Title: Unifying adaptive stress and adaptive habitat selection hypotheses through movement ecology

Authors: Newediuk, Levi[1], Mastromonaco, Gabriela F.[2], & Vander Wal, Eric[1]

[1] Department of Biology, Memorial University, St. John's Newfoundland, Canada A1B 3X9

[2] Reproductive Physiology, Toronto Zoo, Toronto Ontario, Canada M1B 5K7

Corresponding Author: Levi Newediuk

email: ljnewediuk@mun.ca; ORCiD: https://orcid.org/0000-0003-0719-9596

Abstract

1. Glucocorticoid production is often indicative of internal state that underpins movement and resulting habitat selection. Habitat selection is adaptive behaviour, but habitats where animals exhibit atypical glucocorticoid production are often associated with low fitness. Discrepancies between poor fitness outcomes and purported adaptive behaviour have contributed to a lack of consensus about the ecological and evolutionary implications of glucocorticoid production.
2. We aim to demonstrate the adaptive ecological and evolutionary roles of glucocorticoids by integrating stress physiology with habitat selection theory.
3. First, we show how habitat selection theory can benefit from a mechanistic understanding of the relationships between stressors, internal state, and habitat selection. We show that glucocorticoids drive everything from short-term locomotion to large-scale movements. In turn, these movements produce familiar patterns of adaptive habitat selection like habitat specialization and migration. Populations arrive at these evolutionarily stable habitat selection strategies by responding to stressors like predation and food availability. To quantify responses to stressors, we show how to parameterize glucocorticoid data in habitat selection models. Modelling the ecological and evolutionary patterns that make habitat selection adaptive also help clarify relationships between glucocorticoids, stress, and fitness.
4. Our approach delivers a practical framework for testing existing hypotheses about habitat selection and stress physiology. Our framework can also be applied to new questions that integrate both, with the potential to understand adaptations of populations to their

environments, and implications of stressors and habitat selection for ecosystem functioning.

Keywords: Glucocorticoids, stress physiology, optimal foraging theory, integrated step selection analysis, environmental challenges, non-invasive sampling, individual differences

Introduction

Animals respond adaptively to their environments: physiologically they use glucocorticoid production and behaviourally they use habitat selection. The two are intertwined. For example, habitat selection allows individuals to allocate effort among foraging patches to maximize energetic benefit (Charnov, 1976) and mitigates the stress of competition for forage among patches (Fretwell & Lucas, 1969). Adaptive foraging behaviour is driven in part by short-term changes in glucocorticoid hormones that characterize internal state (Jachowski, Montgomery, Slotow, & Millspaugh, 2013). Though internal state has held a theoretical place in habitat selection theory since Nathan et al. (2008) proposed their keystone movement ecology framework, there remains no empirical consensus on the role of glucocorticoids in driving habitat selection. Instead, habitat use is often considered detrimental to fitness when glucocorticoids are elevated because glucocorticoid production is positively associated with stressors in the environment (Bonier, Martin, Moore, & Wingfield, 2009). Viewing long-term associations between glucocorticoid production and habitats as maladaptive, even while short-term glucocorticoid production is adaptive, is a barrier to reconciling the role of internal state in habitat selection theory.

Movement connects internal state with habitat selection behaviour to mitigate the negative effects of stressors. Habitat selection is one way in which animals mitigate stressors like predation risk while foraging to meet energy requirements (Brown & Kotler, 2004). Allocating foraging effort based on energy reserves (McNamara & Houston, 1990) and moving among habitats to reduce forage competition with other individuals (Fretwell & Lucas, 1969; Morris, 2003) make habitat selection adaptive. When proactively responding to stressors through habitat selection is not an available strategy, animals tolerate stressors and use other movement-based

behavioural responses like vigilance to alleviate their effects (Scott Creel, 2018). Many alternative movement behaviours are underpinned by signalling networks between stressors and motor responses. One of the main products of these signalling networks are glucocorticoids (Sapolsky, Romero, & Munck, 2000). Metabolically, glucocorticoids help to allocate energy needed to induce these movement-based behavioural responses (Dallman et al., 1993). Stressors that stimulate glucocorticoid production also increase respiration, altering C:N ratios in the body and stimulating selection for digestible carbon (Hawlena & Schmitz, 2010). Thus, movement and habitat selection are underpinned by both the signalling and metabolic functions of glucocorticoids.

Though glucocorticoids and habitat selection are theoretically connected, they have not yet been integrated to show that glucocorticoid production is partly responsible for adaptive habitat selection behaviour. The delay to integrate glucocorticoid physiology and habitat selection is conceptual and methodological. Conceptually, viewing glucocorticoids as an adaptive driver behind habitat selection challenges the long-standing ideas that persistent environmental stressors (Bonier, Martin, et al., 2009) and chronic stress (Boonstra, 2013) coincide with lower fitness. Moreover, methodological tools to study habitat selection as a response to glucocorticoid production have only recently become readily accessible with increasing access to fine-scale hormone data, biotelemetry data, and modelling approaches to integrate both. In contrast to coarse-scale associations between habitat and glucocorticoid levels, fine-scale approaches are needed to understand how habitat selection strategies are ultimately shaped by short-term changes in glucocorticoids (Box 1).

In this article, we present an empirical roadmap for integrating glucocorticoids into habitat selection theory. First, we synthesize evidence that glucocorticoids underpin adaptive

habitat selection responses to stressors. We show how short-term habitat selection responses to stressors lead to distinct habitat selection strategies that ultimately support divergent life-history stages. Second, we highlight some methodological challenges to integrating glucocorticoids into habitat selection studies. To help address these challenges, we present a proof-of-concept study combining fine-scale glucocorticoid data with movement-based habitat selection analysis. Our proof-of-concept also acts as a template for promising research questions to which our empirical roadmap could be applied in the future (Box 2).

Physiology of glucocorticoids as a mechanism and motivation for movement

According to the marginal value theorem, an animal behaving optimally should remain in the same foraging patch as long as it can gain more energy by remaining than moving to a different patch (Charnov, 1976). Costs and benefits of interpatch movements — calculated in terms of the exchange rate of foraging energy for predation risk — are ultimately determined by the animal's safety and energy reserves (*sensu* McNamara & Houston, 1990). Hungrier animals in richer food patches may be willing to accept a higher risk of predation (Kotler, Brown, Mukherjee, Berger-Tal, & Bouskila, 2010), while the same animals may spend time in poorer patches when sated if those patches offer greater protection from predation risk (J. S. Brown, Morgan, & Dow, 1992). Below we show that the internal states of fear and hunger that modify the net energy gain equation are underpinned by characteristic glucocorticoid profiles. Changing glucocorticoid levels both regulate energy for interpatch movements and motivate foraging behaviour in line with the marginal value theorem, making them a physiological gauge for adaptive habitat selection behaviour.

Glucocorticoids serve a variety of physiological functions. One such function is to make energy available for adaptive movement. Movement between habitats relies on locomotion, the energetic costs of which are met in part by elevating blood glucose levels. Glucocorticoids mobilize glucose by preventing uptake by adipose and muscle tissue (Carroll, Aron & Findling, 2017) and stimulating gluconeogenesis (Dallman et al., 1993), thereby providing the energy needed to either seek forage or escape predation. Animals preparing to respond to long-term changes in predation and forage pressures, such as fledging birds and dispersing animals, also exhibit elevated glucocorticoid levels (Wada, 2008), and without glucocorticoids, movement is impaired. Both adrenalectomized rats without the ability to produce endogenous glucocorticoids (Veldhuis, De Kloet, Van Zoest, & Bohus, 1982), and intact rats treated with the glucocorticoid synthesis inhibitor Metapyrone, have lower capacity for movement (Canini et al., 2009). Locomotion is restored to affected rats within minutes of glucocorticoid replacement (Veldhuis et al., 1982).

Patterns of glucocorticoid production correlate with activity over daily and seasonal time periods. Baseline patterns, 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, Breuner, Gomes, Chappell, & Garland, 2008), and in turn, glucocorticoid rhythms adapt to regular feeding periods when energy is available for movement (Rovirosa, Levine, Gordon, & Caba, 2005). The interplay among energy availability, movement, and these baseline glucocorticoid levels is a hormonal explanation for the well-known diel habitat selection patterns that help prey species access forage while avoiding their predators (e.g., Smith, Donadio, Pauli, Sheriff, & Middleton, 2019). Seasonal activity patterns like migration track longer-term baseline glucocorticoid

rhythms (Landys, Ramenofsky, & Wingfield, 2006). While baseline glucocorticoid levels are seasonally elevated during migration (Landys-Ciannelli, Ramenofsky, Piersma, Jukema, & Wingfield, 2002), birds become 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, Jenni-Eiermann, & Jenni, 2009). Non-migratory birds also elevate baseline glucocorticoids during reproduction when offspring require the most active provisioning (Bonier, Moore, Martin, & Robertson, 2009). Thus, via extension of their effects on activity and locomotion, glucocorticoids form the physiological connection between external factors and adaptive patterns of behaviour.

External factors like predation risk induce stress responses that make prey species avoid risky foraging habitat. Predator cues stimulate a cascade of hormone release via the 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 regulating appetite during the stress response. In times of low stress, baseline glucocorticoids stimulate appetite to regulate energetic balance. Feeding behaviour, however, often interferes with behavioural responses to predators (Laundré, Hernández, & Altendorf, 2001). Thus, appetite is suppressed as glucocorticoids reach stress-induced levels and resulting increases in blood glucose levels stimulate insulin release (Dallman et al., 1993). The overall effect on habitat selection is a drive to escape predation by avoiding foraging habitat when risk is high. 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, Benoît, & Hammill, 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 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 secretion. When reduced glucocorticoids follow a stress response, elevated baseline levels stimulate feeding behaviour (Dallman et al., 1993) and a preference for high-calorie foods (Pecoraro, Reyes, Gomez, Bhargava, & Dallman, 2004). Predation risk elevates respiration rate, changing C:N ratios of animal tissue and stimulating select forage with higher carbon content (Hawlena & Schmitz, 2010). Over time, selection for calories causes animals to 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 intensifying ivory poaching by moving to ranges with higher primary productivity (Goldenberg, Douglas-Hamilton, & Wittemyer, 2018). Preferences for richer foods are reinforced over time because their consumption the stress response gradually blunts it (Foster et al., 2009), further increasing the drive to forage over avoiding risk. Thus, high and low glucocorticoid levels both coincide with different adaptive habitat selection strategies for dealing with the food-safety trade-off.

Typical habitat selection responses to food and safety, however, do not necessarily support both reproduction and survival. For instance, an animal might compromise its body condition and future reproduction if a stress response causes it to forgo foraging in times of low energy availability. As a result, animals in lower energetic states often spend more time in foraging habitats than do healthy animals, even when faced with the same risky situations

(McNamara & Houston, 1990). For example, while risky food patches were avoided by healthy white-footed mice (*Peromyscus leucopus*) relative to safe patches, immunochallenged mice did not discriminate patches based on risk (Schwanz, Previtali, Gomes-Solecki, Brisson, & Ostfeld, 2012). Risk responsiveness diminishes when animals face energy shortages because low glucose levels inhibit HPA axis activity (Kirschbaum et al., 1997), likely blunting selection for safer habitats after encountering predators. At the same time, low energy availability also encourages selection for foraging habitat since reductions in energy storage —adipose tissue and circulating triglycerides — reduces peripheral signals of satiety (Dallman et al., 1993) and keeps baseline glucocorticoids at higher levels that stimulate feeding (DeSimone et al., 2020). In the long term, food limitation leads to familiar seasonal habitat selection patterns where maintaining body condition is prioritized over survival. For example, as body condition declines over winter, species in temperate climates begin to favour productive habitats with higher mortality risk that they would otherwise avoid (Simon, Cherry, & Fortin, 2019).

Incorporating glucocorticoid production into movement ecology through the lens of the marginal value theorem can elucidate their adaptive role in driving habitat selection. In the next section, we consider why many studies still consider glucocorticoid production a consequence of habitat selection rather than also considering it a causal factor. Normalizing a bidirectional relationship between habitat selection and glucocorticoid production requires studying the differences in glucocorticoid-mediated habitat selection both among individuals and within individuals over time. We review evidence that labile individual glucocorticoid levels orchestrate trade-offs between reproduction and survival through habitat selection, thereby maximizing fitness.

Coadaptation between glucocorticoids and habitat selection

Glucocorticoids are normally studied at the population level to understand how habitat selection affects population growth rates. As population sizes change, animals distribute themselves among habitats with varying resources such that their expected fitness is equivalent (Morris, 2003). However, habitat selection strategies, and the resulting balance between survival and reproductive success, vary widely amongst individuals within populations (Stuber, Carlson, & Jesmer, 2022). In turn, individual variation in life history strategies is paralleled by variation in glucocorticoid production and its effects on behaviour (Vitousek, Jenkins, & Safran, 2014). In this section, we describe how this variation in glucocorticoid production, both between and within individuals, can be harnessed to model the adaptive relationship among glucocorticoid levels, habitat selection, and fitness. Glucocorticoid production style can be transferred from parent to offspring (Brass, Herndon, Gardner, Grindstaff, & Campbell, 2020), varies among individuals (Taff, Schoenle, & Vitousek, 2018), and influences survival and reproduction (Vitousek et al., 2014), making it a trait upon which natural selection can act (Hau & Goymann, 2015). Focussing on how short-term changes in glucocorticoid production affect individual habitat selection will reveal how populations adapt to environmental challenges through the habitats they occupy.

Differences in habitat selection and growth rates between populations often correlate with differences in their glucocorticoid levels. These glucocorticoid-fitness relationships are frequently negative because elevated glucocorticoids interfere directly with reproduction (Wingfield & Sapolsky, 2003), and environmental stressors that elicit stress responses shift resources away from offspring production (Creel, Winnie, & Christianson, 2009). For example, male Plateau pikas developed smaller testes and gave up feeding time for vigilance in years of

elevated predation risk, coinciding with elevated circulating glucocorticoids (Yin, Yang, Shang, & Wei, 2017). However, glucocorticoids can also help to prioritize reproduction over survival; levels may rise in anticipation of harsh conditions in predictably unfavourable environments (Michael Romero, 2002) or when reproductive opportunities are few (Bókony et al., 2009; Bonier, Moore, et al., 2009). Associations between reproduction, survival, and glucocorticoid production have led to the use of glucocorticoid levels as a gauge for the environmental challenges facing populations (Bonier, Martin, et al., 2009).

However, even when facing common challenges, glucocorticoid production varies among individuals within populations (Lema, 2020) because they prioritize reproduction and survival differently. Acute production of glucocorticoids by individuals is often repeatable (Bonnot, Bergvall, Jarnemo, & Kjellander, 2018), as are baseline levels in some species (Baldan, Negash, & Ouyang, 2021). The corollary of individual repeatability is consistent differences in glucocorticoid production among individuals, resulting in variation within populations. This variation makes it difficult to determine whether glucocorticoid levels result from environmental challenges facing individuals in the habitats they occupy, or different individual investments in either survival or reproduction made via habitat selection. For example, noisy anthropogenic habitats are associated both with low glucocorticoid production and low reproductive success in birds (Kleist, Guralnick, Cruz, Lowry, & Francis, 2018; Potvin & MacDougall-Shackleton, 2015; Zollinger et al., 2019). Reductions in reproductive success and glucocorticoid production could be considered direct consequences of anthropogenic noise. However, some birds inhabiting noisier environments also experience greater survival (Phillips, Gentry, Luther, & Derryberry, 2018). Thus, as an alternative explanation, lower glucocorticoid production in

response to noise may promote selection of noisier habitats, with those individuals sacrificing current reproductive opportunities in favour of their own survival and future reproduction.

The effect of environmental challenges on glucocorticoid production also changes within individuals over time (Guindre-Parker et al., 2019). This often results from changes in the contributions of survival and reproduction to individual fitness (Schoenle, Zimmer, & Vitousek, 2018). For example, as they age and fewer reproductive opportunities remain, individual terns (*Sterna hirundo*) support reproduction by producing fewer glucocorticoids and adapting behavioural responses to stressors (Heidinger, Nisbet, & Ketterson, 2006). Thus, short-term behaviours must be repeatedly quantified in response to short-term glucocorticoid production by individuals (Bonier & Martin, 2016).

Because glucocorticoids and habitat selection are both transmissible to offspring and affect lifetime reproductive success, habitat-specific glucocorticoid syndromes may evolve over time (Patterson, Hahn, Cornelius, & Breuner, 2014). For example, frogs adapted to environments with long-term exposure to anthropogenic noise both produced fewer glucocorticoids in response to noise and developed physiological coping mechanisms to equalize fitness with their noise-free habitat counterparts (Tennessen et al., 2018). Initially, selection of different habitats may be driven by chance variation in response to the environment among individuals (Bolnick et al., 2003). But because individuals are exposed to different stressors in the habitats they occupy, that chance variation in habitat use could also shape subsequent glucocorticoid production (Palma et al., 2020). Disruptive selection on both glucocorticoid profiles and habitat selection would then reinforce trade-offs between reproduction and survival by different individuals, resulting in both the physiological and spatial separation of populations over time (Lema, 2020). In partially migratory populations, for example, habitat selection phenotypes become spatially segregated

when migrants move to seasonal ranges and residents remain on the same ranges year-round. Despite their spatial separation, both residents and migrants maintain similar energy balance (Bonnet-Lebrun, Somveille, Rodrigues, & Manica, 2020) and overall fitness (Martin, Hebblewhite, & Merrill, 2022) even while glucocorticoid production differs by migratory strategy (Fudickar, Schmidt, Hau, Quetting, & Partecke, 2013). Thus, partial migration may be one example of adaptive result of feedback between habitat selection and glucocorticoid production.

Integrating glucocorticoids into individual habitat selection

In practice, understanding the evolutionary relationships between individual glucocorticoid levels and habitat selection requires quantifying relationships between individual behaviour and sampled levels (Cox, McGlothlin, & Bonier, 2016). Since many behaviours responsible for habitat selection are short-term, glucocorticoids must be sampled as point estimates. Samples like hair and feces normally collected from wild animals, however, reflect circulating glucocorticoids over longer time periods of hours to weeks (Gormally & Romero, 2020). In contrast, the temporal resolution of biotelemetry data is often hourly or finer, potentially mismatching sampled glucocorticoid levels with levels responsible for habitat selection. Sampled glucocorticoids also often come from multiple unknown individuals, making it difficult to separate temporal mismatches between samples and behaviour from mismatches between unidentified samples and individual behaviour. Moreover, additional physiological mechanisms mediate the proportion of circulating glucocorticoids that interact with receptors to cause behaviours (Landys et al., 2006). These downstream mechanisms produce non-linear relationships between behaviour and the circulating glucocorticoids deposited in samples (Lema,

2014). Overall, incongruencies between sampled glucocorticoids and individual glucocorticoid levels and behaviour create noise in the relationship between glucocorticoids and habitat selection. Below, we discuss how this noise might impact our understanding of the adaptive role of glucocorticoids in habitat selection. We also highlight individual-based sampling approaches that promise to clarify the relationship between sampled glucocorticoids and habitat selection.

Repeated samples are needed to understand how glucocorticoid production by individuals shapes their habitat selection decisions over time. However, circulating glucocorticoids are rarely sampled from individual wild animals more than once because repeated captures are often infeasible. Instead, repeated samples come from sources such as hair, feathers, and feces that can be collected non-invasively from the environment. Unlike blood, however, non-invasive samples do not provide a direct measure of circulating glucocorticoids at the time of sampling. Circulating glucocorticoids are processed by the liver and deposited as metabolites in feces within several hours to days depending on species-specific gut transport times (reviewed in Palme, 2019). They are also incorporated into growing hair cells from the plasma, and depending on the rate of hair growth, represent circulating levels over longer periods from weeks to months (Burnard, Ralph, Hynd, Hocking Edwards, & Tilbrook, 2017). Feathers also require weeks or months to incorporate glucocorticoids, but only do so during growth periods prior to moult (Gormally & Romero, 2020). Thus, non-invasive samples represent average, species-specific concentrations of circulating glucocorticoids rather than being precursors to movement in response to short-term stimuli. Moreover, short-term stimuli produce unique behavioural responses by individuals. Consequently, both knowledge of individual identity and an understanding of the period over which sampled glucocorticoids represent circulating levels are beneficial for understanding their relationship to habitat selection.

The bioactive component of glucocorticoids, and not just their production, is responsible for habitat selection. Behaviours at baseline glucocorticoid levels, like foraging and migration, are produced 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). Regardless of circulating glucocorticoid levels, animals can mediate their effects on behaviour by manipulating receptor transcription (Lattin & Romero, 2013). Receptor binding is also regulated by the concentration of corticosterone binding globulins (CBGs). CBGs bind glucocorticoids in the plasma and prevent them from interacting with target tissues (Creagh W. Breuner, Beyl, & Malisch, 2020). The rate of negative feedback on glucocorticoid production during the stress response also tempers the effects of stress-induced concentrations on behaviour (Lattin, Breuner, & Michael Romero, 2016), often mediated by CBG binding (Creagh W. Breuner et al., 2020).

Downstream mechanisms for controlling glucocorticoid actions produce non-linear relationships between circulating glucocorticoids and habitat selection. The effects of glucocorticoids on behaviour may saturate when receptor concentration slows the rate of binding (Lema, 2014). Alternatively, the direction of glucocorticoid effects can change if CBG, negative feedback, or receptor availability prevent binding at higher glucocorticoid concentrations (Lema, 2014). For example, Adélie penguin (*Pygoscelis adeliae*) locomotory behaviour exhibited a U-shaped relationship with glucocorticoid supplementation, where glucocorticoid actions at high circulating concentrations were buffered by CBG (Spée et al., 2011). Quantifying CBG and receptor concentration and negative feedback efficacy can help control error in the relationship between sampled glucocorticoids and habitat selection. However, CBG levels, negative feedback efficacy, and receptor concentration cannot be quantified in non-invasive samples.

Fortunately, repeatedly sampling individuals may control for both the effects of downstream regulation and consistent differences in glucocorticoid production among individuals. When both individual sample identity and time of collection are known, fecal metabolites and hair or feather glucocorticoids can be directly linked to habitat selection during the time when circulating levels affected behaviour. Comparing the relationship between sampled glucocorticoid levels and behaviour between individual life-history stages or seasons may also reveal the non-linear relationships produced by downstream mechanisms. For example, a linear relationship between individual fecal glucocorticoid metabolites and its habitat selection suggests behaviour is proportional to glucocorticoid production. However, a non-linear relationship during some life-history stages or seasons — such as a saturating effect of cortisol supplementation on white-crowned sparrow (*Zonotrichia leucophrys gambelii*) activity when daylengths shorten (Breuner & Wingfield, 2000) — suggests downstream mechanisms mediate whether circulating glucocorticoids at higher levels can bind receptors and influence behaviour. Downstream regulation of glucocorticoid effects is particularly common during reproduction (Lattin & Romero, 2013); at the same time, breeding and offspring provisioning also prompt seasonal changes in habitat selection (Amor et al., 2019).

Because both habitat selection behaviour and glucocorticoid profiles differ consistently between individuals, downstream mechanisms can only be identified through individual-level studies. Assigning individuals to non-invasively collected samples is possible as fine-scale telemetry data become more accessible and genetic capture-mark-recapture techniques are refined. Feathers, hair, and feces contain genetic material in addition to glucocorticoids, allowing samples collected non-invasively from the population to be assigned to individuals (Palme, 2019). When individuals also carry tags that collect telemetry data, areas like trails and locations

of kill or rest sites can be targeted for sampling specific individuals. Timestamped location data link individual movements to their circulating glucocorticoids during the same period. Even without telemetry data, individuals of conspicuous species like ungulates can be observed defecating or shedding hair, eliminating the need for genetic confirmation of sample identities. In the next section, we present a proof-of-concept using individual sampling to link individual habitat selection with non-invasive samples. This approach demonstrates both how short-term changes in glucocorticoid levels are responsible for habitat selection decisions, and that decisions made across life-history stages reveals the adaptive role of glucocorticoids in the habitat selection process.

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 foraging. Increased used of foraging habitat also coincides with elevated baseline glucocorticoid levels typical of ungulate calving periods (Lehman, Rota, & Millspaugh, 2019). However, calves are vulnerable to predation, and 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 security cover habitat despite better foraging opportunities elsewhere (Alves, Alves da Silva, Soares, & Fonseca, 2013).

We used integrated step selection analysis (Box 1; Avgar, Potts, Lewis, & Boyce, 2016) to test whether selection for cover and foraging habitat by 18 female elk (*Cervus canadensis*)

responded to measured fecal glucocorticoid metabolite levels, and whether the response changed between the pre-partum and post-partum periods to support survival versus current reproduction (see Supplementary 1 for detailed methods). A change in response after parturition would be consistent with expectations of the *behavior hypothesis* of seasonal glucocorticoid effects (Romero, 2002), suggesting either glucocorticoid production or its regulation supports adaptive life history transitions through habitat selection. To avoid humans in the largely agricultural landscape, our global positioning system-collared study population in southeastern Manitoba, Canada (49.134, -96.557) uses edge habitat and forest as security cover (Hinton, Freeman, St-Louis, Cornicelli, & D'Angelo, 2020). However, agricultural crops are an important source of calving season forage (Amor et al., 2019). Because animals forage in response to recovery from stressors (Dallman, Warne, Foster, & Pecoraro, 2007), we predicted that prior to calving, elk would increase selection for cropland, and decrease selection for cover habitat, following peaks in fecal glucocorticoids indicative of either intrinsic events leading up to calving or response to a recent stressor. Recovering energy after stress responses risks calf safety by exposing calves to potential encounters with predators. Thus, we expected elk to use less cropland and more cover habitat after parturition. If circulating glucocorticoids directly affect habitat selection, lower fecal glucocorticoid levels after parturition should reduce selection for cropland. The corollary is that parturient elk should select cropland and avoid cover habitat after fecal glucocorticoid peaks. However, if glucocorticoid function is mediated downstream to support calf survival, habitat selection by parturient elk should not reflect circulating glucocorticoids. Instead, we predicted a mismatch between glucocorticoids and habitat use after parturition, where even elk with higher glucocorticoid levels trade off selection for cropland in favour of cover habitat to protect their calves.

Elk habitat selection differed between the pre- and post-parturition periods when their glucocorticoid levels were elevated. While elk were six times less likely to be found in cover habitat with each unit increase in glucocorticoids before parturition, glucocorticoid levels did not change the likelihood of finding elk in cover habitat in the post-parturition period (Fig. 2, left panel). Similarly, despite a two-fold increase in likelihood of cropland use with increasing glucocorticoid levels in the pre-parturition period, elk were just as likely to be found in cropland in the post-parturition period regardless of glucocorticoid levels (Fig. 2, right panel). These results suggest the effects of glucocorticoids on post-partum habitat selection may be mediated downstream by either CBG concentration, mineralocorticoid 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 additional results.

Discussion

By reviewing how glucocorticoid production causes habitat selection, we showed how individuals use it to respond adaptively to stressors. We first integrated stress physiology with habitat selection theory to show that glucocorticoids, as an indicator of internal state, act as a link between stressors and the movement behaviour that results in habitat selection. We then provided evidence that adaptive habitat selection strategies may arise from selection pressure on glucocorticoid production causing movement. Finally, we outlined a movement-based analysis that, given the appropriate data, could be used to reveal habitat selection as a response to internal state. This approach holds promise not only for testing foundational hypotheses in space use ecology and stress physiology, but also for exploring new theoretical links among individuals,

populations, and their environment (Box 1). In our proof-of-concept, internal state and life-history-dependent stressors interacted to shape adaptive habitat selection. The presence of offspring requires safer behaviour. After calving, we found elk with higher glucocorticoid levels did not use risky habitat selection strategies to recover from stressors. For those individuals with calves, glucocorticoid function in habitat selection may have been modified downstream to limit their negative effects on reproduction (Lattin and Romero 2013), highlighting the versatility of glucocorticoids in driving adaptive responses to stressors.

Individual-based approaches highlight the role of glucocorticoids in life-history strategies. Glucocorticoids optimize allocation of energy between reproduction and survival (Schoenle et al., 2018). For example, species and populations favouring current reproduction often have elevated baseline glucocorticoids (Bókony et al., 2009), while higher stress-induced glucocorticoids favour survival (Phillips et al., 2018). But when investment in reproduction and survival varies among individuals, population-level glucocorticoid-fitness relationships become equivocal (Bonier, Martin, et al., 2009). In our proof-of-concept, we found elk reproductive status determined the effect of glucocorticoid levels on habitat selection. We showed that the same glucocorticoid levels characteristic of foraging habitat selection before calving resulted in selection for safer habitat after calving, suggesting calf presence affected glucocorticoid function. The adaptive role of glucocorticoids could be tested explicitly by extending our approach to systems in which individuals vary in both post-reproduction habitat selection strategies and fitness (Box 2). Current reproductive success may be greater for individuals that avoid foraging habitat, but the same individuals may suffer in terms of body condition and future reproduction.

Glucocorticoid-habitat selection relationships can also help us understand the proximate drivers of movements resulting in evolutionarily stable patterns of habitat use at the population level. To equalize fitness, animals distribute themselves relative to available resources, risks, and competition (Charnov, 1976; Fretwell & Lucas, 1969). For example, caribou in calving aggregations that diluted their predation risk had similar average reproductive success to individuals outside that evaded detection (Bonar et al., 2020). Individuals may adopt consistently different habitat selection strategies in response to density, or all may respond similarly; evolutionarily stable patterns do not consider which individuals move, nor how often. Dissecting individual behaviour may reveal specialist strategies, like deep versus shallow water bottlenose dolphins (*Tursiops aduncus*) with similar calving success (Strickland, Mann, Foroughirad, Levengood, & Frère, 2021). Alternatively, some individuals may generalize. In the caribou example, individuals at the periphery of calving aggregations were more likely to calve outside of the aggregation the following season while central individuals remained, suggesting calving site selection by peripheral individuals was more flexible (Bonar et al., 2020). Flexibility could result from exposure to different density-dependent stressors, e.g., predation or forage competition, that drive differences in glucocorticoid production, resulting in habitat selection that exposes individuals to new stressors. Stressor-glucocorticoid-habitat feedbacks could lead to either specialization by reinforcing selection for the same habitats, i.e., central individuals, or generalization by reinforcing flexibility, i.e., peripheral individuals. Comparing variation in glucocorticoid-habitat selection relationships across animal densities would allow us to test whether specialization or generalization underlies evolutionarily stable patterns of habitat selection (Box 2).

Conclusions

Nathan et al. (2008)'s concept of movement ecology encourages an understanding of the ultimate motivations for movement by examining the proximate causes. Our synthesis shows that one such proximate cause — glucocorticoid production — serves as a physiological link between the environment and individual habitat selection behaviour. In theory, individuals respond optimally to environmental pressures by selecting habitat, driven by changing glucocorticoid levels and downstream mediation of their effects. Selection on glucocorticoid production and mediation, when stressors are habitat-specific, could reinforce individual specialization. In turn, individual specialization supports adaptation of populations to their environments. Thus, in addition to their long-standing use as a barometer for stressors, imagining glucocorticoids as a cause of individual habitation selection fosters thinking about how they facilitate responses to changing environments. Ultimately, viewing glucocorticoids as both a cause and consequence of habitat selection fully integrates them with habitat selection theory.

Conflicts of interest: The authors have no conflicts of interest to report.

Author contributions: LN and EVW conceived of the ideas. LN designed the proof-of-concept methodology, analyzed the data, and wrote the manuscript. GFM performed the hormone extractions. All authors contributed to drafts and approved the final manuscript for publication.

Data availability: Data and code to reproduce the analysis are available at https://10.5281/zenodo.6325510

References

Alves, J., Alves da Silva, A., Soares, A. M. V. M., & Fonseca, C. (2013). Sexual segregation in red deer: Is social behaviour more important than habitat preferences? *Animal Behaviour*, *85*(2), 501–509. doi:10.1016/j.anbehav.2012.12.018

Amor, J. M., Newman, R., Jensen, W. F., Rundquist, B. C., Walter, D., & Id, J. R. B. (2019). Seasonal home ranges and habitat selection of three elk (Cervus elaphus) herds in North Dakota. *PLoS ONE*, 1–17. doi:10.1371/journal.pone.0211650

Avgar, T., Potts, J. R., Lewis, M., & Boyce, M. (2016). Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution*, 619–630. doi:10.1111/2041-210X.12528

Baldan, D., Negash, M., & Ouyang, J. Q. (2021). Are individuals consistent? Endocrine reaction norms under different ecological challenges. *Journal of Experimental Biology*, *224*(12). doi:10.1242/jeb.240499

Bókony, V., Lendvai, Á. Z., Likér, A., Angelier, F., Wingfield, J. C., & Chastel, O. (2009). Stress Response and the value of reproduction: Are birds prudent parents? *American Naturalist*, *173*(5), 589–598. doi:10.1086/597610

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, *161*(1), 1–28. doi:10.1086/343878

Bonar, M., Lewis, K. P., Webber, Q. M. R., Dobbin, M., Laforge, M. P., & Vander Wal, E. (2020). Geometry of the ideal free distribution□: individual behavioural variation and annual reproductive success in aggregations of a social ungulate. *Ecology Letters*, 1–10. doi:10.1111/ele.13563

Bonier, F., & Martin, P. R. (2016). How can we estimate natural selection on endocrine traits? Lessons from evolutionary biology. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843). doi:10.1098/rspb.2016.1887

Bonier, F., Martin, P. R., Moore, I. T., & Wingfield, J. C. (2009). Do baseline glucocorticoids predict fitness? *Trends in Ecology and Evolution*, *24*(11), 634–642. doi:10.1016/j.tree.2009.04.013

Bonier, F., Moore, I. T., Martin, P. R., & Robertson, R. J. (2009). The relationship between fitness and baseline glucocorticoids in a passerine bird. *General and Comparative Endocrinology*, *163*(1–2), 208–213. doi:10.1016/j.ygcen.2008.12.013

Bonnet-Lebrun, A. S., Somveille, M., Rodrigues, A. S. L., & Manica, A. (2020). Exploring intraspecific variation in migratory destinations to investigate the drivers of migration. *Oikos*, 187–196. doi:10.1111/oik.07689

Bonnot, N. C., Bergvall, U. A., Jarnemo, A., & Kjellander, P. (2018). Who's afraid of the big bad wolf? Variation in the stress response among personalities and populations in a large wild herbivore. *Oecologia*, *188*(1), 85–95. doi:10.1007/s00442-018-4174-7

Boonstra, R. (2013). Reality as the leading cause of stress: Rethinking the impact of chronic stress in nature. *Functional Ecology*, *27*(1), 11–23. doi:10.1111/1365-2435.12008

Boudreau, M. R., Seguin, J. L., Boonstra, R., Palme, R., Boutin, S., Krebs, C. J., & Murray, D. L. (2019). Experimental increase in predation risk causes a cascading stress response in free-ranging snowshoe hares. *Oecologia*, *191*(2), 311–323. doi:10.1007/s00442-019-04500-2

Boyce, M. S., & Mcdonald, L. L. (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution*, *14*(7), 268–272. doi:10.1016/0363-5023(94)90184-8

Brass, K. E., Herndon, N., Gardner, S. A., Grindstaff, J. L., & Campbell, P. (2020). Intergenerational effects of paternal predator cue exposure on behavior, stress reactivity, and neural gene expression. *Hormones and Behavior*, *124*(June). doi:10.1016/j.yhbeh.2020.104806

Breuner, C. W., & Wingfield, J. C. (2000). Rapid behavioral response to corticosterone varies with photoperiod and dose. *Hormones and Behavior*, *37*(1), 23–30. doi:10.1006/hbeh.1999.1554

Breuner, Creagh W., Beyl, H. E., & Malisch, J. L. (2020). Corticosteroid-binding globulins: Lessons from biomedical research. *Molecular and Cellular Endocrinology*, *514*(October 2019), 110857. doi:10.1016/j.mce.2020.110857

Brown, J. S., Morgan, R. A., & Dow, B. D. (1992). Patch use under predation risk: II. A test with fox squirrels, Sciurus niger. *Annales Zoologici Fennici*, *29*(4), 311–318.

Brown, Joel S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, *7*(10), 999–1014. doi:10.1111/j.1461-0248.2004.00661.x

Burnard, C., Ralph, C., Hynd, P., Hocking Edwards, J., & Tilbrook, A. (2017). Hair cortisol and its potential value as a physiological measure of stress response in human and non-human animals. *Animal Production Science*, *57*(3), 401–414. doi:10.1071/AN15622

Canini, F., Brahimi, S., Drouet, J. B., Michel, V., Alonso, A., Buguet, A., & Cespuglio, R. (2009). Metyrapone decreases locomotion acutely. *Neuroscience Letters*, *457*(1), 41–44. doi:10.1016/j.neulet.2009.03.103

Carroll TB, Aron DC, Findling JW, T. B. (2017). Chapter 9. Glucocorticoids and Adrenal Androgens. In: *Greenspan's Basic & Clinical Endocrinology*, 1–65.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population*

Biology, *9*(2), 129–135.

Cook, R. C., Cook, J. G., Vales, D. J., Johnson, B. K., Mccorquodale, S. M., Shipley, L. A., … Schmitz, L. (2013). Regional and seasonal patterns of nutritional condition and reproduction in elk. *Wildlife Monographs*, *184*(1), 1–45. doi:10.1002/wmon.1008

Cox, R. M., McGlothlin, J. W., & Bonier, F. (2016). Hormones as Mediators of Phenotypic and Genetic Integration: An Evolutionary Genetics Approach. *Integrative and Comparative Biology*, *56*(2), 126–137. doi:10.1093/icb/icw033

Creel, S., Winnie, J. A., & Christianson, D. (2009). Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. *Proceedings of the National Academy of Sciences*, *106*(30), 12388–12393. doi:10.1073/pnas.0902235106

Creel, Scott. (2018). The control of risk hypothesis: reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response. *Ecology Letters*, *21*(7), 947–956. doi:10.1111/ele.12975

Dallman, M. F. (2005). Fast glucocorticoid actions on brain: Back to the future. *Frontiers in Neuroendocrinology*, *26*(3–4), 103–108. doi:10.1016/j.yfrne.2005.08.001

Dallman, M. F., Strack, A. M., Akana, S. F., Bradbury, M. J., Hanson, E. S., Scribner, K. A., & Smith, M. (1993). Feast and famine: Critical role of glucocorticoids with insulin in daily energy flow. *Frontiers in Neuroendocrinology*, *14*(4), 303–347.

Dallman, M. F., Warne, J. P., Foster, M. T., & Pecoraro, N. C. (2007). Glucocorticoids and insulin both modulate caloric intake through actions on the brain. *Journal of Physiology*, *583*(2), 431–436. doi:10.1113/jphysiol.2007.136051

DeSimone, J. G., Ramirez, M. G., Elowe, C. R., Griego, M. S., Breuner, C. W., & Gerson, A. R. (2020). Developing a Stopover-CORT hypothesis: Corticosterone predicts body

composition and refueling rate in Gray Catbirds during migratory stopover. *Hormones and Behavior*, *124*(January), 104776. doi:10.1016/j.yhbeh.2020.104776

Duchamp, J. E., DeVivo, M. T., DeBerti, J. M., Heffernan, L. M., Kougher, J. D., & Larkin, J. L. (2019). Selection of calf bedding sites by female elk in the central Appalachian Mountains. *Journal of Fish and Wildlife Management*, *10*(1), 91–101. doi:10.3996/102015-JFWM-097

Eikenaar, C., Müller, F., Leutgeb, C., Hessler, S., Lebus, K., Taylor, P. D., & Schmaljohann, H. (2017). Corticosterone and timing of migratory departure in a songbird. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1846). doi:10.1098/rspb.2016.2300

Falsone, K., Jenni-Eiermann, S., & Jenni, L. (2009). Corticosterone in migrating songbirds during endurance flight. *Hormones and Behavior*, *56*(5), 548–556. doi:10.1016/j.yhbeh.2009.09.009

Fieberg, J., Signer, J., Smith, B., & Avgar, T. (2021). A 'How to' guide for interpreting parameters in habitat-selection analyses. *Journal of Animal Ecology*, (November 2020), 1–17. doi:10.1111/1365-2656.13441

Fortin, D., Morales, J. M., & Boyce, M. S. (2005). Elk winter foraging at fine scale in Yellowstone National Park. *Oecologia*, *145*(2), 335–343. doi:10.1007/s00442-005-0122-4

Foster, M. T., Warne, J. P., Ginsberg, A. B., Horneman, H. F., Pecoraro, N. C., Akana, S. F., & Dallman, M. F. (2009). Palatable foods, stress, and energy stores sculpt corticotropin-releasing factor, adrenocorticotropic and corticosterone concentrations after restraint. *Endocrinology*, *150*(5), 2325–2333. doi:10.1210/en.2008-1426

Fretwell, S. D., & Lucas, H. L. J. (1969). On territorial behavior and other factors influencing habitat distribution in birds: I Theoretical development. *Acta Biotheoretica*, *19*, 16–36. doi:10.1039/9781847558213-00059

Fudickar, A. M., Schmidt, A., Hau, M., Quetting, M., & Partecke, J. (2013). Female-biased obligate strategies in a partially migratory population. *Journal of Animal Ecology*, *82*(4), 863–871. doi:10.1111/1365-2656.12052

Goldenberg, S. Z., Douglas-Hamilton, I., & Wittemyer, G. (2018). Inter-generational change in african elephant range use is associated with poaching risk, primary productivity and adult mortality. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1879). doi:10.1098/rspb.2018.0286

Gormally, B. M. G., & Romero, L. M. (2020). What are you actually measuring? A review of techniques that integrate the stress response on distinct time-scales. *Functional Ecology*, *34*(10), 2030–2044. doi:10.1111/1365-2435.13648

Guindre-Parker, S., McAdam, A. G., Van Kesteren, F., Palme, R., Boonstra, R., Boutin, S., … Dantzer, B. (2019). Individual variation in phenotypic plasticity of the stress axis. *Biology Letters*, *15*(7), 1–7. doi:10.1098/rsbl.2019.0260

Hau, M., & Goymann, W. (2015). Endocrine mechanisms, behavioral phenotypes and plasticity: known relationships and open questions. *Frontiers in Zoology*, *12*(Suppl 1), 1–15. doi:10.1186/1742-9994-12-S1-S7

Hawlena, D., & Schmitz, O. J. (2010). Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *American Naturalist*, *176*(5), 537–556. doi:10.1086/656495

Heidinger, B. J., Nisbet, I. C. T., & Ketterson, E. D. (2006). Older parents are less responsive to a stressor in a long-lived seabird: A mechanism for increased reproductive performance with age? *Proceedings of the Royal Society B: Biological Sciences*, *273*(1598), 2227–2231. doi:10.1098/rspb.2006.3557

Herman, J. P., Figueiredo, H., Mueller, N. K., Ulrich-Lai, Y., Ostrander, M. M., Choi, D. C., & Cullinan, W. E. (2003). Central mechanisms of stress integration: Hierarchical circuitry controlling hypothalamo-pituitary-adrenocortical responsiveness. *Frontiers in Neuroendocrinology*, *24*(3), 151–180. doi:10.1016/j.yfrne.2003.07.001

Hinton, J. W., Freeman, A. E., St-Louis, V., Cornicelli, L., & D'Angelo, G. J. (2020). Habitat Selection by Female Elk During Minnesota's Agricultural Season. *Journal of Wildlife Management*, (March). doi:10.1002/jwmg.21850

Jachowski, D. S., Montgomery, R. A., Slotow, R., & Millspaugh, J. J. (2013). Unravelling complex associations between physiological state and movement of African elephants. *Functional Ecology*, *27*(5), 1166–1175. doi:10.1111/1365-2435.12118

Kirschbaum, C., Bono, E. G., Rohleder, N., Gessner, C., Pirke, K. M., Salvador, A., & Hellhammer, D. H. (1997). Effects of fasting and glucose load on free cortisol responses to stress and nicotine. *Journal of Clinical Endocrinology and Metabolism*, *82*(4), 1101–1105. doi:10.1210/jc.82.4.1101

Kleist, N. J., Guralnick, R. P., Cruz, A., Lowry, C. A., & Francis, C. D. (2018). Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(4), E648–E657. doi:10.1073/pnas.1709200115

Kotler, B. P., Brown, J., Mukherjee, S., Berger-Tal, O., & Bouskila, A. (2010). Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1687), 1469–1474. doi:10.1098/rspb.2009.2036

Lamb, C. T., Mowat, G., McLellan, B. N., Nielsen, S. E., & Boutin, S. (2017). Forbidden fruit:

human settlement and abundant fruit create an ecological trap for an apex omnivore. *Journal of Animal Ecology*, *86*(1), 55–65. doi:10.1111/1365-2656.12589

Landys-Ciannelli, M. M., Ramenofsky, M., Piersma, T., Jukema, J., & Wingfield, J. C. (2002). Baseline and stress-induced plasma corticosterone during long-distance migration in the bar-tailed godwit, Limosa lapponica. *Physiological and Biochemical Zoology*, *75*(1), 101–110. doi:10.1086/338285

Landys, M. M., Ramenofsky, M., & Wingfield, J. C. (2006). Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. *General and Comparative Endocrinology*, *148*(2), 132–149. doi:10.1016/j.ygcen.2006.02.013

Lattin, C. R., Breuner, C. W., & Michael Romero, L. (2016). Does corticosterone regulate the onset of breeding in free-living birds?: The CORT-Flexibility Hypothesis and six potential mechanisms for priming corticosteroid function. *Hormones and Behavior*, *78*, 107–120. doi:10.1016/j.yhbeh.2015.10.020

Lattin, C. R., & Romero, L. M. (2013). Seasonal variation in corticosterone receptor binding in brain, hippocampus, and gonads in House Sparrows (Passer domesticus). *Auk*, *130*(4), 591–598. doi:10.1525/auk.2013.13043

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, *79*(8), 1401–1409. doi:10.1139/z01-094

Lehman, C. P., Rota, C. T., & Millspaugh, J. J. (2019). Nutritional condition and physiological stress levels of elk in the black hills, South Dakota. *PeerJ*, *2019*(6), 1–16. doi:10.7717/peerj.7185

Lema, S. C. (2014). Hormones and phenotypic plasticity in an ecological context: Linking physiological mechanisms to evolutionary processes. *Integrative and Comparative Biology*, *54*(5), 850–863. doi:10.1093/icb/icu019

Lema, S. C. (2020). Hormones, developmental plasticity, and adaptive evolution: Endocrine flexibility as a catalyst for 'plasticity-first' phenotypic divergence. *Molecular and Cellular Endocrinology*, *502*(September 2019). doi:10.1016/j.mce.2019.110678

MacLeod, K. J., Sheriff, M. J., Ensminger, D. C., Owen, D. A. S., & Langkilde, T. (2018). Survival and reproductive costs of repeated acute glucocorticoid elevations in a captive, wild animal. *General and Comparative Endocrinology*, *268*(June), 1–6. doi:10.1016/j.ygcen.2018.07.006

Majer, A. D., Fasanello, V. J., Tindle, K., Frenz, B. J., Ziur, A. D., Fischer, C. P., … Haussmann, M. F. (2019). Is there an oxidative cost of acute stress? Characterization, implication of glucocorticoids and modulation by prior stress experience. *Proceedings. Biological Sciences*, *286*(1915), 20191698. doi:10.1098/rspb.2019.1698

Malisch, J. L., Breuner, C. W., Gomes, F. R., Chappell, M. A., & Garland, T. (2008). Circadian pattern of total and free corticosterone concentrations, corticosteroid-binding globulin, and physical activity in mice selectively bred for high voluntary wheel-running behavior. *General and Comparative Endocrinology*, *156*(2), 210–217. doi:10.1016/j.ygcen.2008.01.020

Martin, H. W., Hebblewhite, M., & Merrill, E. H. (2022). Large herbivores in a partially migratory population search for the ideal free home. *Ecology*, 0–3. doi:10.1002/ecy.3652

Matthiopoulos, J., Fieberg, J., & Aarts, G. (2020). *Species-Habitat associations*. University of Minnesota Libraries Publishing.

McNamara, J. M., & Houston, A. I. (1990). State-dependent ideal free distributions. *Evolutionary Ecology*, *4*(4), 298–311. doi:10.1007/BF02270929

Michael Romero, L. (2002). Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology*, *128*(1), 1–24. doi:10.1016/S0016-6480(02)00064-3

Morris, D. W. (2003). Toward an ecological synthesis: A case for habitat selection. *Oecologia*, *136*(1), 1–13. doi:10.1007/s00442-003-1241-4

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(49), 19052–19059. doi:10.1073/pnas.0800375105

Palma, A., Blas, J., Tella, J. L., Cabezas, S., Marchant, T. A., & Carrete, M. (2020). Differences in adrenocortical responses between urban and rural burrowing owls: Poorly-known underlying mechanisms and their implications for conservation. *Conservation Physiology*, *8*(1), 1–11. doi:10.1093/conphys/coaa054

Palme, R. (2019). Non-invasive measurement of glucocorticoids: Advances and problems. *Physiology & Behavior*, *199*(July 2018), 229–243. doi:10.1016/j.physbeh.2018.11.021

Patterson, S. H., Hahn, T. P., Cornelius, J. M., & Breuner, C. W. (2014). Natural selection and glucocorticoid physiology. *Journal of Evolutionary Biology*, *27*(2), 259–274. doi:10.1111/jeb.12286

Pecoraro, N., Reyes, F., Gomez, F., Bhargava, A., & Dallman, M. F. (2004). Chronic stress promotes palatable feeding, which reduces signs of stress: Feedforward and feedback effects of chronic stress. *Endocrinology*, *145*(8), 3754–3762. doi:10.1210/en.2004-0305

Peers, M. J. L., Majchrzak, Y. N., Neilson, E., Lamb, C. T., Hämäläinen, A., Haines, J. A., … Boutin, S. (2018). Quantifying fear effects on prey demography in nature. *Ecology*, *99*(8), 1716–1723. doi:10.1002/ecy.2381

Phillips, J. N., Gentry, K. E., Luther, D. A., & Derryberry, E. P. (2018). Surviving in the city: higher apparent survival for urban birds but worse condition on noisy territories. *Ecosphere*, *9*(9), 1–12. doi:10.1002/ecs2.2440

Potvin, D. A., & MacDougall-Shackleton, S. A. (2015). Traffic noise affects embryo mortality and nestling growth rates in captive zebra finches. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, *323*(10), 722–730. doi:10.1002/jez.1965

Rovirosa, M. J., Levine, S., Gordon, M. K., & Caba, M. (2005). Circadian rhythm of corticosterone secretion in the neonatal rabbit. *Developmental Brain Research*, *158*(1–2), 92–96. doi:10.1016/j.devbrainres.2005.06.007

Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews*, *21*(1), 55–89. doi:10.1210/er.21.1.55

Schoenle, L. A., Zimmer, C., & Vitousek, M. N. (2018). Understanding context dependence in glucocorticoid–fitness relationships: The role of the nature of the challenge, the intensity and frequency of stressors, and life history. *Integrative and Comparative Biology*, *58*(4), 777–789. doi:10.1093/icb/icy046

Schwanz, L. E., Previtali, M. A., Gomes-Solecki, M., Brisson, D., & Ostfeld, R. S. (2012). Immunochallenge reduces risk sensitivity during foraging in white-footed mice. *Animal Behaviour*, *83*(1), 155–161. doi:10.1016/j.anbehav.2011.10.020

Simon, R. N., Cherry, S. G., & Fortin, D. (2019). Complex tactics in a dynamic large herbivore–

carnivore spatiotemporal game. *Oikos*, 1318–1328. doi:10.1111/oik.06166

Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., & Middleton, A. D. (2019). Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places. *Oecologia*, *189*(4), 883–890. doi:10.1007/s00442-019-04381-5

Spée, M., Marchal, L., Thierry, A. M., Chastel, O., Enstipp, M., le Maho, Y., … Raclot, T. (2011). Exogenous corticosterone mimics a late fasting stage in captive Adélie penguins (Pygoscelis Adeliae). *American Journal of Physiology - Regulatory Integrative and Comparative Physiology*, *300*(5), 1241–1249. doi:10.1152/ajpregu.00762.2010

Strickland, K., Mann, J., Foroughirad, V., Levengood, A. L., & Frère, C. H. (2021). Maternal effects and fitness consequences of individual variation in bottlenose dolphins ' ecological niche. *Journal of Animal Ecology*, (April), 1–13. doi:10.1111/1365-2656.13513

Stuber, E. F., Carlson, B. S., & Jesmer, B. R. (2022). Spatial personalities: a meta-analysis of consistent individual differences in spatial behavior. *Behavioral Ecology*, 1–10. doi:10.1093/beheco/arab147

Swain, D. P., Benoît, H. P., & Hammill, M. O. (2015). Spatial distribution of fishes in a Northwest Atlantic ecosystem in relation to risk of predation by a marine mammal. *Journal of Animal Ecology*, *84*(5), 1286–1298. doi:10.1111/1365-2656.12391

Taff, C. C., Schoenle, L. A., & Vitousek, M. N. (2018). The repeatability of glucocorticoids: A review and meta-analysis. *General and Comparative Endocrinology*, *260*, 136–145. doi:10.1016/j.ygcen.2018.01.011

Tennessen, J. B., Parks, S. E., Swierk, L., Reinert, L. K., Holden, W. M., Rollins-Smith, L. A., … Langkilde, T. (2018). Frogs adapt to physiologically costly anthropogenic noise. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1891), 1–9.

doi:10.1098/rspb.2018.2194

Veldhuis, H. D., De Kloet, E. R., Van Zoest, I., & Bohus, B. (1982). Adrenalectomy reduces exploratory activity in the rat: A specific role of corticosterone. *Hormones and Behavior*, *16*(2), 191–198. doi:10.1016/0018-506X(82)90018-6

Vitousek, M. N., Jenkins, B. R., & Safran, R. J. (2014). Stress and success: Individual differences in the glucocorticoid stress response predict behavior and reproductive success under high predation risk. *Hormones and Behavior*, *66*(5), 812–819. doi:10.1016/j.yhbeh.2014.11.004

Wada, H. (2008). Glucocorticoids: Mediators of vertebrate ontogenetic transitions. *General and Comparative Endocrinology*, *156*(3), 441–453. doi:10.1016/j.ygcen.2008.02.004

Wingfield, J. C., & Sapolsky, R. M. (2003). Reproduction and resistance to stress: When and how. *Journal of Neuroendocrinology*, *15*(8), 711–724. doi:10.1046/j.1365-2826.2003.01033.x

Yin, B., Yang, S., Shang, G., & Wei, W. (2017). Effects of predation risk on behavior, hormone levels, and reproductive success of plateau pikas. *Ecosphere*, *8*(1), 1–12. doi:10.1002/ecs2.1643

Zollinger, S. A., Dorado-Correa, A., Goymann, W., Forstmeier, W., Knief, U., Bastidas-Urrutia, A. M., & Brumm, H. (2019). Traffic noise exposure depresses plasma corticosterone and delays offspring growth in breeding zebra finches. *Conservation Physiology*, *7*(1), 1–15. doi:10.1093/conphys/coz056

Box 1 – Modelling habitat selection using glucocorticoids

Stress physiologists and space use ecologists alike often define habitat as a spatially discrete set of physical and biological conditions with distinct fitness implications (Morris, 2003). However, more contemporary definitions of habitat distinguish between geographic and environmental space, with the latter comprised of spatiotemporally dynamic combinations of environmental variables that includes stressors (Matthiopoulos, Fieberg, & Aarts, 2020). Mobile animals that face stressors — often marked by changing glucocorticoid levels — can alleviate their negative effects by moving between environmental spaces (Nathan et al., 2008). Thus, the relationship between glucocorticoids and fitness should be considered through the lens of habitat selection.

Habitat selection functions (HSFs) quantify how environmental variables like stressors influence which habitats 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 & 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, Signer, Smith, & Avgar, 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 constrained. 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. 1; 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. 1). 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. 1 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. 1 b)?

Box 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, Sheriff, Ensminger, Owen, & Langkilde, 2018; Majer et al., 2019), 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 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. With emerging evidence habitat selection behaviour is indeed repeatable (Stuber et al., 2022), and that continuous adult exposure 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 & 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.

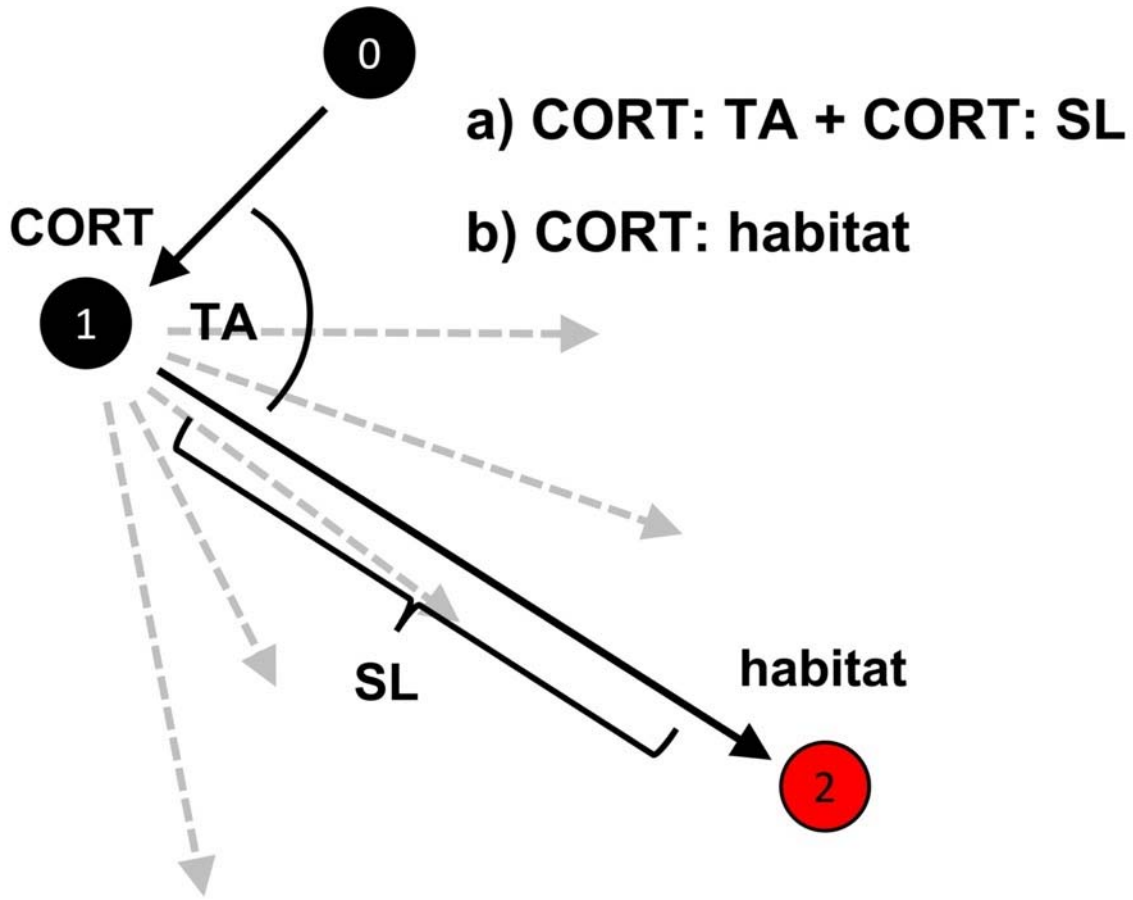

Figure 1. Schematic representation of used locations (circles) along a movement path from $t = 0$ through $t = 2$. Solid arrows represent the movement path between location points, and dashed arrows represent five available trajectories an animal could have taken at $t = 1$, drawn from assumed distributions 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.

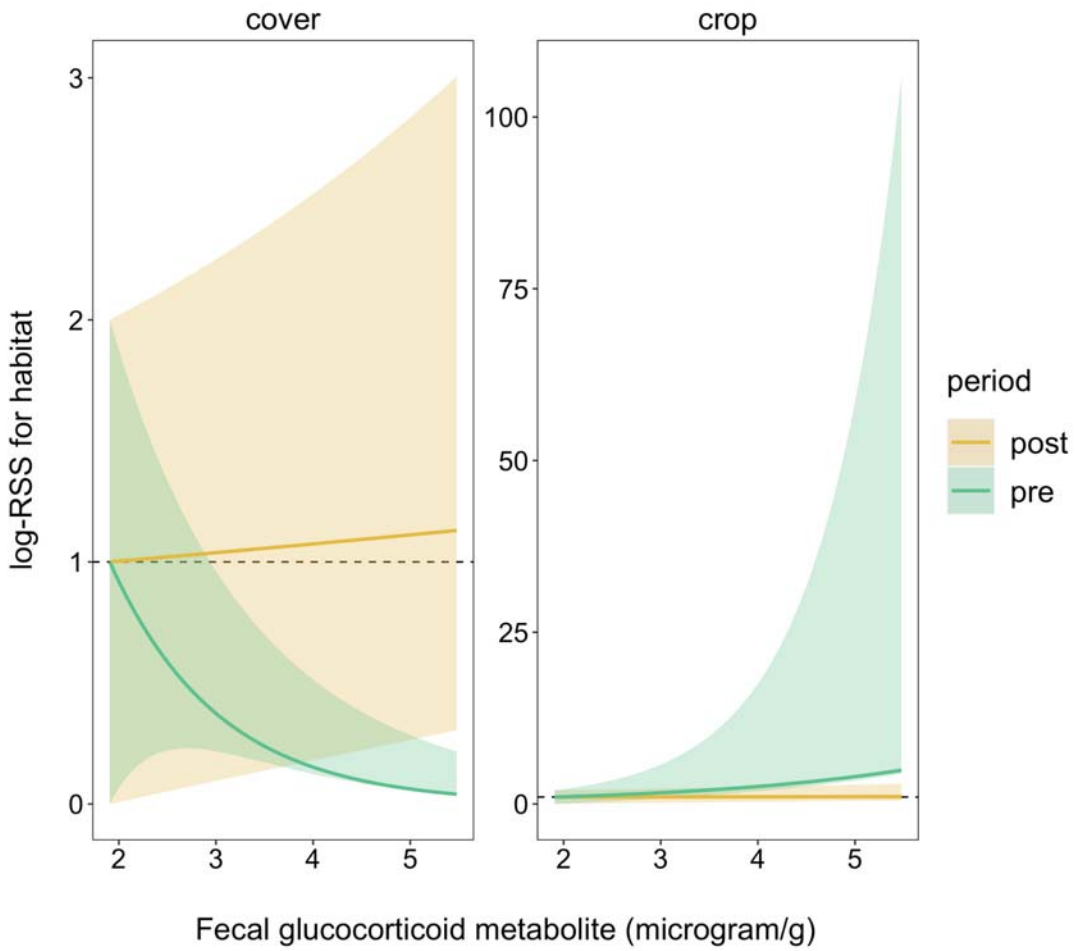

Figure 2. Log relative selection strength (RSS) for a location in cover habitat (left panel) or cropland (right panel), relative to a location in a different land cover type, with increasing fecal glucocorticoid metabolite levels. Green lines show the change in RSS between these locations in the pre-parturition period, and gold lines in the post-parturition period. Ribbons show the bootstrapped 95% confidence interval around the estimated RSS.

Supplementary 1: 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 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, Bildstein, & Mueller, 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 variation in return location, we

used a 300 m radius buffer (Wallace & 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 collected 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 & 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 (caribou, *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, Palme, Zenker, & Möstl, 2003). This makes FGM an integrated proxy for both baseline and stress-induced circulating glucocorticoids during the 18-22 h preceding defecation.

Aside from individual differences in circulating levels, FGM levels are also influenced by metabolism of circulating glucocorticoids and other factors affecting them after defecation. These variables create discrepancies between circulating glucocorticoids and FGM that are not attributable to stressors. For example, FGM concentration in feces can vary considerably with individual diet (Dantzer, McAdam, Palme, Boutin, & Boonstra, 2011) and gut transport time (Scheiber, Kralj, & Kotrschal, 2005), even among fecal samples collected relatively close together in time. To control for the confounding effect of diet and gut transport time on FGM levels, we only included individuals we were able to sample at least three times over the sampling period. FGM recovery from samples is also affected by moisture in the field and failure to promptly store samples after collection (Romero & Wingfield, 2016). Thus, we also avoided sampling after rain, collected samples within 24 hours of suspected defecation, and froze samples as soon as possible (< 8 hours) after collection (Sheriff, Dantzer, Delehanty, Palme, & Boonstra, 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 & 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 1 in manuscript). 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, Potts, Lewis, & Boyce, 2016). Constraining available steps in this way simultaneously estimates movement and habitat selection coefficients (J. Fieberg, Signer, Smith, & Avgar, 2021), making it possible to test the effect of temporally dynamic variables — such as changes in glucocorticoid levels — on habitat selection.

We fit separate population-level iSSA models for selection of cropland and cover habitat (Agriculture and Agri-Food Canada Annual Crop Inventory 2019-2020). To limit our selection inferences to movement bouts associated with known FGM levels, we subsampled GPS data to the 18–h preceding each sample. 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., 2016). 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. Though our question centred around the combined influence of parturition and glucocorticoids on habitat selection, we also expected independent effects of each. To account for all potential relationships in the model, we included four predictors of selection: habitat at the end of each step; habitat interacted with a binary variable for period and habitat interacted with FGM at the start of the movement bout to account for their effects; and a three-way habitat-period-FGM interaction. We also included the natural log of the step length and cosine of the turn angle to account for the movement process. Finally, to account for correlation between samples from individuals (Hebblewhite & Merrill, 2008), differences in sample size among individuals, and individual differences in habitat selection (Gillies et al.,

2006), we included random intercepts and slopes for both habitat 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, Signer, & Fieberg, 2020).

We bootstrapped both the cropland and cover models to obtain confidence intervals around coefficient effect sizes. We sampled individual movement bouts with replacement 1,000 times, in each iteration retaining all the location data belonging to the individual at her corresponding FGM level (J. R. Fieberg, Vitense, & Johnson, 2020). We used relative selection strength (RSS) a measure of habitat selection effect size across the range of FGM levels in the population. RSS quantifies the ratio of the relative probability 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, Lele, Keim, & Boyce, 2017). In our case, we quantified the RSS for cropland and cover habitats at the median FGM level versus a range of elevated levels and compared the difference in effect sizes by period.

We performed simulations and sub-analyses to validate our model inferences. First, we validated our cropland and cover habitat iSSAs with used-habitat calibration (UHC) plots (J. R. 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 detect whether model covariates are important for predicting selection. Unlike other methods, UHC is appropriate for validating

stratified habitat selection analyses like iSSA (J. R. Fieberg et al., 2018). The iSSA approach we used is also appropriate for combined inferences on multiple individuals. Importantly, the model designed to account for missing observations by shrinking random coefficient estimates towards the mean (Muff et al., 2020). However, for redundancy, we also fit a sub-model to ensure our coefficient estimates were not driven by the subset of individuals having FGM data in both the pre- and post-parturition periods (Fig. S1).

Supplementary 2 – Proof-of-concept results

We used 65 fecal glucocorticoid metabolite samples from between May 14 and August 16 in 2019 and 2021, representative of 11 of 13 sampled individuals. We excluded two individuals from which we collected one and two samples to avoid biasing glucocorticoid profiles. The remaining individuals each had between four and 15 fecal samples (median = 5) and between 13 and 157 location points (median = 44) across the pre- and post-parturition periods (Fig. S1). 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 40 to 1,000 available: used points (Fig. S2). Though individual sample sizes and location points per individual were few, small samples are sufficient for RSF inference when selection strength is strong and landscape heterogeneity is low (Street et al. 2021).

Use of cropland and cover habitat differed relative to other land cover types throughout the calving season (Fig. S3). In general, elk were 10 times more likely ($e^{ß}$ = 9.98 95% CI 4.70, 124.24) to be found in cover habitat than other land cover types on the landscape. Their use of cover habitat decreased after parturition when they were less than twice as likely to use cover habitat in comparison to other land cover types ($e^{ß}$ = 1.46, 95% CI 0.91, 1.93). Elk generally

avoided cropland; they were almost three times as likely ($e^{ß}$ = 0.35, 95% CI 0.03, 0.47) to be found in other landcover types over cropland. In contrast to cover habitat, use of cropland increased relative to other land cover types between the pre- and post-parturition periods, when elk were approximately as likely to use cropland as other landcover types ($e^{ß}$ = 1.03, 95% CI 0.53, 1.87).

Glucocorticoid levels affected use of cropland and cover habitats differently before and after parturition (Fig. S3). Elk were more likely to be found in cropland, and less likely to be found in cover habitat, following elevated FGM levels. A single standard deviation increase in FGM corresponded to a 6-fold reduction in the likelihood of elk using cover habitat versus an alternative land cover ($e^{ß}$ = 1.67, 95% CI 1.20, 2.37). For the same unit increase in FGM, there was a corresponding 2-fold increase in the likelihood of elk using cropland versus alternative land cover ($e^{ß}$ = 0.83, 95% CI 0.46, 1.27). However, use of cover habitat and cropland in response to FGM changed after parturition, when a unit increase resulted in similar use of both habitats to the pre-parturition period without elevated FGM (Fig. S3).

Our model validations supported inferences from our cropland and cover habitat models. Coefficients from both crop and cover models discriminated used from available locations in terms of their habitat values (Figs. S4–S5). Both habitat models were also relatively well calibrated, with observed habitat use close to that predicted by models (Figs. S4–S5). Finally, qualitative inferences from our sub-models including only the six individuals with data from both pre- and post-calving were not appreciably different from those of the full models (Table S1).

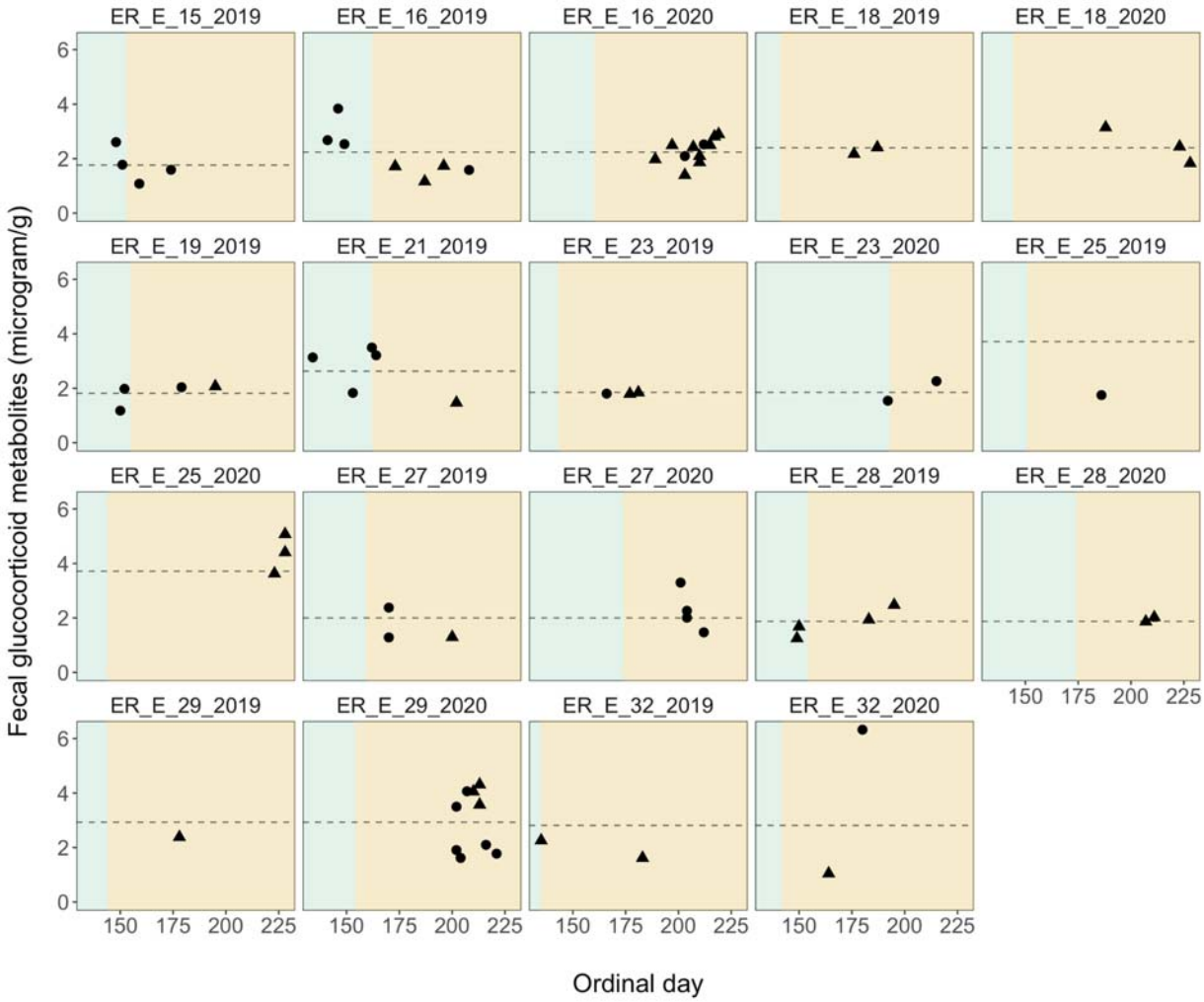

Figure S1. Collection dates and glucocorticoid metabolite levels from 65 fecal samples from 11 individual elk over two years. Each panel represents a single elk, with green indicating the individual's pre-parturition period, and gold indicating the post-parturition period. Circles denote samples identified 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.

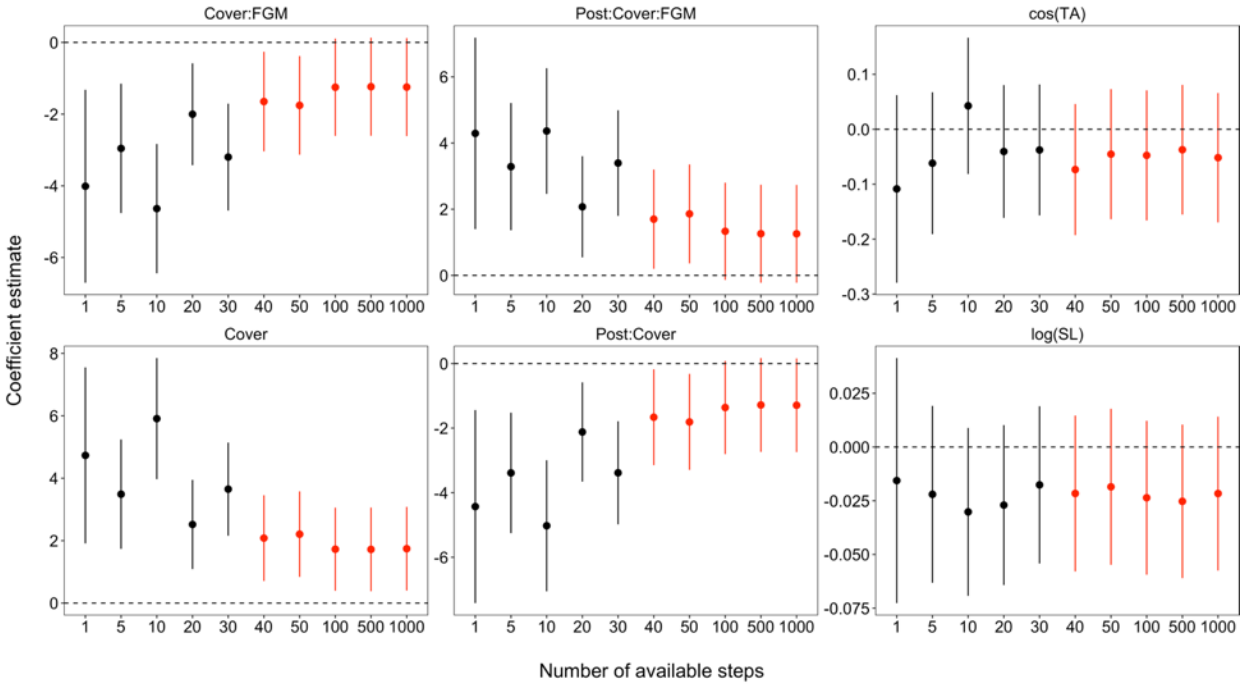

Figure S2. Model coefficient estimates (points) and standard errors (vertical lines) from sub-analysis of cover model varying ratios of used: available points. Black points and lines indicate lower used: available ratios where model coefficients vary, and red points and indicate the used: available ratios after which coefficients remain relatively consistent. SL = step length, TA = turn angle, post = post-parturition period (reference category relative to pre-parturition period), and FGM = fecal glucocorticoid metabolite levels.

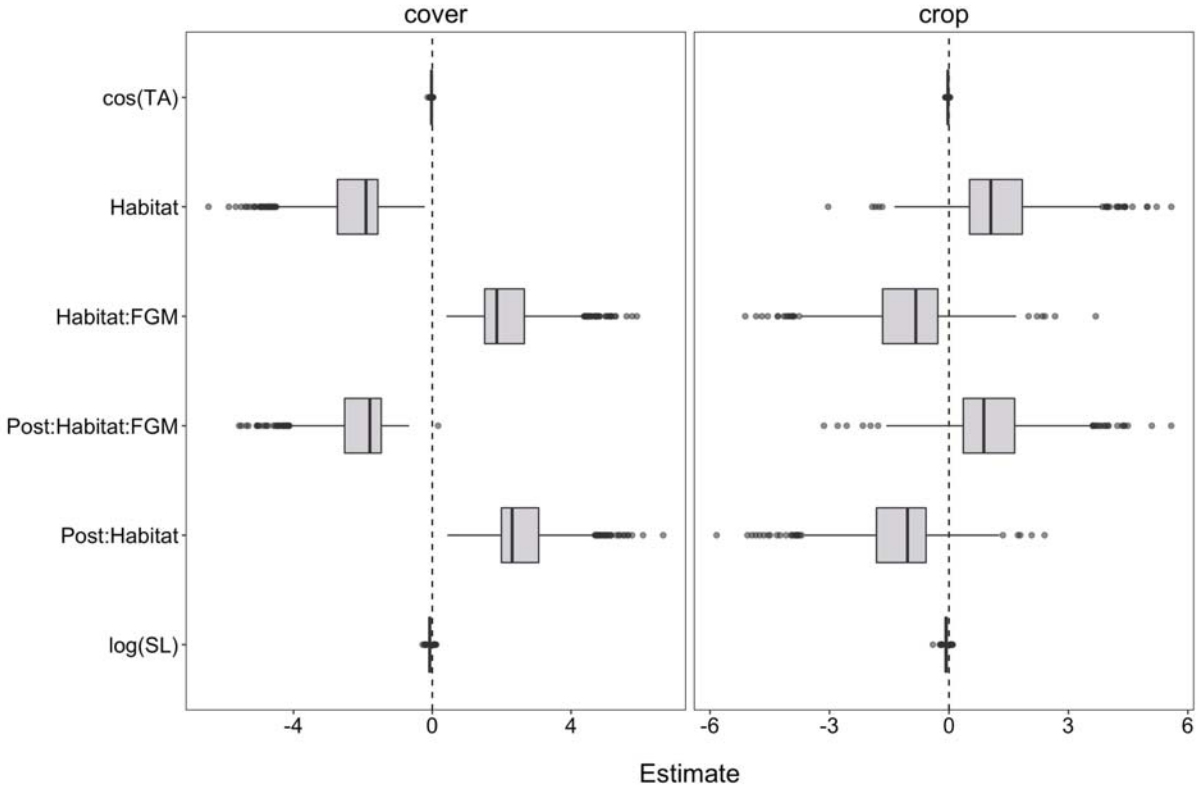

Figure S3. Bootstrapped iSSA coefficient estimates from the cover habitat (left panel) and cropland habitat (right panel) models. Dark lines represent the median coefficient estimate over 500 bootstraps, and whiskers show the 95% confidence interval of the estimates. SL = step length, TA = turn angle, post = post-parturition period (reference category relative to pre-parturition period), and FGM = fecal glucocorticoid metabolite levels.

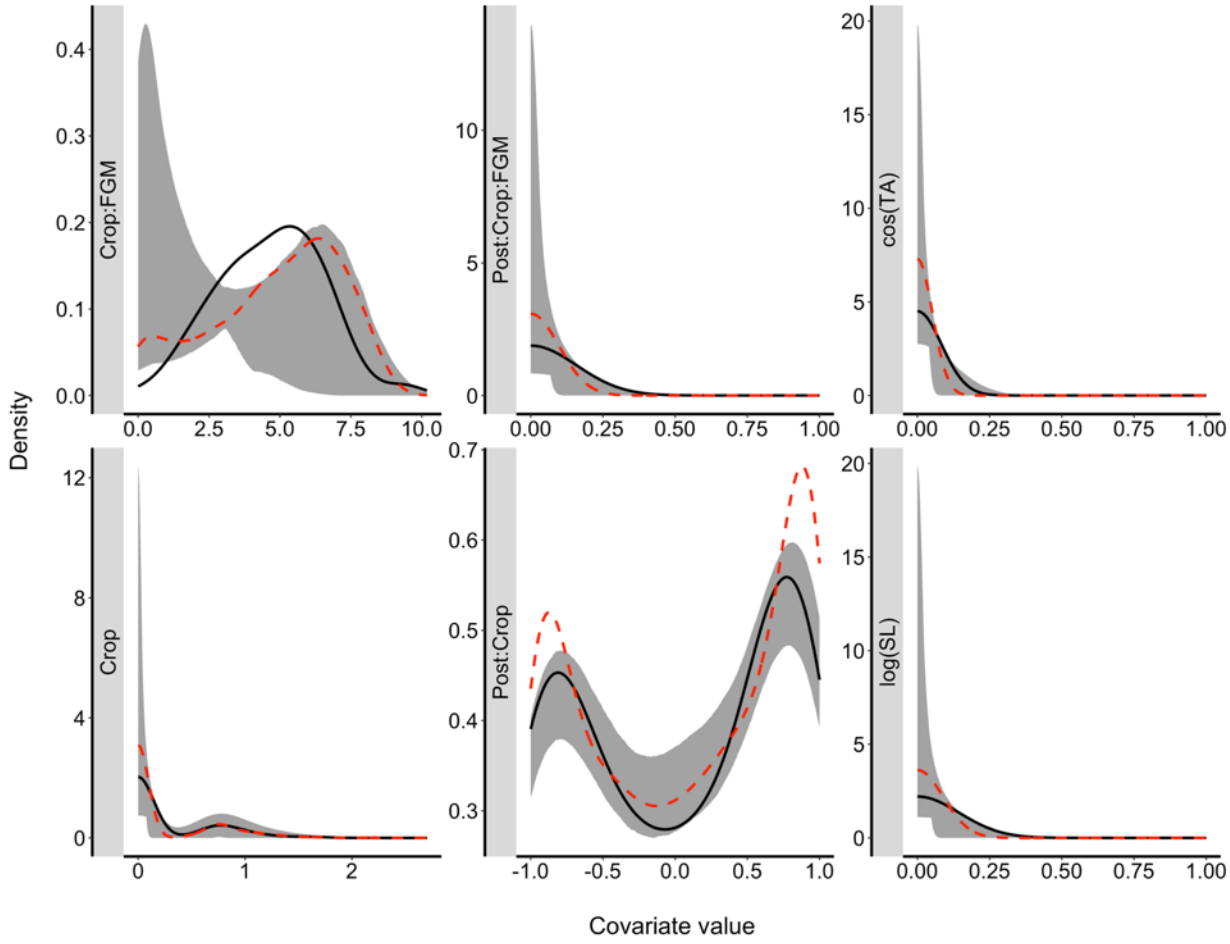

Figure S4. Used-habitat calibration comparing distributions of habitat values at used locations (black solid lines) to habitat values at available locations (red dashed lines) and 95% confidence intervals of used locations predicted by the cropland model (grey ribbons). Predicted values agree with observed values when grey ribbons overlap with black lines. Differences between black-solid and grey-dashed lines indicate elk are likely to be found at locations with dissimilar characteristics to those available. SL = step length, TA = turn angle, post = post-parturition period (reference category relative to pre-parturition period), and FGM = fecal glucocorticoid metabolite levels.

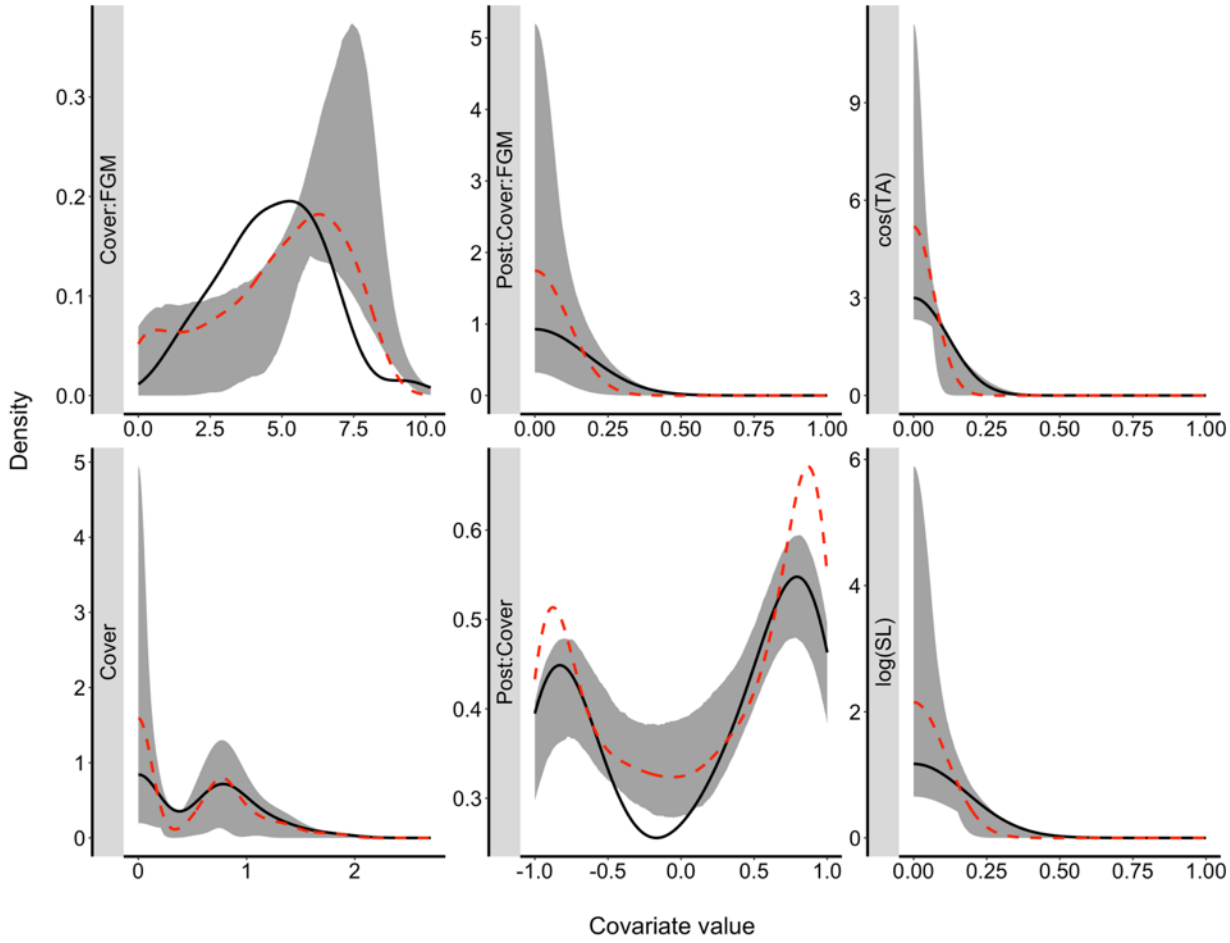

Figure S5. Used-habitat calibration comparing distributions of habitat values at used locations (black solid lines) to habitat values at available locations (red dashed lines) and 95% confidence intervals of used locations predicted by the cover habitat model (grey ribbons). Predicted values agree with observed values when grey ribbons overlap with black lines. Differences between black-solid and grey-dashed lines indicate elk are likely to be found at locations with dissimilar characteristics to those available. SL = step length, TA = turn angle, post = post-parturition period (reference category relative to pre-parturition period), and FGM = fecal glucocorticoid metabolite levels.

Table S1. Model coefficients (95% confidence intervals) from crop and cover sub-models including six of 11 elk having location and hormone data during both the pre- and post-periods. SL = step length, TA = turn angle, post = post-parturition period (reference category relative to pre-parturition period), and FGM = fecal glucocorticoid metabolite levels.

	Crop		Cover	
Coefficient				
Habitat	-0.20	(-1.28, 0.88)	1.31	(0.39, 2.23)
Habitat: FGM	-0.02	(-1.21, 1.17)	-0.74	(-1.72, 0.24)
Post: Habitat	0.91	(-0.61, 2.43)	-0.70	(-2.00, 0.60)
Post: Habitat: FGM	-0.89	(-2.57, 0.79)	0.71	(-0.67, 2.09)
log(SL)	-0.04	(-0.09, 0)	-0.04	(-0.09, 0.01)
cos(TA)	0.02	(-0.13, 0.17)	0.01	(-0.14, 0.16)

References

Ashley, N. T., Barboza, P. S., Macbeth, B. J., Janz, D. M., Cattet, M. R. L., Booth, R. K., & Wasser, S. K. (2011). Glucocorticosteroid concentrations in feces and hair of captive caribou and reindeer following adrenocorticotropic hormone challenge. *General and Comparative Endocrinology*, *172*(3), 382–391. doi:10.1016/j.ygcen.2011.03.029

Avgar, T., Lele, S. R., Keim, J. L., & Boyce, M. S. (2017). Relative Selection Strength: Quantifying effect size in habitat- and step-selection inference. *Ecology and Evolution*, *7*(14), 5322–5330. doi:10.1002/ece3.3122

Avgar, T., Potts, J. R., Lewis, M., & Boyce, M. (2016). Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution*, 619–630. doi:10.1111/2041-210X.12528

Bracis, C., Bildstein, K. L., & Mueller, T. (2018). Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography*, (Watts 1998), 1–11. doi:10.1111/ecog.03618

Brook, R. K. (2010). Habitat selection by parturient elk (Cervus elaphus) in agricultural and forested landscapes. *Canadian Journal of Zoology*, *88*(10), 968–976. doi:10.1139/Z10-061

Dantzer, B., McAdam, A. G., Palme, R., Boutin, S., & Boonstra, R. (2011). How does diet affect fecal steroid hormone metabolite concentrations? An experimental examination in red squirrels. *General and Comparative Endocrinology*, *174*(2), 124–131. doi:10.1016/j.ygcen.2011.08.010

Escribano-Avila, G., Pettorelli, N., Virgós, E., Lara-Romero, C., Lozano, J., Barja, I., … Puerta, M. (2013). Testing Cort-Fitness and Cort-Adaptation hypotheses in a habitat suitability gradient for roe deer. *Acta Oecologica*, *53*(January 2018), 38–48. doi:10.1016/j.actao.2013.08.003

Fieberg, J. R., Forester, J. D., Street, G. M., Johnson, D. H., ArchMiller, A. A., & Matthiopoulos, J. (2018). Used-habitat calibration plots: a new procedure for validating species distribution, resource selection, and step-selection models. *Ecography*, *41*(5), 737–752. doi:10.1111/ecog.03123

Fieberg, J. R., Vitense, K., & Johnson, D. H. (2020). Resampling-based methods for biologists. *PeerJ*, *2020*(3). doi:10.7717/peerj.9089

Fieberg, J., Signer, J., Smith, B., & Avgar, T. (2021). A 'How to' guide for interpreting parameters in habitat-selection analyses. *Journal of Animal Ecology*, (November 2020), 1–17. doi:10.1111/1365-2656.13441

Geist, V. (2002). North America elk: Ecology and management. In D. E. Toweill & J. W. Thomas (Eds.), *North America elk: Ecology and management* (1st ed., pp. 389–433). Washington, DC: Wildlife Management Institute.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., … Jerde, C. L. (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, *75*(4), 887–898. doi:10.1111/j.1365-2656.2006.01106.x

Gormally, B. M. G., & Romero, L. M. (2020). What are you actually measuring? A review of techniques that integrate the stress response on distinct time-scales. *Functional Ecology*, *34*(10), 2030–2044. doi:10.1111/1365-2435.13648

Hebblewhite, M., & Merrill, E. H. (2008). Modeling wildlife-human relationship for social species with mixed-effects resource selection models - Supplementary Materials. *Journal of Applied Ecology*, *45*(3), 834–844. doi:10.1111/j.l365-2664.2008.01466.x

Huber, S., Palme, R., Zenker, W., & Möstl, E. (2003). Non-Invasive Monitoring of the

Adrenocortical Response in Red Deer. *Journal of Wildlife Management*, *67*(2), 258–266.

Johnson, B. K., Mccoy, T., Kochanny, C. O., Cook, R. C., Journal, S., Medicine, W., & Sep, N. (2006). Evaluation of vaginal implant transmitters in elk (Cervus elaphus nelsoni). *Journal of Zoo and Wildlife Medicine*, *37*(3), 301–305.

Marchand, P., Garel, M., Morellet, N., Benoit, L., Chaval, Y., Itty, C., … Marchand, P. (2021). A standardised biologging approach to infer parturition□: An application in large herbivores across the hider- - follower continuum. *Methods in Ecology and Evolution*, 1–14. doi:10.1111/2041-210X.13584

Muff, S., Signer, J., & Fieberg, J. (2020). Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *Journal of Animal Ecology*, *89*(1), 80–92. doi:10.1111/1365-2656.13087

Newediuk, L., & Vander Wal, E. (2021). Predicting the individual identity of non □ invasive faecal and hair samples using biotelemetry clusters. *Mammalian Biology*, (0123456789). doi:10.1007/s42991-021-00173-8

Romero, L. M., & Wingfield, J. C. (2016). *Tempests, poxes, predators, and people: stress in wild animals and how they cope* (1st ed.). New York: Oxford University Press.

Scheiber, I. B. R., Kralj, S., & Kotrschal, K. (2005). Sampling effort/frequency necessary to infer individual acute stress responses from fecal analysis in greylag geese (Anser anser). *Annals of the New York Academy of Sciences*, *1046*(0), 154–167. doi:10.1196/annals.1343.012

Sheriff, M. J., Dantzer, B., Delehanty, B., Palme, R., & Boonstra, R. (2011). Measuring stress in wildlife: Techniques for quantifying glucocorticoids. *Oecologia*, *166*(4), 869–887. doi:10.1007/s00442-011-1943-y

Wallace, M. C., & Krausman, P. R. (1992). Neonatal Elk Habitat in Central Arizona. *The*

Biology of Deer, 69–75. doi:10.1007/978-1-4612-2782-3_10

Willard, S., Sasser, R., Gillespie, J., JT, J., Welsh, T. J., & Randel, R. (1994). Methods for pregnancy determination and the effects of body condition on pregnancy status in Rocky Mountain elk. *Theriogenology*, *42*, 1095–1102.