

Asynchronous vegetation phenology enhances winter body condition of a large mobile herbivore

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Abstract Understanding how spatial and temporal heterogeneity influence ecological processes forms a central challenge in ecology. Individual responses to heterogeneity shape population dynamics, therefore understanding these responses is central to sustainable population management. Emerging evidence has shown that herbivores track heterogeneity in nutritional quality of vegetation by responding to phenological differences in plants. We quantified the benefits mule deer (*Odocoileus hemionus*) accrue from accessing habitats with asynchronous plant phenology in north-west Colorado over 3 years. Our analysis examined both the direct physiological and indirect environmental effects of weather and vegetation phenology on mule deer winter body condition. We identified several important effects of annual weather patterns and topographical variables on vegetation phenology in the home ranges of mule deer. Crucially, temporal patterns of vegetation phenology were linked with differences in body condition, with deer tending to show poorer body condition in areas with less asynchronous vegetation green-up and later vegetation onset. The direct physiological effect of previous winter precipitation on mule deer body condition was much less important than the indirect effect mediated by vegetation phenology.

Additionally, the influence of vegetation phenology on body fat was much stronger than that of overall vegetation productivity. In summary, changing annual weather patterns, particularly in relation to seasonal precipitation, have the potential to alter body condition of this important ungulate species during the critical winter period. This finding highlights the importance of maintaining large contiguous areas of spatially and temporally variable resources to allow animals to compensate behaviourally for changing climate-driven resource patterns.

Keywords Mule deer · Spatial heterogeneity · Temporal heterogeneity · Western Colorado · Climate change

Introduction

Changing climatic patterns are altering the phenology of diverse taxa and the resources on which they depend around the globe (Parmesan 2007; Thackeray et al. 2010; Haenel and Tielboerger 2015). For large-bodied herbivores, the phenology of vegetation is a critical determinant of diet quality (Van Soest 1994; Crawley 1983) that has been linked to diet choice, individual movement and performance (Hjeljord et al. 1990; Albon and Langvatn 1992; Herfindal et al. 2006; Hebblewhite et al. 2008; Mysterud et al. 2008; Hamel et al. 2009; Martinez-Jauregui et al. 2009; Bischof et al. 2012; Nielsen et al. 2012; Singh et al. 2012; Giroux et al. 2014; Monteith et al. 2014), as well as population processes such as survival, reproduction and density dependence (Mysterud et al. 2002; Wang et al. 2006; Pettorelli et al. 2007; Wittemyer et al. 2007; Middleton et al. 2013). The ability of landscapes to support herbivores is ultimately limited by the total amount of aboveground net primary production (ANPP) available for

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consumption (McNaughton et al. 1989; Cebrian and Lartigue 2004). However, when spatial variation in temperature, nutrients, or moisture results in spatially asynchronous pulses of plant growth (Kudo 1991), herbivores are able to prolong the period during which they have access to forage of peak nutritional value. Emerging evidence suggests that limits set by ANPP are modified by the spatial pattern and timing of plant growth. In particular, there is evidence that heterogeneity in plant communities expressed over space, particularly heterogeneity that induces variation in time by influencing plant phenology, offers fundamentally important nutritional benefits to foraging herbivores that enhance the performance of individuals and their populations (Pettorelli et al. 2007; Hebblewhite et al. 2008; Mysterud et al. 2008; Searle et al. 2010; Middleton et al. 2013; Giroux et al. 2014; Hurley 2014; Iversen 2014). For instance, fine-scale dynamics of vegetation green-up across landscapes may determine the length of time during spring when high-quality forage is available for ungulates. This means that access to heterogeneity can be a critically important feature of habitats for mobile herbivores (Owen-Smith 2004; Fryxell et al. 2005; Hobbs et al. 2008; Searle et al. 2010). If access to heterogeneity is limited by habitat fragmentation, mobile herbivores can suffer a reduction in diet quality and food availability leading to deleterious changes to population dynamics and abundance (Hobbs et al. 2008; Hobbs and Gordon 2010; Searle et al. 2010; Blackburn et al. 2011; Herbener et al. 2012). These interactions between access to spatial and temporal heterogeneity and ungulate performance will mediate the response of ungulate populations to environmental change, such as changing land use (including oil and gas development) and climate change. Therefore, understanding the underlying mechanisms and drivers of these interactions is of great importance for informed management of ungulate populations and the changing ecosystems in which they reside.

Large herbivores such as mule deer (*Odocoileus hemionus*) have profound impacts on ecosystem structure and function (Hobbs 1996; Manier and Hobbs 2007; Fornara and Du Toit 2008; Beschta and Ripple 2009; Goheen et al. 2010; Allred et al. 2011; Gass and Binkley 2011; Nkwabi et al. 2011; Bai et al. 2012), and understanding the ways in which their behaviour, individual performance and population dynamics are likely to change under future climate scenarios is crucial for effective management of ecosystems. The condition of ungulates in winter is an important determinant of future fitness because of its impact on individual body condition at the start of the breeding season (Forchhammer et al. 2001; Steinheim et al. 2002; Solberg et al. 2007; Rodriguez-Hidalgo et al. 2010; Taillon et al. 2012; Hurley 2014). In this paper, we mechanistically link changes in annual weather patterns and variation in the spatial and temporal patterns of plant phenology across

landscapes with the winter body condition of adult female mule deer to facilitate understanding of how changing weather patterns may affect this important species. Weather has important direct and indirect effects on ungulate condition. Harsh winters with large snowpacks exert a direct physiological effect on ungulate body condition (Catchpole et al. 2000; Pettoirelli et al. 2005a, c), and also an indirect effect via vegetation phenology and abundance (Albon and Langvatn 1992; Cote and Festa-Bianchet 2001; Pettoirelli et al. 2003, 2005a, c, 2006, 2007; Mysterud et al. 2008; Hamel et al. 2009; Nielsen et al. 2012; Mysterud and Austheim 2014). We explored these direct and indirect effects using hierarchical Bayesian structural equation modelling to link variation in weather and vegetation phenology with winter condition of adult mule deer in Northwest Colorado, USA. Using this framework, we developed hypotheses that first related annual weather conditions and topography with vegetation phenology in the annual home ranges of mule deer, linking the onset and rate of vegetation green-up in the spring with seasonal temperature, rainfall and elevation. We expected that home ranges at lower elevations and with warmer spring temperatures would have earlier onset to vegetation green-up. Additionally, we expected that home ranges with higher winter and spring precipitation would have later vegetation onset in the spring as well as steeper slopes of vegetation green-up. We did not look for direct effects of spring weather on subsequent body condition during winter because previous work has shown for a range of ungulates that effects of weather during spring and summer are more likely to be mediated through their effects on vegetation (e.g. Pettoirelli et al. 2005a, c; Mysterud et al. 2008). As such, we felt that these additional pathways would have over-parameterised the model.

We then considered hypotheses pertaining to how winter body condition of individual deer is influenced by the temporal pattern of vegetation onset and green-up during spring and early summer (4 April–25 June). More specifically, we predicted that individuals inhabiting home ranges with shallower vegetation green-up slopes (slower aggregate rate of vegetation green-up) would experience elongated periods when the vegetation is at peak quality, and that this benefit would accrue during the spring and carry over to winter months resulting in better subsequent winter body condition for these individuals in comparison to those inhabiting home ranges with steeper vegetation green-up slopes (Pettorelli et al. 2005c; Lendrum 2013; Hurley 2014). We also predicted that individuals inhabiting home ranges with an earlier vegetation onset [i.e. a higher value of the normalised difference vegetation index (NDVI) in early spring] would have higher winter body condition than individuals occupying home ranges with a later vegetation onset (Pettorelli et al. 2005c). This is because individuals in home ranges with earlier vegetation onset will have

a prolonged period of access to forage at peak nutritional value (Pettorelli et al. 2007), thereby allowing animals to accrue benefits over a longer time span resulting in better body condition the following winter. In more aggregative terms, we expected that individuals occupying home ranges with higher forage productivity (integrated NDVI; INDVI) would have better winter body condition than those occupying home ranges with lower forage productivity.

We formalised these predictions regarding vegetation phenology and mule deer winter body condition into three hypotheses, each represented by a model that we confronted with 3 years of data to evaluate supporting evidence:

- (a) Individuals inhabiting home ranges with earlier onset of vegetation emergence have higher winter body condition than those individuals inhabiting home ranges with later vegetation onset.
- (b) Individuals occupying home ranges with more asynchronous vegetation green-up have better winter body condition than individuals occupying home ranges with faster, more synchronous vegetation green-up.
- (c) Individuals inhabiting home ranges with greater vegetation productivity will have higher winter body condition than individuals inhabiting home ranges of lower productivity.

More locally, numbers of mule deer in western Colorado declined in the late 1980s up until the early 2000s (White and Lubow 2002; Bergman et al. 2011). Whilst population numbers have since begun to increase in the region, populations remain low such that the Piceance regional population currently represents about half of historic highs from the late 1970s–early 1980s [from Colorado Parks and Wildlife (CPW) quadrat mark-resight survey data; C. Anderson, unpublished data]. Therefore, better understanding of the long-term climatic, annual weather patterns and resource drivers of these population trends is critical for conserving this important species.

Materials and methods

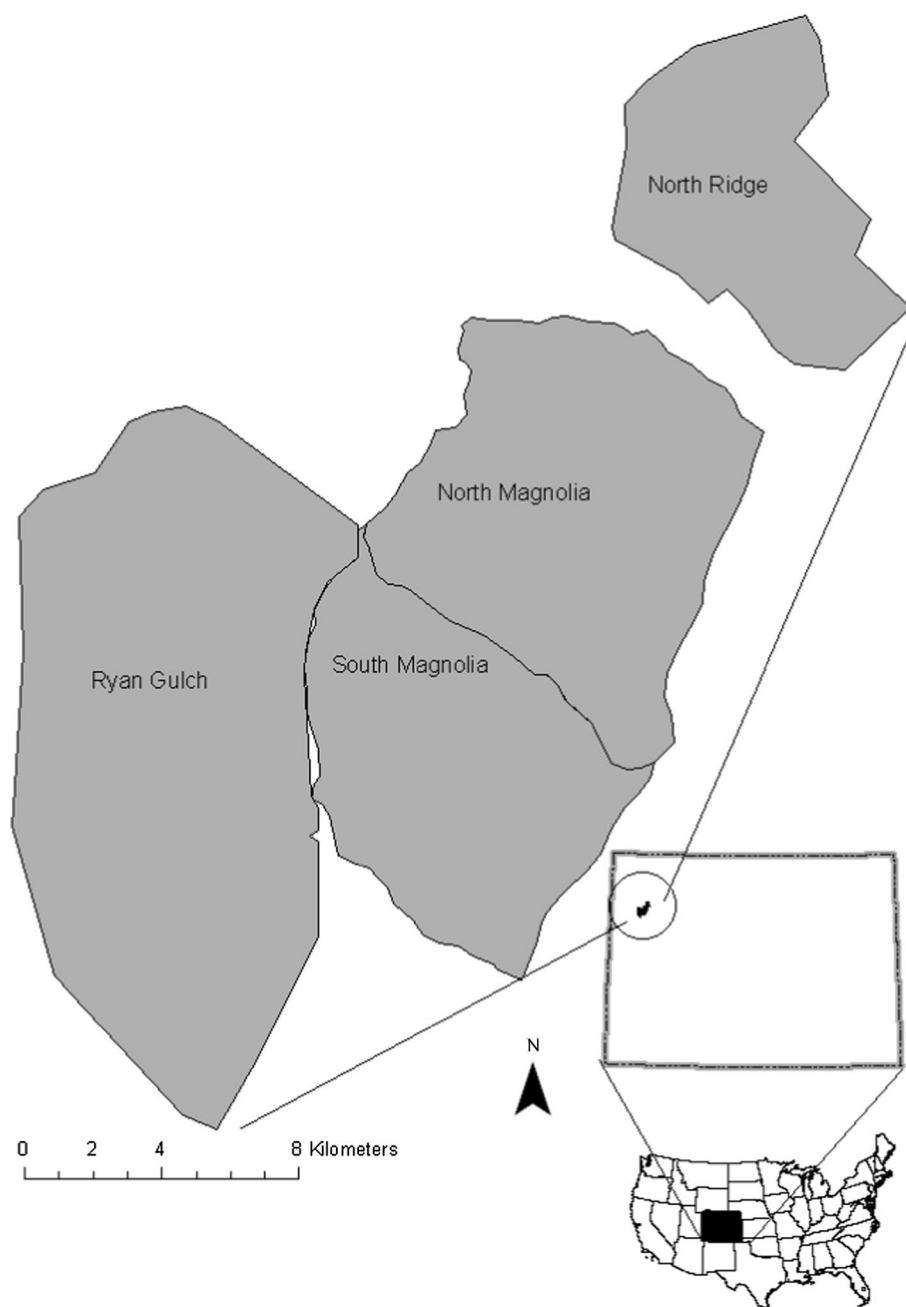
To explore the direct and indirect effects of weather and vegetation phenology on mule deer winter body condition we implemented hierarchical Bayesian structural equation modelling using data from 153 adult female mule deer across four segments of a single winter range population over the period 2009–2011 in Northwest Colorado. Structural equation modelling is well suited to this analysis because it allows a series of hypothesized cause and effect relationships to be captured within a single model, which estimates the magnitude of direct and indirect effects

of independent variables (weather, topography, vegetation phenology) on dependent variables (winter body condition) (Shipley 2002). The four mule deer population segments in this study occupy adjacent winter range areas (Fig. 1), but each segment has distinct seasonal movement patterns. The North Ridge and North Magnolia population segments migrate east to west, while the Ryan Gulch and South Magnolia groups migrate north to south, averaging approximately 40 km between seasonal ranges. Winter ranges are primarily distinct, but there is some overlap within eastern and southern summer ranges. This population does, therefore, provide an opportunity to examine the effects of seasonal variation in vegetation phenology on winter body condition of ungulates. The adjacencies of each population segment's winter range means that individuals experience comparatively similar winter conditions (Fig. 1); however, the migratory behaviour of each segment results in geographically distinct seasonal ranges in the spring and summer. As such, the distinct seasonal migratory patterns and convergent winter ranges for individuals within this population allow us to look for an effect of the temporal pattern of vegetation phenology on body condition in a large, mobile herbivore.

Study area

This study took place in the Piceance Basin located in northwest Colorado, USA, during 2009, 2010 and 2011 (Fig. 1). The Piceance Basin supports one of the largest migratory populations of mule deer in North America (White and Lubow 2002), and contains a diverse mix of pinion pine (*Pinus edulis*)-Utah juniper (*Juniperus osteosperma*) woodland, sagebrush (*Artemisia* spp)-steppe community, Gambel's oak (*Quercus gambelii*)-mountain shrub complex, quaking aspen (*Populus tremuloides*)-Douglas fir (*Pseudotsuga menziesii*) forest, and Englemann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) forest (Lendrum et al. 2014). The region typically experiences warm, dry summers (28 °C mean high) and cold winters (−12 °C mean low), with most of the annual moisture deriving from spring snowmelt (Western Regional Climate Center, 1983–2010). We observed four wintering mule deer population segments in the Piceance Basin: the North Ridge segment (53 km²), just north of the Dry Fork of Piceance Creek including the White River in the northeastern portion of the basin; the Ryan Gulch segment (141 km²), between Ryan Gulch and Dry Gulch in the southwestern portion of the basin; the North Magnolia segment (79 km²), between the Dry Fork of Piceance Creek and Lee Gulch in the north-central portion of the basin; and the South Magnolia segment (83 km²), between Lee Gulch and Piceance Creek in the south-central portion of the basin (Fig. 1).

Fig. 1 Study area containing the four population segments of the Colorado Piceance region mule deer population



Deer capture

We employed helicopter net-gunning techniques (Barrett et al. 1982; van Reenen 1982) to capture 153 adult females between early December and early March across the four study areas over 3 consecutive years of study (Table 1). Capture and handling procedures were approved by the CPW Animal Care and Use Committee (protocol identity 15-2008). In each year of study the number of capture myopathies (includes any mortalities 10 days post-capture) were two (December 2009), three (March 2010), one (December 2010), and zero (March 2011). None of the

Table 1 Number of deer captured from each population segment in each of the 3 years of observation

Year	Population segment			
	North Magnolia	South Magnolia	North Ridge	Ryan Gulch
2009	9	9	16	15
2010	17	19	18	19
2011	10	15	6	0

individuals were re-captured in successive years of observation, therefore each of the 153 observations used in the analysis represents a specific individual. Once netted, all

deer were hobbled and blindfolded. Adult females were transported to localized handling sites for recording body measurements and fitted with global positioning system (GPS) collars (five or 24 fixes/day; G2110D, Advanced Telemetry Systems, Isanti, MN) and released. GPS collars were supplied with timed drop-off mechanisms scheduled to release early in April of the year following deployment. All radio-collars were equipped with mortality-sensing options (i.e. increased pulse rate following 4–8 h of inactivity). All captures were made during the winter for each year of study, with capture dates ranging from December to March.

Body condition and age

We applied ultrasonography techniques described by Stephenson et al. (1998, 2002) and Cook et al. (2001) to measure maximum subcutaneous rump fat (millimetres), loin depth (longissimus dorsi muscle, millimetres), and to estimate percent body fat for each individual. We estimated a body condition score (BCS) for each deer by palpating the rump (Cook et al. 2001, 2007, 2010). Percent body fat was then estimated using a regression equation that incorporated rump fat measurements and BCS (Cook et al. 2007, 2010). Age of individuals was estimated based on tooth replacement and wear (Severinghaus 1949; Hamlin et al. 2000).

Home range calculations

We downloaded and summarized data from GPS collars deployed following collar drop and retrieval in early April of the next year. GPS collars deployed maintained the same fix schedule of attempting fixes every 5 h. For each individual deer, a minimum convex polygon (MCP) was placed around their GPS locations for each year using the Geospatial Modelling Environment (version 0.5.3 Beta; Hawthorne L. Beyer 2009–2011 <http://www.spatialecology.com>). Movement paths were then created between each subsequent location for each deer and the average movement distance was calculated for that deer. A buffer of this distance was applied to each deer's MCP and all spatial data described were extracted for each deer's buffered MCP, hereafter called 'buffer'. We did not separate GPS locations by season because transition from winter to summer range typically occurs rapidly in this population (C. Anderson, unpublished data). We therefore felt that using all GPS locations for the entire year (December/March to April) resulted in the best representation of the yearly home range use of each individual, capturing both winter and summer ranges. We did not attempt to separate winter or summer ranges because we were interested in the combined effect of weather and vegetation over the entire year.

Assessing each individual deer's body condition, movements, and MCP with the previous year's weather variables is supported by the high fidelity of deer to seasonal ranges (Kufeld et al. 1989; Brown 1992; Nicholson et al. 1997). Females in this population of mule deer have occupied identical seasonal ranges over multiple years (Garrott et al. 1987). This fidelity to home ranges allows us to relate annual weather patterns and forage conditions derived from movement patterns observed subsequent to the measurement of winter body condition with a fair degree of certainty.

Plant phenology

We used the NDVI as a proxy for vegetation phenology (greenness), which has been used extensively as a surrogate for vegetation productivity and dynamics (Pettorelli et al. 2005b; Boone et al. 2006; Morissette et al. 2006; Pettorelli et al. 2006; Bellis et al. 2008; Pettorelli et al. 2011). Data were collected from the Global Land Cover Facility Moderate Resolution Imaging Spectroradiometer (MODIS) 16-day composite imagery (NASA 2000–2011). MODIS uses NASA's Terra and Aqua satellites with 16-day orbits, a 2330-km swath, and a 250-m resolution. The NDVI is a ratio of red and near infrared reflectance using bands 1 and 2 of the MODIS sensors [$NDVI = (NIR - RED) / (NIR + RED)$ where NIR is the near-infrared light reflected by vegetation, and RED is the red visible light reflected by vegetation]. NDVI values range from -0.25 to 1 where negative values indicate sparse green vegetation. For each year of observation, we created several different indices for the buffers of individual deer from the satellite-derived NDVI measurements:

Onset of vegetation emergence

The mean value of NDVI for each individual's buffer per year is on 4 April. This date was determined by visual inspection of mean NDVI curves for all individuals in each year to capture the start of the green-up period (sensu Pettorelli et al. 2007; Mysterud et al. 2008). Home ranges with higher NDVI values on this date are expected to have experienced earlier onset to vegetation growth.

Slope of NDVI during vegetation green-up

The slope between the mean NDVI values (termed 'slope') was measured at defined dates for each individual's buffer. The dates defining the start and end of the green-up period were determined visually from plots of mean NDVI curves for all individuals in each year. After visual inspection of NDVI curves, we defined the green-up period as occurring between 4 April and 25 June, and this date range was

used for all individuals in the analysis. This is a measure of the speed of vegetation green-up in the spring, i.e. how elongated or compressed is the phenological development of plants in each individual's home range (Pettorelli et al. 2007; Mysterud et al. 2008)? We also considered the maximum increase in slope during the green-up period to capture any deviations from a linear increase in NDVI during green-up such as very rapid, short flushes of growth (Pettorelli et al. 2007). However, results for maximum slope were similar to those from the slope and so are not discussed further.

Integrated NDVI

The INDVI is the sum of the values for each pixel comprising an individual's buffer per 15 images taken over the year of observation preceding body fat measurements. This metric is commonly used to estimate productivity and biomass of grazing ecosystems (Pettorelli et al. 2005b, 2006, 2011).

Weather and topographic variables

Weather data were collected from the PRISM climate group using their parameter-elevation relationships on independent slopes model (PRISM) data sets of precipitation, minimum temperature, and maximum temperature layers (Daly 1997). The resolution for all weather variables was 4 km. Both precipitation and temperature data were obtained from the year prior to when deer body condition data were collected (e.g. if an individual was captured and measured in December 2010, then climate data from 2009 was used).

Using this data we calculated the sum of precipitation over the green-up period (beginning of April to end of June, hereafter referred to as 'spring precipitation'), and the sum of precipitation over the previous winter (beginning of January to end of March, hereafter referred to as 'winter precipitation'). We also calculated the mean maximum temperature over the green-up period (beginning of April to end of June, hereafter referred to as 'spring temperature').

Elevation and aspect were collected from the US Geological Survey digital elevation model with a 30-m resolution. Elevation units were in metres, and aspect used degree categories based on the following: north (0–22.5), northeast (22.5–67.5), east (67.5–112.5), southeast (112.5–157.5), south (157.5–202.5), southwest (202.5–247.5), west (247.5–292.5), northwest (292.5–337.5), and north (337.5–360).

All data were resampled in ArcGIS to the broadest resolution corresponding to the weather variables at 4 km. Temperature, precipitation, elevation, slope, and NDVI were extracted using spatial analyst in Arc GIS for each individual deer's buffer.

Analysis

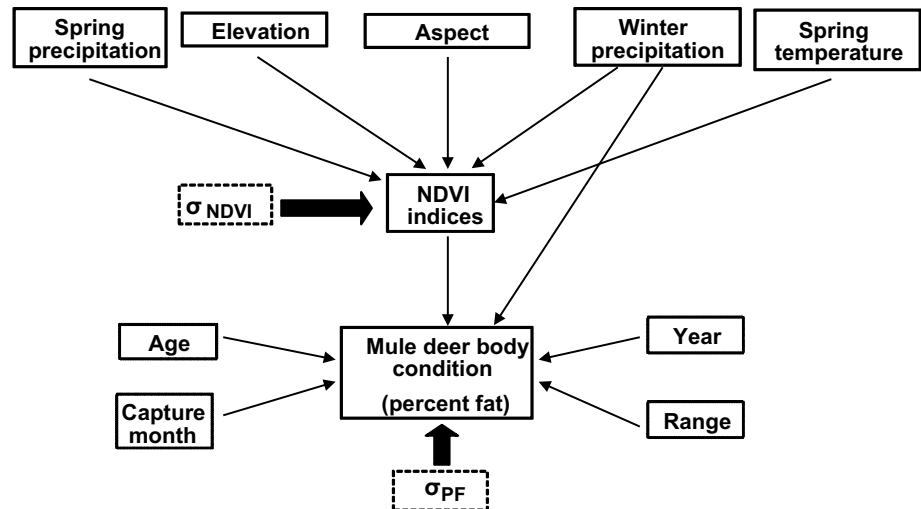
To examine evidence for our hypotheses we used structural equation modelling to examine links between variation in winter body condition (percent fat) of adult female mule deer in northwestern Colorado, plant phenology indices and weather. We used hierarchical structural equation models within the Bayesian framework because this approach can be used to examine both the direct (physiological) and indirect (via plant phenology) effects of weather on ungulate body condition, whilst considering predictor variables from multiple scales (yearly measurements of weather and vegetation phenology, and individual variation between animals), and allowing flexibility in the choice of distributions for likelihoods.

Based on our understanding of the system we surmised a mechanistic model for how weather and plant phenology directly and indirectly affect individual winter body condition of mule deer. The model quantified the direct effects of weather and topography on vegetation phenology (with units of years), the direct effects of plant phenology (defined by the NDVI indices outlined above) on mule deer winter body condition (with units of individuals), the direct effects of annual weather variation on mule deer winter body condition, and the indirect effects of weather, via plant phenology, on mule deer winter body condition (Fig. 2). These relationships were structured to account for variation at the individual level due to animal characteristics (age at capture, population segment). We then fit the model to observations spread over 3 years (2009, 2010, 2011) from the four distinct population segments (Table 1; Fig. 1). Linear relationships were used throughout. We used fixed effects to account for variation amongst the 3 years of study, the age of the deer, the period of capture (early or late winter), and the population segment to which each individual belonged. Capture dates in February and March were classed as a single 'late winter' category because captures generally occurred in late February or early March. Captures in December are classified as 'early winter'.

Structural equation modelling requires hypothesizing causal inferential paths and testing the significance of these paths both directly and indirectly through a mediating variable (vegetation phenology; Fig. 2). To implement this model within a hierarchical Bayesian framework, we specified three separate model parts: data models for percent fat and NDVI metrics, process models for linking weather, topography, vegetation phenology and body condition, and prior distributions of parameters.

The data model is the likelihood linking the data to the model parameters. We have two data models, one linking observations of NDVI metrics to weather and topographic variables, and one linking observations of percent body fat to plant phenology (NDVI metrics) and animal

Fig. 2 Structural equation model diagram for how condition [percent body fat (*PF*) during winter] of mule deer is affected directly and indirectly by weather and plant phenology in northwest Colorado. *NDVI* Normalised difference vegetation index



characteristics (age at capture, capture period, population). NDVI metrics were logit transformed and percent body fat were entered as percentages, such that:

$$\log it(NDVI_{i,t}) \sim \text{normal}(\mu NDVI_{i,t}, \sigma_{NDVI})$$

and

$$PF_{i,t} \sim \text{normal}(\mu PF_{i,t}, \sigma_{PF})$$

where $NDVI_{i,t}$ is the observation for the NDVI metric for the i th deer in the t th year, $\mu NDVI_{i,t}$ is the model prediction for the NDVI metric for the i th deer in the t th year, and σ_{NDVI} is the residual variance across all observations of the NDVI metric not explained by weather or topography. Observations for the body condition (percent fat) for the i th deer in the t th year are denoted by $PF_{i,t}$, residual variance not explained by the model is denoted as σ_{PF} , and $\mu PF_{i,t}$ is the model prediction for the percent fat of the i th deer in the t th year. Observations of percent fat for individual deer are assumed to be independent in this analysis. If captures of individuals tended to target persistent social groups of deer this assumption may be invalid; however, previous work in this area has shown that statistical dependence between survival rates of sibling neonates using the same landscape was minor (C. Bishop, unpublished data). This suggests the assumption of independence is warranted for individuals in our study area.

The process component of the model relates the model predictions for NDVI metrics and percent fat to the parameters of the model. As such, it derives the probability of the model prediction for each NDVI metric for the i th deer in the t th year, $\mu NDVI_{i,t}$, given the respective process model parameters, and the residual variance estimate for unaccounted variation in the modelled NDVI process or measurement error, $\sigma_{NDVI} : P(\mu NDVI_{i,t} | a, b_k, \text{site}_i, \sigma_{NDVI})$, where a is the regression intercept, b_k are the k th regression coefficients for weather and topographical effects, and

site_i is a fixed effect accounting for variation derived from the four distinct mule deer population segments used in the analysis.

The second part of the process model gives the probability of the model prediction for percent fat for the i th deer in the t th year, $\mu PF_{i,t}$, given the respective process model parameters, and the residual variance estimate for unaccounted variation in the modelled percent fat process and measurement error, $\sigma_{PF} : P(\mu PF_{i,t} | c, d_k, \text{age}_i, \text{year}_t, \text{capture_month}_i, \sigma_{PF})$, where c is the regression intercept, d_k are the k th regression coefficients for the effects of phenology and weather on body fat, and age_i , year_t and capture_month_i are fixed effects accounting for variation due to age of individual deer, the year of observation and the period in which individuals were caught for body fat measurements. These probabilities are defined by two structural path equations: firstly for each NDVI metric (Eq. 1) and secondly for each percent fat measurement (Eq. 2):

$$\begin{aligned} \mu NDVI_{i,t} = & a + b_1 \text{springppt}_{i,t} + b_2 \text{winterppt}_{i,t} \\ & + b_3 \text{springtemp}_{i,t} + b_4 \text{elev}_{i,t} \\ & + b_5 \text{aspect}_{i,t} + \text{site}[\text{population}_i] \end{aligned} \quad (1)$$

$$\begin{aligned} \mu PF_{i,t} = & c + d_1 \mu NDVI_{i,t} + d_2 \text{winterppt}_{i,t} + d_3 \text{age}_i \\ & + \text{yr}[\text{year}_t] + \text{cm}[\text{capturemonth}_i] \end{aligned} \quad (2)$$

Because our analysis is fully Bayesian, we specify prior distributions for all model parameters in the hierarchy. All input variables (weather, topography and age) were standardised, therefore all prior distributions were assumed to be normally distributed and uninformative [all parameters \sim normal (0, 1.0E−6)]. Because the data for NDVI indices were logit transformed, these were also assumed to be normally distributed, and uninformative

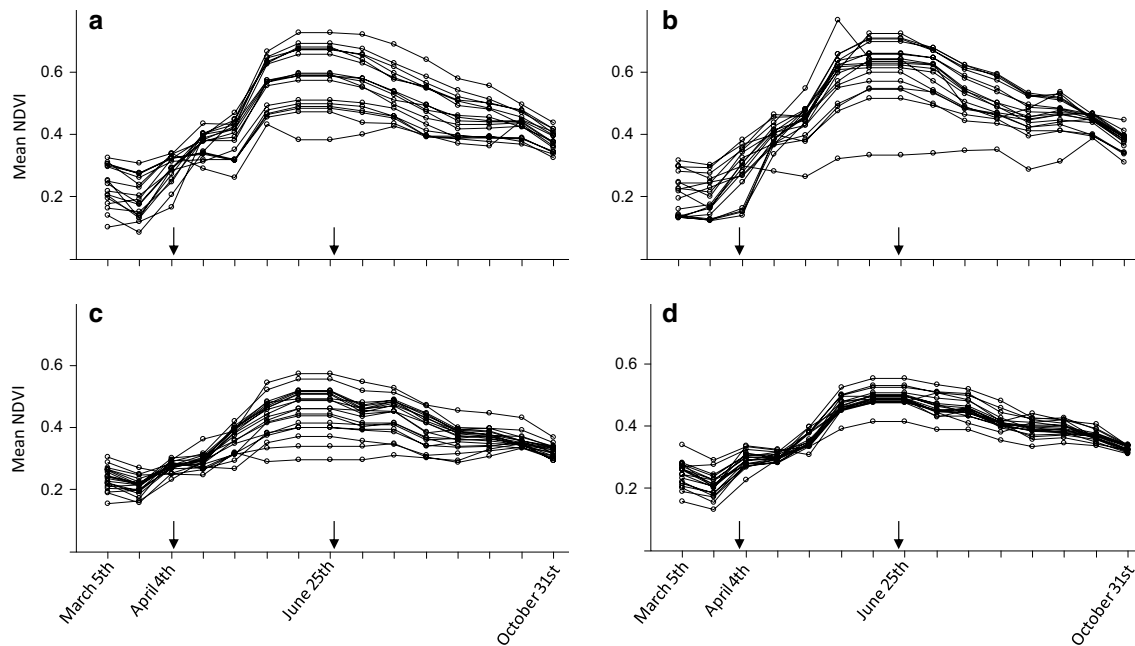


Fig. 3 Mean NDVI curves for each study area in 2009 (**a** North Magnolia, **b** North Ridge, **c** Ryan Gulch, **d** South Magnolia). Each line represents NDVI for an individual deer's annual home range. NDVI values were used from 5 March to 31 October in each year of observation (2009, 2010 and 2011), tick marks represent 16-day intervals, and arrows show vegetation 'onset' (mean NDVI value on

4 April) and the end of the green-up period (25 June). The mean slope of the green-up period was calculated between the two arrows for each individual's annual home range. Integrated NDVI (INDVI) was calculated as the sum of the mean NDVI values over 5 March to 31 October for each individual's annual home range

diffuse gamma priors were used for the inverse of the residual variances of the NDVI model and percent fat model, $\sigma_{\text{NDVI}}, \sigma_{\text{PF}} \sim \text{gamma}(0.001, 0.001)$. All models were fit using WinBUGS (Spiegelhalter 1999) software and a Markov chain Monte-Carlo (MCMC) procedure for each model run for 10,000 iterations after an initial burn-in of 10,000 iterations to ensure convergence of all model parameters. Convergence diagnostics and autocorrelation statistics were used to assess the mixing of three MCMC chains per model, and to assess the MCMC sampling quality for each parameter. Prior to running each model on actual data, models were tested on realistically simulated data to test their ability to converge on reasonable parameter estimates. All models performed well in simulations, converging on known parameter estimates such that 95 % credible intervals for each parameter contained the true, known value.

Results

All models converged satisfactorily on posterior distributions for model parameters. All posterior distributions were approximately normal, and autocorrelation in the MCMC chains was not a factor after the initial burn-in period (Gelman diagnostics for MCMC chains upper credible

interval < 1.05). All model residuals were normally distributed (Pearson χ^2 normality test, onset $P = 19.45$, $p = 0.08$; slope $P = 16.51$, $p = 0.17$; INDVI $P = 19.06$, $p = 0.09$).

Winter body fat measurements varied between 3.0 and 18.3 % across all individuals and years of study. Mean percent fat measurements were approximately similar across the 3 years of observation (2009, 7.0 %, SD 1.5; 2010, 6.9 %, SD 1.5; 2011, 9.1 %, SD 4.0). Body fat measurements across the four study areas were also similar; highest body fat measurements were recorded in North Magnolia (mean 8.0 %, SD 2.6), followed by South Magnolia (mean 7.7, SD 3.0), North Ridge (mean 7.3, SD 2.0), and Ryan Gulch (mean 6.6, SD 1.4). Vegetation phenology followed similar patterns across the four study areas (Fig. 3), with the green-up period commencing around 4 April and reaching a plateau around 25 June. As expected, deer caught in late winter had significantly lower body fat estimates than those caught in early winter (Table 2). In all analyses, age of deer tended to be negatively correlated with body condition (greater than 75–85 % of the posterior density mass was negative; Table 2).

Onset

The onset model explained approximately 36 % of the variation in body condition measurements and approximately

Table 2 Posterior density estimates for parameters in the structural equation models for slope, onset and integrated normalised difference vegetation index (INDVI)

	Slope	Onset	INDVI
<i>a</i> (intercept)	−1.01 (−1.08, −0.94)	−0.94 (−0.98, −0.91)	5.88 (5.79, 5.97)
<i>b</i> ₁ (spring ppt.)	0.12 (0.015, 0.22)*	0.073 (0.022, 0.13)*	−0.11 (−0.25, 0.030)
<i>b</i> ₂ (winter ppt.)	0.21 (0.13, 0.29)*	0.037 (−0.0040, 0.076)	0.22 (0.11, 0.33)*
<i>b</i> ₃ (spring temp.)	−0.26 (−0.36, −0.16)*	−0.13 (−0.18, −0.081)*	−0.10 (−0.24, 0.033)
<i>b</i> ₄ (elevation)	0.21 (0.13, 0.30)*	0.072 (0.030, 0.11)*	0.15 (0.044, 0.27)*
<i>b</i> ₅ (aspect)	−0.072 (−0.14, 0.0014)	−0.068 (−0.11, −0.031)*	0.10 (0.0041, 0.20)*
<i>c</i> (intercept)	11.94 (10.09, 13.78)	12.77 (10.75, 14.8)	10.62 (−1.17, 21.48)
<i>d</i> ₁ (phenology)	−0.82 (−2.25, 0.54)	0.67 (−0.99, 2.27)	0.28 (−1.53, 2.24)
<i>d</i> ₂ (winter ppt.)	0.38 (−0.23, 1.01)	0.0083 (−0.38, 0.39)	−0.026 (−0.67, 0.63)
<i>d</i> ₃ (age)	−0.18 (−0.50, 0.14)	−0.19 (−0.52, 0.14)	−0.19 (−0.52, 0.14)
Residual variance (percent fat model)	3.90 (3.14, 4.97)	3.92 (3.16, 5.00)	3.93 (3.16, 5.01)
Residual variance (phenology model)	0.19 (0.15, 0.24)	0.048 (0.039, 0.060)	0.33 (0.026, 0.41)
Year fixed effect on percent fat	[2] −0.69 (−1.90, 0.51)	[2] 0.18 (−0.90, 0.1.24)	[2] −0.15 (−0.89, 0.60)
	[3] −1.29 (−2.69, 0.10)	[3] −0.86 (−2.25, 0.51)	[3] −1.04 (−2.36, 0.28)
	[4] −0.40 (−1.31, 0.50)	[4] −0.27 (−1.17, 0.62)	[4] −0.26 (−1.17, 0.62)
Population segment fixed effect on percent fat	[2] −0.49 (−1.42, 0.0.46)	[2] −0.42 (−1.37, 0.55)	[2] −0.42 (−1.38, 0.58)
	[3] −0.93 (−0.1.96, 0.084)	[3] −0.77 (−1.75, 0.19)	[3] −0.63 (−1.73, 0.43)
	[4] −0.40 (−1.31, 0.50)	[4] −0.27 (−1.17, 0.62)	[4] −0.26 (−1.17, 0.62)
Capture period fixed effect	−4.93 (−6.37, −3.53)*	−4.89 (−6.34, −3.48)*	−4.85 (−6.32, −3.43)*

Estimates are mean posterior densities with 95 % credible intervals. Fixed effects for different years of study are compared to 2009 (2 = 2010 and 3 = 2011), and for population segment are compared to North Magnolia, with 2 = North Ridge, 3 = Ryan Gulch and 4 = South Magnolia

ppt. Precipitation, *temp.* temperature

* $P < 0.05$

63 % of the variation in NDVI metrics. Precipitation over the green-up period (spring precipitation) had a strong positive relationship with the mean NDVI value during the initial phase of vegetation green-up (4 April), as did elevation (Table 2; greater than 95 % of the posterior density was less than zero). Therefore, home ranges with higher spring precipitation, or those at higher elevations, had significantly earlier onset to vegetation growth. There was also an indication that precipitation during the previous winter (winter precipitation) resulted in earlier onset of vegetation (Table 2; more than 75 % of the posterior density mass was greater than zero). Mean temperature during green-up (spring temperature) had a strong negative relationship with mean NDVI values on 4 April (Table 2; more than 95 % of the posterior density mass was greater than zero) meaning that annual home ranges experiencing warmer spring temperatures had significantly later onset to vegetation growth. Aspect also had a strongly negative relationship with mean NDVI values on 4 April, indicating that home ranges with more southerly or westerly aspects had later vegetation onset values than those with more northerly or eastern aspects (Table 2; more than 95 % of the posterior density mass was greater than zero).

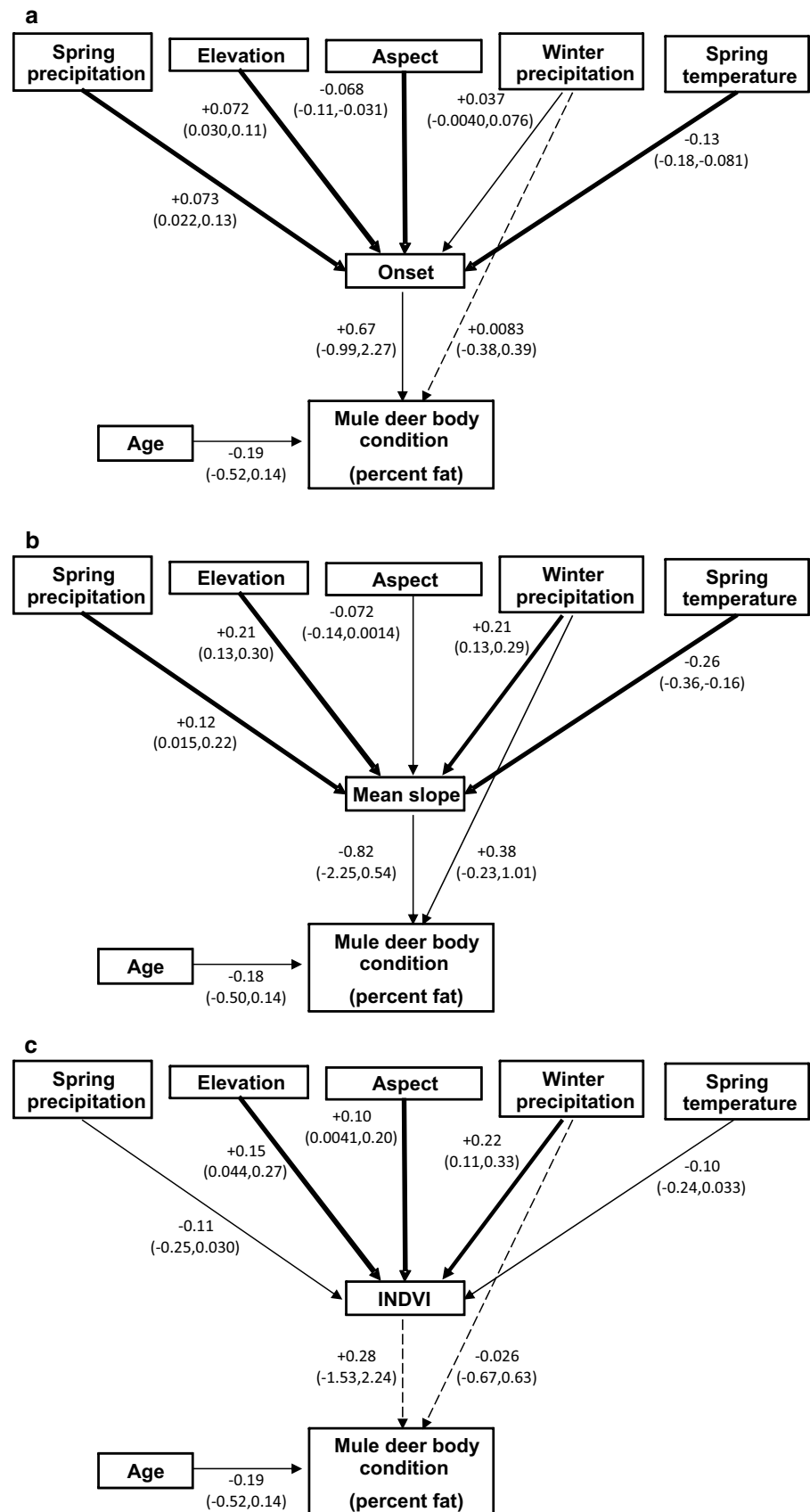
There was weak evidence for a positive relationship between onset of vegetation green-up and body condition

(greater than 75 % of the posterior density mass was positive, Table 2; Fig. 4a), suggesting that deer inhabiting home ranges with earlier vegetation onset tended to have better body condition.

Slope

The slope model explained approximately 36 % of the variation in body condition measurements and approximately 67 % of the variation in NDVI metrics. Precipitation during the previous winter (winter precipitation) and over the green-up period (spring precipitation) had a strong positive relationship with the mean slope of vegetation green-up, as did elevation (Table 2; more than 95 % of the posterior density mass was greater than zero). Mean temperature during green-up (spring temperature) had a strong negative relationship with the mean slope of vegetation green-up (Table 2; greater than 95 % of the posterior density mass was less than zero). Aspect tended to be negatively related to mean slope of vegetation green-up (greater than 75 % of the posterior density mass was negative; Table 2), indicating that home ranges with more southerly or westerly aspects tended to have slower rates of vegetation green-up in the spring. Previous winter precipitation tended to be positively related to body condition (greater than

Fig. 4 Structural equation model diagram for how condition (percent body fat during winter) of adult, female mule deer is affected directly and indirectly by weather and vegetation phenology in northwest Colorado in 2008, 2009 and 2010. Indirect linkages are manifested through a measure of vegetation greenness in the spring derived from NDVI measurements (**a** onset of vegetation, **b** mean slope of green-up, **c** INDVI). *Thick solid lines* represent strong evidence for an effect (95 % credible interval does not overlap zero), while *thin solid lines* represent weak evidence for an effect (95 % credible interval marginally includes zero). *Dotted lines* represent no clear effect. Regression coefficient estimates are given with 95 % credible intervals. *Plus sign* Predicted positive relationship, *minus sign* predicted negative relationship



75 % of the posterior density mass was positive; Table 2). There was a strong indication of a negative relationship between the slope of vegetation green-up and body condition (greater than 87 % of the posterior density mass was negative; Table 2; Fig. 4b), indicating that deer inhabiting home ranges with faster vegetation green-up tended to have poorer body condition than deer inhabiting home ranges with more asynchronous vegetation green-up.

Integrated NDVI

The INDVI model explained approximately 35 % of the variation in body condition measurements and approximately 30 % of the variation in NDVI metrics. Precipitation during the previous winter had a strong positive relationship with INDVI (Table 2; more than 95 % of posterior density mass was greater than zero), and both spring precipitation and spring temperature during the green-up period tended to be negatively related to INDVI (greater than 75 % of the posterior density mass was negative; Table 2). Elevation and aspect both had strong positive relationships with INDVI (Table 2; more than 95 % of the posterior density mass was greater than zero), indicating that home ranges with more southerly or westerly aspects had higher INDVI values than those with more northerly or eastern aspects (Table 2). We found no clear effect of winter precipitation or INDVI on body condition (Table 2; Fig. 4c).

Discussion

In this study, we demonstrate a tangible link between the temporal pattern of vegetation phenology and ungulate body condition during the critical winter period for a migratory mule deer population. Moreover, we identify key variation in annual weather patterns that determine the onset and synchrony of vegetation green-up in this region. Importantly, we demonstrate that the migratory strategies displayed by different segments of a contiguous overwintering population appear to influence the resulting performance of individuals, with variation in the synchrony, and to a lesser extent, the onset of vegetation within seasonal home ranges contributing to subsequent winter body condition. Moreover, we show that this variation in vegetation phenology is a more important driver of subsequent winter body condition than total forage availability, when measured using remotely sensed data.

Weather, topography and vegetation phenology

Precipitation in the spring resulted in significantly earlier onset to vegetation growth, presumably because greater precipitation during this period facilitates the initiation

of plant growth in the spring through enhanced soil water availability. Whilst there were indications of a similar relationship between the onset of vegetation emergence and winter precipitation, the strength of this relationship was not as clear. This is probably due to the contrasting actions of increased soil moisture availability acting to encourage vegetation growth, whilst remaining winter snowpack would act to inhibit earlier growth (e.g. Christianson et al. 2013). The speed of vegetation green-up increased in home ranges experiencing higher winter and spring precipitation, and in those located at higher elevations. This effect is consistent with results from other rangeland systems, and is likely due to a greater flush of available moisture for plant growth in the spring, thereby accelerating green-up of vegetation (Walker et al. 1993, 1995; Bjork and Molau 2007; Christianson et al. 2013). Home ranges with higher winter precipitation had significantly greater productivity (INDVI), probably because the greater moisture availability enhances vegetation growth throughout the spring, and potentially the summer if snowmelt continues into the middle part of the year (Walker et al. 1993, 1995; Bjork and Molau 2007).

Home ranges with higher mean temperature during spring had significantly later onset of vegetation growth, in contrast to results from other regions (e.g. Pettorelli et al. 2005c). Higher temperatures during the spring period may act to delay or reduce onset of vegetation growth if they reduce the moisture available for plant growth, particularly in mountainous semi-arid regions such as the Piceance Basin. Home ranges with higher mean temperatures during spring had shallower slopes of vegetation green-up, which is also in contrast to previous studies (e.g. Pettorelli et al. 2007; Campbell et al. 2013; Middleton et al. 2013). It is possible that warmer spring temperatures resulted in later fulfillment of chilling requirements for some plant species (Yu et al. 2010; Paudel and Andersen 2013). However, the applicability of this mechanism to our study system has yet to be evaluated in the context of warming spring temperatures.

Home ranges with more southerly or westerly aspects had greater INDVI values than those with more northerly or easterly aspects, again probably because of the ameliorated microclimatic conditions for plant growth afforded by these slopes. The significant positive effect of elevation on INDVI is expected in our study area because areas of higher elevation utilized in the summer have greater vegetation productivity over the year than those occupying lower elevations.

Vegetation phenology and ungulate winter body condition

Our findings indicate that deer inhabiting home ranges with earlier vegetation onset tended to have better winter body

condition than those inhabiting home ranges with later vegetation onset. This is because a higher mean NDVI value at the start of the green-up period is thought to be associated with an earlier start to the growing season, and elongated time period at which forage is at peak quality. This result is in line with previous work on the migratory patterns of mule deer in this region, which demonstrated that deer ‘jumped’ rather than ‘surfed’ the green wave (sensu Bischof et al. 2012), arriving on the summer range well before the peak productivity of forage occurs (Lendrum et al. 2014). As such, individuals utilising summer ranges with an earlier vegetation onset would experience a better temporal match between their arrival and the development of higher quality forage. Other studies have demonstrated a positive effect of early season (May) NDVI on body mass of lambs (domestic sheep) in autumn across three alpine ranges in Norway (Nielsen et al. 2012), as well as lower female body mass in free-ranging reindeer in areas with later vegetation onset (Ballesteros et al. 2013). However, Pettorelli et al. (2007) found no positive effect of early vegetation onset on juvenile growth or survival in three ungulate species in Canada and northern Italy, and suggested that there is a greater influence of the average duration of the period of access to high-quality forage, rather than the measure of the average timing of vegetation onset. In combination, these findings suggest that the effect of early vegetation onset differs between ungulate life stages.

Importantly, we found evidence that deer occupying home ranges with steeper, and therefore less asynchronous, vegetation green-up tended to have poorer body condition than deer occupying home ranges with more asynchronous vegetation green-up. Rapid changes in NDVI during vegetation green-up could translate to greater forage availability at a given point in time across a landscape. However, these rapid changes may also serve to compress the time window over which high-quality forage is available to ungulates over a large spatial scale, such as the home range, potentially depressing diet quality over the longer term (Pettorelli et al. 2007; Middleton et al. 2013). Rapid green-up of vegetation during spring has been negatively correlated with growth and survival of bighorn lambs (*Ovis canadensis*), growth of mountain goat kids (*Oreamnos americanus*) in Canada, survival of Alpine ibex kids (*Capra ibex*) in northern Italy (Pettorelli et al. 2007), and declines in recruitment and pregnancy rates amongst migratory elk in the USA (Middleton et al. 2013). Enhanced green-up phenology rates have also been shown to result in lower adult body mass in Eurasian beavers (Campbell et al. 2013). There is mounting evidence that this is a crucial mechanism whereby vegetation phenology directly influences many important life history aspects for large herbivores.

Interestingly, the influence of both vegetation onset and the slope of green-up on body fat were much stronger than

that of overall vegetation productivity. Therefore, whilst total productivity may ultimately determine the capacity of grassland systems to support large herbivores, the condition of individuals and their subsequent fitness and life history components appear to be more strongly driven by the spatio-temporal patterning of forage resources.

Characteristics of individual animals were found to be relatively important determinants of winter body condition. Across all analyses, the age of deer tended to be negatively correlated with body condition indicating that, as expected, older animals tended to have poorer body condition than younger animals. However, we detected little support for a direct effect of previous winter precipitation on percent body fat in any of the analyses, indicating that during the study period the direct, physiological impact of previous winter precipitation was less important than the indirect weather effects on body condition mediated through plant phenology. It may be that mule deer in this region were able to compensate for declines in body condition resulting from previous winter precipitation over the course of the subsequent spring and summer; however, without repeated body condition measurements of individuals over multiple years we are unable to test this assumption. In addition, winter conditions during this study period were relatively mild, and in severe winters we would expect this direct physiological effect to be much stronger. Studies in boreal forests with strong seasonality at northern latitudes have found summer fattening of ungulates linked to plant phenology to be a more important factor for body condition in autumn than winter body mass loss due to harsh conditions (snow depth and temperature) (Myserud et al. 2008). Although body mass of yearling red deer (*Cervus elaphus*) in Norway was linked to winter snow and temperature, it was found that the magnitude of these effects was much smaller than the indirect effects of climate operating through plants (Myserud et al. 2008). Similarly, in our study area, we detected no clear effect of previous winter precipitation on percent body fat of mule deer, whilst effects of previous spring precipitation and temperature on body fat, mediated through plant phenology, were much clearer.

Conclusion

Our findings warrant increased attention to the complexities arising from changing climatic patterns in this region. Although increased spring and winter precipitation resulted in earlier onset of vegetation growth, they also acted to simultaneously compress vegetation green-up periods thereby potentially negatively affecting the body condition of mule deer through a compression of the time period over which high-quality forage is available. However, winter precipitation also had a strong positive impact

on overall vegetation productivity, which would benefit large herbivores (Owen-Smith 1990; Georgiadis et al. 2003). The interplay between precipitation and temperature will ultimately determine vegetation phenology and dynamics in this system. This highlights the need for better understanding of the complexity and non-linearity of weather and vegetation dynamics for predicting the impact of future climate change, particularly in more arid alpine regions with highly seasonal environments. Utilising studies such as this, which facilitate mechanistic links between annual variation in weather patterns and longer-term climate change, will be an important component of addressing this knowledge gap.

We have empirically demonstrated important relationships between temporal patterns of vegetation phenology and winter body condition in this ungulate species. However, the complexity of the differing effects of seasonal weather patterns on the various components of phenologically driven variation in forage quality and quantity warrants further research to better elucidate underlying mechanisms. Our results demonstrate the necessity of conserving sufficient areas of spatially and temporally variable forage resources to allow mobile large herbivores to behaviourally compensate for changing climate and resource patterns. The emerging body of evidence demonstrating that large ungulates will actively track phenological variation in vegetation to enhance diet quality warrants the identification and protection of sufficiently large areas of key resource habitat to conserve large herbivores and the role they play in ecosystems across the globe.

Author contribution statement K. R. S., M. B. R. and N. T. H. conceived, designed and conducted the modelling framework. C. B. and C. R. A. conceived, designed and conducted the field experiments. All authors contributed to the interpretation of data and analysis, ecological inference and manuscript preparation.

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