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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Linking habitat selection to fitness-related traits in herbivores: the role of the energy landscape

Ryan A. Long[1,6] · **R. T. Bowyer**[1] · **Warren P. Porter**[2] · **Paul Mathewson**[2] ·
Kevin L. Monteith[3] · **Scott L. Findholt**[4] · **Brian L. Dick**[5] · **John G. Kie**[1]

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Abstract Animals may partially overcome environmental constraints on fitness by behaviorally adjusting their exposure to costs and supplies of energy. Few studies, however, have linked spatiotemporal variation in the energy landscape to behaviorally mediated measures of performance that ostensibly influence individual fitness. We hypothesized that strength of selection by North American elk (*Cervus elaphus*) for areas that reduced costs of thermoregulation and activity, and increased access to high-quality forage, would influence four energetically mediated traits related to fitness: birth mass of young, nutritional condition of adult females at the onset of winter, change in nutritional condition of females between spring and winter, and neonatal survival. We used a biophysical model to map spatiotemporally explicit costs of thermoregulation and activity experienced by elk in a heterogeneous landscape. We then combined model predictions with data on forage characteristics, animal locations, nutritional condition, and mass and survival of young to evaluate behaviorally mediated effects of the energy landscape on fitness-related traits. During spring, when high-quality forage was abundant, female elk that consistently selected low-cost areas before parturition gave birth to larger young than less-selective individuals, and birth mass had a strong, positive influence on probability of survival. As forage quality declined during autumn, however, lactating females that consistently selected the highest quality forage available accrued more fat and entered winter in better condition than less-selective individuals. Results of our study highlight the importance of understanding the dynamic nature of energy landscapes experienced by free-ranging animals.

Keywords Behavior · Biophysics · Energetics · Thermoregulation · Ingesta-free body fat

Introduction

Behavior represents a key mechanism by which animals buffer themselves against environmental variation (Huey et al. 2003). Through the selection of different habitats, topographies, and microclimates, animals living in heterogeneous landscapes can adjust their exposure to a suite of environmental factors with potential to influence fitness (costs and supplies of energy, risk of predation, etc.). Natural selection should favor behavioral tactics that approximately maximize fitness (Houston and McNamara 2013). Nonetheless, inverse relationships between environmental

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✉ Ryan A. Long
ralong@uidaho.edu

[1] Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, USA

[2] Department of Zoology, University of Wisconsin Madison, Madison, WI 53796, USA

[3] Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA

[4] Oregon Department of Fish and Wildlife, La Grande, OR 97850, USA

[5] US Forest Service, Pacific Northwest Research Station, La Grande, OR 97850, USA

[6] Present Address: Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID 83844, USA

characteristics such as forage availability and risk of predation (Bowyer et al. 1998) often necessitate state- or context-dependent tradeoffs (McNamara and Houston 1996; Long et al. 2014) that can increase variation in behavior among individuals. In addition, optimality problems are complex in heterogeneous landscapes, and animals are rarely able to optimize their behavior with respect to multiple currencies, even in the absence of tradeoffs (Belovsky 1984; Kie 1999). Consequently, individual animals frequently exhibit a broad spectrum of foraging and movement tactics (Morales et al. 2005; Forester et al. 2007; van Beest and Milner 2013), and variation in behavior among individuals may increase as environmental heterogeneity increases (Morales et al. 2005). Yet, few studies have elucidated how differences in habitat selection and space use affect individual performance (Gaillard et al. 2010).

Energetic approaches are ideally suited to evaluating potential relationships between behavior and individual performance (Wilson et al. 2012). Individual energy budgets represent the point of integration for biotic and abiotic factors that influence fitness (Humphries et al. 2004; Parker et al. 2009), and energy balance is the primary mechanistic link between physiological processes occurring at the individual level and ecological patterns and processes observed at the population level (Humphries et al. 2004). In a heterogeneous environment, some individuals will invariably be more selective of the energy landscape (sensu Wilson et al. 2012) than others. Regardless of the reasons for such variation, differences among individuals in strength of selection for the energy landscape likely have important fitness consequences (e.g., van Beest and Milner 2013) because the amount of energy available for growth, storage, and reproduction is determined by the difference between energy intake from foraging, and energy expended on thermoregulation and activity (Porter et al. 1994).

In a previous study, Long et al. (2014) combined spatiotemporally explicit predictions of energy costs experienced by a large, herbivorous mammal (North American elk; *Cervus elaphus*) with detailed data on forage characteristics and animal locations to quantify variation in strength of selection for the energy landscape in two contrasting ecosystems. We collected additional data on condition and survival of elk in one of those systems, and our objective in this study was to relate differences in selectivity among individual elk reported by Long et al. (2014) to variation in four energetically mediated traits related to fitness (Barnett et al. 2015): birth mass of young, nutritional condition at the onset of winter, change in nutritional condition between spring and winter, and neonatal survival.

Numerous studies have demonstrated for a variety of taxa that individuals born small are more vulnerable to mortality from a variety of sources (including predation, because larger individuals are able to effectively evade predators earlier in life) than larger individuals (e.g., Festa-Bianchet et al. 1997; Keech et al. 2000; Côté and Festa-Bianchet 2001; Monteith et al. 2014) and that birth mass may influence reproductive success throughout the lifetime of an individual (Albon et al. 1987). In addition, measures of individual performance such as body mass and condition of adult females (Mysterud et al. 2001a) are positively related to probability of survival (e.g., Loison et al. 1999; Gaillard et al. 2000; Mysterud et al. 2001b). Indeed, for elk in particular, Cook et al. (2004) reported that over-winter survival of females was influenced strongly by condition in early winter. Such strong, positive relationships between birth mass, nutritional condition in early winter, and key correlates of individual fitness such as neonatal and adult survival, have been repeatedly demonstrated for large herbivores. This highlights the utility of those metrics as a means of quantifying the potential fitness consequences of habitat selection. We hypothesized that strength of selection for low-cost areas (i.e., areas that reduce costs of thermoregulation and activity) and high-supply areas (i.e., areas that provide the most abundant, highest quality forage) would be correlated with neonatal mass and survival, as well as maternal condition. Based on this hypothesis, we made the following predictions:

1. Female elk exhibiting the strongest degree of selection for the energy landscape during late gestation (i.e., behavior that reduces costs of thermoregulation and activity and increases access to high-quality forage) will give birth to the largest young, after controlling for effects of mass and condition of the dam, and sex and date of birth of the neonate.
2. Probability of survival of neonates will be positively related to birth mass, maternal condition, and strength of selection for the energy landscape by the dam during early lactation.
3. Female elk exhibiting the strongest degree of positive selection for the energy landscape during summer and autumn will accumulate more fat before winter, and thus will be in better condition at the onset of winter than less-selective individuals, after controlling for carryover effects of condition at the end of the previous winter, and recruitment status (i.e., reproductive allocation associated with recruiting versus not recruiting young).

Materials and methods

Study area

We conducted research at the Starkey Experimental Forest and Range (hereafter “Starkey;” 45°13′N, 118°31′W) in the Blue Mountains of northeastern Oregon, USA. Starkey, which is operated by the US Forest Service, was surrounded by a 2.4-m-high fence that prevented immigration or emigration of elk (Rowland et al. 1997). The main study area, however, was still several times larger (78 km^2) than the average home range reported for elk in the Blue Mountains (Leckenby 1984), and the fence does not affect habitat selection by elk (Stewart et al. 2006). Density of elk at Starkey was low [5 elk/km^2 (Johnson et al. 2000; 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)], good nutritional condition, and large average birth mass of young (Stewart et al. 2005; Long et al. unpublished data). Starkey encompassed a substantial degree of both topographical and vegetative heterogeneity, and included a mosaic of coniferous forests, shrublands, and grasslands dispersed among several major drainages [elevations ranged from 1120 to 1500 m (Stewart et al. 2006)]. Consequently, elk were faced with a diversity of complex choices among factors with potential to influence energy balance. Starkey was characterized by a dry continental climate; the mean maximum temperature recorded by the nearest weather station was 13.9 °C in spring (April–June), 22.9 °C in summer (July–September), and 8.8 °C in autumn (October–November) 1954–2012 (Western Regional Climate Center). Mean total precipitation was 18.4 cm in spring, 6.9 cm in summer, and 6.8 cm in autumn of the same period (Western Regional Climate Center). Common plant communities at Starkey 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*). A detailed description of Starkey was provided by Rowland et al. (1997). No effort was made to control large mammalian carnivores at Starkey, which included mountain lions (*Puma concolor*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*).

Animal capture and handling

We captured adult (≥2 years old) female elk at Starkey by baiting them onto a winter feeding area with an adjacent handling facility during early winter (December–January) 2010–2012 (Rowland et al. 1997). Elk were maneuvered into a squeeze chute upon capture, and each animal was weighed on an electronic platform scale (±1 kg). We quantified nutritional condition at that time using standard protocols developed for elk, which included measuring maximum depth of rump fat via ultrasonography, and assigning a condition score to animals that had catabolized subcutaneous fat reserves (Cook et al. 2010). Those data were combined with data on body mass to estimate percent ingesta-free body fat [IFBF at (Cook et al. 2010)], which is an integrated measure of the energy reserves available for maintenance, growth, and reproduction in capital breeders such as elk (Parker et al. 2009; Cook et al. 2010; Monteith et al. 2013). We also obtained a blood sample from each female to determine pregnancy status based on the concentration of pregnancy-specific protein B (Noyes et al. 1997); elk rarely have more than one offspring (Bubenik 1982). Following data collection, elk were released into the wintering area where they were fed a maintenance diet of alfalfa hay for the remainder of the winter (Rowland et al. 1997). A subset of pregnant females was handled again before being released back into the study area in early spring [March–April (Rowland et al. 1997)]. At that time each female was weighed and fitted with a global positioning system (GPS) collar (model 4400 M; Lotek Wireless, Newmarket, ON) programmed to record hourly locations until early winter (mean positional error of collars was ≤10 m). Each GPS collar also contained a very high frequency (VHF) transmitter.

During spring handling we chemically immobilized elk with an intramuscular injection of 500 mg telazol (Fort Dodge Animal Health, Fort Dodge, IA) reconstituted in 3 mL xylazine hydrochloride [100 mg/mL (Wildlife Pharmaceuticals, Fort Collins, CO; Millspaugh et al. 1995)]. Following injection, we released each animal into a small holding pen until a sufficient anesthetic plane was reached (i.e., laterally recumbent and unresponsive to external stimuli). We applied an ophthalmic ointment to prevent corneal drying and blindfolded elk to reduce stress. In addition, we monitored respiration (breaths/minute), heart rate (beats/minute), and rectal temperature (degrees Celsius) every 5–10 min. If the rectal temperature exceeded 40 °C, we administered 1 L of cold water internally using a veterinary enema bag. We waited 20–60 min post–induction (to allow sufficient metabolism of telazol) before administering 0.25 mg/kg of yohimbine hydrochloride [10 mg/mL; Wildlife Pharmaceuticals (Millspaugh et al. 1995)] intravenously to reverse the xylazine. While each animal was immobilized, we quantified nutritional condition via ultrasonography and body condition scoring (Cook et al. 2010), and fitted each female with a vaginal implant transmitter (VIT; Advanced Telemetry Systems, Isanti, MN) to facilitate capture of neonates immediately after parturition (Johnson et al. 2006; Barbknecht et al. 2009). Each VIT transmitted a temperature–modulated pulse on a unique frequency, and contained a precise event-timing (PET) function that transmitted a coded signal indicating the timing of expulsion in 30-min increments for up to 5.3 days (Johnson et al. 2006; Barbknecht et al. 2009).

We monitored VITs daily throughout birthing seasons (May–June) of 2011 and 2012 using ground-based radiotelemetry. When a parturition event was suspected based on the detection of an expelled VIT, we located the collared female via radiotelemetry; if the neonate was not immediately observed, we initiated a search in the vicinity (≤100-m radius) of the female. When a neonate was located, we blindfolded it, determined its sex, and collected a variety of size- and age-related data (body mass, chest girth, total length, hind foot length, ear length, tooth protrusion, navel diameter, and condition of the hooves, dewclaws, hair, and navel). We generally determined age to the nearest hour using the PET function of the VIT; however, we captured three neonates from GPS-collared females that were not fitted with a VIT, and we estimated the age of those individuals by comparing their morphology and stage of development with that of known-age neonates, as well as with age-specific data reported by Johnson (1951). We fitted each neonate with ear tags and an expandable radio collar (Rearden et al. 2011) equipped with a mortality sensor to monitor survival of young. The mortality sensor was designed to detect movement, and increased the pulse rate of an associated VHF transmitter if the collar was stationary for ≥4 h. We monitored neonatal elk every 1–10 days until winter. When a mortality signal was detected, we located the collar and attempted to verify that mortality had occurred. If we could find no evidence of mortality, we assumed the collar had been slipped, and censored the dam from subsequent analyses of nutritional condition, unless the calf later arrived at the winter feeding area with intact ear tags. We captured 38 neonates from GPS-collared female elk during 2011–2012. Sample sizes in our analyses, however, ranged from 24 to 38, because recapture success of adult females during early winter was <100 %. This resulted in three levels of data resolution: (1) adult females for which we had data on birth mass and survival of young, GPS locations during spring through autumn, and nutritional condition in early winter; (2) adult females for which we had data on birth mass and survival of young and GPS locations during spring through autumn, but no data on early winter condition because we were not able to recover the collar via capture until the following year; and (3) adult females for which we had data on birth mass and survival of young, but no subsequent data on GPS locations or early winter condition because the collar was never recovered (i.e., the animal was never captured again). We were able to include animals in the first category ($n = 24$) in all of our analyses. Animals in the second category ($n = 29$) were included in analyses of birth mass and neonatal survival, but not in analyses of early winter condition or change in condition. Animals in the third category ($n = 38$) were only included in our analysis of neonatal survival. Although we attempted to avoid placing collars on the same adult females in both years to the greatest extent possible, we collected data from seven individuals in both 2011 and 2012. In those instances, we treated the datasets from each year as independent sampling units in our analyses (i.e., the sampling unit was the animal-year). Animal handling was approved by the Institutional Animal Care and Use Committee at Idaho State University (protocol no. 684), the internal Animal Care and Use Committee for the Starkey Experimental Forest and Range, and was in accordance with guidelines established by the American Society of Mammalogists for research on wild mammals (Sikes et al. 2011).

Energy costs: Niche Mapper

Long et al. (2014) modeled spatiotemporally explicit costs of thermoregulation and activity using Niche Mapper (Porter et al. 2002; Porter and Mitchell 2006; Natori and Porter 2007), and results of those analyses provided much of the foundation for our study of potential fitness consequences of behavior. Niche Mapper is based on first biophysical principles, and iteratively solves the energy-balance equation (Porter and Gates 1969) for a model organism as a function of measurable features of the organism and its environment. Two submodels (a microclimate model and an animal model) are integrated to estimate rates of metabolism and evaporative water loss necessary to maintain homeothermy at a particular landscape pixel. Single-site results can then be combined with data on topography and structure of vegetation to model energy and water costs at a landscape scale (Porter et al. 2002; Natori and Porter 2007). Output from Niche Mapper includes a suite of variables related to mass and energy balance (Porter and Mitchell 2006), but the variable of interest both to us and to Long et al. (2014) was the predicted rate of evaporative water loss. Metabolic rate increases in parallel with evaporative water loss above the upper critical limit of the thermal neutral zone (Scholander et al. 1950), and thus rates of water loss (*g*/*d*) predicted by Niche Mapper represented spatiotemporal variation in both energetic and hydric costs imposed on elk by the thermal environment during spring through autumn (Long et al. 2014). Estimates of thermoregulatory costs derived from Niche Mapper have been validated with empirical data for animals ranging in size from mice (*Mus* sp.) to Holstein calves (*Bos taurus*) and Arabian oryx [*Oryx leucoryx* (Porter et al. 1994, 2010)].

Long et al. (2014) used Niche Mapper to model the thermal environment experienced by elk at relatively fine spatial (30 m^2) and temporal (weekly) scales (e.g., Kearney et al. 2012). Therefore, we used results from Long et al. (2014) to represent the “cost” side of the energy landscape available to individual elk on a weekly basis during this study. A detailed description of the methodology used to produce those results, including estimation procedures, input variables and data sources used to parameterize both the microclimate and animal portions of Niche Mapper, landscape–scale implementation of Niche Mapper, and model validation procedures, was provided by Long et al. (2014).

Energy supplies: forage quality and abundance

Long et al. (2014) used a combination of intensive vegetation sampling and geostatistical modeling to quantify spatial variation in quality and abundance of forage available to elk at Starkey. Digestibility, nitrogen content, and abundance of key forage plants for elk were measured at >400 transect locations during spring through autumn (Long et al. 2008), and the product of those three metrics (all expressed as percentages) was then used as an index to overall availability of energy along each transect (Long et al. 2014). Long et al. (2014) subsequently modeled variation in energy supplies as a continuous response surface using spatial interpolation. Preliminary analyses indicated that variation in forage characteristics occurred at a coarser temporal scale than variation in costs imposed by the thermal environment (Long et al. 2014), and thus seasonal (as opposed to weekly) maps of forage quality and abundance provided sufficient temporal resolution for capturing variation in energy supplies. A detailed description of procedures used to produce seasonal maps of energy supplies was provided by Long et al. (2014).

The differences in our approaches to quantifying the cost versus supply sides of the energy landscape precluded the combination of those components into a single metric of net availability of energy (i.e., supplies minus costs). Similarly to Long et al. (2014), however, our primary interest was in accurately representing relative differences in both costs and supplies of energy across the landscape at an appropriate temporal scale—we believe our approach was highly successful in that regard.

Statistical analyses

Long et al. (2014) estimated resource selection functions for elk by fitting generalized linear mixed models with a binomial error distribution and logit link function (Gillies et al. 2006; Bolker et al. 2009; Wagner et al. 2011) to the attribute data from used (GPS locations from elk, coded 1) and random (generated in ArcGIS 10, coded 0) locations at Starkey [analyses conducted using the lme4 package in program R version 2.12 (R Development Core Team 2011)]. Those authors fit separate models for each unique combination of season (spring, summer, and autumn) and diel period (daytime and nighttime), and used standardized predictor variables to facilitate direct comparison of model coefficients (Neter et al. 1996). Our interest here was in the conditional, or individual-level, parameter estimates generated by including a random intercept and uncorrelated random slope for energy costs (grouped by individual elk nested within week so that use and availability were compared at the appropriate weekly time scale), and energy supplies (grouped by individual elk) in each time–specific model (Long et al. 2014). The conditional slopes represented, for each individual elk, the relative strength of selection for both low-cost (i.e., areas that reduced costs of thermoregulation and activity experienced by elk) and high-supply (i.e., areas that provided the most abundant, highest quality forage) areas (Gillies et al. 2006; Wagner et al. 2011); thus, we used those conditional estimates to evaluate the influence of selectivity for the energy landscape on birth mass, nutritional condition at the onset of winter, and change in condition between spring and winter (sensu Wagner et al. 2011) using multiple linear regression (Neter et al. 1996). Other predictor variables considered in models of birth mass of neonates were body mass (kilograms) and nutritional condition (percent IFBFat) of the dam during early spring, sex and date of birth (Julian day) of the neonate, and interactions between sex of the neonate and date of birth, mass of the dam, and conditional parameter estimates for selectivity of the energy landscape (both costs and supplies). Additional predictor variables considered in models of nutritional condition in early winter (or change in condition before winter) were condition of the female during spring, recruitment status of the female ("recruited" indicates that the young were alive at the onset of winter, "did not recruit" indicates that the young died prior to winter), and interactions between recruitment status and conditional parameter estimates for selectivity of the energy landscape. A detailed description of those analyses is provided in Online Appendix S1.

To illustrate relationships between statistically significant predictor variables and each respective response variable (birth mass, nutritional condition in early winter, or change in nutritional condition between spring and early winter), we used the best model from a 95 % confidence set [Δ Akaike information criterion adjusted for small sample size (AIC_c) = 0; see Online Appendix S1 for details], and plotted predicted values of the response variable against values of the predictor variable of interest (across the observed range of the predictor variable), while holding other variables in the model constant at their mean (Monteith et al. 2013). That approach allowed us to illustrate expected effects of each variable of interest (x-axis), while simultaneously controlling for other influential factors included in the model. Raw data are also presented in Online Appendix S2.

We used the known-fate model in program MARK (White and Burnham 1999) to estimate survival of neonatal elk at Starkey, and to evaluate the influence of birth mass, sex, date of birth, maternal mass and condition, and maternal behavior (i.e., selectivity for the energy landscape) on the probability of survival. We estimated pre-weaning survival weekly from birth until 16 weeks of age (approximately June–September). For encounter histories in the known-fate model, we placed all events, including capture, survival monitoring, mortality, and censors into 1-week intervals. All neonates were ≤ 4 days old when captured and thus, entered the survival analysis in the first weekly interval. We right-censored animals that prematurely shed collars ($n = 6$) because censoring likely was independent of the fate of the neonate.

We first modeled survival of neonates up to 16 weeks of age by allowing survival to vary randomly by week, and plotted the resulting weekly estimates of survival to identify periods of time with consistent survival (Barber-Meyer et al. 2008). Survival varied during the first 2 weeks of life, but remained relatively constant thereafter, which was expected because of changing patterns of vulnerability of young to predation, activity of young, and degree of association with the dam (Barber-Meyer et al. 2008; Haskell et al. 2010). Accordingly, we developed a model that was life-stage specific and allowed survival to vary during the first 2 weeks, with constant survival for the remaining 14 weeks. We selected that stage-specific model from among other models (i.e., constant survival and different survival each week) using AIC_c because there were no other candidate models within 2 $\Delta\text{AIC}_\text{c}$. We then used a similar approach to model the time-specific effects of birth mass and maternal condition on survival. Results of that analysis supported an effect of birth mass on survival for the first 4 weeks post-partum, transitioning to an effect of maternal condition on survival thereafter. Finally, using the stage-specific model structure described above, we fit a global model that included all potential covariates (birth mass, sex, date of birth, maternal mass, maternal condition, and maternal selectivity for the cost and supply sides of the energy landscape). Similar to birth mass and maternal condition, we modeled the effects of maternal behavior on survival in a time-specific fashion by allowing each variable to influence survival independently during the first 4 weeks post-partum versus 5–16 weeks post-partum. After fitting the global model, we excluded variables that were clearly uninformative [i.e., 85 % confidence intervals (CI) overlapped 0 (Arnold 2010)] from further analysis. We then modeled all possible combinations of the remaining variables and recorded the AIC_c, $\Delta\text{AIC}_\text{c}$, and Akaike weight ($w_\text{i}$) of each model. We selected a 95 % confidence set of models from the full set based on w_i values, and used model averaging to produce final parameter estimates for each variable (Burnham and Anderson 2002). We concluded that an estimate differed from zero if its 90 % confidence interval did not contain zero (Long et al. 2009; Arnold 2010; Monteith et al. 2013).

Results

The best model for explaining variation in birth mass of neonatal elk included sex and date of birth of the neonate, body mass of the dam, and strength of selection by the dam for areas that reduced costs of thermoregulation and activity (Table S3a, Online Appendix S3); this model explained 44 % of the variation in birth mass. Nutritional condition (fat reserves) and strength of selection for forage quality by the dam were not useful for predicting birth mass (i.e., 85 % CI overlapped zero), and were removed prior to formal model selection. In addition, none of the interactions between sex of the neonate and other predictor variables met our criteria for retention in the model-selection analysis. Model-averaged parameter estimates indicated that male neonates were larger than females, individuals born later in the season were larger than those born earlier, dams exhibiting strong selection for low-cost areas (i.e., areas that reduced costs of thermoregulation and activity) before parturition gave birth to larger young than less-selective individuals, and large dams tended to give birth to large young (although this effect was marginally not significant; Table 1; Fig. 1). Sex of the neonate was the most important variable in the final model (importance weight = 0.84); however, behavior of the dam relative to costs imposed by the thermal environment was the second most important predictor of birth mass, with an importance weight of 0.74 (Table 1).

A total of 13 neonates died during our study, largely from predation by mountain lions ($n = 8$) and black bears ($n = 2$); other sources of mortality included trauma ($n = 1$), malnutrition ($n = 1$), and an unknown cause ($n = 1$). Date of birth, maternal mass, and strength of selection for low-cost areas by the dam from 5 to 16 weeks post-partum were not useful for predicting survival (i.e., 85 % CI overlapped zero), and were removed prior to formal model selection. The best model for explaining variation in probability of survival included sex, birth mass (during the first 4 weeks post-partum), maternal condition (5–16 weeks post-partum), strength of selection for forage quality by the dam, and strength of selection for low-cost areas by the dam during the first 4 weeks post-partum (Table S3b, Online Appendix S3). However, model-averaged parameter estimates and associated 90 % CI indicated that probability of survival was primarily influenced by two variables; birth mass and maternal condition (Table 2). Both of those variables were positively related to probability of survival, whereas CIs for all other variables overlapped zero (Table 2).

The best model for explaining variation in nutritional condition of female elk at the onset of winter included recruitment status, strength of selection for forage

Table 1 Model-averaged parameter estimates, confidence intervals (*CI*), and Akaike importance weights from multiple linear regression analyses of factors affecting birth mass of neonatal elk (*Cervus elaphus*), ingesta-free body fat of adult female elk at the onset of winter (*Winter IFBFat*), and change in IFBFat between spring and winter (Δ Winter IFBFat) at the Starkey Experimental Forest and Range, Oregon, USA, 2011–2012

Model	Parameter	Estimate	90 % CI		Importance weight[a]
			Lower	Upper	
Birth mass	Date of birth (Julian day)	0.040	0.001	0.085	0.609
	Dam mass (kg)	0.031	−0.001	0.063	0.633
	Energetic cost coefficient	−1.032	−1.932	−0.131	0.743
	Sex of neonate	1.392	0.381	2.403	0.842
Winter IFBFat[b]	Spring IFBFat (%)	0.072	−0.033	0.178	0.450
	Forage selection coefficient	−9.679	−13.313	−6.046	0.999
	Recruitment status (recruited young or not)	−4.329	−5.220	−3.438	0.999
	Forage selection × recruitment status	11.453	7.596	15.309	0.999
Δ Winter IFBFat[b]	Spring IFBFat (%)	−0.839	−1.022	−0.656	NA
	Forage selection coefficient	−10.009	−13.595	−6.423	NA
	Recruitment status (recruited young or not)	−4.462	−5.344	−3.580	NA
	Forage selection × recruitment status	11.714	7.909	15.519	NA

[a] Importance weights are not presented for predictor variables in the model of Δ Winter IFBFat because the top model in that set held >95 % of the weight, and thus variables were considered to be of equal importance

[b] All models in the set contained the forage selection × recruitment status interaction term

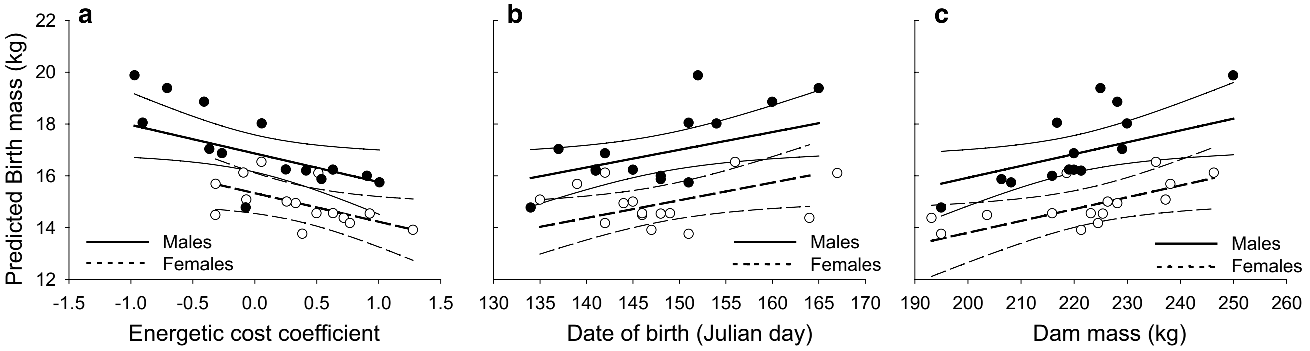

Fig. 1 Model-predicted effects [±90 % confidence intervals (CI)] of **a** selection for low-cost areas, **b** date of birth, and **c** dam mass on birth mass of neonatal male ($n = 14$) and female ($n = 15$) North American elk (*Cervus elaphus*) at the Starkey Experimental Forest and Range, Oregon, USA, 2011–2012. Fitted values for each neonate are also shown (*closed circles* males, *open circles* females). Energetic cost coefficients (**a**) are conditional parameter estimates from a generalized linear mixed model of resource selection by adult female elk, and represent the strength of selection for areas that reduced costs of thermoregulation and activity during the last third of gestation (Long et al. 2014); energetic efficiency of behavior decreases with increasing values of the cost coefficient. Predictions were derived from a multiple regression model, and represent expected effects of the variable of interest (*x-axis*) within the range we observed, while holding all other variables in the model constant at their mean

quality during autumn, and the interaction between those two variables (Table S3a, Online Appendix S3); this model explained 76 % of the variation in early winter condition of female elk. Strength of selection for forage quality during summer, strength of selection for low-cost areas during summer and autumn, and their respective interactions with recruitment status were uninformative, and were removed prior to formal model selection. Model-averaged parameter estimates indicated that nutritional condition at the onset of winter was unrelated to condition in spring, and that females that successfully recruited young entered winter in poorer condition than those that did not (Table 1). The relationship between forage selection during autumn and early winter condition differed in direction between females that did and did not recruit young (indicated by a strong interaction between those two variables; Table 1). Among those females that recruited young, individuals that selected higher quality forage during autumn entered winter in

Table 2 Model-averaged parameter estimates, CIs, and Akaike importance weights of factors that influenced survival of neonatal elk (*C. elaphus*) to 16 weeks of age at the Starkey Experimental Forest and Range, 2011–2012

Parameter	Estimate	90 % CI		Importance weight
		Lower	Upper	
Sex of neonate	−0.777	−1.607	0.054	0.654
Birth mass (kg)	0.267	0.102	0.433	1.000
Dam condition	0.747	0.310	1.183	1.000
Energetic cost coefficient—early[a]	0.720	−0.304	1.743	0.494
Forage selection coefficient—early[a]	−1.883	−4.026	0.260	0.629
Forage selection coefficient—late[a]	3.060	−0.253	6.372	0.622

[a] Energetic cost and forage selection coefficients are conditional parameter estimates from a generalized linear mixed model of resource selection by adult female elk, and represent the strength of selection for areas that either reduced costs of thermoregulation and activity during the last third of gestation or increased access to high-quality forage (Long et al. 2014). Early and late designations indicate whether a variable was allowed to influence survival during the first 4 weeks post-partum (early) or 5–16 weeks post-partum (late) in the known-fate model in program MARK

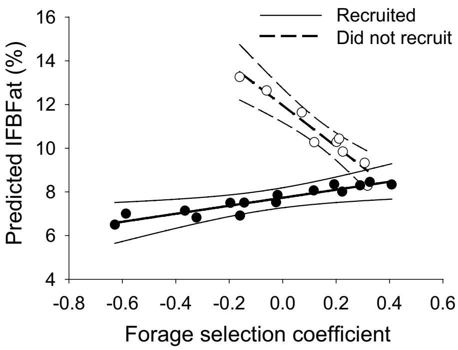

Fig. 2 Model-predicted effect (±90 % CI) of selection for forage quality on ingesta-free body fat (*IFBFat*) at the onset of winter (1 December) of adult female North American elk that either recruited ($n = 15$) or did not recruit ($n = 9$) young at the Starkey Experimental Forest and Range, 2011–2012. Fitted values for each female are also shown (*closed circles* females that successfully recruited young, *open circles* females that did not). Forage selection coefficients are conditional parameter estimates from a generalized linear mixed model of resource selection by adult female elk, and represent the strength of selection for forage quality during autumn (Long et al. 2014); strength of selection for high-quality forage increases with increasing values of the forage selection coefficient. Predictions were derived from a multiple regression model, and represent expected effects of forage selection within the range we observed, while holding all other variables in the model constant at their mean

better condition than those that selected lower quality forage (Fig. 2). The opposite held, however, for females that did not recruit young; selection for forage quality was inversely related to nutritional condition in early winter (Fig. 2). The 95 % confidence set for early winter condition contained only two models; thus, importance weights served only to differentiate between nutritional condition in spring as a relatively unimportant predictor of condition, and the remaining variables, all of which were statistically significant (Table 1).

Factors that influenced the absolute change in nutritional condition of female elk between spring and winter were nearly identical to those that influenced condition in early winter. There were, however, two exceptions to this pattern. First, the top model for explaining change in condition garnered 99 % of the AIC weight, included nutritional condition in spring as a predictor, and explained 89 % of the variation in change in condition between spring and winter (Table S3a, Online Appendix S3). Second, nutritional condition in spring was negatively related to change in condition between spring and winter, and was statistically significant in the final model (Table 1). Female elk that emerged from the previous winter in better condition gained less fat during spring through autumn than those that emerged from winter in poorer condition, regardless of whether they recruited young in that year (Fig. 3). Similar to results of modeling condition in early winter, the relationship between forage selection in autumn and change in condition between spring and winter was positive for females that recruited young and negative for females that failed to do so (Fig. 3).

Discussion

Results of our study largely were consistent with our initial predictions, but also demonstrated that the consequences of behavioral responses to the energy landscape can vary with seasonal changes in costs versus supplies of energy. During spring, when forage at Starkey was both abundant and of high quality (Stewart et al. 2006; Long et al. 2008), strength of selection for forage by female elk during the last third of gestation was unrelated to birth mass of young. In contrast, females that consistently selected areas that reduced costs of thermoregulation and activity gave birth to larger offspring than less-selective individuals, and those offspring had a higher probability of surviving until winter.

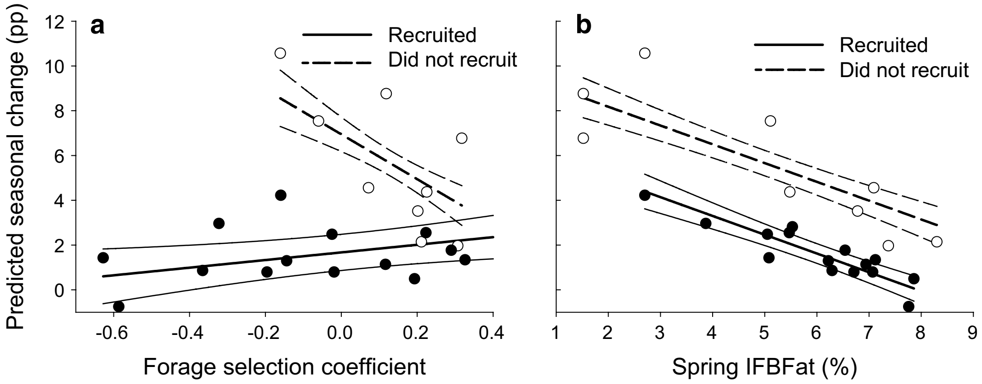

Fig. 3 Model-predicted effects (±90 % CI) of **a** selection for forage quality, and **b** spring IFBFat on absolute change in IFBFat (between spring and winter) of adult female North American elk that either recruited ($n = 15$) or did not recruit ($n = 9$) young at the Starkey Experimental Forest and Range, 2011–2012. Fitted values for each female are also shown (*closed circles* females that successfully recruited young, *open circles* females that did not). Forage selection coefficients (**a**) are conditional parameter estimates from a generalized linear mixed model of resource selection by adult female elk, and represent the strength of selection for forage quality during autumn (Long et al. 2014); strength of selection for high-quality forage increases with increasing values of the forage selection coefficient. Predictions were derived from a multiple regression model, and represent expected effects of the variable of interest (*x-axis*) within the range we observed, while holding all other variables in the model constant at their mean

Those results are consistent with implications of the heat-dissipation limit theory (Speakman and Król 2010), which contends that in situations where availability of energy is effectively unlimited (which frequently coincide with seasonal increases in environmental temperature in many ecosystems), allocation of energy by endothermic animals to growth and reproduction should be constrained largely by the ability to dissipate heat (Speakman and Król 2010). Behavioral implications of the heat-dissipation limit theory are less clear, however, for scenarios in which costs of thermoregulation and activity are high, quality of forage is low, and thus constraints on the allocation of energy to growth and reproduction may be operating on both sides of the energy-balance equation. This scenario likely existed for elk in our study during summer and autumn, and our results indicated that under such conditions, selection of areas that increased access to high-quality forage had a greater influence on net energy balance than selection of areas that reduced costs of thermoregulation and activity.

For female elk that did not recruit young, the negative relationship between forage selection and nutritional condition at the onset of winter (as well as the change in condition between spring and winter) was contrary to our predictions. The most likely explanation for this result is that subtle effects of behavior on energy balance of those individuals were outweighed by the variable costs of reproduction. Lactation represents the most energetically costly period in the life cycle of mammals (Moen 1978; Loudon et al. 1987; Monteith et al. 2014), and female elk typically cease lactation soon after the death of their young (Bubenik 1982). The length of time that a female continues to lactate after losing her young, however, can vary among individuals, and thus the degree to which the duration of offspring survival is correlated with cumulative costs of lactation is unclear. Regardless, among female elk in our study that did not recruit young ($n = 9$), duration of survival of young ranged from 3 to 82 days post-partum ($\bar{x} = 37$ days). Consequently, the magnitude of the trade-off between the direct costs of reproduction and accumulation of body reserves (Fauchald et al. 2004; Monteith et al. 2013) likely varied substantially among those individuals. Although additional post hoc analyses for non-recruiting females were difficult to justify because of small sample size, qualitative inspection indicated that females that reared young for >40 days tended to have higher selection coefficients for forage quality during autumn than females that reared young for <40 days. This pattern indicates that for females that incurred costs of lactation for only a short time, strong selection for forage characteristics was unnecessary for accruing substantial fat reserves before winter. Consequently, those females likely focused their behavior on other potentially limiting factors (e.g., predator avoidance), with a concomitant decrease in the strength of selection for forage.

In an experiment with captive elk, Cook et al. (2004) reported a multiplier effect (sensu White 1983) of forage quality on nutritional condition; reducing the quality (i.e., digestible energy) of forage consumed by elk by 10–20 % resulted in reductions in nutritional condition of 75–300 %. Those authors also reported that increased rates of intake did not allow elk to compensate for a low–quality diet, and that the nutritional treatments used in their study likely were conservative based on the quality of forage available to elk during the summer and autumn in many areas (Cook et al. 2004). Indeed, forage quality is insufficient for meeting energetic demands of large herbivores during lactation in a variety of temperate ecosystems (Cook 2002; Monteith et al. 2013), and frequently reaches minimum values during mid- to late autumn (Cook 2002). We demonstrated that selection for areas that provided relatively high-quality forage during autumn had a positive effect on the accumulation of fat reserves (and, thereby, nutritional condition at the onset of winter) by lactating female elk. In addition, females in better condition likely were able to allocate more energy to lactation, which would explain the positive relationship we observed between maternal condition and probability of survival of neonates 5–16 weeks postpartum. Consequently, our results are consistent with those of Cook et al. (2004), and support the hypothesis that small differences among individuals in the strength and consistency of selection for high-quality forage during periods of nutritional stress can have important, cumulative effects on energy balance and nutritional condition.

Numerous studies have attempted to relate patterns of space use to correlates of individual fitness in large herbivores (e.g., Bender et al. 2007; McLoughlin et al. 2007). Our study, however, is among the first to elucidate the mechanistic underpinnings of such relationships in the context of behavioral responses to spatiotemporal variation in the energy landscape (sensu Wilson et al. 2012). In addition, previous efforts to link behavior to the acquisition and allocation of energy by free–ranging large herbivores rarely have accounted for complex interactions among vegetative structure, topography, animal morphology and physiology, and biophysical factors such as air temperature, wind speed, humidity, and radiation that shape the energy landscape (Porter and Gates 1969; Speakman and Król 2010). Our modeling approach was based on a detailed characterization of such interactions at fine spatiotemporal scales. In contrast, simple correlations between space use and physiographic features of the landscape may produce misleading results with respect to the causes and consequences of animal behavior. For example, on a warm, clear day, a closed-canopy forest could easily represent "optimal" habitat for reducing costs of thermoregulation and activity by minimizing heat gained through radiation, and might be strongly selected as a result. In contrast, on a warm, windy day with substantial cloud cover, open meadow habitat might maximize heat loss through convective means, and thus be strongly selected. In such a scenario, typical analyses of habitat selection would indicate a "change" in behavior, despite the same underlying mechanism driving selection of both habitats. This example highlights the importance of understanding the dynamic nature of the energy landscape experienced by free-ranging animals in heterogeneous environments, and calls into question the utility of simple characterizations of optimal versus suboptimal habitat based on vegetation or topography alone.

Individual animals often possess a substantial ability to modify their behavior in response to environmental factors that influence energy balance and vary across space and time. Our study represents the only example to date in which detailed data on spatiotemporally explicit costs of thermoregulation and activity, as well as forage quality and abundance, have been combined with data on animal locations and fitness correlates to shed light on the functional consequences of habitat selection by a large, herbivorous mammal. Our results complement those of many previous studies by revealing how individual patterns of behavior relative to the energy landscape can translate into effects on energetically mediated correlates of fitness. Population-level responses to environmental variation ultimately reflect the sum of individual responses, and thus additional mechanistic research at the individual level will be critical for predicting long-term patterns of population dynamics and demography in variable environments, and for predicting responses of many species to environmental change.

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Author contribution statement R. A. L. conceived of the study; J. G. K., R. A. L., and R. T. B. designed the study; B. L. D., K. L. M., R. A. L., and S. L. F. conducted fieldwork; P. M., R. A. L., and W. P. P. carried out the biophysical modeling; K. L. M. and R. A. L. analyzed the data; and R. A. L. wrote the manuscript; other authors provided editorial advice.

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