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# Heart rate biologgers reveal individual-specific energy landscapes for mule deer

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## Abstract

**Background** An important, yet often overlooked component of animal movement behaviour is the physiological cost incurred by animals when travelling through an environment, i.e., the “energy landscape”. These include the costs related to movement rate and elevation gain, as well as the mediating influence of variation in cover types and substrate. These costs are likely to be mediated by differences among individuals, with body condition and age likely to modify energy expenditure.

**Methods** Using subcutaneous biologgers paired with GPS collars ( $n = 37$ ), we recorded high-resolution heart rate data from free-ranging mule deer (*Odocoileus hemionus*) across three study sites in Utah, USA. We generated energy landscapes for mule deer by combining heart rate data with the attributes of movement steps derived from GPS locations to quantify how movement and landscape characteristics influenced heart rate, a proxy for energy expenditure.

**Results** Overall, heart rates were higher in summer than in winter. Energy landscapes for mule deer were driven by step length and elevation gain, which increased deer heart rates. We also found a pronounced effect of movement state (encamped versus travelling) on heart rates, suggesting that initiating movement resulted in a larger increase in heart rate compared to distance travelled once movement was initiated. Deer in poorer body condition had an increased average heart rate in winter, as did heavier deer and younger deer. We found a novel trade-off in deer step selection, where deer were more likely to take steps that were energetically costly (associated with an elevated heart rate) when those steps had higher forage quality, suggesting a mediating influence of the energy landscape on forage selection by mule deer.

**Conclusions** Our study highlights the value of quantifying energy landscapes in the field, by revealing how individual energy landscapes can drive movement behaviour decisions and a novel trade-off between energy expenditure and forage quality.

**Keywords** Biologgers, Ecophysiology, Energy landscapes, Foraging tradeoffs, Heart rate, Individual differences, Movement, Mule deer, *Odocoileus hemionus*, Utah

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## Background

Movement decisions made by animals are a result of the integration of perceived costs and benefits of where and when to move across the landscape. Perhaps one of the most studied trade-offs influencing animal movement and space use is the interplay between the (perceived) presence of predators, e.g., “the landscape of fear” [1, 2] and food availability, e.g., “the landscape of food” [3–5]. Another important dimension influencing animals’ movement decisions is the physiological or metabolic cost incurred by an animal when traveling through the landscape, manifesting from the amalgamation of energetic expenditure related to movement speed, incline, substrate and superstrate, and environmental conditions [6, 7]. Elucidating the rate of energy expenditure as a function of the landscape and the environment is critical to fully describing a fundamental dimension of animal movement ecology and represents an often overlooked dimension that may drive trade-offs in animal movement and habitat selection. While ecologists have begun to pay more attention to quantifying energy landscapes [6, 8, 9], models based on direct movement observations and physiological measurements from free-ranging individuals remain rare.

Quantifying the rate of energy expenditure in free-ranging animals is a significant challenge. In laboratory settings, treadmills along with oxygen chambers can be used to quantify oxygen consumption as a function of movement speed and incline [8, 10], however the extent to which such measurements can be applied to real-world scenarios across a range of environmental and topographic conditions is unknown. The doubly labelled water technique can be used to estimate CO<sub>2</sub> production, but only between two blood samples and therefore only at coarse temporal resolution and requires frequent re-handling and sampling of individuals over short time frames which is often not feasible [10, 11]. Many studies use accelerometry to calculate overall dynamic body acceleration as a proxy for energy expenditure [12], and while such models can provide important insight into energy expenditure, such models require calibration and only reflect mechanical activity as opposed to other sources of energy expenditure such as stress or digestion. Heart rate monitoring offers a useful, indirect measure of metabolic rate, given it is closely linked to oxygen consumption [13–15]. As such, the advent of subcutaneous heart rate monitors for free-ranging animals [16] represents a significant opportunity to investigate energetics and the rate of energy expenditure in free-ranging animals.

Energetic costs (and subsequently heart rate) vary as a function of many characteristics of movement and of the environment animals travel through. For animals traveling over level ground, the rate of energy expenditure and

heart rate increases with the speed at which the animal moves [17, 18] with high speeds being associated with high energetic costs [19]. For animals to move up in elevation requires additional work to raise the mass of their bodies [6]. In humans, the cost of walking uphill at a slope of 45° increases the rate of energy expenditure by nearly an order of magnitude [20]. The increased cost of moving uphill has been shown to scale with body mass—while there was no significant cost increase to travelling along a 15° incline compared to flat ground for a mouse (*Mus musculus*), the same difference in incline resulted in a doubling of oxygen consumption in a chimpanzee (*Pan troglodytes*; [21]). Traveling through different land cover types is likely also to alter the cost of movement. Travelling over uneven surfaces requires additional work as limbs must be raised higher [6], which suggests areas such as forests could increase the rate of energy expenditure as animals must navigate obstacles such as thick brush and fallen trees by either stepping over them or detouring around them. Snow depth has also long been known to correlate with increased energy expenditure, particularly in cervids [22, 23].

Seasonality, temperature, and food intake are all also predicted to play a role in regulating heart rate. Heart rates have been shown to be lower in winter in both moose [24] and reindeer [25]. Heart rate has been shown to increase with increasing food intake in reindeer [26], suggesting that seasonal fluctuations in heart rate may be at least partially due to animals being hypometabolic in winter due to restricted food intake. Conversely, other studies have shown a significant decrease in winter heart rate despite ad libitum feeding, suggesting that seasonal changes in heart rate may still be endogenously entrained [27]. In mammals and birds, high ambient temperatures can increase peripheral blood flow and sympathetic activation; heart rate may rise under heat stress, although behavioural down-regulation can also reduce heart rate [28, 29]. Terrain aspect may then also be expected to affect heart rate, with southern and western facing slopes receiving more solar radiation (in the northern hemisphere), which reduces snow cover during winter months and results in greater heat exposure during summer months.

In addition to external environmental drivers of variation in heart rate, differences among individuals are also likely to drive variation in heart rate and its response to activity. In reindeer, heart rate was found to be higher in younger individuals and those currently nursing young [25]. While there exists little evidence to suggest animals in the wild engage in physical activity for the sake of physical fitness (e.g., to be better able to hunt prey or evade predators), many animals have been shown to have increased “athletic capacity” following training in laboratories [30]. As such, we might expect individuals with

higher overall movement rates to be more cardiovascularly fit and therefore have lower overall heart rates and a diminished heart rate response to strenuous activity.

Movement is a fundamental axis of animal behaviour [31]. The rate of energy expenditure represents an oft-overlooked mediating component of key concepts such as the ideal free distribution [32]. Selection favours efficient movement, and therefore animals should be adapted to move through their landscapes efficiently [6, 31, 33]. Animals should therefore find ways to optimize the trade-off between foraging opportunities and movement costs. For example, Wall et al. [34] observed that African elephants (*Loxodonta africana*) in Kenya do not use areas on a local mountain despite the presence of high-quality forage and posited that the energetic cost of climbing compared to travel over level ground (which, due to their large mass is considerable for elephants) make such a trade-off infeasible. Likewise, imperial cormorants (*Phalacrocorax atriceps*) preferentially foraged in areas that reduced their energy-based foraging costs [7]. Effectively elucidating models of optimal animal movement requires knowledge of how animals trade-off perceived benefits and movement costs.

We combined subcutaneous biologgers that record average heartbeat at 2-minute intervals with locational data from GPS collars in three populations of mule deer (*Odocoileus hemionus*) in Utah, USA (total  $n = 37$  individuals) to evaluate how season, landscape characteristics, movement rates, and intrinsic differences among individuals affect heart rates. First, we examined seasonal variation in heart rate across winter, early summer and late summer. We hypothesized that heart rates would be lower in winter when food intake is reduced, and also hypothesized that increased physiological stress and increases in resting metabolic rate [35] in late pregnancy and lactation would increase heart rate in early summer. We hypothesized that thermal stress in late summer may increase heart rates. Conversely, a competing hypothesis is that overheating may lead to a voluntary reduction in feeding and subsequently a reduction in late summer heart rate. Our second goal was to define features structuring the energy landscapes for mule deer, by testing our predictions that longer steps, more elevation gain, deeper snow, higher temperatures, and greater forest cover would increase heart rate. Third, we examined how differences among individuals, including overall average movement, body condition, and age could predict average heart rate. Finally, we used a step selection function framework to test if deer select for steps that are predicted to reduce energy expenditure and how they trade-off physiological movement costs with the acquisition of high-quality forage. Our study represents one of the first examples of the use of biologgers to directly relate heart

rate to the movement ecology and landscape characteristics of free-ranging animals.

## Methods

### Study area

We selected three distinct climatic regions within Utah, USA to conduct our study. Sites were comprised of wildlife management units as defined by the Utah Division of Wildlife Resources (UDWR), and varied with respect to climatic, topographic, and anthropogenic features. The first area (Cache) was in the northeast corner of the state east of Logan, UT (Latitude  $\sim 41^\circ\text{N}$ ; July average temperature  $23.4^\circ\text{C}$ ; January average temperature  $-3.9^\circ\text{C}$ ). The second was in central UT southeast of Salt Lake City (Nebo; Latitude:  $\sim 39.5^\circ\text{N}$ ; July average temperature  $24.1^\circ\text{C}$ ; January average temperature  $-2.0^\circ\text{C}$ ). The third study area was in the southwest corner of the state near St. George, UT (Pine Valley; Latitude:  $\sim 37.3^\circ\text{N}$ ; July average temperature  $30.4^\circ\text{C}$ ; January average temperature  $5.1^\circ\text{C}$ ). The two northernmost sites are located at the interface between lower elevation valleys ( $\sim 1350$  m) with a significant urban footprint and the adjacent mountainous regions (elevation up to 3100 m). For additional information on study sites, see Appendix S1.

### Study population

Mule deer in our study area are generally migratory, with most individuals undertaking relatively short migrations of approximately 25 km between distinct seasonal ranges [36]. Some individuals remain residents year-round. Deer typically spend winters at low elevations (overall mean = 1722 m, Cache = 1902 m, Nebo = 1758 m, Pine Valley = 1529 m), often at the edge of the mountains where they are more often near human infrastructure. Deer then migrate upwards into the mountains in summer (overall mean elevation = 2168 m, Cache = 2246 m, Nebo = 2266 m, Pine Valley = 2040 m).

### Animal handling and collaring

Between November 2021 and April 2024, adult (1 + year) female mule deer were captured via a net gun fired from a helicopter, physically immobilized, and brought to staging areas where they were processed (see [37] for details; Brigham Young University IACUC protocol: #150110). Deer were fitted with GPS radiocollars (Model G5-2DH, Advanced Telemetry Systems Inc., Isanti, MN, USA, 700 g). Most of the collars recorded fix rates every two hours. A few collars collected data every 30 min, but these data were rarefied to only retain one fix every two hours to match the temporal resolution of the other collars. Deer were aged based on tooth wear patterns [38] and were assessed for body condition score using mule deer-specific palpation methods [39]. Individuals in our study (equipped with biologgers, see below) represented

a sample of individuals collared for state-wide monitoring efforts. Focal animals selected for instrumentation represented a random sub-sample from the larger population of deer captured for the broader study.

### **Subcutaneous biologgers**

The recent development of subcutaneous physiological biologgers allows novel insight into animal physiological energetic expenditure during movement. We fit focal animals (Cache = 11, Nebo = 11, Pine Valley = 15; total  $n = 37$ ) within this broader study with biologgers (Medtronic Inc., Reveal Linq II, 1.2 cc; 4.0 mm  $\times$  7.2 mm  $\times$  44.8 mm; 2.4 g). Biologgers were implanted subcutaneously using aseptic techniques above the left shoulder by a veterinarian (Utah State IACUC protocol: #13045). The biologgers were developed for human use but modified by Medtronic to collect data more frequently than in human patients to be able to link heart rate to environmental conditions and movement of individuals at higher temporal resolution [16]. Biologgers monitored cardiac (electrocardiogram - ECG) activity continuously and provided a mean heart rate every two minutes. Data were retrieved by transcutaneous telemetry (CareLink Model 2090 Programmer with software Model SW007, Medtronic Inc., Minneapolis, MN; [16]) when individuals were recaptured in late February or March and late November or December of each year.

### **Environmental/landscape variables**

Elevation was quantified using digital elevation data at 1/3 arc-second resolution ( $\sim 10$  m) from the US Geological survey (<https://apps.nationalmap.gov/download/r/>). Using these data, we created layers of slope and terrain aspect using package *raster* in R [40]. We converted terrain aspect to the solar-radiation aspect index (trasp; [41]), which outputs a value of 1 for land oriented in typically warmer and drier south-southwesterly facing slopes and 0 for land oriented in a north-northeasterly direction which are typically wetter and cooler. We quantified landcover using data from the U.S. National Land Cover Database (NLCD) at a 30 m resolution. We used the 2021 version of the data as it best matched the timeframe of our animal data. We only quantified forest as it was the only significant landcover type in our study area besides shrub/scrub which otherwise dominated in our study area and served as the reference category against forest. To quantify snow depth, we used data from the Snow Data Assimilation System (SNODAS) from the National Snow and Ice Data Center (<https://nsidc.org/data/g02158/versions/1>). These data have a daily temporal resolution and a 1 km<sup>2</sup> spatial resolution. We used data from the PRISM climate group (<https://www.prism.oregonstate.edu>) to define minimum and maximum temperature at

each location at a daily scale with a spatial resolution of  $\sim 4$  km  $\times$  4 km.

To quantify high-quality forage for mule deer, we estimated the instantaneous rate of green-up (IRG; [3]). IRG is defined as the rate of change of a remotely sensed proxy for plant growth through time. While remotely sensed proxies for primary productivity represent imperfect measures, areas with high IRG values have been shown to correlate with increased N: C ratios in plant shoots on bison (*Bison bison*) grazing areas [42] and in increased fat gain in migrating elk (*Cervus canadensis*; [43]). As such, IRG is frequently used as a proxy for high-quality forage for herbivores [44–47]. IRG was calculated as the instantaneous rate of change of normalized difference vegetation index (NDVI) values at a specific location (for further details on processing IRG, see Appendix S2).

### **Defining steps and seasons**

We quantified animal movement data as “steps,” that is, attributes of a line between successive GPS fixes, to which we associated mule deer heart rate data. Within each 2-h step, we took the average of the 2-min average heart rates to define an overall average heart rate associated with that step. We also used migration dates to define summer and winter seasons for our analyses (see Appendix Table S2 for seasonal dates).

### **Seasonal variation in heart rate**

We quantified the differences in heart rate across the winter and early/late summer seasons. Peak parturition in mule deer in Utah occurs around June 16th, and the most intensive period for energy requirements for lactation typically occur in the first month. As such, early summer was defined as starting after spring migration until July 15th (the period of late gestation through parturition and intensive lactation) and late summer from July 16th until fall migration (the period when thermal stress would be the greatest). We took the average heart rate for each individual/year in each season (early summer, late summer, and winter), tested for differences in these seasonal averages using a Tukey test, and plotted the results as density distributions for each population. For all subsequent analyses, we combined both early and late summer into a single summer category.

### **Defining the energy landscape**

To account for behavioural variation in movement, we first fit a two-state hidden Markov model (HMM) to step lengths and turning angles derived from GPS data, where we expected one state to represent slower, less directed movement (interpreted post hoc as “encamped” or locally active behaviour) and the other to represent faster, more directed movement (interpreted as “travelling”) [48]. We emphasize that these states are latent variables inferred

from movement characteristics and therefore represent imperfect proxies for behavioural states.

We then included movement state and its interaction with step length in our heart rate models to test the hypothesis that the energetic consequences of movement differ between behavioural modes. Specifically, we predicted that increases in movement from a resting or locally active state would result in a disproportionately large increase in heart rate relative to additional movement once an individual is already travelling, consistent with costs associated with posture, initiation of movement, and local foraging activity. This formulation allows both the intercept (baseline heart rate) and the slope of the relationship between step length and heart rate to vary between latent movement modes.

We note that an alternative approach would be to model a non-linear relationship between step length and heart rate (e.g., using a quadratic term). However, such an approach assumes a smooth, continuous relationship with movement rate and does not allow for discrete differences in energetic costs between behavioural modes. Our use of a state-based formulation was therefore motivated by our interest in testing state-dependent energetic relationships, rather than solely capturing non-linearity in the effect of step length.

We extracted heart rate and all covariates predicted to influence heart rate to each step (Appendix S3). To define the energy landscape for mule deer in these populations, we fit separate general linear models for each individual/season using the following form:

$$y_i = \beta_0 + \beta_1 \text{StepLength}_i + \beta_2 \text{State}_i + \beta_3 (\text{StepLength}_i \times \text{State}_i) + \beta_4 \text{Elevation}_i + \beta_5 \text{Gain}_i + \beta_6 \text{Forest}_i + \beta_7 \text{trasp}_i + \beta_8 \text{Temp}_i + \beta_9 \text{Snow}_i + \epsilon_i \quad (1)$$

where  $y_i$  = estimated heart rate. Note that snow was estimated in winter models only. Forest was coded as a binary variable indicating whether the animal was located in forested habitat, and state was also coded as a binary variable (encamped = 0, travelling = 1). In this model, the index  $i$  refers to individual time steps (observations within an individual). Given that the step length data and elevation gain spanned several hundred meters, we opted to put both on a scale of 100s of meters (e.g., m/100).

Due to collinearity with elevation gain, we excluded slope from our models. We assumed thermal stress would be related to high temperatures in the summer and extreme cold in winter; therefore, we used maximum daily temperature in the summer models and minimum daily temperature in the winter models. We also included an interaction between movement state and step length to determine how step length affected heart rate as a function of movement behavioural state. We included

movement state and its interaction with step length to test whether the relationship between movement and heart rate differed between behavioural modes. We predicted that step length would have a stronger effect on heart rate for animals in an encamped state, reflecting the energetic costs associated with posture and local movement relative to resting [49, 50]. In contrast, we expected additional movement to have a smaller incremental effect on heart rate once animals were in a travelling state. We therefore included state and its interaction with step length rather than modelling this relationship solely as a continuous non-linear function of movement rate.

Elevation and temperature were mean-centered and scaled (elevation at the population-level within a season; temperature at the individual/season scale), but step length and elevation gain were not. This was done so that the intercept in each individual model can be interpreted as the average heart rate at the average population elevation and individual temperature, for an animal that is not travelling, outside of forest, with no snow on the ground, on a north-northeasterly aspect.

To estimate population-level means and associated uncertainty for each iSSA covariate, we used a case resampling bootstrap applied to individual-level coefficient estimates. For each combination of season, population, and covariate, we resampled deer-season beta estimates with replacement 1,000 times and computed the mean at each iteration using the R package “boot” [51, 52]. We report the mean of the original sample as the population-level estimate and derived 95% confidence intervals from the empirical bootstrap distribution (basic bootstrap method). This two-stage approach fits models at the individual level and bootstraps to population-level inference, which avoids parametric assumptions about the distribution of individual responses and propagates individual-level variation into population estimates [53]. To quantify population-level trends, we bootstrapped the estimates of each covariate by season/population and extracted the mean and 95% confidence interval using R package *boot*. We also ran these models as mixed effects models for each season/population with individual mule deer fit as a random intercept using package *lme4* [54].

### Demographic/movement model

We were also interested to see if variation in average heart rate could be explained by individual-level movement, demographic, or body condition parameters. For our winter models, explanatory variables included animal weight, body condition score, age (assessed at capture in December or late November), and average seasonal movement rate. For the summer models, we included weight, body condition score (as assessed at the start of the previous winter), the change in body condition over winter, and mean seasonal movement rate. Mean seasonal movement rate was calcu-

lated as the mean of step length divided by the time between GPS locations for steps in that season. We then fit, for each season, a model predicting the intercept of each individual's seasonal average heart rate. For the winter model:

$$y_i = \beta_0 + \beta_1 \text{Weight}_i + \beta_2 \text{Body Condition}_i + \beta_3 \text{age}_i + \beta_4 \text{Movement Rate}_i + \epsilon_i \quad (2)$$

And for the summer model:

$$y_i = \beta_0 + \beta_1 \text{Weight}_i + \beta_2 \text{Body Condition}_i + \beta_3 \Delta \text{body condition over summer}_i + \beta_4 \text{Movement Rate}_i + \epsilon_i \quad (3)$$

where  $y_i$  equals the intercept of the individual heart rate model from each season. In contrast to Eq. (1), in Eqs. (2) and (3).  $i$  indexes individual  $\times$  season combinations. Prior to fitting models, we tested for issues with collinearity by examining variance inflation factors and found all variables to have a VIF less than 3.

### Step selection functions

To test the influence of the energy landscape on mule deer movement we used step selection functions (SSFs) [55, 56] developed for each population in the summer to test how mule deer resource selection is influenced by both energetic costs and forage availability. To generate our random steps to compare with our observed steps in the SSF, we simultaneously sampled both the step lengths and turning angles from a random step within our data (drawn from all individuals within the focal season and only from the distribution of points in the same movement state) and generated the resultant random step/end point. We generated a total of 10 random locations for each used step. We then extracted, for each step, all environmental covariates used to fit our energy landscape plus the instantaneous rate of green-up (IRG) layer described above. We then predicted the heart rate of mule deer for all available steps (we used the actual/observed heart rate for used steps) using each individual's energy landscape model. We then fit step selection functions for each population in the summer. The model included predicted energy cost (heart rate) of the step, IRG, and their interaction as we hypothesized deer may be more likely to take "costlier" energetic steps if they were associated with forage rewards. Models were fit using the *clogit* function in R package *survival* [57]. Each step and associated random steps were fit as a conditional "stratum" in the model. Responses were then plotted as the log of the relative selection strength, comparing selection for different values of predicted heart rate and forage availability against a step at the mean of both [58].

We were also interested in quantifying differences in green-up phenology across our three study sites to

contextualize the trade-offs in energy expenditure and forage selection across study sites. We were specifically interested in the overall greenness of each study area to quantify forage availability, and the speed at which green-up occurred, as rapidly maturing vegetation tends to be higher quality but for a shorter period of time. To do so, we generated a 95% minimum convex polygon around all GPS locations for each population in each summer and then sampled 10,000 random locations within each population's range. We then extracted the mean and standard deviation of NDVI values for each day throughout the year, as well as an annual measure of spring speed. This measure was based on the 2nd derivative of the time series of NDVI, and therefore represented the number of days between when green-up was accelerating most quickly (maximum value of the 2nd derivative), to when the rate of green-up was decelerating the fastest (minimum value of the 2nd derivative).

### Results

Our sample included data from 37 unique adult female mule deer, with 52 ID-seasons in winter, and 26 ID-seasons in summer. Across all three of our study populations, the overall mean of individual mean heart rate was lowest in winter ( $\bar{x} = 72.8$ ,  $SD = 11.8$ ) and higher in early summer ( $\bar{x} = 88.4$ ,  $SD = 9.0$ ) and late summer ( $\bar{x} = 82.8$ ,  $SD = 10.4$ ). We found a significant effect of season on mean heart rate (ANOVA:  $F_{2,101} = 19.76$ ,  $p < 0.001$ ). Tukey's HSD post hoc tests revealed that mean heart rate was significantly lower in winter compared to both early summer (estimate =  $-15.55$ ,  $SE = 2.60$ ,  $p < 0.001$ ) and late summer (estimate =  $-9.89$ ,  $SE = 2.60$ ,  $p < 0.001$ ). The difference between early summer and late summer was not statistically significant (estimate =  $-5.67$ ,  $SE = 3.00$ ,  $p = 0.146$ ). There was some variation among populations with individuals in the Nebo population generally having the highest overall heart rate (Fig. 1).

The two-state HMM identified movement modes that were consistent with our expectations, with one state characterized by shorter step lengths and less directed movement (interpreted as "encamped") and the other by longer, more directed steps (interpreted as "travelling"; Figure S2). Deer movements, as measured by increased step length, exhibited an increased heart rate across all populations/seasons with increased distance travelled, and this effect was stronger in winter than in summer, and this seasonal contrast appeared strongest in the Cache population (Fig. 2a), although we did not formally test between-season differences at the population level in this analysis (Fig. 2a). When individual deer were in a travelling state (as estimated by our hidden Markov models), heart rates were also higher (Fig. 2b). However, we also found a significant negative interaction between the effect of step length and the travelling state on heart rate

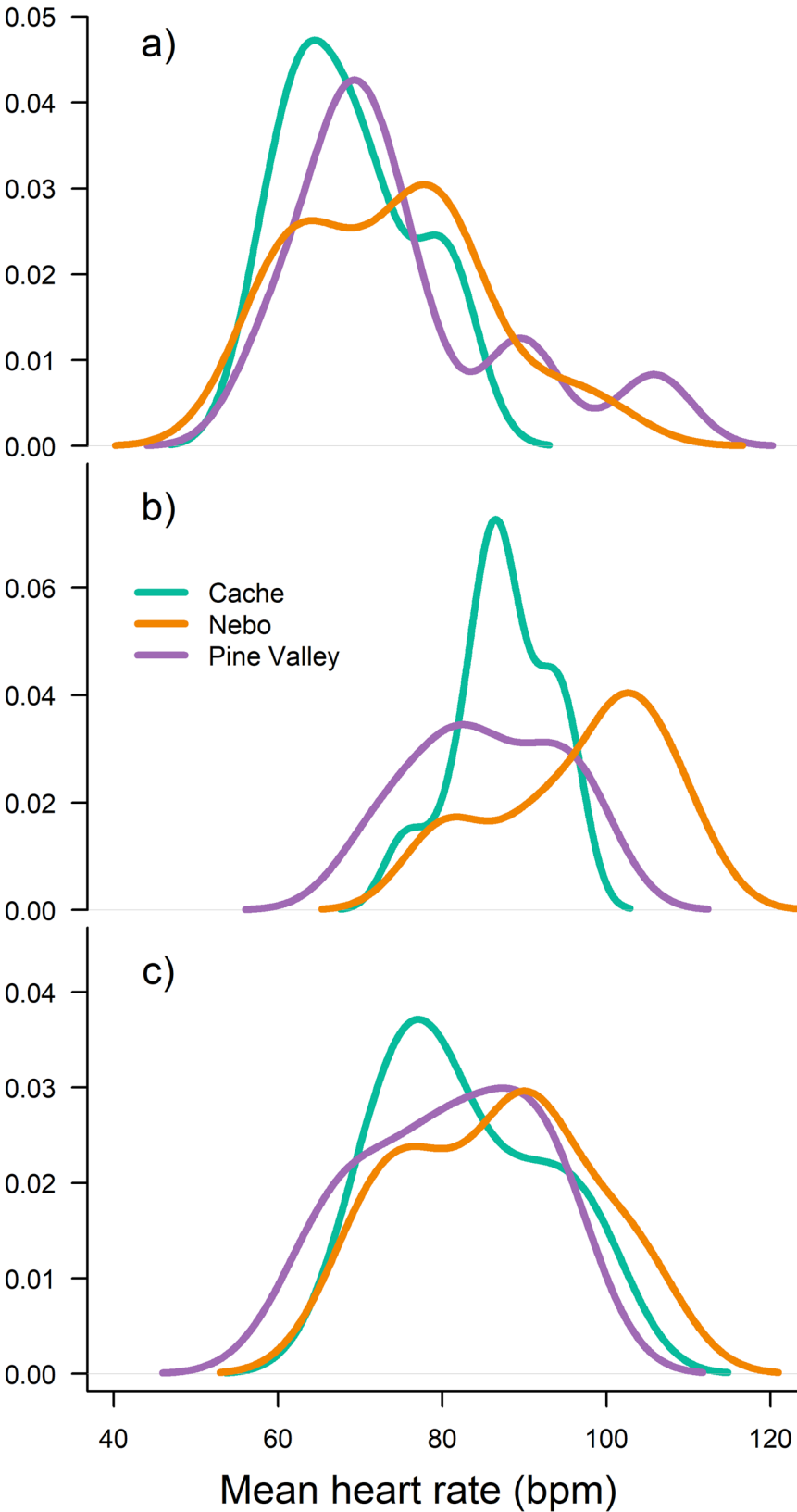


**Fig. 1** Density distribution of individual mean seasonal mule deer (*Odocoileus hemionus*,  $n=37$ ) heart rate by population in winter (a), early summer (b) and late summer (c) in Utah, USA, 2021–2024. Winter and summer are defined by seasonal migration dates, with the cut-off between early and late summer occurring on July 15th

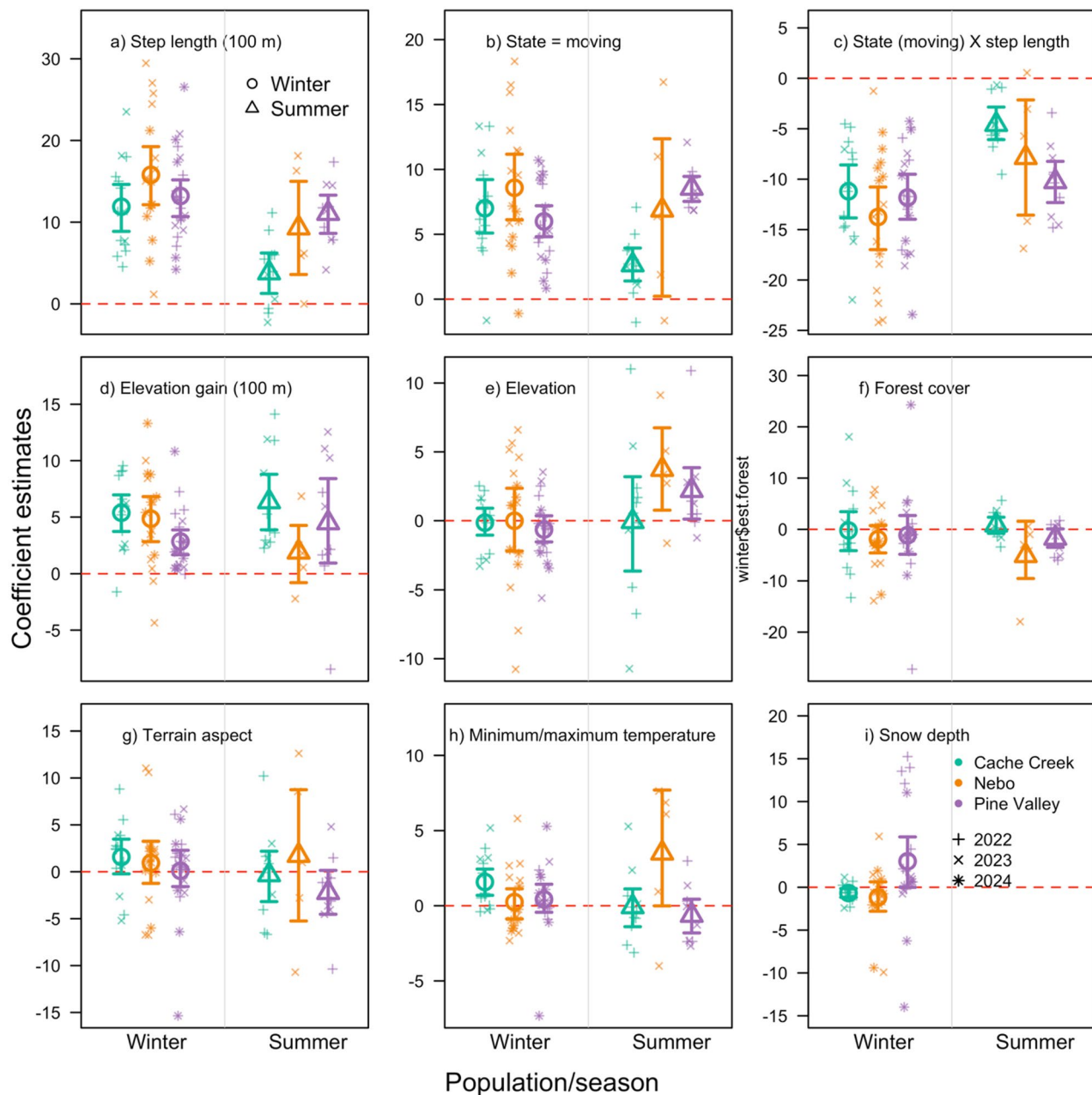


**Fig. 2** Parameter estimates for individual-level models of energy landscapes of mule deer (*Odocoileus hemionus*,  $n = 37$ ) in Utah, USA, 2021–2024. Small symbols represent individual beta coefficient estimates for the effect of each parameter on heart rate (year is represented by symbol type), large symbol and lines represent the bootstrapped mean estimate of the beta coefficient estimates along with the 95% confidence intervals. Circles (left side of each panel) represent data for winter, and triangles (right side of each panel) represent data for summer. Each population is represented by a different color

(Fig. 2c). Taken together, this suggests that increasing movement speed has a strong cost on deer who were not travelling large distances, but that this effect is lessened for individuals undertaking longer displacements (in a travelling state), in which the increased rate of energy expenditure is primarily a binary one (e.g., an effect based on movement state not on speed). Coefficient estimates are also presented in Table S3, along with the results from our mixed effects approach (Table S4).

We also found that deer movements resulting in elevation gain resulted in a significantly elevated heart rate, although this relationship was not significant for Nebo in summer (Fig. 2d). Absolute elevation only affected heart rate for the Nebo and Pine Valley populations in summer (Fig. 2e). Forest cover and terrain aspect did not influence deer heart rate at the population level, and temperature only drove intra-seasonal variation in heart rate in the winter for the Cache population (Fig. 2f-h). Snow depth

**Table 1** Model outputs from predictive models of heart rate for mule deer (*Odocoileus hemionus*,  $n = 37$ ) in Utah, USA highlighting individual variation in heart rate intercept in summer and winter as a function of individual demographic and body condition variables

| Parameter                               | Estimate | 95% CI          | Sig. |
|-----------------------------------------|----------|-----------------|------|
| <b>Intercept of heart rate - winter</b> |          |                 |      |
| Intercept                               | 13.932   | -43.349, 71.214 |      |
| Weight                                  | 1.558    | 0.455, 2.660    | **   |
| Body condition score                    | -5.234   | -10.209, -0.259 | *    |
| Age                                     | -2.592   | -5.343, 0.160   | .    |
| Mean step length                        | -0.147   | -0.358, 0.064   |      |
| <b>Intercept of heart rate - summer</b> |          |                 |      |
| Intercept                               | 79.896   | 14.511, 145.282 | *    |
| Weight (previous winter)                | 0.005    | -1.249, 1.259   |      |
| Change in body condition over summer    | 1.508    | -3.409, 6.426   |      |
| Body condition (previous winter)        | 2.905    | -2.967, 8.776   |      |
| Mean step length                        | -0.065   | -0.280, 0.149   |      |

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

was positive but not significant in predicting heart rate for the Pine Valley population (Fig. 2i). Mule deer in our study had an average weight of 62.3 kg (SD=6.8). The mean body condition score (5-point scale) was 3.43 (SD=1.17). The average estimated age of deer in our sample was 5.55 years (SD=2.42). In winter, heavier deer had a higher average heart rate as defined by the intercept of the individual energy landscape model (Table 1; Fig. 3). In contrast, the effects of body condition

score and age on mean heart rate were both estimated to be negative, though age was not statistically significant. This model had an adjusted  $R^2$  of 0.125. We found no significant factors influencing heart rate intercept in summer. Finally, our step selection functions revealed an important interaction between the predicted heart rate of a step and the forage benefit of the end point of the step in the summer. Across all populations, individuals were more likely to take steps that resulted in increased heart rate when the end point had higher quality forage (Fig. 4g-i). This response was strongest in Cache and Nebo, where green-up occurred faster compared to Pine Valley, the more southern site (Fig. 4a-f). These results indicate that mule deer were increasingly willing to accept energetically costly steps when those steps were associated with higher forage rewards (dark shades in panels g-i). Conversely, when forage reward was low, selection declined with increasing energetic cost (light shaded lines). Thus, predicted energetic cost acted as a deterrent to choice of step when IRG was low, but this deterrent weakened near the median value of IRG, and the relationship reversed when IRG was high, consistent with a trade-off between movement cost and forage benefit.

Discussion

Correlating physiological responses of animals to environmental conditions and landscape features is important to elucidate animal habitat selection and therefore resilience to change [6]. Using physiological biologgers, we found mule deer in Utah had higher heart rates in summer than in winter, likely due to limited food intake

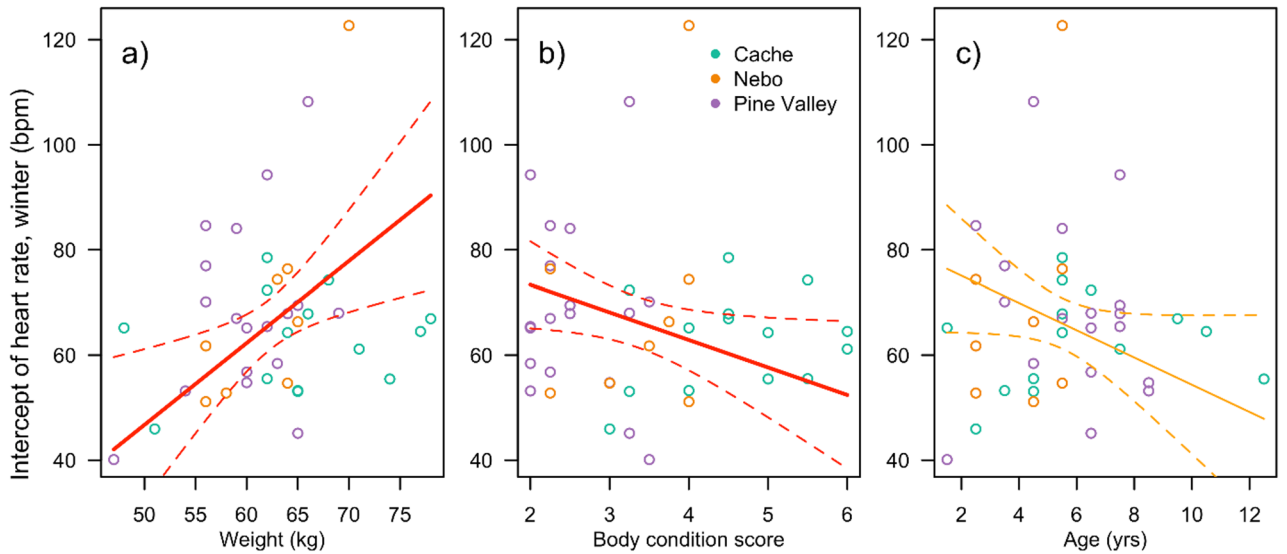


**Fig. 3** Effect of demographic/movement attributes of mule deer (*Odocoileus hemionus*,  $n = 37$ ) on average heart rate (intercept of individual heart rate models) in winter from individual-level energy landscape models. Plots represent relationships that were significant at the  $\alpha = 0.05$  level (red regression lines) and one relationship that was negative but only significant at the  $\alpha = 0.10$  level (orange regression line)

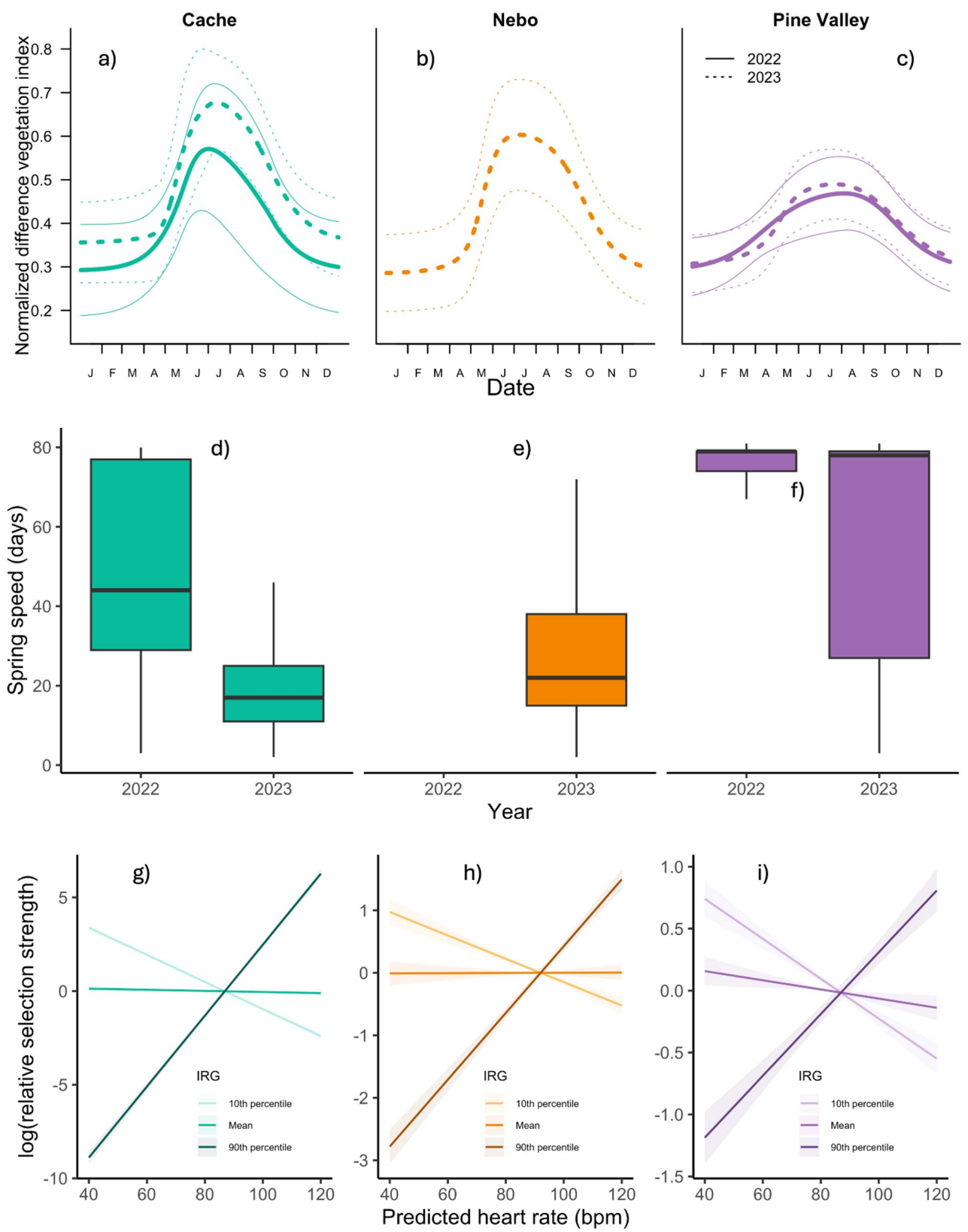


**Fig. 4** (See legend on next page.)

(See figure on previous page.)

**Fig. 4** Plant phenology across years/study areas and results from individual-level step selection functions of mule deer (*Odocoileus hemionus*,  $n=37$ ) in Utah, USA, 2021–2024. Panels **a–c** show the annual curve of mean NDVI values (thick lines) plus/minus one standard deviation (thin lines). Solid lines are data from 2022 and dashed lines are data from 2023. Panels **d–f** show the speed of spring green-up across the study areas. Values represent the number of days between when green-up speed is increasing fastest (maximum of the 2nd derivative of the time series of NDVI at a location), and when green-up speed is decreasing the fastest (minimum of the 2nd derivative of the time series of NDVI at a location). Data for panels **a–f** are based on sampling 10,000 locations within a 95% minimum convex polygon of all animal locations within each study area for each year. Green-up occurs at a slower rate in the Pine Valley study area (**c, f**). Panels **g–i** represent the log of the relative selection strength for predicted heart rate of used/available steps from the step selection function at low, mean, and high levels of high-quality forage (instantaneous rate of green-up; IRG). Selection is relative to selection for a step at the mean value of both IRG and predicted heart rate. Lines show the relationship between predicted step heart rate and relative selection strength at fixed IRG values. Positive slopes at high IRG (dark lines) indicate that deer were more willing to accept energetically costly steps when the expected forage reward was high

in winter [25, 26] and increased costs related to reproduction in spring [35] (Fig. 1). We also found that heart rate increased as a function of movement state more so than movement speed, particularly when comparing animals in an encamped state versus those moving locally at small scales (e.g., for foraging; Fig. 2a–c). Our analysis of the heart rate/landscape interaction (e.g., the energy landscape) showed that deer had increased energy costs associated with longer movements and when climbing uphill. We were also able to describe important individual-level relationships between body condition, weight, and age on heart rates in winter. Finally, our results suggest important variation among populations, outlining that energy landscapes are both individual- and study-area specific.

Our results suggest that mule deer experience seasonal fluctuations in heart rate related to intake of higher quality food in much the same way as other ungulate species such as moose and reindeer [24, 25]. Notably, this included the Pine Valley population which would have experienced much milder winter conditions. This supports the notion that such variation in heart rate may also be endogenously entrained and not linked solely to food intake [27]. Relative to winter, we found elevated heart rates in both early and late summer; we note that in addition to increased metabolism, energy demands for reproduction (late gestation, parturition and lactation) also likely influence this result, particularly in early summer [59].

Although step length had a strong effect on mule deer energy landscapes, a strong negative interaction between deer in a travelling state and step length suggests that this effect is most pronounced for individuals that are encamped and moving relatively slowly (e.g., moving relatively minimally to forage). This suggests a significant difference in heart rate between behavioural states (namely between encamped versus small movements presumably for local foraging) which may be more important in determining energetic costs than the absolute distance travelled for individuals in a travelling state. That is, changes in body posture or simply standing to move locally and forage appear to increase the energetic burden for mule deer compared to being at

rest. This increase could be related to both movement/posture, as well as due to food intake altering heart rates due to digestion. Resting animals may also have lower heart rates due to less forage intake and consequently less additional heart rate burden for digestion [26]. Periodic disturbances (e.g., by humans), even if it does not cause animals to flee but merely to stand and be vigilant, could have an important metabolic cost. Increased energy costs related to factors that disrupt rest bouts (e.g., human activity) and increase movement could influence fitness by resulting in additional energy expenditure and non-optimal movement and space use [60, 61]. Interestingly, these results indicate a relatively minor additional cost to increased movement rate once an animal is in a travelling state, suggesting that travelling at a slow pace could be more costly than travelling at an intermediate pace due to the postural cost of movement which results in increased costs simply related to being in a movement state as opposed to a resting state for longer timeframes [50]. This may be the energetic function underlying the use of stopover points [62] during longer migrations, whereby relatively rapid movement over long distances punctuated by extended rest and refueling may be more efficient overall than consistent but slower/meandering migrations. Conversely, however, excessive stop-and-go movements could incur increased energetic costs as could there be a cost of actual transitions between movement modes, however we were not able to quantify this at the scale that we examined.

Our findings outline the fact that energy landscapes vary by individual, suggesting that there is not a single generic energy landscape for mule deer. This suggests that deer may adapt or acclimate their physiology to the conditions they experience, which in turn determines their energy landscape. Such individual differences are important as they can provide a buffer against changing environmental conditions [63]. Notably, some individual variation was explained by weight and body condition. Individuals in poorer body condition had higher average heart rates in winter when controlling for movement step length (Fig. 3). This may indicate a feedback loop for individuals in poor condition, in which they must expend even more energy in winter simply on basic metabolism

(perhaps in relation to maintaining body temperature). It is also important to acknowledge the fact that the relationship between heart rate variation and  $O_2$  consumption can also vary by individual, and so some variation in energy landscapes or average heart rate may simply be driven by intrinsic individual differences that may not be easily measurable or at least immediately apparent [64]. Finally, heart rate responses will also vary due to stressful events (e.g., encounters with predators or road crossings) which were not quantified in our study but could play an important role in regulating heart rate. Regardless, the variation in heart rate responses across individuals highlights the fact that energy landscapes, whenever possible, should be derived from direct observations of animals in the wild. While other proxies such as overall movement or dynamic body acceleration provide important inference for energy expenditure [12], accounting for intrinsic individual variation is difficult and requires calibration or hierarchical models. As such, while measuring energy expenditure in a lab setting (e.g., via measuring  $O_2$  expenditure on a treadmill [8]) and extrapolating to the field represents highly useful information, direct measurements of heart rate allow for the integration of additional factors unrelated to movement such as autonomic, thermoregulatory, and digestive loads.

Energy landscapes provide a unique opportunity to quantify dispersal and migration corridors from a new lens. Many studies quantify the potential for animal population dispersal using habitat selection tools such as step selection functions [65], or habitat suitability models combined with least-cost path analysis [66] or circuit-based models [67, 68]. Other models, such as spatial absorbing Markov chains, allow for the inclusion of additional factors such as mortality risk and habitat quality in connectivity modelling [69]. Such dispersal models could be improved by incorporating energy landscapes at the population level as cost surfaces for animal dispersal, which could have significant impact when assessing population distributions and dispersal capacity, and therefore habitat connectivity. Likewise, energy landscapes could also be used to map migration corridors [70], both in terms of quantifying current corridors as well as quantifying potential future corridors if perturbations from climatic conditions or human development alter current routes.

Our results show compelling evidence that the energy landscape modifies mule deer movement and foraging behaviour. Notably, across all populations, deer in the summer were more willing to take steps that increased their heart rate if those steps ended in areas with high-quality forage. That is, when forage quality at the end of a step was high, deer were more likely to use steps that are predicted to increase heart rate and therefore energy expenditure. We emphasize that the positive relationship

between predicted heart rate and log-RSS at high IRG should not be interpreted as selection for energetic expenditure itself; rather, it indicates that deer tolerated or accepted higher energetic costs when those costs were offset by improved forage conditions, which was not observed when forage quality was low, in which case deer selected to conserve energy by selecting for steps with a lower energetic cost. This outlines the importance of the energy landscape as a key, but often overlooked, dimension of optimal foraging theory [71]. As such, the true influence of energy landscapes on individual movement appears to be mediated by the reward, or food landscape [3, 4]. Here, IRG is interpreted as a remotely sensed index of phenological change that is most informative during the green-up/growing period, rather than a direct measure of forage quality across all cover types. In heterogeneous mountain systems, IRG/NDVI-based signals can also reflect non-forage vegetation phenology (e.g., tree leaf-out) and be influenced by background reflectance and illumination conditions (e.g., soil/rock, snow, and shade [72]). Green-up occurred much more quickly in the northern sites compared to the southern site (Fig. 4a-f). The result is that forage is likely of higher quality but for a much shorter period of time in the more northern sites compared to the southern site, which would likely increase the value of selection for areas of peak green-up in sites characterized by intense, brief growing seasons [73]. An alternative explanation to these findings is that heart rate increases as animals increase selection for higher quality forage as higher intake of higher quality food increases heart rate to facilitate digestion [26]. As climate continues to change and the West becomes hotter and more arid with less predictable precipitation, the distribution of forage resources is likely to shift [74]. If high-quality forage shifts to even higher elevations, the physiological cost of exploiting these resources could increase, which could be exacerbated by increased thermal stress. All of this suggests potential changes in the distribution and recruitment patterns of mule deer in the mountain West.

As with any study that relies on nascent technological advances, our study was somewhat limited in scope owing to a relatively small sample size and a geography that spanned a single US state. Despite this, we were able to test relationships between heart rate and movement ecology across a breadth of ecological contexts within the state of Utah. We also did not detect a strong influence of temperature intra-seasonally on deer heart rates, however micro-climate effects may have provided more evidence of a temperature effect compared to the broader spatial scales at which temperature was evaluated in our study. Further studies across species and considering micro-climatic effects will strengthen the important inferences we have found in the present study.

Our use of HMM-derived movement states introduces some caveats and limitations. The inferred states represent latent classifications based on movement characteristics and therefore do not correspond perfectly to discrete behavioural states, with some overlap in movement distributions between states. In addition, we relied on the most likely (Viterbi-decoded) state sequence and did not propagate uncertainty in state assignment into downstream models, which may lead to overconfidence in estimated state effects. Finally, while we modelled linear relationships between step length and heart rate within states, additional non-linear relationships may exist within movement modes. As such, the state-based formulation should be interpreted as capturing broad differences between movement modes rather than precise behavioural or physiological thresholds.

New and emerging technologies have the capacity to revolutionize the questions ecologists can ask to inform our knowledge on the hidden lives of animals. The advent of GPS collars and the ability to quantify animal movement over relatively short timescales opened a world of movement-related questions that hitherto could not be asked [31]. Biologgers also have the capacity to unlock a suite of novel questions on the ecophysiology of animals in the wild, by linking movement, habitat selection, and physiology [75]. For example, heart rate can be used to quantify stress responses to anthropogenic features or to the risk of predation to refine landscape of fear models. Our models did not directly examine how acute and contextual stressors from predators and roads affect heart rate as a measure of acute stress. Heart rate variability can also be used as a measure of chronic stress. When linked with measures of survival and reproductive success, heart rate variability could provide researchers new insight into the physiological drivers of fitness.

## Conclusion

Our study revealed energy landscapes for mule deer across a climatic gradient and outlined specific drivers of heart rate in deer related to both movement and the environment as well as intrinsic factors such as body condition. As climate continues to change, many populations will face increased stressors as environments shift to become less optimal. Such perturbations will also result in changing costs and benefits associated with travel through the landscapes that animals inhabit. As such, the use of biologgers provides novel opportunities for ecologists to acquire physiological data from wildlife in the field. This will provide researchers the means to elucidate animal physiological responses to their environments and changes therein in situ, and therefore represent powerful emerging tools in wildlife research and management.

## Abbreviations

|      |                                             |
|------|---------------------------------------------|
| IRG  | Instantaneous rate of (vegetation) green-up |
| NDVI | Normalized difference vegetation index      |
| SSF  | Step selection function                     |

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40462-026-00654-w>.

Supplementary Material 1

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## Author contributions

MPL, MAD, and GW conceived of the study and generated hypotheses and predictions. MPL wrote the manuscript. TGL provided biologgers and support for biollogger technology. Data were collected by MPL, MAD, DCS, VS, KRH, KRM, RTL, and BRM. Manuscript was revised and edited by MPL, MAD and GW. All authors read and provided feedback on earlier drafts.

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## Data availability

All data and code for this manuscript is available on Zenodo at (<https://doi.org/10.5281/zenodo.13732583>). Due to concerns around poaching of deer, spatial locations have been anonymized (mean-centered).

## Declarations

### Ethics approval and consent to participate

All animal capture and handling was approved by University Animal Care guidelines, Brigham Young University IACUC protocol: #150110. Biologgers were implanted subcutaneously using aseptic techniques above the left shoulder by a veterinarian (Utah State IACUC protocol: #13045).

### Consent for publication

Not applicable.

### Competing interests

The authors declare no competing interests.

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