EXAMINING THE INTRINSIC AND EXTRINSIC DIMENSIONS OF UNGULATE MOVEMENT AND RESOURCE SELECTION

By

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ABSTRACT

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Large mammalian herbivores are extensively-studied worldwide, often to gain new insights into the relationship between these animals and their environment. Elucidating a mechanistic basis of processes such as movement and resource selection can inform conservation and management practice. Therein, relating these processes to intrinsic (both state- and stagerelated) and extrinsic dimensions (abiotic and biotic characteristics of the environment) is of paramount importance. I center my thesis on the role of these two dimensions in ungulate movement and resource selection. In chapter 1, I focused on the extrinsic dimension by employing both linear and non-linear regression techniques to evaluate the plausibility of "critical temperatures" in movement of moose (Alces alces) in Norway, using a rich dataset of GPS-location data. I found weak evidence for these thresholds in the movement of moose, and I discuss this finding in light of a changing climate. In Chapter 2 I studied the intrinsic dimension via an examination of individual variation in resource selection of elk (*Cervus elaphus*) in the Ozark Mountains of Missouri. I investigated the consequences of prevailing practice, whereby individual information is pooled to fit an aggregate-level model, by fitting models at the level of each individual elk and making comparisons. I found that important inferences can be missed if resource selection is only considered at the aggregate level. In summary, my research demonstrates the importance of using wild-living individuals and multiple modeling perspectives to develop functional population- or species-level inferences regarding the roles of intrinsic and extrinsic factors in animal-environment relationships of ungulates.

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iii

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TABLE OF CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	viii
INTRODUCTION REFERENCES	1 5
CHAPTER 1	9
INVESTIGATING SIGNATURES OF HEAT STRESS IN WILD-LIVING MOOSE	9
Abstract	9
1.1. Introduction	11
1.2. Methods	14
1.2.1. Study area	14
1.2.2. GPS-tracking and temperature	15
1.2.3. Movement Metric Calculation	15
1.2.4. Mixed-effects modeling	17
1.2.5. Probabilistic Movement Metrics	19
1.3. Results	20
1.4 Discussion	23
1.5. Conclusions	27
Acknowledgements	29
APPENDIX	30
REFERENCES	46
CHAPTER 2	53
EVALUATING THE CONSEQUENCES ON ECOLOGICAL INFERENCE OF	
AGGREGATING WILDLIFE TELEMETRY DATA WHEN ESTIMATING RESOURCE	
SELECTION FUNCTIONS	53
Abstract	53
2.1. Introduction	55
2.2. Methods	58
2.2.1. Resource selection data	58
2.2.2. Environmental variables	59
2.2.3. RSF modeling	59
2.2.4. Comparison between aggregate- and individual-level RSFs	62
2.3. Results	64
2.3.1. Number and composition of parameters	65
2.3.2. Parameter estimates	65
2.3.3. Predicted relative probabilities	66
2.4. Discussion	67
Acknowledgements	73
APPENDIX	74

REFERENCES	
CONCLUSION	
REFERENCES	89

LIST OF TABLES

Table 1.1. R te or	Review of articles published between 2010-2015 that have directly referenced the emperature thresholds suggested by Renecker and Hudson (1986) to develop models r discuss climate related impacts on moose
Table 1.2. C N cr du be	Counts of temperatures recorded by GPS collars of GPS-tracked moose in central Norway from July through August of each year during 2006-2010. Counts during repuscular period ($20:00 - 06:00$ next day) above, counts of temperatures recorded uring daytime period ($08:00 - 18:00$) middle, differences of temperature (Δ T) etween crepuscular and daytime periods below
Table 1.3. C	Comparison of ARMA error structure for linear mixed models of crepuscular (left alf) and daytime (right half) movements of moose, sorted by ascending AIC score. 34
Table 1.4. C m cr	Comparison of best approximating LMMs. The top three linear mixed models of novement rate (Rate) and mean turning angle (Turn) response variables during repuscular and daytime movement metrics, sorted by increasing AIC score
Table 1.5. C m cr	Comparison of best approximating AMMs. The top three additive mixed models of novement rate (Rate) and mean turning angle (Turn) response variables during repuscular and daytime movement metrics, sorted by increasing AIC score
Table 1.6. B ap M m	Best approximating LMMs, daytime hours. Parameter estimates for best pproximating linear mixed models of daytime movements, as determined by AIC. Max. daytime collar temperature (T_{day}) was the temperature covariate used in these nodels
Table 1.7. B ap T cr –	Best approximating LMMs, crepuscular hours. Parameter estimates for best pproximating linear mixed models of crepuscular movements, as determined by AIC. The temperature covariate used in each model is indicated in parentheses. $T_{crep} = max$. repuscular collar temperature, $T_{day} = max$. daytime collar temperature, and $\Delta T = T_{day} - T_{crep}$
Table 2.1. W in in tr as w p	VAIC values for top 10 aggregate-level resource selection function models. + ndicates an environmental variable included in the model, spaces left blank if not ncluded. Environmental variable abbreviations as follows: D2t = distance to two- rack road; Dpav = Distance to paved road (m); Slope = slope (degrees); Aspect = spect (degrees); Rd dens = road density (km/km ²); D edge = Distance to nearest wooded edge; % Can = percent forested canopy cover; Rx burn = years since rescribed fire; Habitat = indicator variables for 8 cover types

LIST OF FIGURES

Figure 1.1	. Summer locations of GPS-tracked moose in Central Norway during 2006-2010. Norway is shaded light blue, other countries colored olive
Figure 1.2	. Mean ln-transformed speeds (\pm SE) of moose movement in Central Norway, during the months of July and August of each year from 2006-2010 (n = 152 moose). Speeds were estimated from continuous-time correlated random walk movement models fit to each summer track using the package <i>crawl</i> in R
Figure 1.3	. Boxplots of daytime (a) and crepuscular (b) movement metrics calculated from GPS data on moose tracked during July-August of 2006-2010. Movement metrics are binned by maximum collar temperature recorded during the respective period for which the movement metric was calculated
Figure 1.4	. Predictions based on best approximating AMMs (\pm 95% CI shaded grey) for movement rates of male moose at median elevation during daytime (a) and crepuscular periods (b-d). Daytime movement rates predicted as a function of daytime temperature, and crepuscular movement rates predicted as a function of crepuscular temperature (b), daytime temperature (c), and the difference between daytime and crepuscular temperature (d)
Figure 1.5	Predictions based on best approximating AMMs (\pm 95% CI shaded grey) for mean turning angles of male moose at median elevation during daytime (a) and crepuscular periods (b-d). Daytime turning angles predicted as a function of daytime temperature, and crepuscular turn angles predicted as a function of crepuscular temperature (b), daytime temperature (c), and the difference between daytime and crepuscular temperature (d)
Figure 1.6	Predictions based on best approximating AMMs of movement rates calculated from probabilistic movement paths. Predictions for daytime (a) and crepuscular (b-d) movement rates of male moose. Daytime movement rates predicted as a function of daytime temperature, and crepuscular movement rates predicted as a function of crepuscular temperature (b), daytime temperature (c), and the difference between daytime and crepuscular temperature (d)
Figure 1.7	Predictions based on best approximating AMMs of mean turning angles calculated from probabilistic movement paths. Predictions for daytime (a) and crepuscular (b-d) movement rates of male moose. Daytime movement rates predicted as a function of daytime temperature, and crepuscular movement rates predicted as a function of crepuscular temperature (b), daytime temperature (c), and the difference between daytime and crepuscular temperature (d)
Figure 2.1	. Inclusion of parameters at the individual level in top models (a panel) and top 5% of models (b panel) as ranked by WAIC for elk reintroduced into the Missouri Ozarks

INTRODUCTION

The collective ability to measure and map various ecological phenomena has expanded dramatically over the last two decades, as evidenced by a myriad of novel data types and volumes, ushering in a new era of inquiry that has been likened to the bioinformatics movement of the early 2000's (Jones et al., 2006; Michener and Jones, 2012). Unprecedented rates of data volume and data acquisition have now become commonplace due to advancements in technology and networking, leading to a "data deluge" (Baraniuk, 2011). Novel data collection methods including sensor networks, such as the National Ecological Observatory Network (NEON), automated sensing (including camera trap technology), and both aircraft- and satellite-borne remote sensing platforms are now regularly used to collect environmental observations that have great utility for ecological research (Keller et al., 2008; Pfeifer et al., 2012; Porter et al., 2009, 2012). Not surprisingly, developments that facilitate the quantitative analysis of big ecological data have emerged in tandem, from best practices in data management to statistical methods and software tools (Borer et al., 2009; Purves et al., 2013; Steiniger et al., 2009).

These advancements have altered the trajectory of scientific discourse in virtually all types of applied ecological research, but one area of particular growth has been animal movement ecology. This previously marginal sub-discipline only received cursory attention until recent years, when a paradigm shift has been facilitated by decreasing costs and increasing flexibility of tracking methods, most notably those based on Global Positioning System (GPS) technologies (Hussey et al., 2015; Kays et al., 2015; Nathan et al., 2008). A central theme of this new paradigm is a shift in focus from Eulerian (i.e. place- or population-based) approaches to Lagrangian (i.e. individual-based) approaches for studying movement and space use (Nathan et al., 2008; Smouse et al., 2010). When combined with data derived from sensor networks and

remote sensing systems, high-resolution tracking data holds promise for revealing mechanistic connections between individual animals and their environment (Cooke et al., 2004; Schick et al., 2008). Recent advancements in Global Positioning System (GPS) telemetry technology provide a venue to study the mechanisms underlying fundamental concepts in animal ecology, such as home range estimation and resource use (Cagnacci et al., 2010).

A mechanistic understanding of species movement through human-dominated landscapes is of critical importance to both conservation and management (Fleishman et al., 2011). Indeed, animal-borne telemetry and Geographic Information System (GIS) software have been indispensable tools to wildlife biologists and managers for at least 25 years (Millspaugh and Marzluff, 2001). Barriers to a mechanistic mode of inquiry have traditionally been driven by lack of data however, reflecting the advancements outlined above, animal movement data has recently become voluminous and ubiquitous enough to earn the "big" data title (Kays et al., 2015; Urbano et al., 2010). Databases specific to animal movement data have been created to archive data and facilitate collaboration. For example, as of January 2017, the open-access repository known as Movebank included over 387 million locations on 635 taxa (Wikelski and Kays, 2017). Coupled with the growth across these data collection/management spheres, there has been ongoing development of statistical and software tools necessary to accommodate these increasingly resolute data (Calabrese et al., 2016; Gurarie et al., 2016). Many methods have been proposed for modelling the behavioral mechanisms of animal movement using both Fisherian and Bayesian techniques, but the Bayesian framework offers an intuitive way to accommodate uncertainty of latent states in these types of models (Calabrese et al., 2016; Clark, 2005; Gurarie et al., 2016; Hobbs and Hooten, 2015; Johnson et al., 2008).

Studies of ungulate ecology can particularly benefit from sophisticated analyses of telemetry and remotely-sensed data. Movements and behaviors of these animals typically occur over vast spatiotemporal scales, and their relatively large body size permits the attachment of tracking devices that can collect precise data over long periods of time (Kays et al., 2015). Given the ecological and cultural significance of many ungulate species across the globe, there is growing concern around the ways in which these species will respond to continued anthropogenic disturbance and changing climate patterns. Herein, my thesis investigates questions in ungulate ecology arising from the complex interaction between individuals, their movement and resource selection behaviors, and the intrinsic and extrinsic factors affecting these processes. In chapter 1, I explored the relationship between Scandinavian moose movements and a changing climate, specifically rising ambient temperatures. Using five years' worth of relocation data from over 150 GPS-tracked moose in Norway, I derived movement metrics over daytime and crepuscular periods and employed linear and non-linear regression techniques to test established theory pertaining to the "critical temperatures" beyond which moose behavior is expected to change considerably (Renecker and Hudson, 1986). In discussing this analysis, I address the support for these established thresholds and the importance of using free-roaming animals to delineate threshold responses to extrinsic factors. In chapter 2, I explored the consequences of analyzing resource selection by elk in an aggregate manner, as is conventionally done to achieve statistical inference at the population level. With four years of relocation data on elk introduced into southern Missouri, along with associated GIS layers mapping environmental features in the landscape, I fit discrete-choice models at the aggregate and individual levels and compared inferences between these two broad methodologies. I report on the significance of discounting individual variation in this key ecological process when informing conservation and

management. My thesis examines both intrinsic and extrinsic factors on ungulate behavior and in this way, provides a novel computational and analytical framework for assessing movement and resource selection using Bayesian statistical methods. REFERENCES

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CHAPTER 1

INVESTIGATING SIGNATURES OF HEAT STRESS IN WILD-LIVING MOOSE

Abstract

Heat stress from rising ambient temperatures associated with global climate change threatens the persistence of numerous species of wildlife as heat-induced behavioral changes can decrease fitness and alter population dynamics. Moose (Alces alces) are purported to be heatsensitive mammals that become stressed when ambient temperatures rise above specific temperature thresholds. However, these temperature thresholds were established in a study which linked physiological changes in thermoregulation to ambient temperatures in a small study group (n = 2) of captive-reared moose. Temperature thresholds for organisms vulnerable to climate change should be rigorously evaluated from wild-living animals whenever possible. Here, I examined the effects of ambient temperature on movements of wild-living moose to investigate potential temperature thresholds beyond which movement is altered. Analyzing animal movement in this manner provides a natural way to relate environmental conditions to behavior. I fit both linear and additive mixed models to daily movement metrics (movement rate and mean turning angle) calculated from GPS locations collected on 152 moose tracked in central Norway during 2006-2010. I modeled these movement metrics as a function of temperature recorded by GPS collars during different periods of the day, as well as sex, mean elevation, and month. I found little evidence of a threshold response in moose movement to temperature during either period, but note responses to high within-day temperature differences. I documented differences between crepuscular and daytime movement responses to temperature, suggesting that moose

exhibit a compensatory strategy for mitigating the effects of high temperatures by moving more during the crepuscular and night hours when temperatures are high. These results suggest that onset of problematic heat stress in wild-living moose may not occur at the previously proposed temperature thresholds, or that heat stress mitigation strategies are not well-correlated with the movements considered. Additionally, within-day variability in ambient temperature may be an important factor to consider when determining the onset of heat stress in moose.

1.1. Introduction

Warming temperatures associated with global climate change have been causally linked to changes in the behavior, reproduction, distribution, and abundance of a variety of species (Harley et al., 2006; Humphries et al., 2004; Parmesan and Yohe, 2003; Root et al., 2003; Thomas et al., 2004). Moose (Alces alces) are temperate-zone obligates that are well-adapted to the cold and can tolerate temperatures as low as -32 °C (Karns, 2007; Renecker and Hudson, 1986), but unseasonably warm temperatures purportedly induce physiological heat stress (Renecker and Hudson, 1986; Schwartz and Renecker, 2007). In response to heat stress, moose are expected to engage in thermoregulatory behaviors such as the selection of habitat providing thermal refuge, and compensatory activity schedules (Broders et al., 2012; Dussault et al., 2004). This heat sensitivity supports the notion that a warming climate is linked with recent (within the last three decades) declines in moose populations at the southern extent of the species' range globally (Dou et al., 2013; Lenarz et al., 2009; Murray et al., 2006). Other possible drivers implicated in these declines include pathogens and underestimated effects of wolf (*Canis lupus*) predation (Lankester, 2010; Mech and Fieburg, 2014; Murray et al., 2006). While temperature is likely a factor limiting the southern geographic range of this species, and continued trends in climate change may affect moose survivability in certain populations, the precise effect of warming temperatures on population viability remains poorly understood (Lenarz et al., 2010; van Beest et al., 2012). For example, a viable population of moose with relatively ideal demographic characteristics resides in southern Ontario despite exposure to apparently unfavorable climatic conditions (Murray et al., 2012). Identifying the mechanism(s) by which

rising ambient temperature affects individual animal fitness is crucial to assessing the risks that changing climate patterns may pose to populations.

Studying animal movement is a useful way to examine climate-related impacts for many species (McKellar et al., 2005; Nathan and Giuggioli, 2013; Patterson et al., 2009; Schick et al., 2008). In the case of ungulates, temperature and precipitation have been linked to movements of white-tailed deer (*Odocoileus virginianus*; Brinkman et al., 2005) and wild boar (*Sus scrofa*; Thurfjell et al., 2014). In addition, fine-scale movements of migratory caribou (*Rangifer tarandus caribou*) in the Arctic can be affected by availability of ice (Leblond et al., 2016), and the interaction of plant phenology and climate can affect large-scale movements of red deer (*Cervus elaphus*; Pettorelli). Exploring the movement-temperature relationship in moose provides an ideal opportunity to investigate potential fitness impacts of rising temperatures, for two reasons: 1) there are physiological temperature thresholds that have been proposed for moose (McCan et al., 2013; Renecker and Hudson, 1986); 2) there is support for altered behavior in response to ambient temperatures near these thresholds (Melin et al., 2014; Street et al., 2015; van Beest et al., 2012, 2013).

It has been suggested that moose are stressed by heat when ambient temperatures rise above 14° C (57° F) in summer and above -5° C (23° F) in winter (Renecker and Hudson, 1986, 1990). These seasonal thresholds however, were derived from a study of 2 captive-reared cow moose kept in a provisioned fenced enclosure (Renecker and Hudson, 1986). Evidence of heat stress in this study was based on physiological responses, namely increased respiratory rate and open-mouth panting. The authors postulated that when moose are stressed by heat they reduce both activity and food intake (Renecker and Hudson, 1986). Despite the narrow scope of this assessment, these thresholds have been referenced scores of times since 1986. For example, > 15

papers published between 2010 and 2015 in 11 different journals studying 10 moose populations worldwide have either used these thresholds to develop models or cited them in discussing climate-related impacts on moose (see Table 1.1). However, because the exact mechanism by which rising ambient temperatures could have population-level consequences for moose still remains unclear, the utility of the thresholds presented by Renecker and Hudson (1986) has been questioned (Lowe et al., 2010; McGraw et al., 2012).

One possible mechanistic explanation is that when ambient temperature rises above some seasonal thresholds, moose movement would be compromised to the point where foraging effort would be reduced. If these effects were sustained because of heat stress, weight loss would be incurred which, in turn, would deteriorate body condition potentially leading to a reduction in fecundity and fitness. Despite support of this explanation as a conceptual model in the literature, the first connection (altered movement and activity beyond these thresholds) has received only marginal support (DelGuidice et al., 2011; Sand, 1996; Testa and Adams, 1998). For instance, while there is support for temperature-induced changes in moose movement behavior (resource selection and habitat use) at temperatures near the proposed thresholds (Broders et al., 2012; Melin et al., 2014; van Beest et al., 2012, 2013), another study found no difference in such behavior of moose (e.g., habitat use) with respect to these temperature thresholds (Lowe et al., 2010). More specific changes in wild-living moose movement behavior observed during warm periods include reduced activity, decreased distance traveled, and selection for habitat providing thermal refugia (Demarchi and Bunnell, 1995; Dussault et al., 2004; Street et al., 2015). A compensatory effect has also been suggested whereby, during warm periods, moose shift the bulk of their activity to night-time hours when conditions are comparatively cooler (Dussault et al., 2004). That being said, no mechanistic link has connected variation in movement to

population-level consequences given the thresholds suggested by Renecker and Hudson (1986). Therefore, while the Renecker and Hudson thresholds have been often applied by the research community as benchmarks for understanding moose response to heat stress (Renecker and Hudson, 1986; McCan et al., 2013; Table 1.1), their adequacy for describing population-level processes in free-living moose is blurred by inconsistencies in behavioral responses to ambient temperature and possible compensatory behaviors during warm periods.

Here, I analyzed a large set of movement data from a population of moose in central Norway to answer a fundamental research question: are there thresholds in ambient temperature above which wild-living moose movement changes significantly? Specifically, I searched for changes in daytime and crepuscular movements in relation to temperature during these periods. I also investigated the possibility of compensatory movement schedules by relating both daytime temperature and within-day temperature difference to crepuscular movements. Analyzing animal movement in this manner provides a framework to assess the mechanistic role that climate change phenomena may have for species population trajectories. I discuss the implications of this research for understanding how warming temperatures might affect moose fitness, and I examine the utility of my approach for detecting climate-induced changes in moose behavior from movement paths and associated environmental data.

1.2. Methods

1.2.1. Study area

Through a partnership with the Norwegian Institute for Nature Research (NINA), I obtained data on moose that were tracked across central Norway (64°32' N, 12°15 E), in Nord-Trøndelag, Sør-Trøndelag, and southern parts of Nordland counties from 2006 to 2010 (Fig. 1.1). The study area ranged from coastal regions to alpine zones containing mountain, boreal forest,

and cultivated land biomes (Van Moorter et al., 2013). The majority of the study area was forested, consisting primarily of coniferous stands and to a lesser extent deciduous forests (Bjørneraas et al., 2010). Cultivated land was particularly common at lower elevations, along the fjords on the west coast (Moen, 1999).

1.2.2. GPS-tracking and temperature

During February-March or November 2006, and February-March 2007 and 2008, moose were darted from a helicopter to immobilize them, and a sedative administered to facilitate attachment of GPS collars (Bunnefeld et al., 2011). 171 moose (145 adults, 26 calves) were fit with GPS/Global System for Mobile communications (GSM) collars, 7 of which were Tellus GPS collars (Followit AB/Televilt, Lindesburg, Sweden) and the remaining 164 were GPS PLUS/GPS PRO Light collars (VECTRONIC Aerospace GmbH, Berlin, Germany). 50 moose (37 F, 13 M) were collared in 2006, 87 moose (63 F, 24 M) were collared in 2007, and 31 moose (17 F, 14 M) were collared in 2008. Locations were recorded during 2009 and 2010 as well, tracking 67 moose (54 F, 13 M) in 2009 and 25 moose (22 F, 3 M) in 2010. The collars had an expected battery life of 3 years while attempting a locational fix every 2 hours (Bjørneraas et al., 2011; Bunnefeld et al., 2011). These GPS collars recorded ambient temperature from an onboard sensor at each successful location fix. Although these temperatures might be biased by factors such as prevailing conditions or placement on the body, the offset tends to be consistent and collar temperatures provide a reliable index of ambient air temperature (Ericsson et al., 2015).

1.2.3. Movement Metric Calculation

Using the data acquired from these efforts, I calculated moose movements from 214,024 GPS locations (107,049 daytime fixes, 106,975 crepuscular fixes) of 152 moose in central

Norway recorded during the summer months (July and August) of 2006-2010. I centered my assessment on summer because this is the time of year when behavior-altering heat stress in moose is suggested to be most obvious (Broders et al., 2012; Dussault et al., 2004), when migratory individuals in this region are likely to be occupying summer home ranges, and to minimize effects of parturition and rearing that occur during the early summer (Bjørneraas et al., 2011; Rolandsen et al., 2016; Solberg et al., 2007). After screening the GPS data for erroneous fixes following established procedures, I subdivided the data so as to assess variation in moose movement response to temperature between daytime and crepuscular periods (Bjørneraas et al., 2010). Crepuscular periods of each day were defined as the time from 8 p.m. to 6 a.m. the following day, so as to encapsulate the movement path between both onset of civil twilight at night and offset of civil twilight in the morning during July and August. This approach allowed me to assess the effects of temperature on moose movements when activity/foraging effort is typically at the highest, and it is consistent with daily activity patterns of other large herbivores in temperate regions (Cederlund, 1989; Ensing et al., 2014). I defined the daytime period of each day as the hours between 8 a.m. and 6 p.m., given the remainder of the recorded locations fell within these hours. I calculated two movement metrics during both the daytime and crepuscular periods of each summer day: i) movement rate - calculated as the distance travelled (the sum of the inter-location distances) divided by the length of the period (10 hours), and *ii*) mean turning angle - where the turning angle of a location is the angle formed between the line extending beyond that location in the direction of travel from the previous point, and the line segment between the current location and the next. I considered angles to be constrained by 180°, such that a clockwise angle of 270° would be equivalent to a counter-clockwise angle of 90° in the opposite direction.

1.2.4. Mixed-effects modeling

I modeled movement rates and mean turning angles as a function of temperature in a linear mixed model (LMM) framework for movements during each period. In models of daytime movements, I used the maximum collar temperature recorded (T_{dav}) during the respective daytime period. To directly assess crepuscular movements in relation to ambient temperature, I used maximum collar temperature recorded during the respective crepuscular period (T_{crep}) as the temperature covariate. I used the maximum recorded temperatures because I was interested in moose response to specific thresholds rather than average conditions; however, a preliminary analysis using mean daily temperatures estimated by local weather stations did not differ qualitatively from the results presented here. Additionally, to test the possibility of compensatory movements during warm periods, I modeled crepuscular movements in two other cases, each utilizing a different temperature covariate: T_{day} of the prior daytime period, and ΔT , the difference between maximum collar temperatures recorded during the daytime prior and the current period ($\Delta T = T_{day} - T_{crep}$). I included individual moose (id) and year within id as random intercepts. Year was modeled as a random effect within id because these factors were only partially crossed, meaning the variation in movements between years is confounded by the differences in movements between the different groups of moose tracked each year (Pinheiro and Bates, 2000). The remaining fixed effects for each model were sex; elevation, calculated by taking the average of the digital elevation model estimates (resolution 25 m, altitude 1 m) at each location recorded during the corresponding period; and month. Thus, the global LMM was of the form:

$$Y_{ijk} = \beta_0 + \beta_{temp} x_{1ijk} + \beta_{elev} x_{2ijk} + \beta_{mo} x_{3ijk} + \beta_{sex} x_{4ijk} + u_{1j} + u_{2jk} + \varepsilon_{ijk}$$
(1)

where Y_{ijk} is the *i*th observation of any of the three movement metrics calculated for the *j*th individual in year k; β -parameters correspond to population mean response and effects of temperature, elevation, month (base July), and sex (base female); u_{1-2} correspond to normallydistributed random effects of moose id j and year k within id j; and ε_{ijk} is a temporallyautocorrelated error term. I included both sex and month in the model because of differences observed in preliminary analysis of within-day variation in movement rate (Fig. 1.2), and because males may regularly travel greater distances than females (Bjørneraas et al., 2012; Van Moorter et al., 2013). Elevation was included in the models because altitude is one of the main environmental gradients in this region, and preliminary analyses revealed a large variation across the study population relative to variation within individuals (Bakkestuen et al., 2008). I tested temporal autocorrelation structures, prior to fitting LMMs, by fitting the global linear mixed models for each movement metric with an autoregressive (AR) moving-average (MA) error structure. I separately fit all 8 combinations of orders 0-2 for both the AR and MA components, as well as AR(0) MA(3) and AR(3) MA(0). Models were compared using AIC, ranking models according to ascending AIC value. I conducted these tests separately for both crepuscular and daytime movements, and selected the AR-MA structure having the lowest AIC value for each. To ensure reliable estimates of collar temperature and elevation were available for a given period, I only included crepuscular and daytime periods having at least 5 (out of 6 possible) recorded GPS locations. Although other factors influence fine-scale movements of moose I focused on examining the relationship between moose movements and temperature while minimizing model complexity (Leblond et al., 2010).

In addition to the linear mixed models, I also wanted to test for the potential of nonlinear relationships in these data. Specifically, I hypothesized that the relationship between movement

metrics and temperature measures could be curvilinear. Therefore, I evaluated non-linear patterns by developing an additive mixed model (AMM) framework. Additive models are especially useful for this analysis because they would help reveal a specific temperature threshold at which movements significantly change, as might be expected if movement is affected at the Renecker and Hudson thresholds (i.e., 14° and 20° C in the summer (Fewster et al., 2000; Large et al., 2013; Renecker and Hudson, 1986). I tested the same fixed effects as above (sex and month), with thin plate regression splines placed on the continuous terms (temperature and elevation; Wood, 2003). The same random effects structure used for the LMMs was employed in the AMMs, as well as the best ARMA structure. These models took the form: $Y_{ijk} = \beta_0 + f_{temp}(x_{1ijk}) + f_{elev}(x_{2ijk}) + \beta_{mo}x_{3ijk} + \beta_{sex}x_{4ijk} + u_{1j} + u_{2jk} + \varepsilon_{ijk}$ (2)

where f_{temp} and f_{elev} are unknown smooth functions of temperature and elevation to be estimated from the data, and all other terms are the same as in (1). The best approximating models were selected by the lowest AIC score (Burnham and Anderson, 2003). This resulted in a total of 16 LMMs and 12 AMMs (additive models without the continuous covariates are equivalent to linear models, thus they were not re-fit in the AMM analysis) for each response, giving a total of 28 models under evaluation for the movement metrics in each period. I conducted all statistical analyses in the R statistical computing environment using packages *nlme* and *mgcv* (Pinherio et al., 2015; R Core Team, 2015; Wood, 2011).

1.2.5. Probabilistic Movement Metrics

I also developed a companion modeling effort using a probabilistic movement estimator to quantify the moose movement metrics. I performed these additional steps to assess sensitivity of results to differences in sample size and periods of time where GPS locations were closer in space, as these factors could influence the bias of movement metric estimates. I predicted these

movement paths from continuous-time correlated random walk (CTCRW) models fit separately for each moose in each summer using the R package *crawl* (Johnson et al., 2008). The CTCRW is a state-space model based on Brownian motion, where the estimated GPS location at time = t + 1 is a function of the current movement state. This includes the current velocity, and parameters for velocity autocorrelation and velocity variation, which influence both the predicted location and the associated Brownian error (Johnson et al., 2008). I then used these models to predict GPS locations at the same two hour intervals the GPS fixes were attempted and, using these predicted locations, calculated movement metrics for the same exact periods used before (i.e., those having 5 or 6 locations obtained on the particular moose during the respective time of day). With these metrics in hand, I repeated the analysis outlined above exactly as described and evaluated the similarity in the predictions with tests of correlation. My goal here was thus to evaluate whether probabilistic movement paths that accounted for autocorrelation and variation in velocity revealed different patterns from those developed using the straight-line calculations performed on the raw GPS locations.

1.3. Results

After screening the GPS data and omitting periods having less than 5 successful GPS fixes, 17,531 daytime periods and 16,799 crepuscular periods each consisting of 5 or 6 GPS fixes remained for calculating movement metrics, represented by 152 moose. 95% of the maximum daytime (T_{day}) and maximum crepuscular collar temperatures (T_{crep}) recorded were between 17 and 41 °C and 13 and 29 °C, respectively. Temperature differences between daytime and respective crepuscular periods ($\Delta T = T_{day} - T_{crep}$) fell between 0 and 17 °C for 95% of the time. The collars consistently recorded temperatures near and above the proposed thresholds, during both daytime and crepuscular hours (Table 1.2). The movement rates calculated in both periods

were positively skewed, which was improved by log-transformation prior to all analyses. Although bounded by 0 and 180°, mean turning angles were approximately normally distributed, with 97.5% of data falling within 55.3 and 151.2°. Variation in both movements during periods of similar temperatures was large, although movement rates were characterized by more outliers than mean turning angles during both daytime and crepuscular periods.

The best autocorrelation structure for crepuscular movement rate was ARMA(2,1) as determined by both the lowest AIC values, and all other models scored best with the ARMA(1,1) structure, including all models of daytime movement metrics (Table 1.3). The best approximating AMMs and LMMs for both daytime and crepuscular movement rate as determined by lowest AIC included all four terms, with the exception that month was excluded from the top LMM for daytime movement rate (Tables 1.4 and 1.5). The best approximating AMMs and LMMs of turning angle during the crepuscular period were of the same form, including temperature for each estimate tested (T_{day} , T_{crep} , and ΔT), as well as sex and month. However, temperature was not included in the best approximating AMM for daytime turning angle, although the global model was within $\Delta AIC = 1$ (Table 1.5). I report the mean turning angle predictions of the global model in this case (Fig. 1.5), as the main focus here is on the effect of temperature, and a $\Delta AIC = 1$ suggests weak evidence to prefer one over the other (Burnham and Anderson, 2003). The runner-up LMM for each model of mean crepuscular turning angle was the global model, and was within $\Delta AIC = 2$ for each estimate of temperature tested (Table 1.4).

The top AMM for crepuscular movement rate revealed a positive relationship with increasing T_{crep} and increasing T_{day} , indicating that moose moved greater distances at night when it is warm during both day and night (Figs. 1.4b and 1.4c). Further, the linear effect of ΔT on

crepuscular movements evidenced by the top LMMs was much less than the effects of T_{crep} and T_{day} on crepuscular movement rate (Table 1.7). This corresponded to a decreasing relationship between T_{day} and daytime movement rates, which was also reflected in the opposite signs of the temperature effects in the LMMs between periods (Tables 1.6 and 1.7). Interestingly, this decreasing relationship between T_{day} and daytime movement rate leveled off near ~ 30 °C, while the increasing relationship between temperatures (both T_{day} and T_{crep}) and crepuscular movements did not exhibit a tapering off effect (Fig. 1.4a). This suggests rate of movement during the day may reach a limit even as temperatures during this period continue to rise relatively high. These findings support the notion that moose move greater distances at night, even as T_{crep} increases.

A distinct temperature threshold was not evident in any of the best approximating models, although the best approximating AMM for mean turning angle during the daytime period, as well as that for crepuscular movement rate in relation to ΔT , both indicated a curvilinear relationship with increasing estimates. There is a notable concave downward relationship predicted for movement rate as ΔT approaches the extreme observed values, which suggests the possibility of a threshold in within-day temperature variability on crepuscular movements (Fig. 1.4d). That mean daytime turning angles began to increase beyond $T_{day} = 30$ °C, co-occurring with the leveling off of daytime movement rate, indicates that although moose may have stopped moving less with increasing temperature, their movement metrics went unexplained by the best approximating models, as evidenced by the substantial amount of residual variation relative to the variation of the random effects (Tables 1.3 and 1.4). The effect sizes of the temperature terms in the LMMs were small relative to the scale of the response

variables, and effects of the other predictors (Tables 1.3 and 1.4). Conducting the same analyses using movement metrics calculated from CTCRW-derived GPS locations did not reveal any differences in either LMMs or AMMs; responses were highly correlated at r = 0.949 and r = 0.993 for mean turning angle and movement rate, respectively. Subsequent predictions from models fit to movement metrics calculated on predicted and raw GPS locations ways were nearly identical, as evidenced by high correlations between predicted values for the two movement modeling approaches (r > 0.995 for Figs. 1.6 and 1.7).

1.4 Discussion

I found little evidence of summer temperature thresholds beyond which moose movement significantly changed. This result comes after I carried out a rigorous assessment of the movement of 152 wild-living moose, evaluated across vast spatio-temporal extents and over two different periods (daytime and crepuscular), using two separate modeling frameworks (linear and additive) for each of two techniques for quantifying movement (raw GPS locations and predicted locations based on CTCRW models). I did not find any concordance with the temperature thresholds proposed by Renecker and Hudson (1986), despite repeated exposure to higher temperatures in both periods. Rather, the effect of maximum daytime and crepuscular temperature (T_{day} and T_{crep}) on crepuscular movement metrics as estimated in the AMMs indicated linear relationships between movements and temperature, and of the same direction for each metric (Figs. 1.4b and 1.4c; 1.5b and 1.5c). These results do not dismiss the possibility that a temperature threshold in moose movement exists. Rather, they suggest that at a 12-hour scale, such thresholds do not scale-up to the population-level movement metrics I employed, or are not applicable to this population of wild-living moose during the summer months. Indeed, this study is limited by a restriction to the summer months. Additional research should quantify this relationship during times where altered movement could have more obvious fitness implications

(e.g., mating season). The broad-scale nature of this approach also limits the ability to document behavioral responses to temperature at fine scales (e.g., within-hour movements in a small habitat patch) and does not necessarily rule out behavioral responses at such scales. Yet the lack of any threshold response resulting from exposure to previously proposed critical temperatures is a key finding in light of the evidence that moose alter their behavior (habitat selection and use) near these same temperatures (Broders et al., 2012; McCan et al., 2013; Melin et al., 2014; Renecker and Hudson, 1986; Street et al., 2015; van Beest et al., 2012, 2013). The predicted relationship of crepuscular movement rate with ΔT is also interesting, as it provides evidence that within-day fluctuations in ambient temperature could be a potential indicator for threshold responses in movements at the daily scale. Thus, my study supports the notion that 'thresholds' may be better referred to as a general range in which ambient temperature could start to trigger summer heat stress in moose (McGraw et al., 2012; Renecker and Hudson, 1990). Furthermore, considering variability in temperature in addition to ambient temperature levels may allow for more precise prediction of the onset of this heat stress.

The stronger positive effects of T_{day} and T_{crep} on crepuscular movement rates that I documented relative to the effect of ΔT provides evidence that moose move more at night during warm periods in general (Figs. 1.4b and 1.4c; Table 1.4), which is consistent with previous findings of Dussault et al., (2004). In that assessment, the authors identified a positive effect of increasing temperature on nighttime activity, where activity was estimated from motion sensors affixed to the GPS collars. While they did not find a negative effect of ambient temperature on daytime moose activity, these results suggest that this may be the case if there exists a positive relationship between moose activity and movement rates. This is a reasonable assumption, as a recent study found decreased daytime activity levels of moose during warm periods (Street et al.,

2015). These results suggest that moose may exhibit compensatory movement or activity schedules, moving more at night and less during the day as temperatures increases. That being said, the size of this effect was much less than the effects of either temperature estimate on crepuscular movement rate (Tables 1.6 and 1.7). This is likely due to the leveling-off phenomenon displayed in predictions of daytime movement rates as T_{day} approached 30 °C (Fig. 1.4a), where the movement rate remained steady at about 48.9 m/hr (SD ± 57.6 m/hr) thereafter. Coupled with the concave upward trend of T_{day} with daytime turning angle near this temperature range (Fig. 1.5a), these results suggest that moose may start engaging in different behavior at this point, possibly avoiding harassment by insects or searching for thermal refuge (Renecker and Hudson, 1990). The differences revealed between the AMMs of mean turning angle for each period paint a similar picture. While a negative linear relationship was found between crepuscular turning angles and T_{day} , T_{crep} , and ΔT (Table 1.6), the nonlinear relationship during the day indicates moose may not exhibit the same behavioral responses to warm temperatures during the day as they do during the crepuscular and night hours (Figs. 1.4a-1.4d).

The challenge of achieving a mechanistic understanding for the demographic consequences of high ambient temperatures is further complicated by how intrinsic factors such as body mass and maturity may affect the movement-temperature relationship. Because I assessed coarse population-level relationships between movements and temperature, I only included sex as a fixed effect. This assumes calves do not move any differently than adults, and that sex captured some of the variation in movement caused by body mass. However, the large random effect variation suggests that including these other factors in analyses could strengthen the model fits. Regional variability in other interacting factors, such as disease prevalence, predation, and changes in both forage quality and selection are also important for informing a

mechanistic understanding. If the range of moose is limited by operative temperatures in summer, assessing the influence of these other biotic factors would be necessary. That mature conifer stands may be selected during warm periods, but are typically lacking in abundance of high-quality forage compared to younger forests, suggests a possible trade-off between thermoregulation and forage availability (Bjørneraas et al., 2011; van Beest et al., 2012). But careful evaluation of the implications of this general concept for individual and population-level moose fitness is necessary and currently lacking. In North America, parasites such as the winter tick (Dermacentor albipictus) might affect fitness, and increased transmission of the meningeal worm (Parelaphostrongylus tenuis) to moose has been implicated as an overlooked cause of population declines (Lankester, 2010; Murray et al., 2006). Elevated infection rates have been attributed to a warming climate, especially during winter, as this has been associated with greater abundance of the primary mammalian host (white-tailed deer; Odocoileus virginianus) in moose range (DelGuidice et al., 2002; Whitlaw and Lankester, 1994). Additional examination of the multifaceted ways in which external biotic factors and ambient temperature regimes can interact to affect moose populations is necessary if underlying mechanisms do exist.

This study highlights the complex nature of the relationship between abiotic stimuli and animal movement at broad scales. Studying the effects of abiotic conditions on physiological stress of captive animals (e.g. Renecker and Hudson, 1986; McCan et al., 2013) provides a helpful, but perhaps limited, reference point from which to understand the behavior of wildliving animals. Analysis of animal movement data can be illustrative of the physiological and behavioral states of free-ranging individuals as they interact with their environment (Gurarie et al., 2016). For instance, increasingly high resolution data can facilitate models that account for different "modes" or "states" of movement, which depict the interaction of an individual's

internal state and the environment (Morales et al., 2004; Nathan et al., 2008; Patterson et al., 2009; Schick et al., 2008). Employing flexible frameworks to account for the effects of environment on these different characterizations of movement might grant an enhanced understanding of the relationship between physiology and abiotic conditions in wild-living moose. However, the ability to precisely characterize the abiotic conditions experienced in the wild will continue to be challenging, particularly where compared to the access that captive studies afford. For instance, the reliability of collar temperature measurements may diminish as habitat selection varies with temperature (e.g. selection of open water and marshes; Street et al., 2015). Such behavioral influence on collar estimates of ambient temperature could possibly buffer the effects of a threshold response at the temperature extremes. Therefore, there are pluses and minuses to studies that occur along the captive-to-wild continuum. This point emphasizes the more philosophical position that choosing the most appropriate modeling techniques from such a wide, often esoteric range of possible methods can prove to be restrictive for many ecologists (Gurarie et al., 2016; Schick et al., 2008).

1.5. Conclusions

Declines in moose population abundance have been attributed to a variety of factors beyond rising ambient temperatures, but the southern edge of the moose range is still predicted to shift northward as the climate continues to warm and heat stress becomes more likely (Lenarz et al., 2010; Murray et al., 2012). However, the thermal conditions under which heat stress in moose might negatively affect fecundity after accounting for these factors remains unknown, and the physiological temperature thresholds for moose as inferred from a small sample of captive animals (Renecker and Hudson, 1986; Table 1.1) should be applied with caution. Determining temperature thresholds for wild-living moose movement would enhance our ability to predict the
effects of abiotic conditions on body condition, and thus survival. My study took an important step towards that end by identifying a relatively smooth and continuous relationship between temperature and moose movements. Additional work could build on this study by exploring this relationship at different scales, in other seasons, or in the context of other potentially important biotic factors (e.g., habitat heterogeneity).

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APPENDIX

Table 1.1. Review of articles published between 2010-2015 that have directly referenced the temperature thresholds suggested by Renecker and Hudson (1986) to develop models or discuss climate related impacts on moose.

Citing article	Journal	Context
Lenarz et al., 2010 [16]	Journal of Wildlife Management	"These upper critical temperatures," p. 1013
Lowe et al., 2010 [32]	Canadian Journal of Zoology	"Thus, when temperatures exceeded critical thresholds," p.1033
Bjørneraas et al., 2011 [42]	Wildlife Biology	"thresholds that are regularly exceeded," p. 51
Rolandsen <i>et al.</i> , 2011 [67]	Ecosphere	"respiratory rate, and metabolic rate when ambient temperatures rise above -5°C in winter and 14°C in summer," p. 9
Rempel 2011 [68]	Ecological Modeling	"In summer, thermal stress begins at about 14 °C and is fairly severe at 20 °C," p. 3360
Broders et al., 2012 [10]	Alces	"relatively low, upper critical temperature limit," p. 54
Murray et al., 2012 [18]	Canadian Journal of Zoology	"upper critical temperature limits can cause," p. 431
van Beest <i>et al.</i> , 2012 [17]	Animal Behaviour	"Upper critical temperature thresholds for moose under captive conditions," p. 724
Dou et al., 2013 [13]	Ecological Research	"critical temperature of the moose," p. 630
McCan <i>et al.</i> , 2013 [27]	Canadian Journal of Zoology	"indicate heat-stress thresholds for moose at 14 and 20 °C," p. 893
van Beest <i>et al.</i> , 2013 [28]	PLoS ONE	"locations were classified by temperature in relation to seasonal thermoregulation thresholds," p. 3
Melin et al., 2014 [29]	Global Change Biology	"The thresholds for thermal stress in moose, as suggested by," p. 1116

Table 1.1 (cont'd).

Citing article	Journal	Context
Olson <i>et al.</i> , 2014 [69]	Alces	"estimated upper critical temperatures (T _{uc}) of moose as," p 105
Street et al., 2015 [30]	Journal of Wildlife Management	"particularly at temperatures exceeding the upper thresholds," p. 3
Monteith et al., 2015 [70]	Oecologia	"and have the lowest upper critical temperature of any northern ungulate," p. 1145

Year T_{crep} (°C) < 15 [15:17) [17 - 19) [19 - 21) [21 - 23) [23 - 25) [25 - 27) $[27 - 29) \ge 29$ $\overline{T_{day}(^{\circ}C)}$ Year [21 - 23) [23 - 25) [25 - 27) [27 - 29) [29 - 31) [31 - 33) $[33 - 35) \ge 35$ < 21 Year $\Delta T (^{\circ}C)$ < 1 [1 - 3) [3 - 5) [5 - 7) [7 - 9) [9 - 11) [11 - 13) $[13 - 15) \ge 15$

Table 1.2. Counts of temperatures recorded by GPS collars of GPS-tracked moose in central Norway from July through August of each year during 2006-2010. Counts during crepuscular period (20:00 - 06:00 next day) above, counts of temperatures recorded during daytime period (08:00 - 18:00) middle, differences of temperature (Δ T) between crepuscular and daytime periods below.

Model	df	AIC	Model	df	AIC		
Response = ln(Movement Rate)							
ARMA(2,1)	11	33803.96	ARMA(1,1)	10	34916.56		
ARMA(2,2)	12	33805.50	ARMA(2,1)	11	34917.42		
ARMA(1,1)	10	33881.73	ARMA(2,2)	12	34920.34		
ARMA(3,0)	11	33956.68	ARMA(3,0)	11	34931.68		
ARMA(1,2)	11	33992.39	ARMA(0,3)	11	34937.96		
ARMA(0,3)	11	33998.61	ARMA(2,0)	10	34944.88		
ARMA(2,0)	10	33999.84	ARMA(1,2)	11	34948.26		
ARMA(1,0)	9	34040.00	ARMA(0,2)	10	34953.78		
ARMA(0,2)	10	34032.73	ARMA(1,0)	9	34989.14		
ARMA(0,1)	9	34086.27	ARMA(0,1)	9	34996.7		
ARMA(0,0)*	8	34491.44	ARMA(0,0)*	8	35065.97		
Response = Strai	ghtne	ess Index					
ARMA(1,1)	10	-529.156	ARMA(1,1)	10	-2063.72		
ARMA(2,1)	11	-528.701	ARMA(2,0)	10	-2062.65		
ARMA(2,2)	12	-526.248	ARMA(0,2)	10	-2062.47		
ARMA(3,0)	11	-507.374	ARMA(2,1)	11	-2061.73		
ARMA(0,3)	11	-505.425	ARMA(3,0)	11	-2061.5		
ARMA(2,0)	10	-494.310	ARMA(0,3)	11	-2061.46		
ARMA(0,2)	10	-492.866	ARMA(1,0)	9	-2061.22		
ARMA(1,2)	11	-491.816	ARMA(0,1)	9	-2060.92		
ARMA(1,0)	9	-485.026	ARMA(1,2)	11	-2060.65		
ARMA(0,1)	9	-484.701	ARMA(2,2)	12	-2059.92		
ARMA(0,0)*	8	-480.498	ARMA(0,0)*	8	-2052.76		
Response = Mean	n turi	ning angle					
ARMA(1,1)	10	-20749.8	ARMA(1,1)	10	-23009.4		
ARMA(2,1)	11	-20748.1	ARMA(2,1)	11	-23007.4		
ARMA(2,2)	12	-20746.6	ARMA(2,2)	12	-23006.3		
ARMA(3,0)	11	-20690.2	ARMA(3,0)	11	-22987.4		
ARMA(0,3)	11	-20687.5	ARMA(0,3)	11	-22986.6		
ARMA(2,0)	10	-20686.0	ARMA(1,0)	9	-22982.2		
ARMA(0,2)	10	-20684.2	ARMA(0,1)	9	-22982.1		
ARMA(1,2)	11	-20683.4	ARMA(2,0)	10	-22981.5		
ARMA(1,0)	9	-20673.8	ARMA(0,2)	10	-22981.2		
ARMA(0,1)	9	-20672.7	ARMA(1,2)	11	-22979.5		
ARMA(0,0)*	8	-20655.9	ARMA(0,0)*	8	-22976.1		

Table 1.3. Comparison of ARMA error structure for linear mixed models of crepuscular (left half) and daytime (right half) movements of moose, sorted by ascending AIC score.

* denotes global model with no autocorrelation structure

Table 1.4. Comparison of best approximating LMMs. The top three linear mixed models of movement rate (Rate) and mean turning angle (Turn) response variables during crepuscular and daytime movement metrics, sorted by increasing AIC score.

Response	Model				df	AIC	
Daytime movements							
Rate	T _{day}	+ Elevation	+ Sex		11	36261.37	
Rate	T_{day}	+ Elevation	+ Sex	+ Month	12	36270.40	
Rate	T_{day}		+ Sex		10	36270.55	
Turn	T _{day}	+ Elevation	+ Sex	+ Month	10	167026.1	
Turn		Elevation	+ Sex	+ Month	9	167027.1	
Turn		Elevation	+ Sex		8	167043.6	
		Crepuscula	r movem	nents			
Rate	Tcrep	+ Elevation	+ Sex	+ Month	11	36727.61	
Rate	Tcrep		+ Sex	+ Month	10	36729.52	
Rate	Tcrep	+ Elevation	+ Sex		10	36767.34	
Turn	T _{crep}		+ Sex	+ Month	10	158862.0	
Turn	T _{crep}	+ Elevation	+ Sex	+ Month	11	158863.3	
Turn	T_{crep}		+ Sex		9	158868.4	
Rate	T _{day}	+ Elevation	+ Sex	+ Month	11	35914.53	
Rate	T_{day}		+ Sex	+ Month	10	35924.94	
Rate	T_{day}	+ Elevation	+ Sex		10	35942.18	
Turn	T _{day}		+ Sex	+ Month	10	154935.6	
Turn	T_{day}	+ Elevation	+ Sex	+ Month	11	154937.6	
Turn	T_{day}		+ Sex		9	154948.4	
Rate	ΔΤ	+ Elevation	+ Sex	+ Month	11	36204.18	
Rate	ΔT		+ Sex	+ Month	10	36208.70	
Rate	ΔT	+ Elevation	+ Sex		10	36209.52	
Turn	ΔΤ		+ Sex	+ Month	10	154990.4	
Turn	ΔT	+ Elevation	+ Sex	+ Month	11	154992.3	
Turn			Sex	+ Month	9	154993.7	

Table 1.5. Comparison of best approximating AMMs. The top three additive mixed models of movement rate (Rate) and mean turning angle (Turn) response variables during crepuscular and daytime movement metrics, sorted by increasing AIC score.

Response	Model				df	AIC	
Daytime movements							
Rate	s(T _{day})	+ s(Elevation)	+ Sex	+ Month	14	36206.89	
Rate	s(T _{day})	+ s(Elevation)	+ Sex		13	36220.19	
Rate	s(T _{day})		+ Sex		11	36241.85	
Turn		s(Elevation)	+ Sex	+ Month	10	167029.1	
Turn	s(T _{day})	+ s(Elevation)	+ Sex	+ Month	12	167030.1	
Turn		s(Elevation)	+ Sex		9	167045.1	
		Crepuscular	moveme	nts			
Rate	s(T _{crep})	+ s(Elevation)	+ Sex	+ Month	13	36693.45	
Rate	s(T _{crep})		+ Sex	+ Month	11	36731.52	
Rate	s(T _{crep})	+ s(Elevation)	+ Sex		12	36731.62	
Turn	s(T _{crep})		+ Sex	+ Month	11	158864	
Turn	s(T _{crep})	+ s(Elevation)	+ Sex	+ Month	13	158867.3	
Turn	$s(T_{crep})$		+ Sex		10	158870.4	
Rate	s(T _{day})	+ s(Elevation)	+ Sex	+ Month	13	35872.33	
Rate	s(T _{day})	+ s(Elevation)	+ Sex		12	35898.85	
Rate	s(T _{day})		+ Sex	+ Month	11	35926.94	
Turn	s(T _{day})		+ Sex	+ Month	11	154937.6	
Turn	s(T _{day})	+ s(Elevation)	+ Sex	+ Month	13	154941.6	
Turn	s(T _{day})		+ Sex		10	154950.4	
Rate	s(ΔT)	+ s(Elevation)	+ Sex	+ Month	13	36164.86	
Rate	$s(\Delta T)$	+ s(Elevation)	+ Sex		12	36170.36	
Rate	$s(\Delta T)$		+ Sex	+ Month	11	36206.41	
Turn	$s(\Delta T)$		+ Sex	+ Month	11	154992.4	
Turn	$s(\Delta T)$	+ s(Elevation)	+ Sex	+ Month	13	154996.3	
Turn		s(Elevation)	+ Sex	+ Month	11	154997.7	

Table 1.6. Best approximating LMMs, daytime hours. Parameter estimates for best approximating linear mixed models of daytime movements, as determined by AIC. Max. daytime collar temperature (T_{day}) was the temperature covariate used in these models.

Fixed effect	Estimate	SE	Random effect		Std. Dev.
Movement Rate					
Intercept	3.714	0.041	Moose ID	Intercept	0.222
Temp (T _{day})	-9.3E-3	9.6E-4	Year: Moose ID	Intercept	5.2E-4
Elevation	2.4E-4	2.4E-4		Residual	0.696
Sex	0.424	0.049			
Mean Turning Angle					
Intercept	92.58	1.236	Moose ID	Intercept	3.163
Temp (T _{day})	-0.020	0.038	Year: Moose ID	Intercept	0.035
Elevation	-8.8E-3	1.8E-3		Residual	28.36
Sex	-6.903	0.886			

Table 1.7. Best approximating LMMs, crepuscular hours. Parameter estimates for best approximating linear mixed models of crepuscular movements, as determined by AIC. The temperature covariate used in each model is indicated in parentheses. $T_{crep} = max$. crepuscular collar temperature, $T_{day} = max$. daytime collar temperature, and $\Delta T = T_{day} - T_{crep}$.

Fixed effect	Estimate	SE	Random effect		Std. Dev.
Movement Rate					
Intercept	3.880	0.056	Moose ID	Intercept	0.261
Temp (T _{crep})	0.033	1.7E-3	Year: Moose ID	Intercept	7.0E-4
Elevation	-1.6E-4	7.9E-5		Residual	0.760
Sex	0.577	0.064			
Month	0.119	0.018			
Mean Turning Ar	ıgle				
Intercept	111.61	1.254	Moose ID	Intercept	1.828
Temp (T _{crep})	-0.485	0.053	Year: Moose ID	Intercept	1.299
Sex	-5.774	0.693		Residual	24.36
Month	1.249	0.451			
Movement Rate					
Intercept	4.069	0.050	Moose ID	Intercept	0.259
Temp (T _{day})	0.020	1.0E-3	Year: Moose ID	Intercept	6.5E-4
Elevation	-3.0E-4	7.9E-5		Residual	0.759
Sex	0.570	0.063			
Month	0.098	0.017			
Mean Turning Ar	ıgle				
Intercept	108.4	1.073	Moose ID	Intercept	1.707
Temp (T _{day})	-0.269	0.035	Year: Moose ID	Intercept	1.261
Sex	-5.620	0.680		Residual	24.39
Month	1.740	0.442			
Movement Rate					
Intercept	4.550	0.041	Moose ID	Intercept	0.244
Temp (Δ T)	0.011	1.3E-3	Year: Moose ID	Intercept	9.1E-4
Elevation	-2.1E-4	8.0E-5		Residual	0.765
Sex	0.567	0.061			
Month	0.049	0.018			
Mean Turning Angle					
Intercept	101.3	0.489	Moose ID	Intercept	1.562
Temp (Δ T)	-0.105	0.045	Year: Moose ID	Intercept	1.491
Sex	-5.606	0.668		Residual	24.42
Month	2.584	0.433			

Figure 1.1. Summer locations of GPS-tracked moose in Central Norway during 2006-2010. Norway is shaded light blue, other countries colored olive.



Figure 1.2. Mean ln-transformed speeds (\pm SE) of moose movement in Central Norway, during the months of July and August of each year from 2006-2010 (n = 152 moose). Speeds were estimated from continuous-time correlated random walk movement models fit to each summer track using the package *crawl* in R.



Figure 1.3. Boxplots of daytime (a) and crepuscular (b) movement metrics calculated from GPS data on moose tracked during July-August of 2006-2010. Movement metrics are binned by maximum collar temperature recorded during the respective period for which the movement metric was calculated.



Maximum temperature bins (°C)

Figure 1.4. Predictions based on best approximating AMMs (± 95% CI shaded grey) for movement rates of male moose at median elevation during daytime (a) and crepuscular periods (b-d). Daytime movement rates predicted as a function of daytime temperature, and crepuscular movement rates predicted as a function of crepuscular temperature (b), daytime temperature (c), and the difference between daytime and crepuscular temperature (d).



Figure 1.5. Predictions based on best approximating AMMs (± 95% CI shaded grey) for mean turning angles of male moose at median elevation during daytime (a) and crepuscular periods (b-d). Daytime turning angles predicted as a function of daytime temperature, and crepuscular turn angles predicted as a function of crepuscular temperature (b), daytime temperature (c), and the difference between daytime and crepuscular temperature (d).



Figure 1.6. Predictions based on best approximating AMMs of movement rates calculated from probabilistic movement paths. Predictions for daytime (a) and crepuscular (b-d) movement rates of male moose. Daytime movement rates predicted as a function of daytime temperature, and crepuscular movement rates predicted as a function of crepuscular temperature (b), daytime temperature (c), and the difference between daytime and crepuscular temperature (d).



Figure 1.7. Predictions based on best approximating AMMs of mean turning angles calculated from probabilistic movement paths. Predictions for daytime (a) and crepuscular (b-d) movement rates of male moose. Daytime movement rates predicted as a function of daytime temperature, and crepuscular movement rates predicted as a function of crepuscular temperature (b), daytime temperature (c), and the difference between daytime and crepuscular temperature (d).



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CHAPTER 2

EVALUATING THE CONSEQUENCES ON ECOLOGICAL INFERENCE OF AGGREGATING WILDLIFE TELEMETRY DATA WHEN ESTIMATING RESOURCE SELECTION FUNCTIONS

Abstract

Telemetry data are commonly used to assess animal-habitat relationships via the quantification resource selection functions (RSFs). As the output of these models are often designed to inform conservation or management practice, inference is typically desired at the population-level. Thereby, it has become common practice to aggregate data from all telemetered animals prior to fitting an RSF. To account for individual variation in selection among telemetered animals, these models typically include a random effect by animal id. These approaches are valuable for quantifying broad scale selection, but when the focal population may be comprised of various intrinsic categories (e.g. sex or age class) or clustered spatially (e.g. two sub-populations occupying different areas of the landscape), information relating to individual animal decision-making may be obscured by the act of aggregating data. Here I investigated individual variation in resource selection among a population of reintroduced elk (Cervus elaphus) in the Missouri Ozarks. I modeled elk location data, collected from Global Positioning System (GPS) collars, using a Bayesian discrete choice RSF model. I fit an aggregate-level model, according to prevailing practice, and then batch-processed models at the level of each individual elk. I compared the outputs of the top aggregate- and individual-level models via examination of three metrics; 1) the number and composition of parameters in top models, 2) the estimates of parameters in global models, and 3) the predicted relative probabilities of use. Via

this comparison I discovered substantial variation in all three metrics. Furthermore, I could not detect any conformity at the individual level by age, sex, or year of reintroduction and telemetry-collaring. My work demonstrates that important ecological variation is lost when resource selection analyses are aggregated at the population level. I discuss the implications of this analysis for management and conservation practice and present some guiding principles for developing RSFs at the individual level.

2.1. Introduction

Research on animal-habitat relationships is a cornerstone of ecological inquiry providing insights across both theoretical and applied dimensions (Johnson 1980; Morris 2003). Evaluating animal decision-making in relation to habitat characteristics has implications for optimal foraging, predator-prey interactions, survivorship, reproduction, life history, and, correspondingly, population-level processes (MacArthur and Pianka 1966; Charnov 1976; Rosenzweig 1981, 1991; Morris 2003). Applied assessments of animal-habitat relationships are predicated on the ability to track animal movement over time. While a variety of data collection methods inform these efforts, much of habitat selection research rely upon telemetry data (Craighead and Craighead 1971; Craighead et al., 1971; Kenward 2001; Thomas and Taylor 2006; Montgomery and Roloff 2013). Telemetry technology has expanded dramatically in the last 50 years with subsequent growth in the methods necessary to model these data. Sophisticated and complex models have been developed to rigorously quantify animal movement, selection, habitat suitability, as well as population abundance and performance (Hirzel and Lay 2008; Gaillard et al., 2010; Thurfjell et al., 2014; Avgar et al., 2016; Boyce et al., 2016).

Examples of the formative techniques for quantifying habitat selection include compositional analysis (Aebischer et al., 1993), Chi-square goodness-of-fit tests (Neu et al., 1974; Byers et al., 1984), ranking methods (Arthur et al., 1996), and logistic regression (Thomasma et al., 1991). Many of these models operate in a similar fashion in that used habitat units (e.g., at locations detected via telemetry) are compared to habitat units which is deemed to be either unused or available (i.e., locations not detected via telemetry). The statistical comparison of used to unused/available was unified under the broader resource selection function (RSF) framework (Boyce and McDonald 1999; Manly et al., 2002). Herein, the RSF

models the use versus unused/available data as a function of environmental variables, or resources, where the output is a value proportional to the probability that location is used given the resources present (Manly et al., 2002). In other words, an RSF is always proportional to an RSPF (resource probability selection function) that quantifies the *actual* probability of using landscape units. The ability to accurately estimate an RSPF, which can be desirable in a number of scenarios, is determined by the extent to which non-use habitat units can be reliably quantified (Manly et al., 2002). Given that estimation of *availability* is typically much more feasible than determination of *non-use* in wildlife studies, the use/available framework tends to be most common (Johnson 1980; Thomas and Taylor 1990, 2006). In this way, RSFs can provide insight into the combinations of resources that are necessary to sustain wildlife populations (Manly et al., 2002). While there are important sampling elements to consider including the ways in which available or unused habitat units are measured, the RSF framework has become a widely-used approach among wildlife ecologists to model animal-habitat relationships (Erickson et al., 2001; Keating and Cherry, 2004; Arts et al., 2008; Fieburg et al., 2010; Montgomery and Roloff, 2013).

Given that management and conservation efforts are typically developed at the population-level, researchers typically deploy telemetry collars/tags on a number of animal subjects and then aggregate the resultant telemetry data at the population-level to fit one RSF (Thomas and Taylor 2006). Importantly, aggregating telemetry data across animal subjects obscures any individual variation that may exist in the ways in which these animals respond to the environment. This can bias inference, particularly when relocation data are unbalanced across individual animals, as is often the case (Gillies et al., 2006; Aarts et al., 2008). To account for individual variation, researchers may fit models where animal id is included as a random effect.

This random effects component (fit as either a random intercept or random slope) relaxes the assumption of independence among data points, potentially mediating issues with unbalanced sampling efforts by allowing parameters in an RSF to vary according to an aggregate-level probability distribution (also called population-level or top-level; Mysterud and Ims, 1998; Gillies et al., 2006; Thomas, Johnson and Griffith 2006; Aarts et al., 2008; Hebblewhite and Merrill 2008; Duchesne et al., 2010; Hooten et al., 2016). However, adjustments to the slope or intercept of a model may be insufficient to account for the true variation inherent to the input data. At risk here is the potential to misidentify resource selection which can confound inference and problematize prevailing management or conservation philosophy. As Marzluff et al. (2004) note, individuality in wildlife resource selection can be extreme, warranting an examination of the consequences of that individuality.

Here I investigated the consequences of aggregating animals, where variation is assumed to be constrained statistically, in RSF analyses. Modeling elk (*Cervus elaphus*) resource selection in a reintroduced population in southern Missouri, I compared aggregate-level to individual animal RSFs. Using a hierarchical discrete choice model to evaluate these RSFs, I treated individuals as random effects at the aggregate level according to conventional practice. I then fit the same model at the level of each individual elk to compare variation in selection tendencies using multivariate techniques. I based this comparison on three areas of inference common to resource selection analyses: 1) the number and composition of parameters in top models, 2) the estimated RSF parameters of global models, and 3) the predicted relative probabilities of use. I discuss the ramifications of variation across these three metrics for management and conversation practice. Finally, I provide guidance on the framing of future analyses of RSFs and habitat selection research more broadly.

2.2. Methods

2.2.1. Resource selection data

Elk (n = 88) were captured in Kentucky for relocation to the Missouri Ozarks in June of 2011 (14 males, 19 females), 2012 (8 males, 26 females), and 2013 (3 males, 36 F). After a period of acclimation in a fenced enclosure, these elk were introduced onto Peck Ranch Conservation Area (Fremont, MO), a 9,327 ha plot of land managed by the Missouri Department of Conservation. Both of these areas are contained within the broader elk restoration zone, an 896 km² study area in southeast Missouri delimited by the Missouri Department of Conservation because of the region's high density of abundant public lands and high predicted habitat suitability for elk (MDC 2010). Prior to release, all elk \geq 1 year old were fitted with a GPS collar (RASSL custom 3D cell collar, North Star Science and Technology, LLC, King George, VA, or G2110E Iridium/GPS series model, Advanced Telemetry Systems, Insanti, MN). These collars were set to a 2.5 hour fix attempt schedule, storing locations internally at this frequency and uploading information every 5 hours (aside from two collars, set at 2 and 4 hours, respectively). Capture and handling protocols were approved by the University of Missouri Animal Care and Use Committee (Protocol 6909). Environmental variables were measured at the used locations (as determined by the GPS telemetry system) and available locations, which were defined using the radius of available habitat method (Durner et al., 2009). This involved delimiting a circle around each used location having radius equal to c(a + 2b), where a, b, and c represent the mean hourly movement rate, the standard deviation of the movement rate, and the number of hours between locations, respectively. Locations were then randomly sampled from within these circles to determine the corresponding available locations for the subsequent used locations, hereafter referred to as a "choice set".

2.2.2. Environmental variables

I used a geographic database of environmental variables developed by Smith (2015) to describe the study area. These included 11 different variables each depicted as rasters at a resolution of 30 m. This database included percent tree canopy cover (2011 US Forest Service National Land Cover Database (www. mrlc.gov/nlcd11_data.php, accessed 8 Jan 2015), number of years since prescribed burn, aspect (degrees), slope (percent), distance to wooded edge (m), the interspersion and juxtaposition index (IJI; Griffith et al., 2000), road density (km paved or gravel road/km² within 95 km² circle), distance to paved road (m), distance to closed two-track roads (m), and distance to public gravel roads (m; for more information see Smith (2015)). Finally, I also considered habitat type, the only categorical variable considered, which had eight categories: warm-season grassland, cool-season grassland, shrubland, woodland, savannah, forest, glade, and forage opening.

2.2.3. RSF modeling

I fit discrete choice RSFs because they can accommodate availability data that is defined separately for each location, which can provide a more realistic approximation of animal choice (Cooper and Millspaugh, 1999, 2001; McCracken et al., 1998). I selected a Bayesian framework given the difficulties of likelihood-based approaches and the flexibility of Bayesian methods when fitting random-effects logistic regression models (Browne and Draper 2005; Gelman et al., 2014a). For every used location I developed 5 available locations to define each discrete choice set. I developed the RSFs at the aggregate- and individual-levels. The individual-level model is defined as follows, where the probability of an individual elk choosing alternative l from a set of *C* feasible habitat units at unit *i* is given by

$$P_{il} = \frac{e^{\beta X_{il}}}{\sum_{c=1}^{C} e^{\beta X_{ic}}}$$
(1)

where

$$\boldsymbol{\beta}\boldsymbol{X}_{il} = \beta_1 \boldsymbol{X}_{il1} + \beta_2 \boldsymbol{X}_{il2} + \dots + \beta_k \boldsymbol{X}_{ilk} \tag{2}$$

is the *utility* of unit l to the individual being considered, consisting of k slope parameters measured on each used and available unit. The concept of utility derives from economic theory and is analogous to satisfaction; eqn. (1) is valid under the assumption that the individual in question always chooses the resource unit having the greatest utility (Cooper and Millspaugh 1999). I slightly extended eqns. (1) and (2) to develop the aggregate-level model, where I make explicit the probability of individual j choosing alternative l from a set of C feasible alternatives to unit i, defined as

$$P_{ijl} = \frac{e^{\beta_j X_{ijl}}}{\sum_{c=1}^{C} e^{\beta_j X_{ijc}}}$$
(3)

with utility function now defined as

$$\boldsymbol{\beta}_{j}\boldsymbol{X}_{ijl} = \beta_{j1}X_{ijl1} + \beta_{j2}X_{ilj2} + \dots + \beta_{jk}X_{ijlk}$$
(4)
and $\beta_{ik} \sim Normal(\mu_k, \sigma_k^2)$

where the individual parameters for selection of environmental variable k (the β_{jk} for all j = 1, 2, ..., 88 individuals), are assumed to be normally-distributed random effects following some population distribution. The parameters of the population distributions for each environmental variable k (μ_k and σ_k^2) are referred to as "hyperparameters"(Hobbs and Hooten 2015). Thus, the aggregate-level model was a hierarchical random slopes model, where inference can be made on

the central tendency of selection for each environmental variable k, or the "mean hyperparameter" μ_k , as well as variation among individuals, or the "standard deviation hyperparameter" σ_k . I conducted aggregate-level model estimation using the following uninformative priors for all hyperparameters:

$$\mu_{k} \sim Normal(0, 10)$$
(5)
$$\sigma_{k} \sim Uniform(0, 10)$$

Prior to model fitting, I examined evident collinearity among the environmental variables on a per-individual basis, and excluded redundant environmental variables until all pairwise correlations were $|\mathbf{r}| \le 0.6$. I then constructed a global model at the aggregate and individual levels consisting of all remaining environmental variables such that this condition was satisfied.

I fit these models in the Bayesian package Stan (Stan Development Team 2016a) using R and RStan as an interface (R Core Team 2016; Stan Development Team 2016b). For each individual model, I used four chains of 1000 draws each, with a burn-in period of 200. This was likely more simulation than necessary, given the simple structure of the models (i.e. nonhierarchical) and in most cases 1000 iterations is more than enough to reach convergence to the posterior distribution using Stan (Vehtari et al., 2016). However, I used this approach to ensure that any individual differences that may arise in the comparisons (next section) would not be attributable to Monte Carlo error. Additionally, to fit all models, I used the high-performance computing cluster developed and maintained by the Institute for Cyber-Enabled Research at Michigan State University. With the large number of processors and excess RAM, I was able to fit the models in parallel and remotely. I assessed convergence of all models by ensuring that for all parameters the potential scale reduction factor, \hat{R} , was below 1.1 and the effective sample

size, \hat{n}_{eff} , was greater than 100 (Gelman et al., 2013). I assessed goodness of model fits using posterior predictive checks, whereby I computed the probability that a test statistic, *T*, calculated on new data simulated from the model, y^* , is more extreme than *T* calculated on observed data, y (Gelman et al., 2013; Hobbs and Hooten 2015). I used the chi-square test statistic to conduct these checks for the aggregate-level global model and all individual-level global models as follows

$$\Pr(T(\boldsymbol{y}^*, \boldsymbol{\theta}) \ge T(\boldsymbol{y}, \boldsymbol{\theta}) | \boldsymbol{y})$$

$$T(\boldsymbol{y}, \boldsymbol{\theta}) = \sum_{i} \frac{(y_i - p_i)^2}{p_i}$$
(6)

where $\boldsymbol{\theta}$ represents the parameters for the fitted model, and p_i is the probability associated with the *i*th choice. The first expression in (6) returns a Bayesian "*p*-value", P_B , which I used to diagnose lack of model fit (Gelman et al., 2013; Hobbs and Hooten 2015).

2.2.4. Comparison between aggregate- and individual-level RSFs

I assessed patterns of individual variation in resource selection among the individual and aggregate levels by comparing: 1) the parameters included in top models, 2) parameter estimates of all global models, and 3) predictions of the relative probability of use expressed across the study area. To make comparisons based on the model selection approach, I fit all subsets of the global model for each individual following examination for collinearity, carrying out estimation as described above to perform what was essentially a "dredge" (Wiens et al., 2008; Cade 2015). I ranked models using WAIC, a fully Bayesian estimate of out-of-sample predictive ability, determining the top model for each individual to be that with the lowest WAIC score (Watanabe 2010; Vehtari et al., 2015; Gelman et al., 2014b). I evaluated the inclusion of parameters in the

top and runner-up models by calculating "inclusion rates" in the top 5% of models for each individual. To make this calculation, I ordered all models by increasing WAIC score and, using only the models contained in the top 5% of this ordering, divided the number of models in which a parameter was included by the total number of models in this list. I used WAIC to rank models because it is both fully Bayesian and computationally efficient (Vehtari et al., 2015). I also performed this selection procedure for the aggregate-level model, where sub-models retained the same hierarchical format used in the global model, but varied with respect to the RSF parameters and associated hyperparameters.

I compared individual variation in parameter estimates to the estimated aggregate-level distribution on a per-parameter basis using a graphical approach. As an aggregate-level estimate of the individual variation in parameter estimates, I added the lower and upper limits of the mean hyperparameter CIs to their corresponding limits for the standard deviation hyperparameters for each environmental variable, giving the following interval $[\hat{\mu}_k^{(l)} - \hat{\sigma}_k^{(l)}, \hat{\mu}_k^{(u)} + \hat{\sigma}_k^{(u)}]$ for all k parameters, where *I* and *u* represent the lower and upper limits for the 95% CIs, respectively. This calculates conservative intervals within which one standard deviation of the individual random effects (~ 66% of theoretical individuals' parameters) is expected to be contained under the aggregate-level model assumptions. I refer to this metric as the 95% "random-effect CI", as it characterizes the random-effect distributions with uncertainty around the hyperparameter estimates incorporated. Additionally, I investigated patterns of estimated selection tendencies (i.e., the composites of individual parameter estimates) among individuals using principal components analysis on the RSF parameter point-estimates. Ordination in parameter space has been used previously to investigate variation in selection and movement patterns among individuals (Hanks et al., 2011; Pape and Löffler 2015). I only used the individual-level
estimates for which uncertainty was comparable among individuals, and I compare among intrinsic factors and year of GPS-collaring and release, hereafter referred to as "cohort".

For the final comparison, I produced predictive maps of the relative probabilities of use for each top model across the entire study area. I evaluated the logistic of the estimated RSFs, $\exp(RSF)/(1 + \exp(RSF))$, at each 30m resolution cell within the study area, returning the predicted relative probability of use of that unit under the estimated model(s).

2.3. Results

The 88 elk in this study were GPS-tracked between June 1, 2011 and September 15, 2014 (35 elk released in 2011 (22 female, 13 male), 24 elk released in 2012 (17 female, 7 male), and 29 elk released in 2013 (26 female, 3 male)). At the aggregate level, I fit the global discrete choice RSF model and sub-models using 141,197 choice sets consisting of 1 used location and 5 available locations. I detected high collinearity $(0.61 \le |r| \le 0.84)$ between the distance to gravel road and road density variables for all individuals, and I excluded the former variable from consideration given that two other variables (distance to paved road and distance to two-track road) quantified proximity to roads. Thus, an identical set of sub-models was fit to all individuals. Individual-level models were estimated based on 95 to 4865 choice sets depending on the elk, and more than 50% of the models were fit with between 783 and 2071 choice sets. I achieved convergence of all models fit ($\hat{R} < 1.1$ for all parameters at the individual level and hyperparameters at the aggregate level). The Bayesian p-value test for the global aggregate-level model indicated no lack of fit, i.e. could have reasonably generated the observed data (P_B = 0.35, Hobbs and Hooten 2015). Bayesian *p*-values for all individual-level global models fell between 0.16 and 0.58, with an average value of 0.33.

2.3.1. Number and composition of parameters

The global model at the aggregate level had the highest predictive ability of all submodels considered (see Table 2.1), while the top individual-level models had an average of 14.4 parameters with a range of 7 to 17 (Fig. 2.1a). The order of importance of parameters for predictive ability was also mixed, although habitat and slope were in all but two and five of top models, respectively. Conversely, aspect was only included as a predictor in the top model for 44% of the elk (39 of the 88 top models). The exclusion of any one parameter from top models did not appear to be linked with patterns of exclusion for other parameters. The remaining parameters were included in top models for between 62% and 86% of the elk (between 54 and 76 of the 88 top models, respectively). Habitat and slope also had the highest inclusion rates, having a value of 1.0 for the majority of elk (i.e., included in the top model and all of the 5% runner-up models; Fig. 2.1b) I observed low inclusion rates (\leq 0.2) of the distance to two-track roads parameter for four elk and the distance to paved roads parameter for three elk, as well as IJI for one elk (Fig. 2.1b).

2.3.2. Parameter estimates

At the aggregate level, thirteen of the seventeen μ_k estimates under the global model had 95% credible intervals (CIs) which did not overlap zero. These included estimates for all μ_k for continuous environmental variables as well as all categorical habitat types except forest, shrubland, glade, and warm-season grassland. However, the estimated 95% random-effect CIs contained zero in only two cases: slope and forage opening. Aggregate-level point estimates of individual variation (the σ_k estimates) varied from a minimum of 0.04 for aspect, to 1.71 for distance to two-track. The latter was large relative to estimates of σ_k for the remaining environmental variables, as all other estimates fell below 0.67 (Fig. 2). There was a high degree

of variation in the individual-level estimates of selection, and point estimates of the habitat type parameters were exceptionally variable, extending far beyond random-effect CIs (Fig. 2). However, uncertainty around these point estimates was high for most individuals, as evidenced by the large CI's around these estimates (Fig. 2.2). Conversely, variability among individuals in selection for distance to two-track roads appeared much smaller than was estimated at the aggregate-level, as virtually all point estimates fell within the random-effect CIs (gray boxes, Fig. 2.2). Given the relatively large uncertainty around individual-level habitat type parameter estimates, I based the principal components analysis (PCA) on parameters for only the continuous environmental variables. Ordination by PCA revealed that some individuals were much more different from one another in terms of combined selection estimates of the nine resource covariates, yet none of the factors examined accounted for the observed extreme selection tendencies (Fig. 2.3a). A small degree of clustering was evident based on cohort (Fig. 2.3b).

2.3.3. Predicted relative probabilities

Predictive mapping of the relative probability of use throughout the elk restoration zone under the global models was vastly different among individuals, and when compared to the aggregate-level predictions (Fig. 2.4a). Of the randomly-selected individuals I used to inform these plots, less than half displayed patterns of selection similar to the estimated population-level predictions. The remaining individuals varied with respect to both general areas of relative use probability and uniformity of this use. For example, elk, at an aggregate level, were predicted to select habitat units found in the southeastern portion of the elk restoration zone where the predicted probability of use was very low for many of the individual elk (Fig. 2.4b). Yet even

among these individuals, areas of high predicted relative use varied along a gradient of uniform patterns to being much more clustered, varying in scales (Fig. 2.4b).

2.4. Discussion

Under the current paradigm for evaluating wildlife resource selection, telemetry data of collared/tagged individuals are typically aggregated prior to model-fitting (Thomas and Taylor, 2006). Aggregating data among individuals is done in the interest of making inferences about animal populations that can provide, among other things, information that is relevant to management and conservation. My study revealed substantial differences between models fit at the aggregate and individual animal levels across three metrics including the number and composition of parameters in top models, the estimated parameters among global models, and predicted relative probabilities of use. This analysis demonstrates that variation in resource selection among individual animals may not be well accounted for by simply including a random effect in aggregate models. While results speak to variation among one population of elk in this ecosystem in Missouri, I find this variation to particularly interesting given that my study animal is highly gregarious and often expected to respond similarly to the environment. These results support existing research which demonstrates the importance of considering individual animal differences in habitat selection, even when the species of interest exhibits sociality (Gillingham and Parker, 2008; Putman and Flueck, 2011; Pape and Löffler, 2015). Further, I could not detect any real conformity in elk-habitat relationships by age or sex class (Figs. 2.3a and 2.3b).

At the aggregate-level, the global model received the most support based on ranking by WAIC, yet the inclusion of parameters among individual top models was highly variable. The assumption that observations (i.e. choices between available habitat units) follow some population process with parametric form may have influenced which variables are considered

important to selection by all individuals. The fact that the global aggregate-level model achieved the best ranking by WAIC could also be affected by the large sample size, given the tendency for information criteria-based ranking methods to favor more complex models with large sample sizes (Piironen and Vehtari, 2016). The individual variation revealed by our model-ranking analysis suggests that a particular resource may influence decision-making for certain elk more than others. Differential selection may arise in cases where there is a functional response in resource selection, or differences in resource selection/avoidance among individuals (Mysterud and Ims 1998; Haydon et al., 2008). It is difficult to distinguish the effect of overall available habitat from the effect of individual differences in selection, but analysis at the individual level affords the opportunity to explore why individual animals may apparently select habitat units differentially based on available resources. For example, a comparison of RSF models for individual moose made by Gillingham and Parker (2008) revealed that inclusion of a particular selection parameter in the top model varied with the availability in an individual's home range. Investigating why individuals may differ in this way can provide information that would be obscured if telemetry data were aggregated and only one model was fit.

Variation in parameter estimates at the individual level was not commensurate with the variation identified by the σ_k estimates (representing random effect of animal ID) of the aggregate-level model. For example, with respect to distance to two-track roads, variation among individual-level parameter estimates was much lower than what would be suggested by the aggregate-level model (Fig. 2.2). This observation reflects a potential issue with standardizing variables when evaluating RSFs at the aggregate level. It is common practice to standardize predictor variables to facilitate comparison of effects when evaluating RSFs (e.g. Thomas et al., 2006). In the present study, the aggregate-level hyperparameter estimates were all based on the

standardized environmental data at used and available habitat units for 88 elk, while our individual-level parameter estimates were based on data standardized for each individual separately. This should provide a more accurate depiction of the comparative effects between environmental variables on an individual basis; in the case of distance to two-track roads, it suggests that elk respond much more consistently to this environmental variable than would be depicted by the aggregate-level model, where it has a small, negative effect on selection of a resource unit, as opposed to an unknown effect that could vary in both magnitude and direction (Fig. 2.2). Differential use of habitat units based on habitat type may, in part, account for the relatively large uncertainty of corresponding individual-level parameter estimates (Fig. 2.2). If avoidance of specific habitat types by individuals occurs, low use or non-used of these habitat types can bias parameter estimates, which is a known issue with categorical covariates in such models (problem of separation; Menard 2002). Modelling at the individual level allows further investigation into relationships between sampling and RSF parameter estimates (Gillingham and Parker, 2008).

Spatial variation in the predicted relative probability of use indicated broad-scale differences in selection strategies between aggregate- and individual-level models (Figs. 2.4a and 2.4b). Because these predictive maps do not reflect parameter uncertainty, it is difficult to quantify the extent that this variation may be attributed to error as opposed to real differences in habitat selection strategies among individual elk. It may be that individual animals are selecting for specific environmental features, and the configuration of those features should be expected to be heterogeneously distributed (Aarts et al., 2008; Paton and Matthiopolous, 2015). Additionally, given that predictive mapping with RSFs is a very useful tool for management of ungulate species, assessing individual-based predictions could offer unique advantages (Johnson et al.,

2004). For example, predicting relative probability of landscape use (or the absolute probabilities of use when using an RSPF) for individuals could help inform predictions of space use as populations increase following a reintroduction. Predictive mapping based on individual RSF models may present greater potential opportunities for conservation and management of solitary animals, or animals of conservation concern whereby efforts may be focused on managing habitat to meet the needs specific individuals.

With recent developments in technologies that can produce highly resolute movement and remotely-sensed data, we have an unprecedented ability to model habitat use by individual animals that can even reveal insights into specific behavioral and ecological mechanisms (Kays et al., 2015). The idea that consistent individual differences among animals (i.e., personality) have important evolutionary and ecological consequences has been amassing a large amount of support for many processes, including habitat selection (Réale et al., 2010; Leclerc et al., 2016; Merrick et al., 2017; Spiegel et al., 2017). Indeed, the potential to derive fitness implications for populations based on differences in movement among individuals has been demonstrated for elk (Haydon et al., 2008; Morales et al. 2010). In this study, aggregate models missed important inferences for conservation and management, including: the importance of certain resource covariates in predicting selection, such as aspect; the inflated effects of certain resource covariates on selection, such as distance to paved roads; that more extreme individuality in combined selection habits could not be attributed to intrinsic factors; and that selection of resource units across the greater landscape may not be as consistent. These results are consistent with an emerging body of research demonstrating potentially substantial variation in habitat selection strategies within populations of highly gregarious species (e.g., elk and reindeer *Rangifer tarandus*; Sawyer et al., 2007; Pape and Löffler, 2015)

My study demonstrates that modelling resource selection at the individual level can reveal important variation in selection strategies within populations of animals that could have been missed by aggregate-level models. That being said, I did identify some consistencies between the aggregate and individual levels. For example, the consistent inclusion of slope and habitat type in top individual models compliments the result that slope and forage openings had the greatest effects on selection at the aggregate level. However, apparent inter-individual differences in selection as determined by RSF modelling can only be investigated by fitting individual-level models, because the selection tendencies of individuals is a prerequisite that is not estimable when fitting typical aggregate (i.e. hierarchical) models. Other benefits to modelling resource selection at the individual level were beyond the scope of our study but provide opportunities for future study. Quantifying variation in the movement process at the individual-animal level could be particularly relevant. There have been a number of individualbased movement models developed in recent years, and methods that simultaneously estimate resource selection and movement have been introduced (Thurfjell et al., 2014; Avgar et al., 2016). Employing models of animal movement can be useful for defining more biologically feasible unused or available habitat units.

In conclusion, via this assessment we do not suggest that researchers should abandon aggregate-level RSF modelling with random-effects to quantify individual variation. In this study, relatively strong effects of slope and forage opening on selection of a habitat unit were found at both the aggregate and individual levels. However, I caution against discounting individual variation in habitat selection. Recent developments in this area highlight the common consideration of individual differences in studies of behavioral or population ecology, a viewpoint which should be adopted in applied wildlife conservation research (Merrick and

Koprowski, 2017). Thus, researchers and managers should fit models at the individual level so that they can appreciate the consequences of that variation on management practice. When using RSFs to quantify resource selection, I reiterate the importance of multi-scale efforts that have been advocated by others, and assert that both individual- and aggregate-level models can provide valuable inference for management (Gillingham and Parker, 2008; Pape and Löffler, 2015). The methods that we used here provide a framework that other ecologists and managers can use to assess the role of individual variation in their study system. These approaches can be useful for evaluating the utility of population inference from RSFs which will vary among systems and research objectives (Hanks et al., 2011). Computational improvements to hierarchical methods for estimating movement and resource selection are also being developed (Hooten et al., 2016). For researchers and managers limited by computational resources or statistical expertise, fitting individual models provides a better alternative, or at least a supplement to, aggregating across individuals for population-level inference in resource selection analyses. In studies of resource selection, approaches that do not consider individual-level selection are liable to giving superficial weight to certain resources and/or habitats, while underestimating the importance of others and potentially missing interesting ecological relationships. I therefore recommend that whenever feasible, practitioners model habitat selection at the individual level if aggregate approaches will be used to inform management decisions.

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APPENDIX

Table 2.1. WAIC values for top 10 aggregate-level resource selection function models. + indicates an environmental variable included in the model, spaces left blank if not included. Environmental variable abbreviations as follows: D2t = distance to twotrack road; Dpav = Distance to paved road (m); Slope = slope (degrees); Aspect = aspect (degrees); Rd dens = road density (km/km²); D edge = Distance to nearest wooded edge; % Can = percent forested canopy cover; Rx burn = years since prescribed fire; Habitat = indicator variables for 8 cover types.

D2t	Dpav	Slope	Aspect	Rd dens	D edge	% Can	Rx burn	Habitat	WAIC
+	+	+	+	+	+	+	+	+	321786.1
+	+	+		+	+	+	+	+	323171.8
+	+	+	+	+		+	+	+	323894.1
+		+	+	+	+	+	+	+	324310.7
+	+	+	+		+	+	+	+	324410.7
	+	+	+	+	+	+	+	+	324608.6
+	+	+	+	+	+		+	+	324759.4
		+	+	+	+	+	+	+	324865.3
+	+		+	+	+	+	+	+	326220.7

Figure 2.1. Inclusion of parameters at the individual level in top models (a panel) and top 5% of models (b panel) as ranked by WAIC for elk reintroduced into the Missouri Ozarks (2011-2014). Green boxes (panel a) indicate the selection parameters in line with the row was included in the top model as ranked by WAIC. Shade of purple (panel b) is proportional to the number of times the corresponding parameter was included in the top 5% of sub-models, where the darkest shade corresponds to all models and lightest shade indicates that parameter was not included in any of the top models.



Individual elk

Figure 2.2. Aggregate-level random effects distributions (boxes) and individual-level RSF parameter estimates (blue dots) with 95% Bayesian credible intervals (CIs, in translucent blue) for reintroduced elk in the Missouri Ozarks (2011-2014). The middle horizontal bars within the boxes are the point estimates of the mean hyperparameters of the random effects distributions. The light gray horizontal bars within the boxes are point estimates for the standard deviation hyperparameters, and the ends of the boxes represent 95% Bayesian credible intervals on mean + standard deviation point estimates.



Figure 2.3. Principal components analysis (PCA) ordination of the 88 individual elk reintroduced into the Missouri Ozarks (2011-2014) based on individual-level parameter estimates for selection of 9 resource covariates. Grouped by intrinsic factors (panel a) and by GPS-collaring and release year (cohort; panel b).



Figure 2.4. Predicted relative probabilities of use of the elk restoration zone based on and aggregate-level RSF (panel a) and individual-level RSFs for 20 randomly selected elk (panel b) reintroduced to the Missouri Ozarks (2011-2014).



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CONCLUSION

Conservation and management of ungulate species will require a mechanistic understanding of the ways in which extrinsic and intrinsic factors change movement and habitat selection. The ability to obtain location data on these animals at relatively fine temporal resolutions for long periods of time suggests that the movement ecology paradigm is well-suited for discovering these mechanistic links. When coupled with on-board data-loggers (e.g., temperature) and data from remote sensing platforms or autonomous sensor networks, there is opportunity to study the influence of both extrinsic characteristics of an individual's surroundings, and of intrinsic properties. My study took important steps towards identifying the underlying mechanisms while developing quantitative techniques to model these data with increased accuracy. I envision the contributions of my thesis to be two-fold. First, in chapter 1 non-linear modeling revealed little evidence of heat stress thresholds in movement of moose in central Norway. Using a population-level model, I was able to demonstrate that physiological thresholds of moose established about 30 years ago may not affect moose movement as much as had previously been thought. The results further verified the importance of studying free-living animals whenever possible. Second, in chapter 2 I evaluated the pitfalls of the practice of analyzing the process of resource selection at the aggregate level. Even when accounting for individual variation by incorporating mixed-effects models (i.e., random effect by individual animal) to fit resource selection functions, this work demonstrated that potential inferences could still be missed. This finding has important implications for wildlife management and conservation practice.

The main strength of this study is to simultaneously treatment of both the aggregate- and individual-level perspectives, while remaining in the Lagrangian framework of treating the individual as the sample unit, in accordance with prevailing discourse in movement ecology. Specifically, I used movement data derived from individual tracks and associated temperature readings from collar-borne loggers to evaluate my research question in an aggregate perspective. Additionally, I employed a Bayesian discrete choice modelling framework to estimate resource selection, which is predicated on the notion of individual choice and was therefore highly appropriate for estimating choice at the individual level. In this way, it makes intuitive sense to think about individual heterogeneity in the process of resource selection that may not be effectively captured by aggregate methods. Admittedly, a salient weakness of my study is that I did not account for both processes (habitat selection and movement) in either of the focal analyses. These processes are intricately linked; habitat likely plays a major role in deciding how and when ungulates move, and vice versa (Thurfjell et al., 2014). Thus, quantifying both simultaneously could better inform the mechanistic roles of important intrinsic and extrinsic dimensions.

Clearly, efforts to conserve ungulate species will be greatly benefitted by the quantitative analysis of movement and habitat selection, in addition to other processes (Nathan et al., 2013). However, scaling up inference to the population level is paramount for making management decisions. Development of holistic methods to do this is an area of active research, and computationally efficient hierarchical modeling approaches show much promise (Hooten et al., 2016; Jonsen, 2017). However, besides the fact that many recent open-source software packages have been developed with analysis of individual movement tracks in mind (e.g., Calabrese et al., 2016), the notion that consistent differences among individuals (i.e., personality) could have

implications for management is gaining attention, which raises questions about the scenarios in which such aggregate methods make biological or ecological sense, or are even practical (Merrick and Koprowski, 2017; Speigel et al., 2017). Nevertheless, it remains critical to combine the power of open-source analytical tools and mechanistic models of movement and habitat selection with data collected from distributed sensor networks, remote sensing platforms, and telemetered individuals, as well as intrinsic biological information. This thesis is a testament to the need for multiple analytical perspectives when nurturing a mechanistic understanding of ungulate space use and fitness at multiple scales. REFERENCES

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