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Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate

Ryan A. Long,[1,4] R. Terry Bowyer,[1] Warren P. Porter,[2] Paul Mathewson,[2] Kevin L. Monteith,[3] and John G. Kie[1]

[1]*Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209 USA*
[2]*Department of Zoology, University of Wisconsin Madison, Madison, Wisconsin 53796 USA*
[3]*Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA*

Abstract. Temporal changes in net energy balance of animals strongly influence fitness; consequently, natural selection should favor behaviors that increase net energy balance by buffering individuals against negative effects of environmental variation. The relative importance of behavioral responses to climate-induced variation in costs vs. supplies of energy, however, is uncertain, as is the degree to which such responses are mediated by current stores of energy. We evaluated relationships among behavior, nutritional condition (i.e., energy state), and spatiotemporal variation in costs vs. supplies of energy available to a large-bodied endotherm, the North American elk (*Cervus elaphus*), occupying two ecosystems with contrasting climates and energy landscapes: a temperate, montane forest and an arid, high-elevation desert. We hypothesized that during spring through autumn, behavioral responses to the energy landscape would be both context dependent (i.e., would vary as a function of the contrasting environmental conditions experienced by elk in the forest vs. the desert), and state dependent (i.e., would vary as a function of the energy balance of an individual). We tested several predictions derived from that hypothesis by combining output from a biophysical model of the thermal environment with data on forage quality, animal locations, and nutritional condition of individuals. At the population level, elk in the desert selected areas that reduced costs of thermoregulation over those that provided the highest-quality forage. In the forest, however, costs imposed by the thermal environment were less pronounced, and elk selected areas that increased access to high-quality forage over those that reduced costs of thermoregulation. At the individual level, nutritional condition did not influence strength of selection for low-cost areas or high-quality forage among elk in the forest. In the desert, however, strength of selection for low-cost areas (but not forage quality) was state dependent; individuals in the poorest condition at the end of winter showed the strongest selection for areas that reduced costs of thermoregulation during spring and summer, and also expended the least amount of energy on locomotion. Our results highlight the importance of understanding the roles of behavior and nutritional condition in buffering endotherms against direct and indirect effects of climate on fitness.

Key words: biophysical model; Blue Mountains, northeastern Oregon, USA; Cervus elaphus; *climate change; elk; nutritional condition; resource selection function; Snake River Plain, southeastern Idaho, USA; thermal environment; thermoregulation.*

Introduction

Many effects of climate change on ecosystem structure and function are driven by environmental temperature (Pörtner and Farrell 2008, Rosenzweig et al. 2008), and the earth is currently in the midst of a pronounced warming trend (Humphries et al. 2004, Collins et al. 2005, Braconnot et al. 2012). Consequently, understanding linkages among broadscale climatic variability, local weather patterns, and ecological processes has emerged as a critical challenge facing ecologists. In terrestrial ecosystems, considerable effort has been devoted to determining how the distribution (Walther et al. 2002, Van der Putten et al. 2010), population dynamics (Mysterud et al. 2001, Chan et al. 2005, Post et al. 2009), and timing of life-history events (Bowyer et al. 1999, Stenseth and Mysterud 2002, Winkler et al. 2002, Monteith et al. 2011) of a variety of species are, or will be, affected by climatic variability. Nevertheless, many important questions remain largely unaddressed. For example, what role has climate played in the evolution of behavioral strategies used to enhance fitness in heterogeneous landscapes (Levy et al. 2012, van Beest and Milner 2013)? Behavior is a primary mechanism by which animals buffer themselves against a variable

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[4] Present address: Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544 USA. E-mail: ralong@princeton.edu

environment (e.g., the "Bogert effect"; Huey et al. 2003), and the capacity for such buffering against climatic variability is likely to play a critical role in determining responses of many species to future changes in climate (Kearney et al. 2009).

Endothermic organisms frequently encounter trade-offs as they strive to maximize fitness (Berger 1991, Barten et al. 2001), and females, in particular, must balance energy invested in current offspring against the probability of surviving to reproduce again (Trivers 1974, Stearns 1992). In heterogeneous landscapes, such trade-offs often cause individuals to modify their behaviors in response to environmental factors that influence energy balance. Climate can affect energy balance of endotherms indirectly by influencing the quality, distribution, or phenology of forage (Post and Stenseth 1999, Mysterud et al. 2001, 2008, Humphries et al. 2004), or directly by producing spatiotemporal variation in the thermal environment that determines thermoregulatory costs incurred by individuals choosing to occupy a particular site (Porter et al. 2000, 2002, Dussault et al. 2004). Because patterns of net energy balance through time strongly influence fitness correlates such as body mass, nutritional condition, and birth mass of young (Cook et al. 2004, Parker et al. 2009), natural selection should favor behaviors that optimize net energy balance, depending on time of year and individual condition (Speakman and Król 2010). Nevertheless, the degree to which endotherms should select low-cost areas (i.e., areas that reduce costs of thermoregulation and activity) vs. those that increase access to supplies of energy is unclear. Much previous research on relationships between behavior and energy balance of endotherms has focused on the supply side of the energy balance equation (e.g., McNab 2002, Brown et al. 2004). The heat dissipation limit theory of Speakman and Król (2010), however, contends that, in many circumstances, trade-offs in energy allocation by endothermic organisms are governed more by their capacity to dissipate heat and avoid hyperthermia than by their ability to harvest energy from the environment.

Although Speakman and Król (2010) did not include quantitative predictions of animal behavior as an implicit component of the heat dissipation limit theory, a number of important behavioral implications can be derived from their model. For example, the theory implies that in situations where energy is readily available (and thus intake is not limited) and environmental temperatures are relatively warm (a common occurrence during spring through autumn in many temperate ecosystems), endotherms should focus their behavior on reducing costs associated with heat dissipation. By actively selecting areas that reduce environmental heat loads, endotherms should increase their capacity to allocate energy to growth and reproduction rather than to thermoregulation and activity. Similarly, Parker et al. (2009) and Wilson et al. (2012) argued that, during much of the year, behavioral control over energy balance is more likely to be manifested through minimization of energy expenditures for thermoregulation and activity than through maximization of energy intake. This related hypothesis ostensibly stems from the observation that variation in availability of energy (i.e., forage quality) often occurs at broader temporal (e.g., seasons to years vs. hours to days) and spatial (e.g., among vs. within habitat patches) scales than variation in costs of thermoregulation and activity. Thus, fine-scale decisions made by animals as they navigate a landscape are more likely to be influenced by energy costs than benefits, even if the latter has a greater effect on broad patterns of demography and population dynamics (Mysterud et al. 2001, Chan et al. 2005).

Behavioral implications of the heat dissipation limit theory are particularly germane to large-bodied endotherms in the face of a warming climate. In contrast to smaller species, large endotherms tend to be especially sensitive to warm temperatures, and can develop high internal heat loads relatively easily because thick boundary layers and small surface-to-volume ratios reduce rates of heat loss to the environment (Porter and Gates 1969, Renecker and Hudson 1986, Cain et al. 2006, Porter and Kearney 2009). Indeed, previous eras of high global temperature (e.g., the Paleocene–Eocene Thermal Maximum) have resulted in average body size reductions of $>30\%$ for mammals (Jardine 2011). Thus, large, herbivorous mammals are a useful model for evaluating behavioral responses of endotherms to variation in the energy landscape (i.e., costs and supplies of energy). Such questions are more challenging to address for other large-bodied taxa (e.g., cetaceans or carnivores) because of the mobility of their prey, which results in a continual state of flux in the spatial distribution of energy supplies.

In contrast to the dearth of information on behavioral responses of endotherms to fine-scale variation in the energy landscape, several studies have elucidated the influence of endogenous individual traits, including energy balance, on behavior of large, herbivorous mammals (McNamara and Houston 1996, Monteith et al. 2013). For example, Montgomery et al. (2012) demonstrated that when moose (*Alces alces*) in Isle Royale National Park, USA, were faced with a trade-off between forage and risk of predation, prime-aged individuals traded access to forage for less risky habitats, whereas senescent individuals showed stronger selection for riskier habitats with abundant forage. Similarly, Monteith et al. (2011) demonstrated that in a migratory population of mule deer (*Odocoileus hemionus*), older individuals and those in good nutritional condition were more likely to delay autumn migration and risk encountering severe weather and reduced foraging opportunities than were younger individuals or those in poor condition. In contrast to many other individual characteristics, nutritional condition integrates a suite of responses of large herbivores to the environment (Parker et al. 2009), is an excellent metric of energy reserves available for maintenance, growth, and reproduction (Cook et al. 2004, 2010, Parker et al. 2009), and is positively related to survival and reproductive success (Gaillard et al. 2000, Mysterud et al. 2001). Therefore, individual responses to the energy landscape should vary as a function of nutritional condition.

We combined output from a biophysical model (Niche Mapper) designed to predict spatiotemporally explicit metabolic and hydric costs imposed on endothermic animals by the thermal environment, with data on forage quality, nutritional condition, animal locations, concealment cover, and proximity to human disturbance, to quantify behavioral responses of a large-bodied endotherm, the North American elk (*Cervus elaphus*; see Plate 1), to the energy landscape in two ecosystems with markedly different climates: a temperate, montane forest and an arid, high-elevation desert. We hypothesized that during spring through autumn, the relative importance of costs vs. supplies of energy as determinants of behavior would be both context dependent (i.e., would vary as a function of the contrasting environmental conditions experienced by elk in the forest vs. the desert), and state dependent (i.e., individual-level responses would vary as a function of energy state at the end of winter). We tested that hypothesis by evaluating the following series of seven predictions, which integrate central principles of the heat dissipation limit theory of Speakman and Król (2010), and the Bogert effect of Huey et al. (2003):

1) After accounting for non-energetics-related determinants of behavior, such as perceived risk of predation (concealment cover) and anthropogenic disturbance, seasonal and diel patterns of behavior by elk at the population level will be influenced more by spatiotemporal variation in costs imposed by the thermal environment than by spatiotemporal variation in forage quality.
2) Relative importance of the thermal environment as a determinant of behavior at the population level will be greater for elk in the desert than in the montane forest because of the higher temperatures and radiant heat loads (and thus higher costs of thermoregulation and activity) that characterize the desert.
3) Locomotion increases metabolic heat production, and thus diel (day–night) differences in energy expended on locomotion will be more substantial for elk in the desert than for those in the montane forest, because diel differences in environmental heat loads will be more extreme in the desert.
4) In both study systems, individuals in poor nutritional condition at the end of winter will show stronger selection for areas that reduce thermoregulatory costs during spring through autumn than individuals in good nutritional condition. Conversely, because high-quality forage is readily available in both systems during spring through autumn, strength of selection for forage quality will not vary with nutritional condition of elk in either system.
5) As a result of the higher overall cost of living in the desert, and thus the greater potential importance of behavioral control over energy balance, the relationship between nutritional condition and strength of selection for areas that reduce thermoregulatory costs will be stronger for elk in the desert than for those in the montane forest.
6) If a threshold in nutritional condition can be detected below which costs imposed by the thermal environment begin to play a role in influencing behavior of elk, that threshold will occur at a higher level of condition among elk in the desert than among those in the montane forest.
7) Although costs of locomotion represent only a small proportion of the energy budget of many large herbivores, the higher overall cost of living in the desert will force elk in poor condition to limit the amount of energy that they expend on locomotion, whereas elk in good condition will be able to move greater distances in their search for resources (i.e., energy expended on locomotion by individual elk in the desert will be positively related to nutritional condition). In contrast, energy expended on locomotion will be independent of nutritional condition of elk in the montane forest because of the lower overall cost of living in that environment.

Materials and Methods

Study areas

We conducted research in two ecosystems with substantially different climates, topographies, and vegetation associations. The Starkey Experimental Forest and Range (hereafter Starkey; 45°13′ N, 118°31′ W; Fig. 1), our first study area, was situated in the Blue Mountains of northeastern Oregon, USA. Starkey was a 101-km^2 research site operated by the U.S. Forest Service and surrounded by a 2.4 m high fence that prevented immigration or emigration of large herbivores (Rowland et al. 1997), but played no role in habitat selection by elk (Stewart et al. 2002, 2006). The fence also divided Starkey into several distinct research areas; we conducted our study in the largest of those, which, at 78 km^2 was several times larger than the average home range reported for elk in the Blue Mountains (Leckenby 1984). Density of elk at Starkey was low (<5 elk/km^2; Johnson et al. 2000; R. A. Long et al., *unpublished data*), and the population was probably well below carrying capacity (K), based on consistently high pregnancy rates (assessed by pregnancy-specific protein B; Noyes et al. 1997), excellent nutritional condition, and large birth mass of young (Kie et al. 2003, Stewart et al. 2005; R. A. Long et al., *unpublished data*). Traffic levels and recreational activities (e.g., hunting) were similar to patterns of use on nearby public lands (Rowland et al.

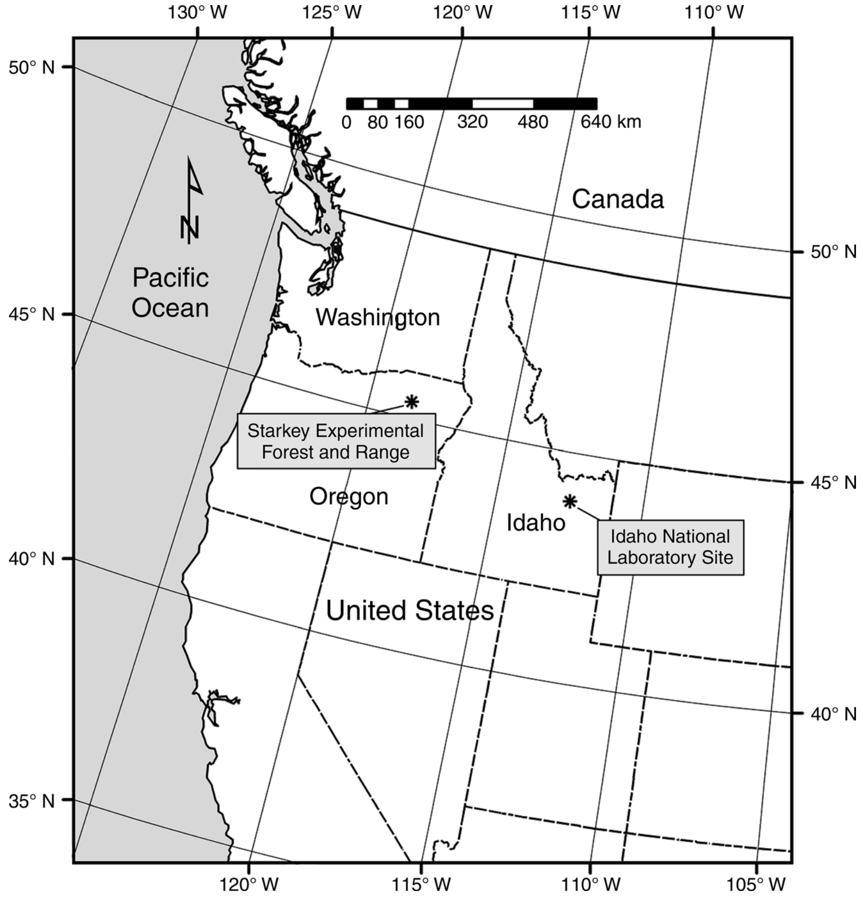

FIG. 1. The locations of our study areas: the Starkey Experimental Forest and Range in northeastern Oregon (temperate, montane forest), and the Idaho National Laboratory Site (an arid, high-elevation desert) in southeastern Idaho, USA.

1997). Starkey was subject to a dry continental climate; mean maximum temperature recorded by the nearest weather station (maintained by the National Oceanic and Atmospheric Administration; elevation 1102 m) was 13.9°C during spring (April–June), 22.9°C during summer (July–September), and 8.8°C during autumn (October–November) of 1954–2012 (Western Regional Climate Center). Mean total precipitation was 18.4 cm during spring, 6.9 cm during summer, and 6.8 cm during autumn of the same period (Western Regional Climate Center). Elevations ranged from 1120 to 1500 m, and common plant communities included bunchgrasses (*Festuca idahoensis*, *Poa secunda*, *Pseudoroegneria spicata*), ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and lodgepole pine (*Pinus contorta*; Long et al. 2008). Primary predators at Starkey were mountain lions (*Puma concolor*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*), although no study animals died from predation during our research.

Our second study area was the Idaho National Laboratory Site and surrounding Snake River Plain in southeastern Idaho, USA (hereafter INL; 43°40′ N, 112°41′ W; Fig. 1). The INL proper encompassed 2303 km^2, and was administered by the U.S. Department of Energy as a nuclear research and testing site. Adjacent public lands were managed primarily by the U.S. Bureau of Land Management; most nearby private lands supported agricultural fields. Public access to the INL was restricted, whereas most of the neighboring public lands provided unrestricted access for travel and recreation. Elk densities at the INL during spring through autumn (<3 elk/km^2; R. A. Long et al., *unpublished data*) were probably well below carrying capacity of that environment (pregnancy rates $\geq 80\%$, most individuals were in good to excellent nutritional condition; McCorquodale et al. 1988, McCorquodale 1991; R. A. Long et al., *unpublished data*) during our study. The INL and surrounding river plain supported a sagebrush–steppe ecosystem characterized by an arid desert climate. Mean maximum temperature recorded by the nearest weather station (maintained by the National Oceanic and Atmospheric Administration; elevation 1430 m) was 19.2°C during spring (April–June), 30.4°C during summer (July–August), and 19.8°C during autumn (September–October) of 1954–2012 (Western Regional Climate Center). Mean total precipitation was 8.2 cm during spring, 2.4 cm during summer, and 3.1 cm during autumn of that same period (Western Regional Climate Center). Elevations ranged from 1316 to 2585 m, although elevations above 1600 m constituted <10% of the study area, and occurred only on a series of local buttes and in the foothills of the Lemhi and Lost River mountain ranges. The two most common plant communities were big sagebrush (*Artemisia tridentata*) and recent (<25-yr-old) burns dominated by grasslands (*Hesperostipa comata*, *Pseudoroegneria spicata*, *Oryzopsis hymenoides*, *Bromus tectorum*; Strohmeyer et al. 1999). Agricultural lands consisted primarily of alfalfa (*Medicago sativa*), barley (*Hordeum vulgare*), and potatoes (*Solanum tuberosum*). Primary predators at the INL were mountain lions and coyotes; no study animals died from predation during our research.

Animal handling, condition, and location data

We captured adult (≥2-yr-old) female elk at Starkey during early winter (December–January) of 2010–2012 by baiting them onto a winter feeding range with an adjacent handling facility (Rowland et al. 1997). Elk were fed a maintenance diet of alfalfa hay during the remainder of the winter, and in early spring (March–April), 25–40 individuals were maneuvered into a squeeze chute for processing prior to being released back into our study area (Rowland et al. 1997). During spring handling, individual elk were weighed on an electronic scale (±1 kg) and fitted with Global Positioning System (GPS) collars (model 4400M, Lotek Wireless, Newmarket, Ontario, Canada) programmed to record hourly locations during spring through autumn; the mean positional error of collars was ≤10 m (M. J. Wisdom, *unpublished data*). We also quantified nutritional condition of a subset of those animals using standard protocols developed for elk, which included measuring maximum depth of rump fat via ultrasonography, and assigning a condition score to those animals that had catabolized subcutaneous fat reserves (Cook et al. 2010). Those data were combined with data on body mass to estimate percentage ingesta-free body fat for each individual as an overall measure of nutritional condition (Cook et al. 2010). We obtained hourly GPS locations for 32 elk at Starkey during 2010, 26 elk during 2011, and 28 elk during 2012, resulting in 345 075 total locations included in our population-level analyses. From the full set of collared animals, we obtained data on nutritional condition of 19 elk in 2011 and 20 elk in 2012 for use in individual-level analyses of state-dependent behaviors.

We captured adult female elk at the INL during late winter (February–March) 2010–2012 using either a handheld net gun fired from a helicopter or drive nets. Individuals were hobbled and blindfolded at the site of capture and fitted with a GPS collar (model GPS-LOG-V2, Kedziora Innovation Group, Mannsville, New York, USA; or model NSG-D3, North Star Science and Technology, King George, Virginia, USA) that was programed to record hourly locations during spring through autumn; mean positional error of collars (based on a series of tests performed at a known location) was ≤15 m. Each collar contained both a drop-off mechanism (model R1C, Sirtrack, Hawke's Bay, New Zealand) programmed to release from the animal on 1 December, and a very high frequency (VHF) radiotransmitter, which facilitated retrieval of stored location data at the end of each year. We estimated body mass as a function of chest girth (Cook et al. 2010), and quantified nutritional condition using an ultrasound with procedures identical to those used at Starkey (Cook et al. 2010). We obtained hourly locations and data on nutritional condition for four elk at the INL during 2010, 19 elk during 2011, and 12 elk during 2012 (128 854 total locations included in our analyses).

We screened GPS data from both study sites based on the recommendations of Lewis et al. (2007) for using the maximum amount of information and minimizing effects of location error on analyses of space use; we retained all locations with a three-dimensional fix in our analyses, and excluded locations that had both a two-dimensional fix and a dilution of precision >5. All animal handling at both study sites was approved by the Institutional Animal Care and Use Committee at Idaho State University (protocol #s 639 and 684), and was in accordance with guidelines established by the American Society of Mammalogists for research on wild mammals (Gannon et al. 2007).

Energetics modeling: Niche Mapper

We used Niche Mapper (Porter et al. 2002, Porter and Mitchell 2006, Natori and Porter 2007) to model spatiotemporally explicit costs imposed on elk by the thermal environment at each study site. Niche Mapper is based on first biophysical principles, and is designed to solve the energy balance equation (Porter and Gates 1969, Campbell and Norman 1998) for a model organism as a function of directly measurable properties of the organism and its environment. The model consists of two submodels (a microclimate model and an endotherm model) that are integrated to produce estimates of hourly rates of metabolism and evaporative water loss necessary to maintain homeothermy (within user-specified bounds) at a particular landscape pixel. Those estimates are derived from pixel-specific data on topography and vegetation characteristics that are used to model the local sun–shade microclimates that define the environmental determinants of energy and water costs at a landscape scale (Porter et al. 2002, Natori and Porter 2007, Huang et al. 2013). A variety of experimental tests have indicated that energy and water costs estimated by Niche Mapper are strongly correlated with empirical estimates for animals ranging in size from mice to Holstein calves (*Bos primigenius*) and Arabian oryx (*Oryx leucoryx*; Porter et al. 1994, 2010).

The microclimate model, which has been tested and validated in a wide variety of ecosystems (e.g., Natori and Porter 2007, Huang et al. 2013), calculates hourly temperature, wind speed, and humidity profiles, as well as clear-sky solar radiation, at a single reference location (usually the location of the weather station collecting the microclimate data, located near the geographic center of the study site) for the "average" day of a user-specified temporal window, *x*, where *x* can be a day, week, month, and so forth. The model assumes that the average day for each value of *x* is representative of all other days within that window, and the goal is to choose a value of *x* that is small enough to justify this assumption, yet large enough to make data management as tractable as possible. Based on preliminary analysis of microclimatic data collected in 2010, we chose to model spatial variation in the thermal environment on a week-by-week basis during our study; this degree of temporal resolution represented a satisfactory balance between absolute realism and a manageable amount of output (i.e., Niche Mapper produced a map of the thermal environment for each week of our study, rather than a map for each day or hour). Diverse input data (e.g., temperature, wind speed, and humidity minima and maxima averaged across days within each week; Appendix A: Table A1) were provided to parameterize the microclimate model, and the resulting hourly profiles for the average day of each week were then passed on to the endotherm model, which iteratively solved the steady-state heat balance equation for the animal (Porter and Mitchell 2006). Input variables and associated data sources for the microclimate model are described in Appendix A.

The endotherm model estimates hourly values of a suite of variables for the average day during each time period of interest (weeks, in our study) by combining outputs from the microclimate model with detailed physiological and morphological data for the animal being modeled (Porter and Mitchell 2006). Hourly estimates are then integrated to produce a single estimate of the costs that would be incurred by the animal if it were standing at the reference location for the duration of the average day during each week. Output from the endotherm model includes numerous variables related to mass and energy balance (Porter and Mitchell 2006), but the variable of greatest interest to us was the predicted rate of evaporative water loss. Because metabolic rate increases in concert with evaporative water loss above the upper critical limit of the thermal-neutral zone (Scholander et al. 1950), rates of water loss predicted by Niche Mapper represent spatiotemporal variation in relative metabolic and hydric costs imposed by the thermal environment when environmental temperatures are warm (e.g., during spring through autumn in our study).

After accounting for all major pathways of environmental heat exchange (i.e., radiative, convective, and conductive), the endotherm model calculates the metabolic rate that will allow the steady-state heat equation for the animal to balance. If the calculated metabolic rate is below a user-specified minimum determined by the basal metabolic rate and minimum energy expended on activity (standing and foraging), then the model allows the animal to thermoregulate to achieve heat balance with a realistic rate of metabolic heat production. The thermoregulation routine consists of a series of behavioral and physiological steps (Natori and Porter 2007): first, the animal is oriented away from the sun to minimize exposure to solar radiation (the default assumes maximal exposure to the sun); second, the animal is allowed to use shade; third, thermal conductivity of the flesh is incrementally increased to a user-specified maximum; and finally, the rate of latent heat loss via evaporation (both respiratory and, for elk, sweating; Parker and Robbins 1984) is incrementally increased (coincident with user-specified increases in allowable core temperature; Appendix B: Table B1) until heat balance is achieved. If both latent heat loss and core temperature reach user-specified maxima and the animal continues to gain heat from the environment, then the predicted metabolic rate is forced to remain below the basal value, and the model assumes that the animal has overheated. Thus, costs predicted by the endotherm model constitute a "best-case scenario" in which the animal is assumed to achieve heat balance as efficiently as possible by a combination of behavioral (primary) and physiological (secondary) means. Given our focus on heat dissipation and behavioral responses to costs imposed by high environmental temperatures, we used the predicted rate of evaporative water loss from Niche Mapper as our metric of overall costs imposed by the thermal environment. Additional details on the endotherm model, including input variables and associated data sources, modifications from previous versions, and validation procedures, are provided in Appendix B.

The landscape-scale version of Niche Mapper processes the microclimate and endotherm models for each pixel in a landscape after adjusting the microclimatic input data to account for spatial variation in topography and vegetation. Pixel-specific air temperatures are calculated from measured temperatures at the reference location, elevation of the new pixel, and the adiabatic lapse rate (−5.3°C/km). Similarly, relative humidity for each pixel is calculated as a function of measured values at the reference location corrected to pixel-specific air temperatures assuming the same mass of water/unit volume of air. Clear-sky solar radiation is calculated for each pixel based on its location and topography (elevation, slope, and aspect; McCullough and Porter 1971). In addition, the vegetation association of each pixel is allowed to modify wind speed and percentage of solar radiation reaching the ground surface (details are provided in Appendix C). Landscape-scale input data are stored in a MySQL database (version 4.1, 2008 release), and model execution is controlled by a Perl program (Porter et al. 2002, Natori and Porter 2007) that outputs results for each pixel and time period to a new table in the MySQL database. Spatial resolution of our input data was 30 m^2, and thus landscape-scale output from Niche Mapper for our study also was 30 m^2. The final result of the landscape-scale simulations in our study was a series of weekly maps for each study area during spring through autumn 2010–2012 that depicted, for each pixel, the average daily rate of evaporative water loss (g/d) predicted to be experienced by an individual elk standing in that pixel.

Cost of locomotion

In addition to using Niche Mapper to quantify costs imposed by the thermal environment, we calculated energy expended on locomotion by elk at both study sites as a function of body mass, distance moved between successive hourly locations, and slope (uphill, downhill, or flat). We calculated distance moved between successive locations using the Home Range Tools extension for ArcGIS (Rogers et al. 2007), and the elevation of each location was determined from a digital elevation model. We used the equation of Parker et al. (1984:478) to calculate mass-specific cost of horizontal locomotion for individual elk ($\mathrm{kcal \cdot kg^{-1} \cdot km^{-1}}$), and then multiplied the resulting value by late-winter body mass and distance moved between successive locations to estimate energy (in kJ) expended on horizontal locomotion. Although late-winter body mass represents a minimum annual value for elk, predicted increases in mass between spring and autumn during our study (see Appendix B for predictive equation) averaged $\sim$5%, and such changes have minimal effect on costs of locomotion incurred by adult elk weighing $>$150 kg (Parker et al. 1984). We assumed that movement distances and elevation changes $\leq$10 m resulted from location error and represented no movement. In addition, GPS collars occasionally failed to record a location, and when this occurred (i.e., successive locations were $\geq$2 h apart), we excluded that movement segment from our analyses. When the elevation change between successive locations was $>$10 m, we adjusted the horizontal cost of locomotion to account for slope (degrees). For downslope movements, we used the equation of Robbins (2001:137) to calculate the efficiency of moving downslope as a percentage of the cost of horizontal locomotion. We then adjusted the estimated cost of the movement segment based on that percentage; negative efficiencies increased the cost above that of horizontal locomotion, whereas positive efficiencies reduced the cost. Zero efficiency (i.e., cost of moving downslope = cost of moving horizontally) occurred at a slope of 12.5° for a 240-kg individual, which was consistent with empirical results reported by Robbins (2001). For upslope movements, we estimated cost of the vertical component of the movement (i.e., the change in elevation) as 5.73 $\mathrm{kcal \cdot kg^{-1} \cdot km^{-1}}$ (Parker et al. 1984, Robbins 2001) and added that cost to that of the horizontal component. Costs were converted to kilojoules (kJ) prior to analysis.

Additional environmental variables

Our study was designed to provide a direct, mechanistic comparison of behavior of elk in two substantially different ecosystems, and thus habitat type (i.e., vegetation association) per se was not included as a predictor variable in our analyses. Nevertheless, it still was necessary to differentiate among habitat types, both to parameterize Niche Mapper and to facilitate efficient sampling of other environmental variables of interest. Therefore, we delineated habitat types at both study sites based on the following factors: (1) differences in vegetative structure that influenced parameterization of Niche Mapper (i.e., effects of vegetation on wind speed and percentage shade; Appendix C: Table C1); (2) differences in forage quality; (3) differences in the degree of concealment cover provided by vegetation and, in some instances, topography; and (4) habitat classification accuracy. We visited 200 random locations at each study site during 2012 and collected data on vegetative cover, dominant plant species, and topography. We then combined that information with data on forage quality (described in the following section) and existing vegetation layers to create habitat maps for each study site that maximized classification accuracy and clearly differentiated among levels of vegetative structure, forage quality, and concealment cover. Additional details on habitat classification are provided in Appendix D.

We quantified spatiotemporal variation in quality of forage using the best available data for each study site; an index of vegetation greenness at the INL, and data on forage digestibility, percentage nitrogen (N), and abundance of key forage plants for elk at Starkey. A detailed description of forage-quality analyses is provided in Appendix E. Although our approach to quantifying forage quality differed between study sites, our primary interest was not in a direct comparison of quality between sites, but rather in accurately representing relative differences in forage quality across space within each site on a seasonal basis; we believe that both approaches were effective in that regard (Appendix E). Nevertheless, because the degree of measurement error associated with each approach was uncertain, and because forage quality at both study sites was substantially more variable among than within habitat types, we created both ordinal (mean forage quality value for each habitat type assigned to all pixels within that type) and ranked (by habitat type based on mean forage quality values) transformations of forage quality for consideration in subsequent models of resource selection by elk.

Although perceived risk of predation and proximity to human disturbance do not directly influence energy balance, those variables can have important effects on behavior of large herbivores, which should be accounted for in analyses of space use and movement (e.g., Rowland et al. 2000, Middleton et al. 2013). Consequently, we quantified availability of concealment cover (a commonly used index to perceived risk of predation in both forested and non-forested environments; Bowyer et al. 1999, Dussault et al. 2005, Barbknecht et al. 2011) and proximity to open, maintained roads at both study sites. Details are provided in Appendix F.

Statistical analysis

We quantified the relative influence of thermoregulatory costs, forage quality, concealment cover, and proximity to roads on behavior of elk at both study sites using resource selection functions (RSFs) and a use–availability design (Manly et al. 2002, Johnson et al. 2006). We used GPS locations from individual elk to quantify habitat use, and generated random locations to quantify habitat availability at the landscape scale (Johnson 1980, Bowyer and Kie 2006). We chose that scale because our primary interest was in determining to what degree individuals at each study site were using portions of the landscape available to them that reduced costs of thermoregulation and activity, and increased access to high-quality forage. Thus, we used the same set of random locations for each individual. At Starkey, we distributed random locations within the study area boundary delineated by the ungulate-proof fence (78 km^2); at the INL, we distributed random locations within the boundary of a 100% minimum convex polygon surrounding all locations obtained during 2010–2012 (9036 km^2; estimated using the Home Range Tools extension for ArcGIS; Rogers et al. 2007). We determined the minimum number of random locations necessary to accurately represent available habitat at each study site by: (1) calculating the "true" mean value of each habitat variable using all 30-m^2 pixels in the landscape; (2) generating sequential sets of random locations in 250-point increments from 500 to 10 000 locations; (3) overlaying each set of random locations on the appropriate habitat layers in ArcGIS; (4) calculating the mean value of each habitat variable for each set of random locations; and (5) plotting the means as a function of sample size ($n = 500–10\,000$) and identifying when an asymptote was reached that was within $\pm 5\%$ of the true mean (Kershaw 1964). Using this approach, we determined that 750 random locations was sufficient for quantifying habitat availability at Starkey, and 2000 locations was sufficient at the INL.

All energy variables in our study were time specific, so we partitioned GPS locations for elk by year, season, week, and time of day. Seasons were delineated independently for each study site by using a climograph (e.g., Stewart et al. 2002) to group months that had similar ranges of average temperature and precipitation during 1954–2012. Mean timing of sunrise and sunset within each season was used to differentiate daytime from nighttime locations at both study sites. We overlaid each subset of locations on the appropriate layers in ArcGIS and spatially joined them to predicted rates of evaporative water loss from Niche Mapper on a weekly basis, and values of forage quality on a seasonal basis. Values of concealment cover (both ordinal and ranked) and distance to roads did not vary temporally. We used this same approach to sequentially join the random locations for each study site to the appropriate underlying habitat layers on a time-specific basis.

We estimated RSFs by fitting generalized linear mixed models with a binomial error distribution and logit link function (Gillies et al. 2006, Bolker et al. 2009, Zuur et al. 2009) to the used (coded 1) and random (coded 0) locations for each study site. We modeled resource selection independently for each combination of season (spring, summer, and autumn) and diel period (daytime and nighttime), which resulted in a total of six candidate model sets for each study site. We were primarily interested in estimation of effects rather than prediction, so we standardized all predictor variables by subtracting the mean and dividing by the standard deviation prior to analysis to facilitate direct comparison of the resulting model-averaged coefficients (Neter et al. 1996). A detailed description of our approach to model selection, model averaging, and interpretation of marginal (i.e., population-level) parameter estimates is provided in Appendix G. With only one exception (spring daytime in the desert), however, the best-fit model, determined by the lowest value of the marginal Akaike's information criterion ($_{\mathrm{m}}$AIC; Hall and Clutter 2004, Bolker et al. 2009) for each season and time of day, included a random intercept and uncorrelated random slopes for thermoregulatory costs (grouped by individual elk nested within week so that use and availability of those variables were compared at the appropriate weekly time scale) and forage quality (grouped by individual elk). The conditional parameter estimates produced by inclusion of those random effects represented, for each individual elk, the relative strength of selection for low-cost areas, and for forage quality, during each season and diel period (Gillies et al. 2006, Indermaur et al. 2009, Wagner et al. 2011); accordingly, we used those conditional estimates to evaluate patterns of state-dependent behavior among individual elk in a series of subsequent analyses (sensu Indermaur et al. 2009, Wagner et al. 2011).

We modeled the relative strength of selection (i.e., conditional parameter estimates from generalized linear mixed models) for low-cost areas and forage quality, as well as the amount of energy expended by elk on locomotion, for each study site and season separately as a function of late-winter nutritional condition (i.e., percentage ingesta-free body fat) using multivariate linear regression (Johnson and Wichern 2002). For thermoregulatory costs, we averaged conditional parameter estimates across weeks within each diel period and season, so that a total of six unique estimates (two diel periods × three seasons) were produced for each individual elk. Conditional estimates for forage quality, and estimates of mean daily energy expended on locomotion by elk, were obtained on a seasonal basis for each study site. Up to five response variables (conditional slopes for thermoregulatory costs and forage quality by diel period, and mean daily energy expended on locomotion) were included in regression models for each season and study site. Prior to analysis, we used a correlation matrix to identify pairs of variables that could not be included in the same model because of collinearity ($|r| > 0.6$). If daytime and nighttime parameter estimates for thermoregulatory costs or forage quality were positively correlated (indicating that individual patterns of selection were similar during day and night), we used the average estimate across diel periods as a response variable. In addition, we evaluated residual plots for each response variable to assess adherence to assumptions of linear regression. When a reasonable level of evidence existed ($P \leq 0.15$) for a multivariate effect of nutritional condition on behavior (i.e., strength of selection for low-cost areas or forage quality, or energy expended on locomotion), we used canonical correlation analysis to determine which variables were responsible for the overall effect (Johnson and Wichern 2002). For variables identified in the canonical analysis, we used simple linear regression to evaluate direction and strength of the relationship with nutritional condition (Neter et al. 1996).

In a separate analysis, we plotted all bivariate relationships between nutritional condition and our metrics of behavior, and attempted to identify breakpoints that might represent a threshold below which nutritional condition influenced behavioral choices. In instances where a potential threshold was detected, we used iterative piecewise regression (Bates and Watts 1988, Neter et al. 1996, Ryan and Porth 2007) to estimate the breakpoint, the slopes of the fitted regression lines above and below the breakpoint, and statistical significance of both the slopes and the difference between them. We initialized iterative models by visually estimating the breakpoint, fitting separate linear regressions to those data on either side of the breakpoint, and providing the resulting intercept and slopes as starting values in the piecewise model (Bates and Watts 1988, Ryan and Porth 2007). We performed all regression analyses using SAS software v9.3 (PROC GLM and PROC NLIN; SAS Institute 2011), and adopted $\alpha \leq 0.10$ to facilitate detection of subtle behavioral responses to nutritional condition at the end of winter, and to the energy landscapes at Starkey and the INL.

RESULTS

Cost comparison: forest vs. desert

Weekly thermoregulatory costs predicted by Niche Mapper for elk generally were higher in the desert (INL) than in the montane forest (Starkey; Appendix H: Fig. H1). Predicted rates of evaporative water loss at the reference locations (weather stations) averaged 11.6% higher in the desert than the forest during spring (range across weeks was −15.6% to 69.5% higher in the desert), 20.6% higher in the desert during summer (range −16.9% to 62.6% higher in the desert), and 0.1% higher in the desert during autumn (range −7.2% to 10.5% higher in the desert). The landscape-scale distribution of costs also differed substantially between study sites (Appendix H: Fig. H2). Ranges in available rates of evaporative water loss overlapped between sites during all seasons, but minimum rates of water loss in the forest typically were 150–400 g/d lower than those available in the desert (Fig. H2, Appendix H). At both sites, predicted rates of water loss were highest during summer (Fig. H2, Appendix H), and the lowest rates available in summer were comparable to, or higher than, the maximum rates predicted during spring and autumn (Fig. H2, Appendix H).

Population-level results

Seasonal and diel patterns of resource selection differed markedly between elk in the desert and their forest counterparts. For elk in the desert, standardized RSF coefficients for costs of thermoregulation were negative and significant during all seasons and times of day, indicating strong selection for areas that reduced those costs (Fig. 2). A significant difference from 0 was determined when the 95% confidence interval of the parameter estimate (based on the unconditional SE), did not overlap 0 (see Appendix G). Coefficients for forage quality also were negative across seasons and times of day, indicating general avoidance of areas that provided the highest-quality forage available in the desert (Fig. 2). This result could have stemmed from the highest-quality forage being located in agricultural fields, which may be avoided by elk because of their proximity to human disturbance. To evaluate this possibility, we removed all used and random locations from agricultural fields (i.e., we considered agricultural fields to be "unavailable") and repeated our modeling analyses for the desert. Reanalysis produced no substantive changes in parameter estimates for other variables, but estimates for forage quality generally were closer to 0. Temporal changes in the magnitude of selection for low-cost areas and forage quality were negligible for elk in the desert. In contrast, elk selected low-cost areas more consistently (based on 95% confidence intervals bounding standardized coefficients) during summer–autumn than during spring, whereas selection for forage quality was substantially less consistent during summer–autumn than during spring (Fig. 2).

For elk in the montane forest, positive coefficients for forage quality in spring indicated selection for areas that provided higher-quality forage than was available at random during that season (Fig. 2). The relative importance of forage quality as a predictor of selection, however, declined between spring and summer–autumn (Fig. 2). Coefficients for costs of thermoregulation generally did not differ from 0, and were never negative (Fig. 2), indicating that such costs were not a principal predictor of space use by elk in the montane forest at the population level. Indeed, patterns of selection for low-cost areas were highly variable among elk in the forest;

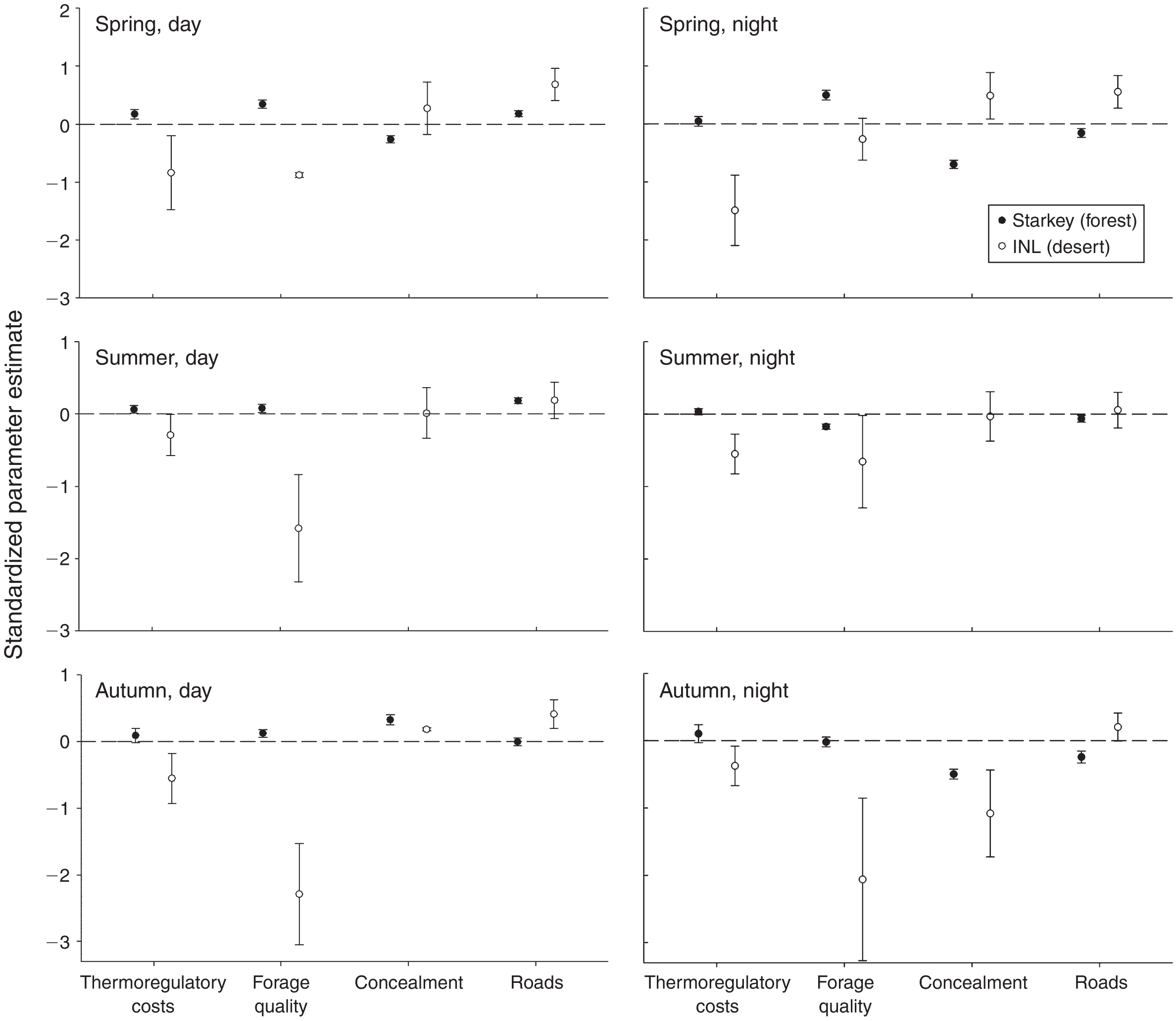

FIG. 2. Model-averaged, standardized parameter estimates (with 95% confidence intervals) obtained from resource selection functions for North American elk (*Cervus elaphus*) during daytime and nighttime hours in spring (April–June), summer (July–September), and autumn (October–November), 2010–2012, at the Starkey Experimental Forest and Range, Oregon, USA ($n = 86$ elk), and the Idaho National Laboratory Site, Idaho, USA ($n = 35$ elk). Predictor variables included energy and water costs imposed by the thermal environment (Thermoregulatory costs), forage quality, concealment cover (Concealment), and distance to roads (Roads). Resource selection functions were derived from generalized linear mixed models fit to used and random locations from each study site. Concealment cover was not included in the summer model for Starkey, because it was correlated with forage quality ($r > 0.6$).

coefficients of variation calculated from conditional (i.e., individual-level) parameter estimates for costs of thermoregulation were, on average, 2.98 times and 0.30 times higher for elk in the forest than for those in the desert during daytime and nighttime hours, respectively.

Proximity to roads was an important predictor of space use by elk at both study sites. In the desert, elk generally avoided roads during all seasons and times of day, whereas in the montane forest, elk avoided roads during the day and moved closer to roads at night (Fig. 2). Patterns of selection for concealment cover were more variable. During the day, concealment cover was a significant predictor of space use by elk in the desert only during autumn, when individuals showed some selection for increased cover (Fig. 2). At night, elk in the desert selected increased concealment cover during spring and avoided cover during autumn (Fig. 2). During summer in the montane forest, concealment cover and forage quality were positively correlated ($r \geq 0.7$), and forage quality was selected as the better predictor of space use during that season (based on $_{\mathrm{m}}$AIC). Of the remaining time periods, however, daytime in autumn was the only instance in which elk at Starkey showed positive selection for concealment cover (Fig. 2).

Mean daily energy expended on locomotion did not differ between elk in the desert and those in the montane forest during spring (Fig. 3). Similarly, diel patterns of

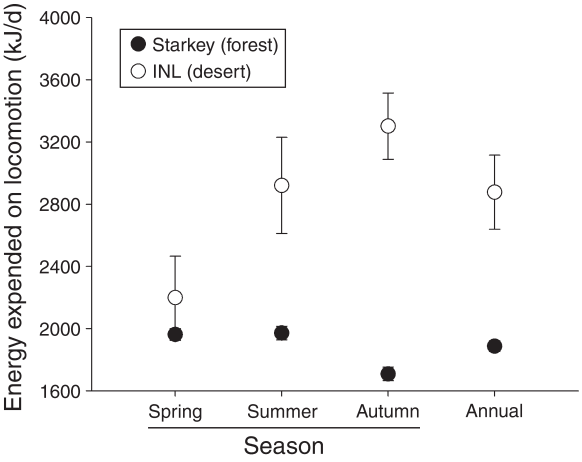

FIG. 3. Daily energy expended on locomotion (mean and 95% CI) by North American elk (*Cervus elaphus*) during spring (April–June), summer (July–September), and autumn (October–November), 2010–2012, at the Starkey Experimental Forest and Range, Oregon, USA ($n = 86$ elk; mean body mass $= 219.9$ kg), and the Idaho National Laboratory Site, Idaho, USA ($n = 35$ elk; mean body mass $= 241.6$ kg). Mean values across all three seasons also are presented (annual).

investment in locomotion during spring largely were comparable between study sites (Fig. 4), although elk in the desert expended more energy on locomotion at night than did their forest counterparts (Fig. 4). In contrast, elk in the desert devoted significantly more energy to locomotion during summer and autumn than did those in the forest (Fig. 3), but >75% of that investment occurred after 20:00 hours and before 09:00 hours (Fig. 4), when heat gain from solar radiation was minimal. During those hours, energy invested in locomotion by elk in the desert consistently was 2–4 times that invested by elk in the forest. From 15:00 to 20:00 hours in summer and from 15:00 to 18:00 hours in autumn, however, elk in the desert expended significantly less energy on locomotion than those in the montane forest (Fig. 4). Indeed, during the hottest portion of the day, elk in the desert ceased movement almost entirely.

Individual-level results

Multivariate regressions of metrics of behavior (conditional parameter estimates for costs of thermoregulation and forage quality, and energy expended on locomotion) against nutritional condition never were significant for elk in the montane forest (all Wilks' $\Lambda \geq 0.93$, $P \geq 0.54$). In contrast, multivariate models for elk in the desert were marginally significant in spring (Wilks' $\Lambda = 0.83$, $P = 0.16$) and significant in summer (Wilks' $\Lambda = 0.74$, $P = 0.05$) and autumn (Wilks' $\Lambda = 0.66$, $P = 0.08$). Subsequent canonical analyses indicated that conditional parameter estimates for costs of thermoregulation were almost exclusively responsible for significance (or marginal significance) of multivariate models in spring and summer, and that conditional estimates for costs of thermoregulation and forage quality contributed to multivariate significance in autumn.

For elk in the desert, conditional parameter estimates for costs of thermoregulation were positively related to nutritional condition during spring and summer, indicating that individuals in relatively poor condition at the end of winter showed stronger selection for areas that reduced costs of thermoregulation during spring and summer than did individuals in relatively good condition at the end of winter (Fig. 5). In contrast, strength of

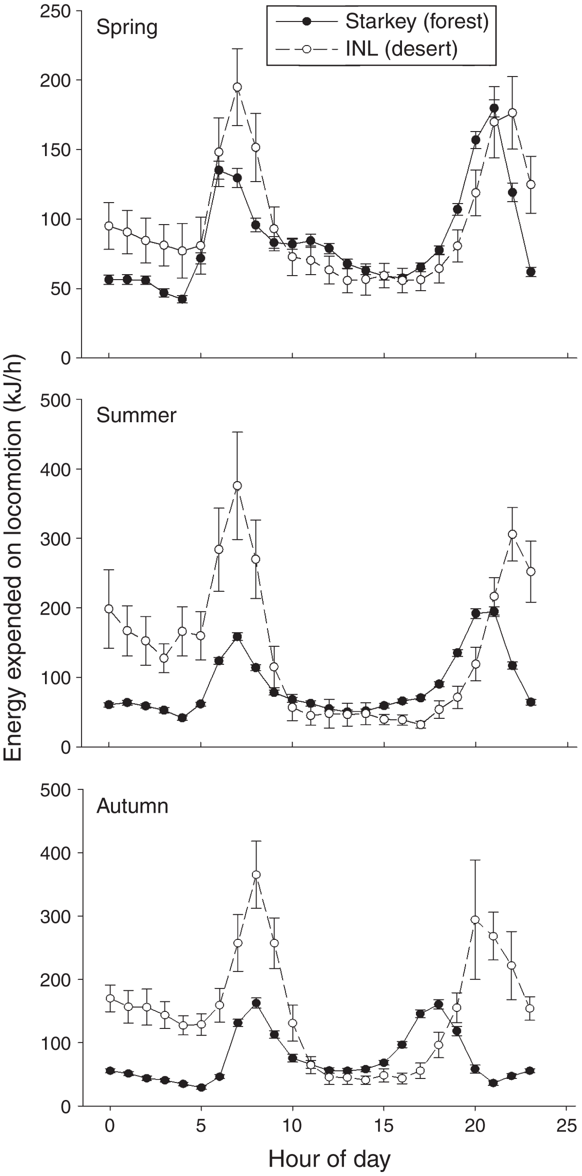

FIG. 4. Energy expended on locomotion (mean and 95% CI) by North American elk on an hourly basis throughout the day during spring (April–June), summer (July–September), and autumn (October–November), 2010–2012, at the Starkey Experimental Forest and Range, Oregon, USA ($n = 86$ elk), and the Idaho National Laboratory Site, Idaho, USA ($n = 35$ elk). Hour 0 begins at 12:01 hours.

PLATE 1. An adult female elk (*Cervus elaphus*) returns to the native sagebrush-steppe habitat that characterizes much of the Idaho National Laboratory Site, southeastern Idaho, USA, after being fitted with a GPS collar and assessed for late-winter nutritional condition. Photo credit: Kort Duce Photography.

selection for forage quality by elk in the desert was unrelated to nutritional condition during spring and summer (Fig. 5). During autumn, the relationship between selection for low-cost areas and nutritional condition was reversed for elk in the desert; individuals in the best condition at the end of winter showed the strongest selection for areas that reduced costs of thermoregulation (Fig. 5). Individuals in the best condition at the end of winter also exhibited the strongest selection for high-quality forage during autumn, indicated by a positive relationship between strength of selection for forage quality and nutritional condition in that season (Fig. 5).

Thresholds in the relationship between nutritional condition and strength of selection for low-cost areas or forage quality by elk at either study site were ambiguous. For elk in the desert, however, careful inspection of the relationship between late-winter nutritional condition and energy expended on locomotion during spring and summer revealed the possible existence of a threshold. Simple linear regressions of energy expended on locomotion against nutritional condition were not significant in either season ($P \geq 0.17$). Iterative piecewise regressions, however, were significant in spring ($P = 0.04$) and marginally significant in summer ($P = 0.11$), which revealed a breakpoint at ~8% ingesta-free body fat in both seasons. Below this level, energy expended on locomotion was positively related to nutritional condition (i.e., individuals in better condition expended more energy on locomotion; 90% confidence intervals did not include 0), whereas above this level, energy expended on locomotion was unrelated to condition (Fig. 6). Slopes of the regression lines above and below the breakpoint differed significantly in both seasons (based on nonoverlap of 90% confidence intervals; Fig. 6).

DISCUSSION

Behavior is a primary mechanism used by animals to cope with environmental constraints on fitness, and regulatory behaviors can both dampen environmental heterogeneity and effectively constrain the selective environment experienced by animals (e.g., the "Bogert effect"; Huey et al. 2003). Consequently, clarifying the role of behavior in mediating dynamic patterns of energy acquisition and allocation is critical for understanding relationships between environmental variability and individual life-history strategies. Small differences in the ratio of energy intake to expenditure through time can have "multiplier" effects (White 1983, Cook et al. 2004) on fitness parameters such as body mass and condition, and thus behavioral responses to environmental factors affecting energy balance can have important fitness consequences. Energy balance, however, can be both a cause and a consequence of behavior (Monteith et al. 2011), and although the form and

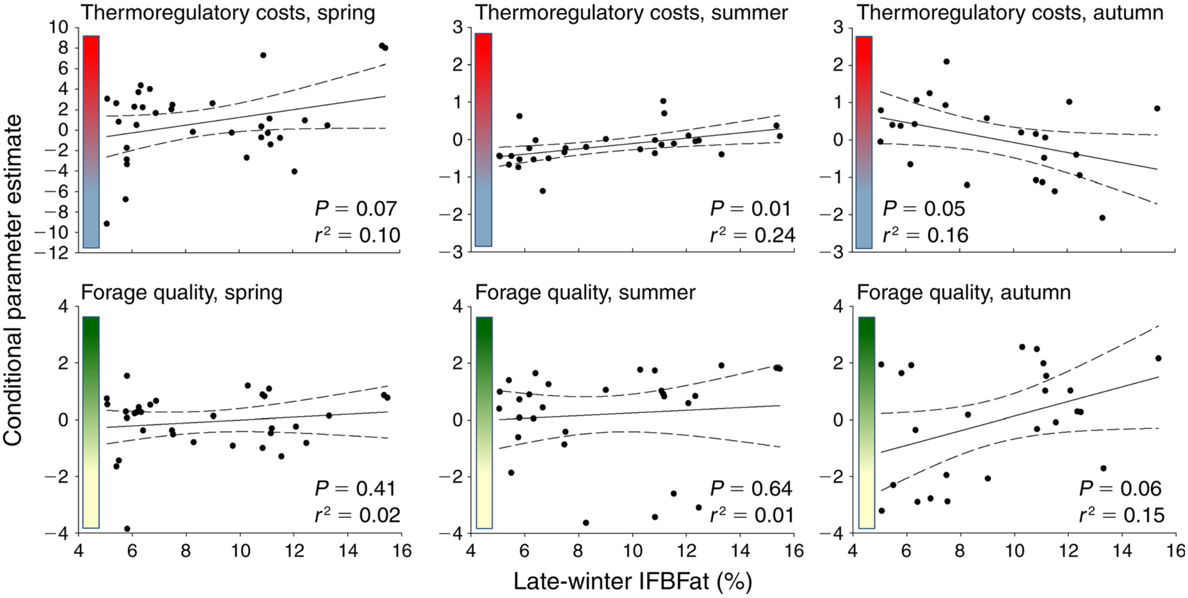

FIG. 5. Conditional (individual-level) parameter estimates from resource selection functions for North American elk during spring (April–June), summer (July–September), and autumn (October–November), 2010–2012, in the desert site (Idaho National Laboratory). Parameter estimates are plotted against late-winter nutritional condition (percentage ingesta-free body fat in February or March; IFBFat) and indicate, for each individual, the relative strength of selection for areas that reduced costs of thermoregulation (selection for lower cost, blue; selection for higher cost, red), or increased access to high-quality forage (selection for lower quality, yellow; selection for higher quality, green). Resource selection functions were derived from generalized linear mixed models fit to used and random locations from each study site. Fitted lines from simple linear regression analyses are shown, along with 95% confidence intervals (dashed lines) and test results.

strength of feedbacks between nutritional condition and behavior have received little attention, such relationships probably are an integral part of the life histories of many species. Considered together, the heat dissipation limit theory of Speakman and Król (2010) and the "Bogert effect" of Huey et al. (2003) provide an integrative framework for evaluating effects of climate on endotherms, and for predicting future responses of endotherms to climate change. We used this integrative framework to generate a series of testable predictions about the interplay among behavior, the energy landscape, and nutritional condition of a large-bodied endotherm.

Population-level predictions

Our first prediction, that seasonal and diel patterns of behavior by elk would be influenced more by thermoregulatory costs than by forage quality at the population level, was strongly supported in the desert environment but not in the montane forest. Elk in the desert consistently selected areas that reduced costs over those that provided the highest-quality forage during all seasons and times of day. Increased consistency in selection for low-cost areas between spring and summer–autumn, coincident with decreased consistency in selection for forage quality, also was in keeping with our prediction. Although we observed no substantial changes in the strength of selection for low-cost areas through time, a likely explanation for this result is that most animals in the desert already were selecting the least costly areas available during spring; thus, increasing the degree of selection for low-cost areas during summer and autumn was not generally possible.

Lack of a significant, population-level relationship between thermoregulatory costs and behavior of elk in the montane forest may be explained in one of several ways. First, this result could indicate the existence of a cost threshold, beyond which endotherms are increasingly forced to focus their behaviors on reducing negative effects of the thermal environment on net energy balance; conditions in the montane forest frequently may have been below such a threshold, whereas conditions in the desert may have exceeded it. This explanation seems unlikely, however, because of the degree of overlap between the montane forest and the desert in thermoregulatory costs available to elk. Second, the ability of individual elk in the montane forest to consistently optimize their behavior relative to costs imposed by the thermal environment may have been compromised by the substantially higher degree of spatial heterogeneity at that site. Optimality problems are complex in heterogeneous landscapes, and individuals may lack the ability to synthesize all information necessary for optimizing patterns of space use and movement (Belovsky 1984). Individual elk in the montane forest were more variable in their responses to the thermal environment than were elk in the desert, which indicates that elk in the forest either had greater

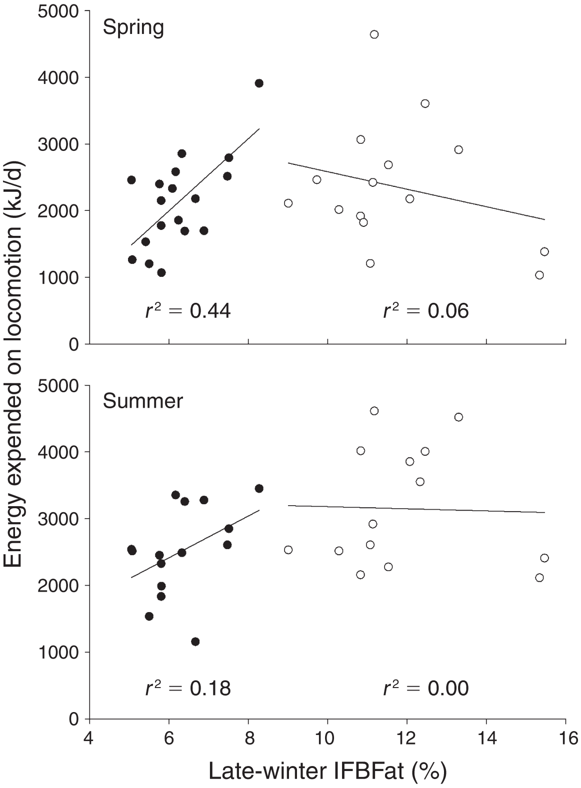

FIG. 6. Piecewise linear regressions of mean daily energy expended on locomotion by North American elk (mean body mass = 241.6 kg) against late-winter nutritional condition (percentage ingesta-free body fat in February or March; IFBFat) during spring (April–June) and summer (July–September), 2010–2012, in the desert site (Idaho National Laboratory). Breakpoints (at ~8% ingesta-free body fat in both seasons) and slopes were estimated iteratively (Bates and Watts 1988, Ryan and Porth 2007). Below the breakpoint (solid circles), energy expended on locomotion was positively related to nutritional condition (i.e., individuals in better condition expended more energy on locomotion), whereas above that level (open circles), energy expended on locomotion was unrelated to condition.

difficulty consistently selecting the lowest-cost areas available to them, or that they simply paid little attention to such costs. Our results provide greater support for the first of those explanations, but additional research designed to relate individual patterns of behavior to energetics-oriented fitness correlates (e.g., nutritional condition or birth mass of young) probably would help to disentangle such alternatives.

Both seasonal and diel patterns of behavior were more strongly influenced by spatiotemporal variation in thermoregulatory costs in the desert than in the montane forest, which is consistent with our second prediction regarding relative importance of the thermal environment as a determinant of behavior at each study site. In addition, at both study sites, the importance of energy costs relative to forage quality as predictors of space use by elk was greatest in summer or autumn (indicated by relative consistency of the marginal parameter estimates for costs of thermoregulation across seasons, vs. declining parameter estimates for forage quality), when environmental heat loads were maximal but forage quality was declining (Cook et al. 2004, Long et al. 2008). This result is consistent with expectations of the heat dissipation limit theory, and is especially striking, given that summer and autumn represent periods of peak energy demand for lactation by elk. Lactation represents the most costly period in the life cycle of mammals, in terms of energy balance (Moen 1978, Loudon and Racey 1987), and rates of energy intake increase dramatically during lactation to support milk production (Cook 2002). Based on our results, we hypothesize that higher rates of energy intake during lactation may have been accomplished by increased forage consumption rather than selection of higher-quality forage. This hypothesis is consistent with results of previous studies in which females have been shown to use lower-quality forage than is generally available during lactation in favor of reducing the effects of other environmental constraints on fitness (Bleich et al. 1997, Barten et al. 2001, Corti and Shackleton 2002). Similarly, in many species, changes in gut morphology allow maternal females to extract nutrients from low-quality forages more efficiently during lactation (e.g., Barboza and Bowyer 2000). Thus, natural selection often may have favored the combination of "time-minimizing" regulatory behaviors (Schoener 1971, Belovsky 1984, Kie 1999), and targeted physiological development in endotherms, rather than favoring behaviors that simply maximize energy intake.

Our third prediction, that diel differences in energy expended on locomotion would be more substantial for elk in the desert than for those in the montane forest, also was supported. Wickstrom et al. (1984) reported that elk generally devote 40–60% of each day to finding and consuming food, and that this value changed little with range conditions (presumably because of constraints associated with rumination time and other necessary activities; Bowyer 1981, Cook 2002). Additionally, however, the expense of foraging can approach 20% or more of basal metabolism (Wickstrom et al. 1984, Hudson and Haigh 2002), and thus movements associated with foraging generate a substantial amount of heat. Although elk are capable of dissipating much of this heat through sweating (Parker and Robbins 1984), thermoregulation under heat stress is substantially less costly at night or near dawn and dusk, when temperatures are low and solar radiation is absent or minimal. Elk also may seek shade during the day to dissipate heat and facilitate activity (McCorquodale 1991, Merrill 1991), but an almost complete lack of thermal cover for elk in the desert largely precluded this form of behavioral thermoregulation. Consequently, as costs imposed by the thermal environment increased in the desert during summer and autumn, elk adjusted their daily activity patterns accordingly by foraging almost exclusively at night and near dawn and dusk. In contrast, energy expended on locomotion in the montane forest during summer and autumn was similar during daytime and nighttime, and in some instances was higher in the middle of the day than at night. Daily activity patterns of elk in the montane forest probably were less constrained by the need to dissipate heat because of the lower costs imposed by the thermal environment in that ecosystem.

In contrast to diel patterns of movement, differences in the thermal environment between sites cannot account for our observation that mean daily energy expended on locomotion was significantly higher for elk in the desert than for those in the forest. The ungulate-proof fence at Starkey also is an unlikely explanation for that result, because radio-collared individuals at that site rarely utilized >50% of the study area during the course of an entire year (R. A. Long et al., *unpublished data*). Instead, differences in the distribution of forage between sites probably explain higher overall rates of movement among elk in the desert. McCorquodale (1991) quantified quality and distribution of forage for elk in a coniferous forest and a sagebrush-steppe desert, and reported that forage was highly concentrated in the forest, but widely and evenly distributed in the desert. Our own maps of forage quality were consistent with that result, and thus we hypothesize that elk in the desert must move more continuously than their forest-dwelling counterparts to attain required intake of food. Greater movements to obtain food also would provide impetus for elk inhabiting the desert to concentrate their foraging efforts at night and avoid the additional heat production associated with high rates of movement during the day.

Individual-level predictions

Lack of a significant relationship between nutritional condition and behavior of elk in the montane forest was consistent with our fifth prediction that such relationships would be stronger in the desert environment, where costs of thermoregulation were higher. This result made it difficult, however, to evaluate the relative strength of state-dependent selection for low-cost areas and forage quality by elk in the montane forest, our fourth prediction. Costs of thermoregulation were substantially lower in the montane forest than in the desert during spring through autumn, and thus the energy consequences of individual variation in behavior probably were reduced for elk in the forest. Consequently, there may have been less incentive (or opportunity) for individuals in that environment to adjust the energy efficiency of their behavior during spring through autumn in an attempt to compensate for low levels of stored energy at the end of winter. Similar to results observed at the population level, however, this result might be explained by differences in the degree of heterogeneity between sites. As a result of the more complex landscape at Starkey, elk at that site may have lacked the ability to synthesize all information necessary to consistently optimize their patterns of space use and movement relative to the thermal environment (Belovsky 1984). Indeed, whether environmental heterogeneity has a stabilizing or destabilizing effect on population dynamics of large herbivores is uncertain (Illius and O'Connor 2000, Owen-Smith 2004), and may be related to the capacity of individuals to optimize their behavior relative to environmental factors that influence energy balance. Disentangling such relationships would improve our understanding of a wide variety of ecological phenomena, including responses of species to climate change, and warrants additional comparative and experimental research.

Also consistent with our fourth and fifth predictions, elk in the desert that were in relatively poor condition at the end of winter showed stronger selection for areas that reduced thermoregulatory costs during spring and summer than did elk in good condition, whereas the strength of selection for forage quality was not state dependent. In energetically costly (or, potentially, less heterogeneous) environments, regulatory behaviors that reduce exposure to costs imposed by the thermal environment may play an important role in allowing individual herbivores to compensate for seasonal reductions in energy reserves that result primarily from costs of reproduction (Moen 1978, Cook 2002, Stewart et al. 2005). Patterns of forage intake and selection by large herbivores are under strong endogenous control (Arnold 1985, Schwartz et al. 1988, Frost et al. 2008), and numerous studies have demonstrated state dependency in the catabolism of energy reserves during winter (e.g., Cook et al. 2004, Bårdsen et al. 2010, Monteith et al. 2013) that result primarily from individual regulation of food intake and metabolism. In contrast, the potential for state-dependent regulation of energy balance to be mediated through energy expended on thermoregulation and activity rather than energy intake during warmer seasons had not been demonstrated previously.

The implications of our results for allocation of energy to reproduction are particularly striking. Monteith et al. (2013) reported that: (1) investment in reproduction by female mule deer was a function of nutritional condition following winter; (2) females exiting winter with fat reserves that exceeded threshold values determined by number of young recruited preferentially allocated those reserves to reproduction rather than storage; and (3) although probability of successfully recruiting young was positively related to post-winter nutritional condition, poor condition did not directly translate into reproductive failure, and females spanning a range of post-winter condition successfully recruited young. Although we had no data on recruitment of young, pregnancy rates of elk inhabiting the desert environment in our study were high across years, and were not related significantly to post-winter nutritional condition within the ranges that we observed. The combination of results from our study and Monteith et al. (2013) indicates a degree of flexibility in the mechanisms by which female herbivores allocate energy to reproduction and avoid reproductive pauses; individuals in good condition following winter rely primarily on the catabolism of stored reserves (i.e., capital), whereas individuals in poor condition rely on short-term gains produced by maximizing net energy balance (i.e., income). We hypothesize, therefore, that the capital–income continuum (Jönsson 1997) may represent a plastic behavioral strategy rather than a fixed evolutionary trait. Resolving that question, however, will require additional research that combines data on seasonal dynamics in energy reserves with detailed information on reproductive success, individual behavior, and distributions of energy costs and benefits in space and time.

Reversal of the relationship between post-winter nutritional condition and selection for low-cost areas by elk in the desert during autumn was contrary to our fourth prediction; we propose two competing explanations for that result. The first could be described as a behavioral extension of the "individual quality" hypothesis (Hamel et al. 2009); individuals in the best condition at the end of winter were in that condition because they consistently maximized the energy efficiency of their behavior (i.e., maximized net energy balance) in the months immediately preceding winter. This explanation seems unlikely for two reasons: (1) previous studies in which nutritional condition has been measured both at the beginning and end of spring through autumn have failed to document a positive correlation between the two (i.e., the same individuals are rarely in the best condition both coming out of and going into winter; Monteith et al. 2013); and (2) although smaller mammals have been demonstrated to accumulate, in just a few weeks, the energy reserves necessary to survive winter (e.g., Kenagy et al. 1989), energy balance of large herbivores varies over longer time scales, with potential carryover effects between seasons (Monteith et al. 2013), which is likely to preclude an overriding influence of behavior during any one season. An alternative explanation for our autumn results is simply that the very nature of the relationship between post-winter nutritional condition and selection for low-cost areas during spring and summer (i.e., elk in the poorest condition selected the least costly areas) may have allowed individuals that were in poor condition at the end of winter to fully compensate by autumn. If individuals in poor condition also allocated a smaller proportion of their fat reserves to support reproduction than did individuals in good condition (i.e., produced smaller young, reduced milk production, and so forth; Monteith et al. 2013), then a reversal in the overall ranking of individuals with respect to nutritional condition may have occurred between spring and autumn. If such a reversal took place, then the "real-time" relationship between nutritional condition in autumn and selection of low-cost areas in autumn probably would have remained positive, with individuals in the poorest condition in autumn selecting the least costly areas.

The existence of a threshold in the relationship between nutritional condition and energy expended on locomotion by elk in the desert during spring and summer provides partial support for our sixth and seventh predictions. Such a threshold further highlights the importance of behavioral regulation of energy balance as a means of compensating for low stores of energy at the end of winter, as well as the relative importance of regulating expenditure as opposed to intake of energy when thermoregulatory costs are high and energy is readily available. Individual elk in the desert that were in poor condition at the end of winter not only showed the strongest degree of selection for areas that reduced costs of thermoregulation, but also, below ~8% ingesta-free body fat, those individuals invested the least energy in locomotion. Because costs of locomotion constitute a relatively small proportion of the overall energy budget of elk (Cook 2002), these results provide strong support for the hypothesis that, under some conditions (e.g., seasons or areas in which costs of thermoregulation and availability of energy are both high), allocation of energy by large herbivores may be constrained by costs of thermoregulation and activity rather than by availability of energy (Speakman and Król 2010).

Additional considerations and conclusions

The biophysical model used for mapping the thermal environment in our study operated by averaging microclimatic conditions predicted for each 30-m^2 pixel on a week-by-week basis. As a result, pixel-specific estimates of evaporative water loss did not represent field rates per se, but rather costs that would be experienced by an individual elk if it were standing in a specific location during the course of each week. Our primary objective, however, was to quantify how differences in predicted costs among pixels influenced behavior of elk. Consequently, relative differences in predicted costs across space and time were of greater importance than absolute cost values predicted for each location. Consistent selection for "low-cost" pixels during a week was equivalent to standing in a low-cost pixel throughout that week, and thus combining output from Niche Mapper with high-frequency location data for elk represented a novel and robust approach to quantifying behavioral responses to the thermal environment. In addition, "noise" in predictions from Niche Mapper that resulted from averaging microclimatic data on a weekly basis should have made it more difficult to detect a significant relationship between predicted thermoregulatory costs and behavior, and thus our results are likely to be conservative.

Climate variability unequivocally affects demography and population dynamics of endotherms by altering the quality, distribution, and phenology of forage (Aanes et al. 2000, Mysterud et al. 2001, Chan et al. 2005). Such variation, however, occurs at broad spatial and temporal scales that probably reduce the effectiveness of behavioral buffering by most species (Huey et al. 2003). In addition, the capacity of endotherms to allocate energy obtained from forage to growth and reproduction may be constrained by their ability to effectively dissipate internal heat loads (Speakman and Król 2010). Direct effects of climate on endotherms are manifested at relatively fine scales, and behaviors designed to regulate exposure to costs imposed by the thermal environment probably will play a critical role in responses of many species to future climate change. Our study represents the only example to date in which detailed data on costs of thermoregulation and activity have been combined with data on animal locations, forage quality, and nutritional condition to shed light on complex relationships among climate, the energy landscape, behavior, and energy state of a large herbivore. Our results indicate that large herbivores possess substantial ability to adjust their behavior in response to endogenous and exogenous factors related to energy balance, but that the magnitude of such adjustments is both context and state dependent, and may be mediated by thresholds in the energy landscape. Indeed, if differences in behavior between elk in the montane forest and the high desert were even partially a result of the higher temperatures and radiant heat loads experienced by elk in the desert, then our results have important implications for predicting future responses of large herbivores to climate change. As global temperatures continue to rise, the capacity of endotherms to buffer themselves behaviorally against direct effects of climate on survival and reproductive success are likely to determine thresholds beyond which changes in demography, population dynamics, or distribution begin to occur.

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SUPPLEMENTAL MATERIAL

Appendix A

Description of primary variables and data sources used to parameterize the microclimate model (*Ecological Archives* M084-019-A1).

Appendix B

Description of primary variables and data sources used to parameterize the endotherm model (*Ecological Archives* M084-019-A2).

Appendix C

Description of vegetation effects on wind speed and percentage shade (percentage of solar radiation reaching the ground) in the landscape-scale energetics model (*Ecological Archives* M084-019-A3).

Appendix D

Description of procedures used to classify habitat types at both study sites (*Ecological Archives* M084-019-A4).

Appendix E

Description of procedures used to quantify spatiotemporal variation in forage quality at both study sites (*Ecological Archives* M084-019-A5).

Appendix F

Description of procedures used to quantify concealment cover and proximity to roads at both study sites (*Ecological Archives* M084-019-A6).

Appendix G

Description of model selection and averaging procedures (*Ecological Archives* M084-019-A7).

Appendix H

Representative single-site and landscape-scale simulation results from Niche Mapper (*Ecological Archives* M084-019-A8).

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.ss548