20_m.dist_nearest_pt	0.48660714	0.25178048	0.7214338
knn	n_within_dist	0.4828869	0.30566926	0.66010455
knn	n_within_dist.nn_avg	0.4672619	0.29314799	0.64137582
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt	0.46279762	0.22296577	0.70262947
knn	beds_in_20_m.dist_nearest_pt.nn_avg	0.46205357	0.27468805	0.6494191

rpart	n_within_dist	0.46056548	0.25260452	0.66852643
svmRadial	beds_in_20_m.dist_nearest_pt.nn_avg	0.46056548	0.18774763	0.73338332
rpart	nn_avg	0.453125	0.22085136	0.68539864
knn	beds_in_20_m.nn_avg	0.44717262	0.26704631	0.62729893
nb	beds_in_20_m.dist_nearest_pt.nn_avg	0.43973214	0.17752987	0.70193442
rpart	beds_in_20_m.dist_nearest_pt.nn_avg	0.4360119	0.18010566	0.69191815
knn	nn_avg	0.42633929	0.23778878	0.61488979
rpart	n_within_dist.nn_avg	0.42559524	0.22654573	0.62464475
svmRadial	n_within_dist	0.42559524	0.29350826	0.55768222
rpart	beds_in_20_m.dist_nearest_pt	0.42410714	0.13771699	0.71049729
nb	n_within_dist	0.41889881	0.24524299	0.59255463
knn	dist_nearest_pt.nn_avg	0.40178571	0.2316981	0.57187333
rpart	n_within_dist.dist_nearest_pt	0.38095238	0.16206631	0.59983845
nb	n_within_dist.nn_avg	0.37872024	0.2639179	0.49352258
knn	dist_nearest_pt	0.3764881	0.12943859	0.6235376
knn	n_within_dist.dist_nearest_pt	0.3735119	0.16682294	0.58020087
lda	nn_avg	0.35416667	0.11616043	0.59217291
lda	dist_nearest_pt.nn_avg	0.35119048	0.12409196	0.578289
nb	n_within_dist.dist_nearest_pt.nn_avg	0.34077381	0.11268308	0.56886453
knn	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.33705357	0.1468695	0.52723764
nb	dist_nearest_pt.nn_avg	0.33035714	0.07703876	0.58367552
svmRadial	nn_avg	0.3125	0.11245834	0.51254166
lda	dist_nearest_pt	0.29910714	0.08454599	0.5136683
svmRadial	dist_nearest_pt.nn_avg	0.27232143	0.07356742	0.47107544
knn	n_within_dist.dist_nearest_pt.nn_avg	0.25967262	0.04075475	0.47859048
nb	dist_nearest_pt	0.23660714	0.04010715	0.43310714
rpart	dist_nearest_pt	0.22767857	0.0072013	0.44815584
nb	nn_avg	0.171875	0.02040733	0.32334267

svmRadial	dist_nearest_pt	0.11160714	0.03354265	0.18967164

Table S.4-8: Model specificity output from blocked cross validation of models for distinguishing positively from negatively identified samples. Predictor variables include *n_within_dist* = cluster tightness; *nearest_pt*= distance from sample to nearest cluster centre; *nn_avg* = average nearest neighbour distance among points in cluster; *beds_in_20_m* = number of beds within 20 m of sample. Classifiers include naïve Bayes (nb), linear discriminant analysis (lda), radial support vector machines (svmRadial), K-nearest neighbour (knn), and classification and regression trees (rpart).

Classifier	Model predictor variable set	Specificity	Lower 95% CI	Upper 95% CI
lda	beds_in_20_m	0.82222222	0.60553607	1.03890838
nb	dist_nearest_pt.nn_avg	0.80432099	0.67661869	0.93202329
nb	beds_in_20_m.dist_nearest_pt	0.79753086	0.58441144	1.01065029
nb	beds_in_20_m.dist_nearest_pt.nn_avg	0.74197531	0.55847902	0.9254716
knn	n_within_dist.beds_in_20_m	0.73888889	0.53848384	0.93929393
nb	nn_avg	0.71481481	0.53209933	0.8975303
nb	n_within_dist	0.71296296	0.49120018	0.93472575
nb	beds_in_20_m	0.71111111	0.44609165	0.97613057
nb	n_within_dist.dist_nearest_pt	0.70617284	0.50860187	0.90374381
nb	beds_in_20_m.nn_avg	0.7037037	0.49541287	0.91199454
lda	n_within_dist.beds_in_20_m.dist_nearest_pt	0.70185185	0.5098242	0.8938795
nb	n_within_dist.dist_nearest_pt.nn_avg	0.69691358	0.49946767	0.89435949
lda	n_within_dist.beds_in_20_m.nn_avg	0.69567901	0.50821167	0.88314636
lda	beds_in_20_m.dist_nearest_pt	0.68641975	0.4284536	0.9443859
lda	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.68333333	0.4967144	0.86995227
svmRadial	n_within_dist.beds_in_20_m	0.68333333	0.42810347	0.9385632
nb	n_within_dist.nn_avg	0.67901235	0.47827963	0.87974506
lda	n_within_dist.beds_in_20_m	0.67716049	0.47050329	0.8838177

lda	beds_in_20_m.nn_avg	0.67716049	0.42525459	0.92906639
nb	n_within_dist.beds_in_20_m	0.65864198	0.41183323	0.90545072
svmRadial	beds_in_20_m.nn_avg	0.65864198	0.43233787	0.88494608
rpart	beds_in_20_m.nn_avg	0.65740741	0.44782683	0.86698798
knn	beds_in_20_m	0.65555556	0.39608492	0.91502619
svmRadial	beds_in_20_m	0.65555556	0.39608492	0.91502619
lda	beds_in_20_m.dist_nearest_pt.nn_avg	0.65246914	0.40495172	0.89998656
nb	n_within_dist.beds_in_20_m.nn_avg	0.65246914	0.3985035	0.90643477
svmRadial	n_within_dist.beds_in_20_m.nn_avg	0.65246914	0.45524172	0.84969656
lda	n_within_dist	0.65123457	0.43577199	0.86669715
svmRadial	n_within_dist.nn_avg	0.64876543	0.47109886	0.826432
lda	n_within_dist.dist_nearest_pt.nn_avg	0.64753086	0.44750866	0.84755307
nb	n_within_dist.beds_in_20_m.dist_nearest_pt	0.6462963	0.39543257	0.89716002
svmRadial	dist_nearest_pt	0.64444444	0.42364981	0.86523908
lda	n_within_dist.nn_avg	0.64074074	0.4601391	0.82134238
rpart	n_within_dist	0.63888889	0.43287452	0.84490326
lda	dist_nearest_pt	0.63580247	0.44305969	0.82854525
svmRadial	n_within_dist	0.62962963	0.44518207	0.81407719
nb	dist_nearest_pt	0.61975309	0.43481594	0.80469024
rpart	beds_in_20_m	0.61851852	0.37030048	0.86673655
rpart	n_within_dist.beds_in_20_m.nn_avg	0.61851852	0.44507138	0.79196566
knn	n_within_dist	0.61604938	0.43507924	0.79701952
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt	0.61481481	0.41621976	0.81340987
rpart	n_within_dist.beds_in_20_m	0.61234568	0.37264518	0.85204618
lda	nn_avg	0.60925926	0.42717165	0.79134687
rpart	n_within_dist.dist_nearest_pt	0.60864198	0.46769584	0.74958811
svmRadial	n_within_dist.dist_nearest_pt	0.60802469	0.39998557	0.81606382
svmRadial	nn_avg	0.60308642	0.4781215	0.72805134

svmRadial	beds_in_20_m.dist_nearest_pt.nn_avg	0.60061728	0.37753125	0.82370332
lda	n_within_dist.dist_nearest_pt	0.5962963	0.39407081	0.79852178
knn	nn_avg	0.59444444	0.44831778	0.74057111
rpart	n_within_dist.dist_nearest_pt.nn_avg	0.59382716	0.41818431	0.76947001
lda	dist_nearest_pt.nn_avg	0.59074074	0.39655016	0.78493132
svmRadial	dist_nearest_pt.nn_avg	0.59012346	0.37136555	0.80888137
nb	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.56604938	0.34649429	0.78560448
knn	n_within_dist.beds_in_20_m.dist_nearest_pt	0.55925926	0.37458538	0.74393313
knn	n_within_dist.dist_nearest_pt	0.55	0.3674542	0.7325458
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt	0.54444444	0.31684085	0.77204803
rpart	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.54444444	0.32223252	0.76665637
knn	dist_nearest_pt	0.53148148	0.33390672	0.72905624
rpart	dist_nearest_pt	0.52839506	0.32074921	0.73604091
svmRadial	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.52037037	0.30580877	0.73493198
svmRadial	beds_in_20_m.dist_nearest_pt	0.51666667	0.30912755	0.72420578
rpart	beds_in_20_m.dist_nearest_pt.nn_avg	0.51358025	0.27848642	0.74867408
rpart	beds_in_20_m.dist_nearest_pt	0.48271605	0.25782542	0.70760668
rpart	dist_nearest_pt.nn_avg	0.48148148	0.30698107	0.65598189
knn	n_within_dist.beds_in_20_m.dist_nearest_pt.nn_avg	0.47962963	0.32905268	0.63020657
knn	dist_nearest_pt.nn_avg	0.46728395	0.31121947	0.62334843
svmRadial	n_within_dist.dist_nearest_pt.nn_avg	0.45493827	0.27602728	0.63384926
knn	beds_in_20_m.dist_nearest_pt	0.44876543	0.27760337	0.61992749
knn	n_within_dist.beds_in_20_m.nn_avg	0.44753086	0.30291392	0.59214781
knn	beds_in_20_m.dist_nearest_pt.nn_avg	0.43765432	0.24436938	0.63093926
rpart	nn_avg	0.43333333	0.25665369	0.61001297
knn	n_within_dist.nn_avg	0.41728395	0.2875544	0.5470135
knn	n_within_dist.dist_nearest_pt.nn_avg	0.41728395	0.28636547	0.54820243
rpart	n_within_dist.nn_avg	0.40987654	0.18654704	0.63320605

knn	beds_in_20_m.nn_avg	0.34691358	0.17306986	0.5207573

References

Knopff KH, Knopff AA, Warren MB, Boyce MS (2009) Evaluating Global Positioning System Telemetry Techniques for Estimating Cougar Predation Parameters. J Wildl Manage 73:586–597. https://doi.org/10.2193/2008-294

S.5 Supplementary materials for Chapter 5

Table S.5-1: Weights assigned to landcover classes for calculating contrast weighted edge density. Adjacent classes with more dissimilar edge weights result in larger contrast weights when adjacent.

Land cover class	Land use type	Weight
Forest	Natural	0.025
Shrubland	Natural	0.050
Water	Natural	0.075
Wetland	Natural	0.075
Grassland	Semi-anthropogenic	0.100
Sod	Semi-anthropogenic	0.100
Grains	Crop	0.300
Barley	Crop	0.300
Millet	Crop	0.300
Oats	Crop	0.300
Rye	Crop	0.300
Spelt	Crop	0.300
Triticale	Crop	0.300
Wheat	Crop	0.300
Switchgrass	Crop	0.300
Sorghum	Crop	0.300
Winter Wheat	Crop	0.300
Spring Wheat	Crop	0.300
Oilseeds	Crop	0.400
Camelina	Crop	0.400
Flaxseed	Crop	0.400
Mustard	Crop	0.400
Safflower	Crop	0.400
Sunflower	Crop	0.400
Soybeans	Crop	0.500
Peas	Crop	0.500
Lentils	Crop	0.500
Corn	Crop	0.600
Tobacco	Crop	0.700

Hops	Crop	0.700
Herbs	Crop	0.700
Buckwheat	Crop	0.700
Vetch	Crop	0.700
Tomatoes	Crop	0.800
Potatoes	Crop	0.800
Sugarbeets	Crop	0.800
Other Crops	Crop	0.800
Exposed Land and Barren	Anthropogenic	0.975
Fallow	Anthropogenic	0.975
Urban and Developed	Anthropogenic	1.000

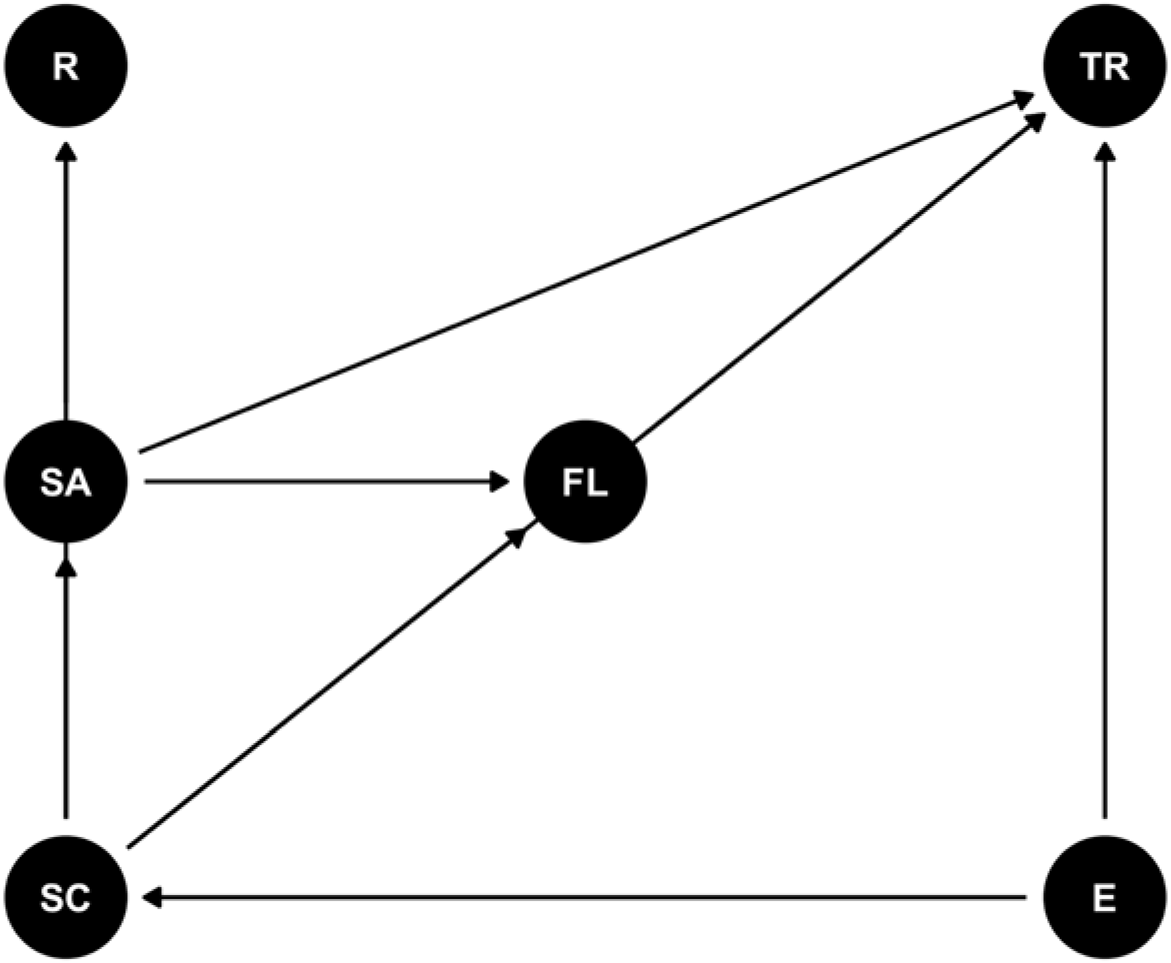

Figure S.5-1: Directed acyclic graph demonstrating assumed causal relationships between predictor variables (R = perceived predation risk (fecal glucocorticoid metabolites μg/g), SC = degree of home range overlap with other individuals, SA = degree of social association with other individuals (simple ratio index), FL = familiarity with other individuals with overlapping home ranges, E = total difference in the environment between years), and TR (resource-tracking, either vegetation quality or habitat structure).

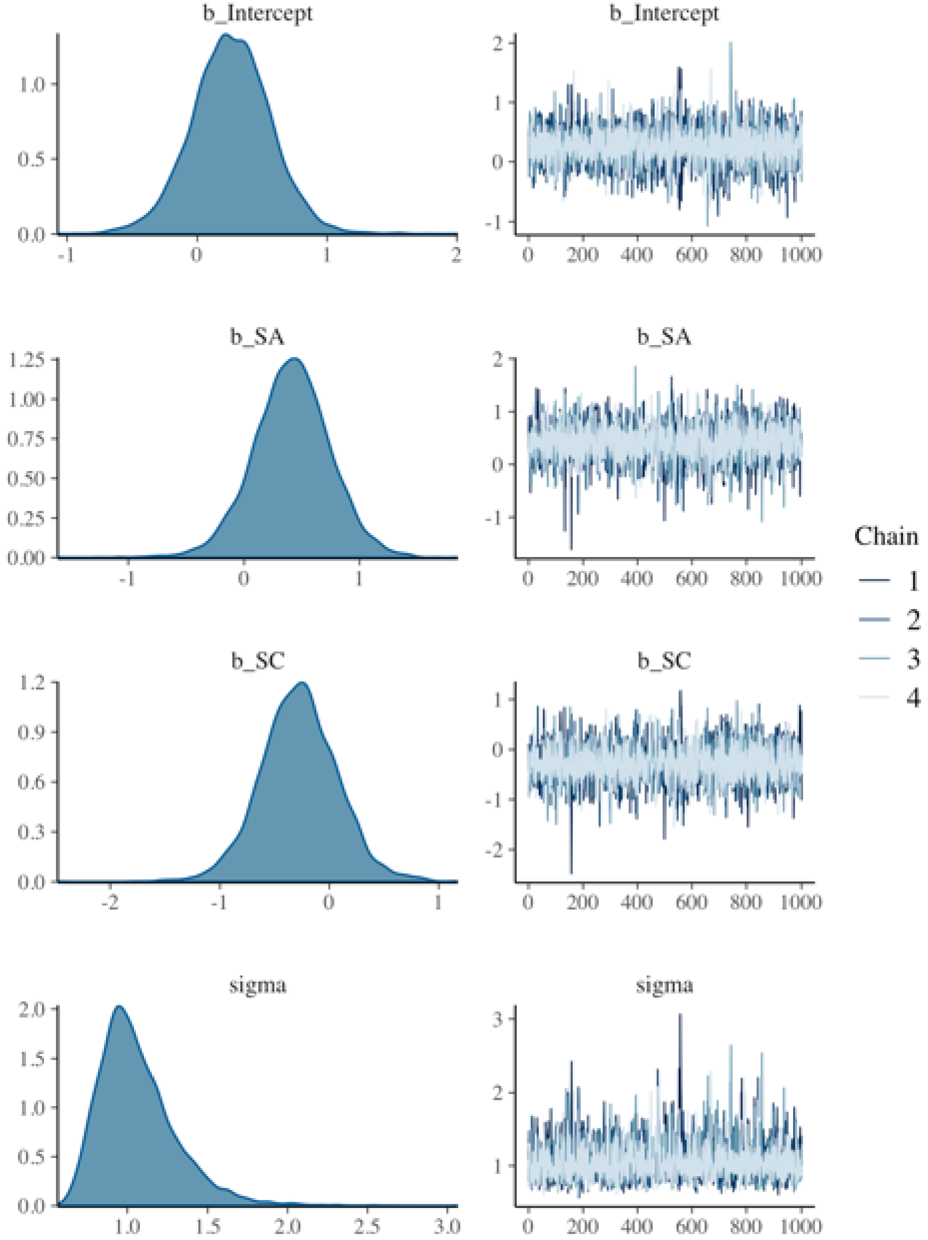

Figure S.5-2: Posterior distributions (left panel) and trace plots (right panel) of MCMC coefficients from model testing the effect of social associations on tracking habitat structure (i.e., contrast-weighted edge density, CWED). SC = shared spatial overlap, included to control for its effect on social associations (SA).

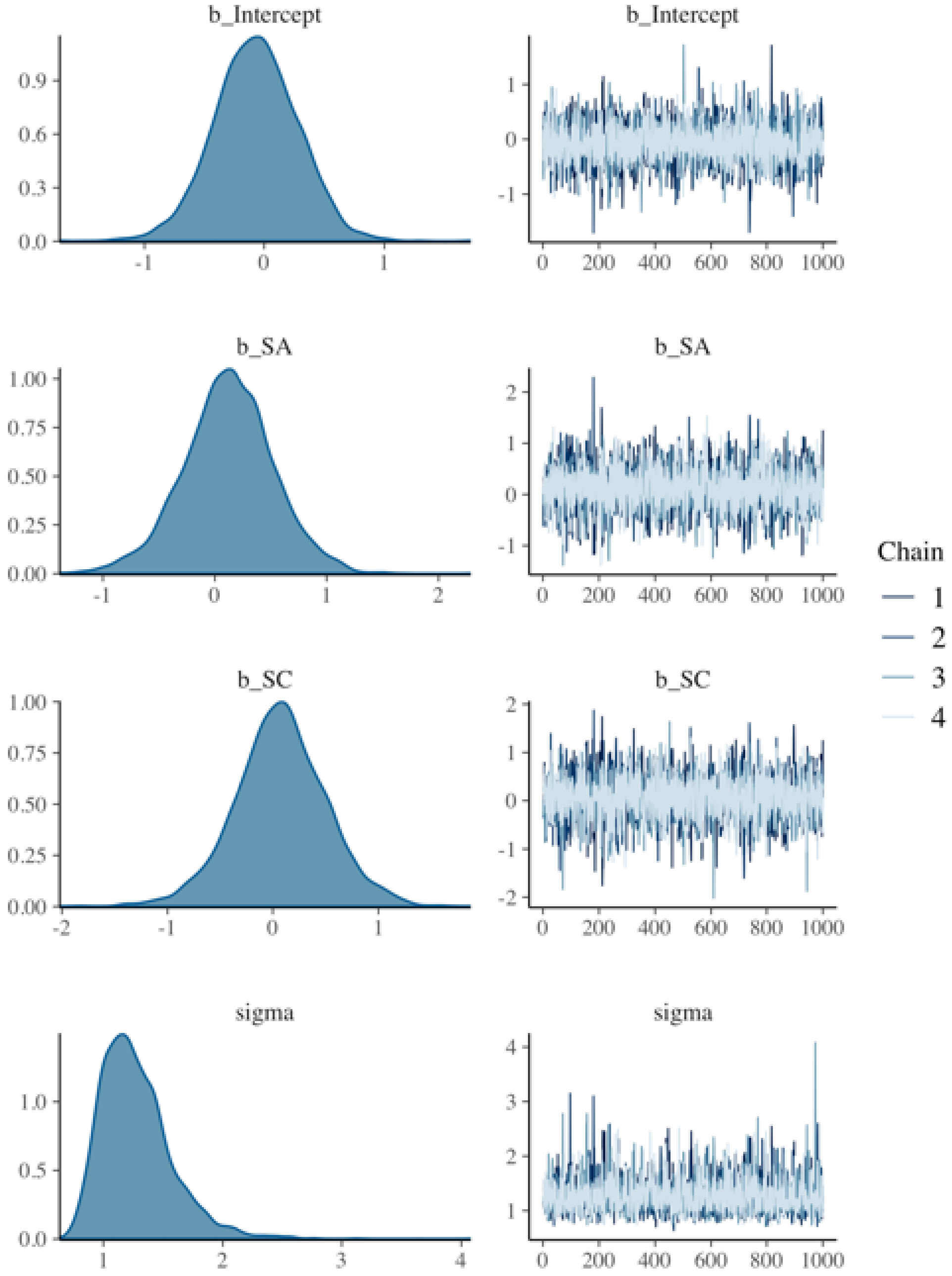

Figure S.5-3: Posterior distributions (left panel) and trace plots (right panel) of MCMC coefficients from model testing the effect of social associations on tracking vegetation quality (i.e., normalized vegetation difference index, NDVI). SC = shared spatial overlap, included to control for its effect on social associations (SA).

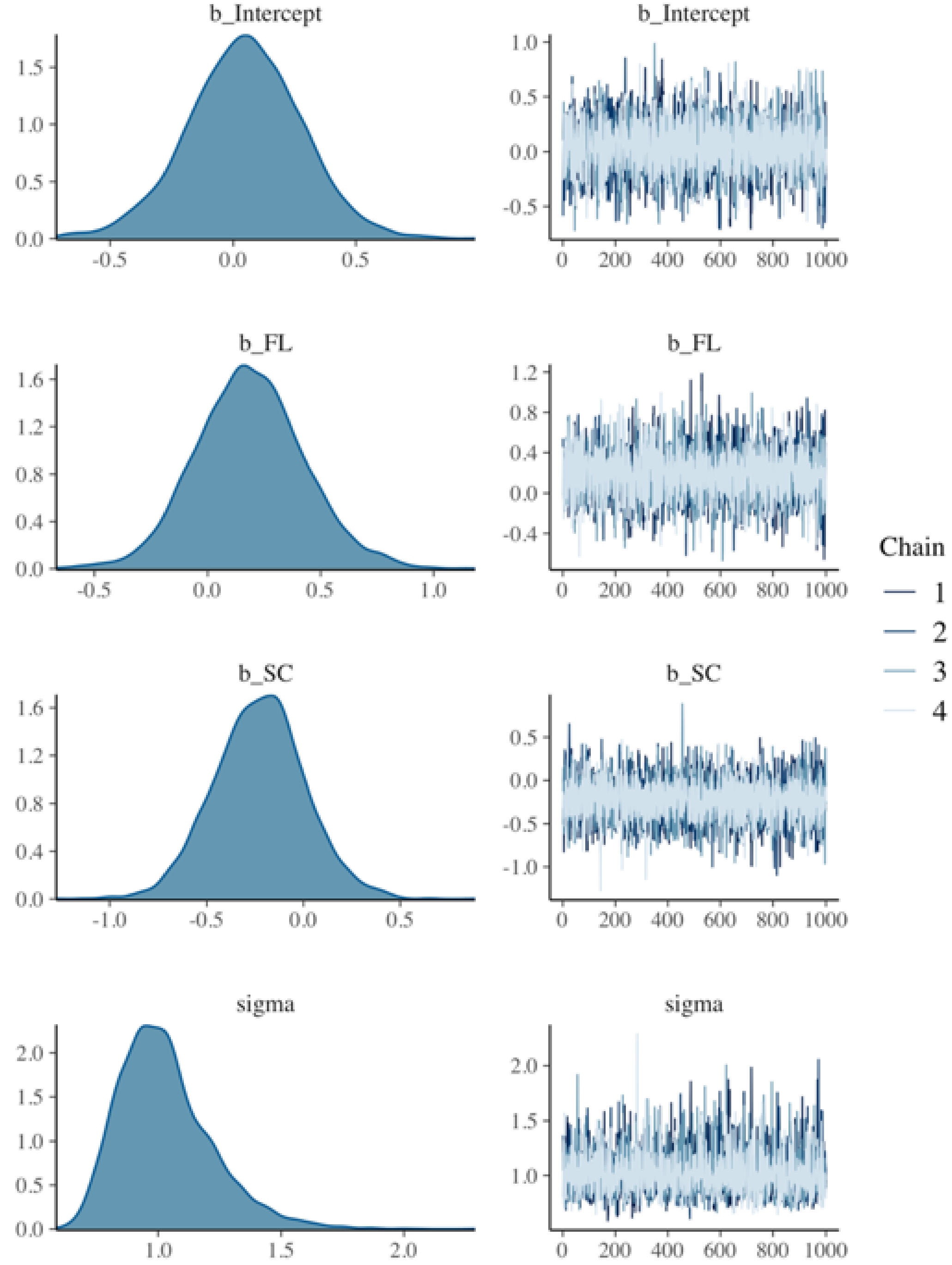

Figure S.5-4: Posterior distributions (left panel) and trace plots (right panel) of MCMC coefficients from model testing the effect of familiarity with social connections on tracking habitat structure (i.e., contrast-weighted edge density, CWED). FL = familiarity and SC = shared spatial overlap, included to control for its effect on familiarity with social connections.

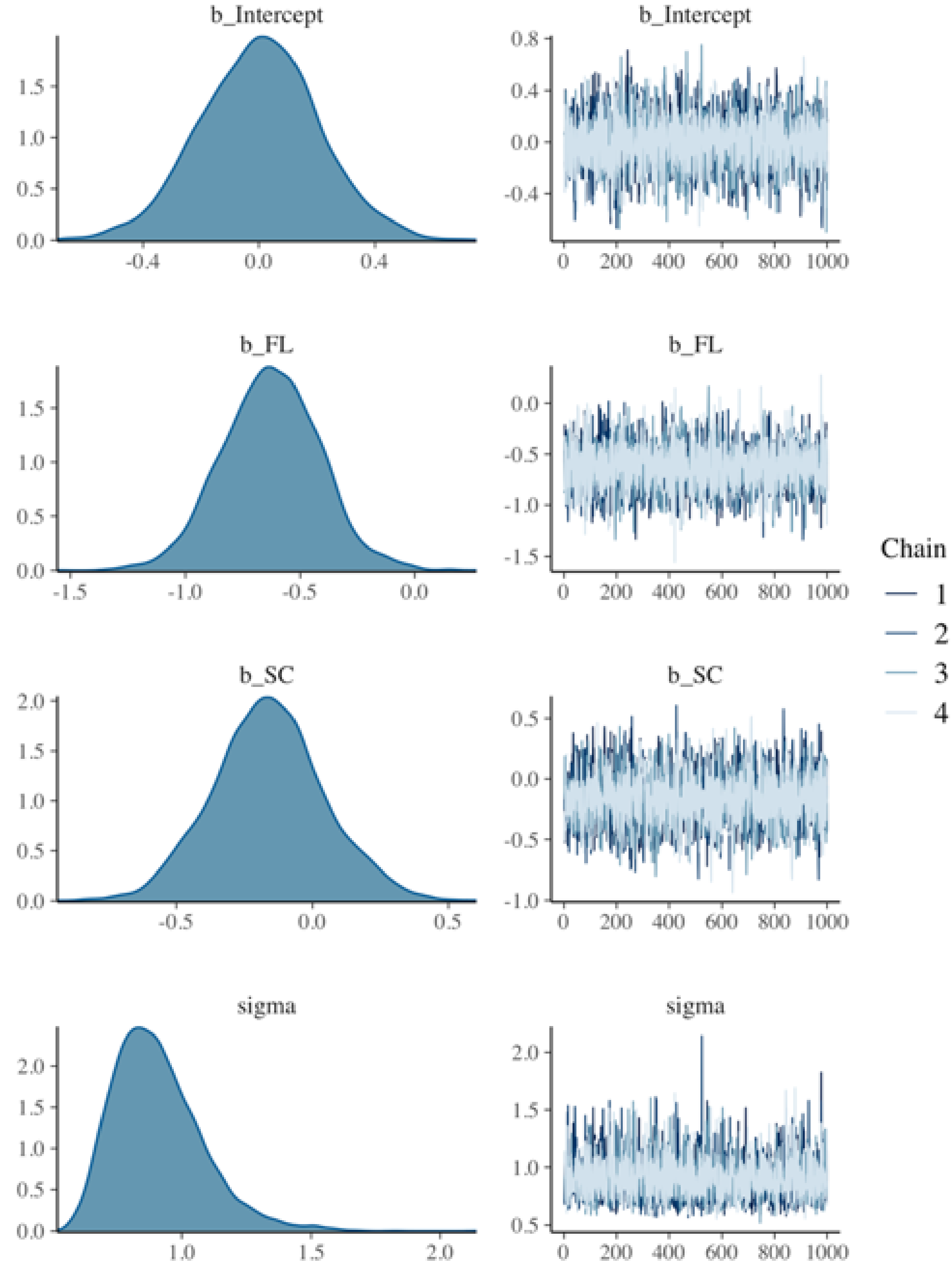

Figure S.5-5: Posterior distributions (left panel) and trace plots (right panel) of MCMC coefficients from model testing the effect of familiarity with social connections on tracking vegetation quality (i.e., normalized vegetation difference index, NDVI). FL = familiarity and SC = shared spatial overlap, included to control for its effect on familiarity with social connections.

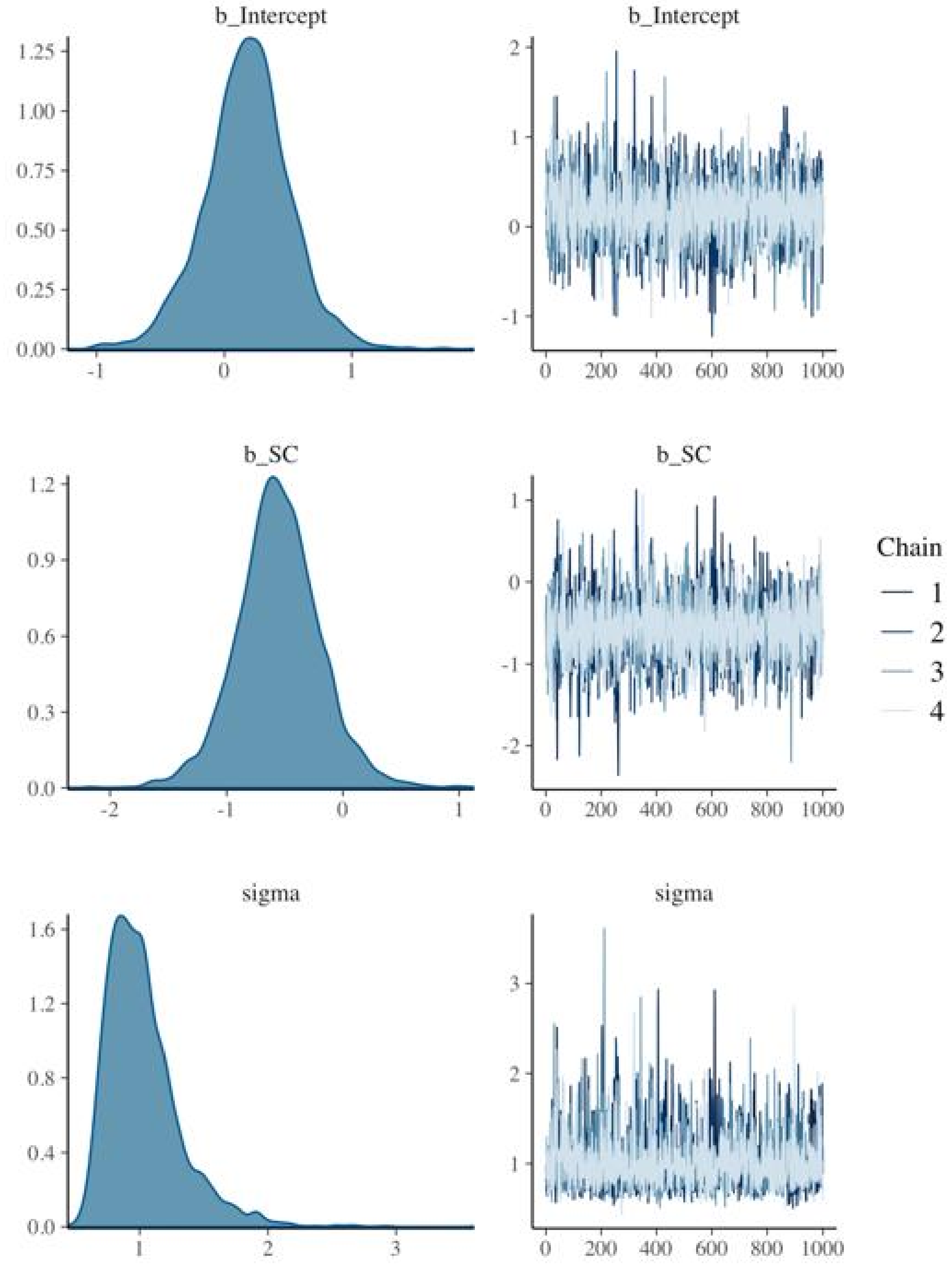

Figure S.5-6: Posterior distributions (left panel) and trace plots (right panel) of MCMC coefficients from model testing the effect of shared spatial overlap on glucocorticoid levels. SC = shared spatial overlap.

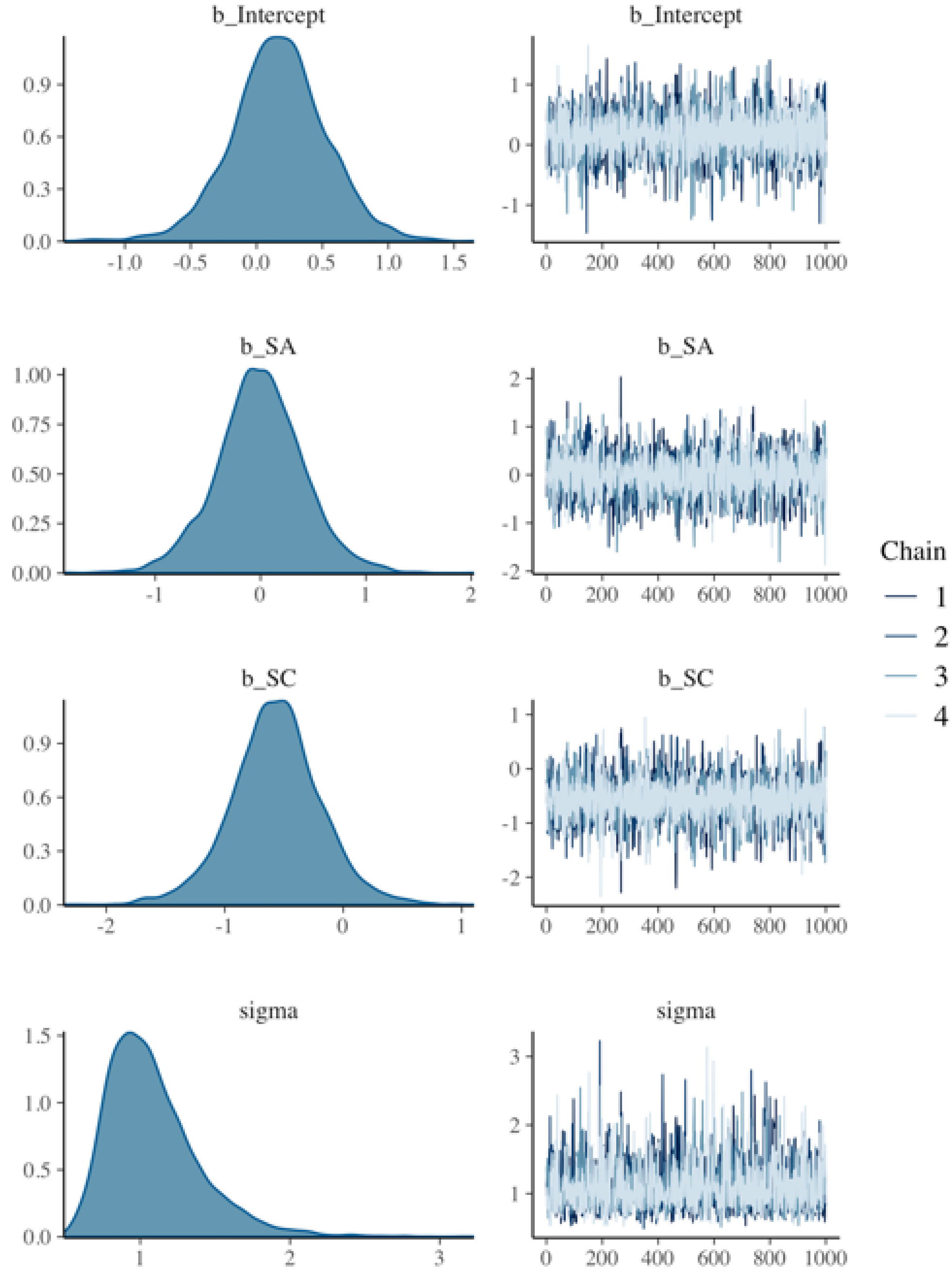

Figure S.5-7: Posterior distributions (left panel) and trace plots (right panel) of MCMC coefficients from model testing the effect of social associations on fecal glucocorticoid levels. SA = social associations, SC = shared spatial overlap, included to control for its effect on risk perception with social associations.

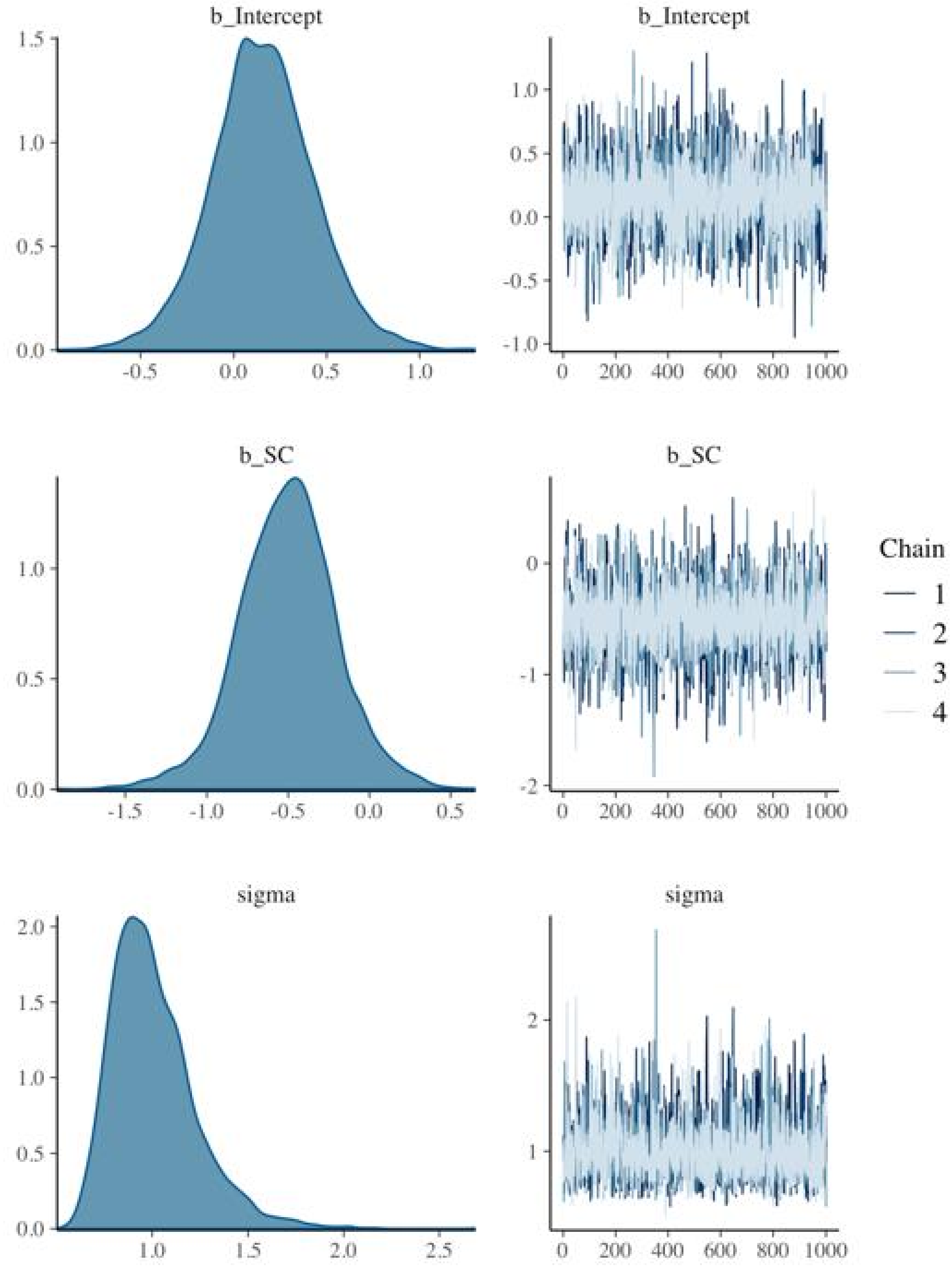

Figure S.5-8: Posterior distributions (left panel) and trace plots (right panel) of MCMC coefficients from model testing the effect of shared spatial overlap on social associations. SC = home range overlap.